U.S. Fish and Wildlife Service

Strategic modeling to assist conservation of bull trout in the Lower Clark Fork River

Final Report

February 2015

By Doug Peterson

Abernathy Fish Technology Center
Longview, Washington

Shana Bernall[1], Kenneth Bouwens[2], Kenny Breidinger[3], Joe DosSantos[1], Doug Grupenhoff[4], Wade Fredenberg[5], Ryan Kreiner[3], Sean Moran[1], Brendan Naples[4], Lee Nelson[3], Rob Ryan[2], and David Schmetterling[3]

Affiliations
[1] Avista Corporation, Noxon, Montana
[2] Idaho Department of Fish and Game
[3] Montana Fish, Wildlife and Parks
[4] US Forest Service, Trout Creek, Montana
[5] US Fish and Wildlife Service, Creston, Montana

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Douglas P. Peterson

Abernathy Fish Technology Center

US Fish and Wildlife Service

Longview, WA 98632

doug_peterson@fws.gov

With

Shana Bernall[1], Kenneth Bouwens[2], Kenny Breidinger[3], Joe DosSantos[1], Doug Grupenhoff[4], Wade Fredenberg[5], Ryan Kreiner[3], Sean Moran[1], Brendan Naples[4], Lee Nelson[3], Rob Ryan[2], and David Schmetterling[3]

Final report February 26, 2015

Affiliations

[1] Avista Corporation

[2] Idaho Department of Fish and Game

[3] Montana Fish, Wildlife and Parks

[4] US Forest Service

[5] Montana Ecological Services Field Office, US Fish and Wildlife Service

ABSTRACT

The Native Salmonid Restoration Plan (NSRP) for the lower Clark Fork River has been implemented for nearly 15 years, and a systematic effort to evaluate which management actions are providing the greatest conservation benefit for native fishes was needed. To address this, we conducted a strategic modeling exercise with the objective of guiding and prioritizing future conservation actions. Through a participatory modeling exercise that included workshops, webinars, and individual and group assignments and exercises, we developed a probabilistic decision support model that would allow biologists to systematically evaluate management alternatives for the migratory life history of bull trout (*Salvelinus confluentus*) across ten local populations (or patches) in the lower Clark Fork River system, in Idaho and Montana. Specifically, we used the model to explore management scenarios related to three major programs being implemented under the NSRP: juvenile and adult bull trout capture and transport, habitat restoration in the natal patch, and manipulation of nonnative trout. Population status was judged by the likelihood that a local population – or set of local populations – was stable or increasing, with a finite population growth rate (λ) of 0.9-1.1 or greater. Under the current environmental conditions and management intensity, the model predicted there were: three patches with a high likelihood (>85%) of a stable or increasing bull trout population – Lightning, Johnson, and Graves creeks; four with moderate likelihood (>59 to 76%) – Rock Creek, Swamp Creek, Trout Creek, and Vermilion River; and three where the likelihood (48-54%) did not strongly indicate stability– Bull River, Prospect Creek, and Thompson River. Using a scheme that weighted population growth rate by intrinsic habitat potential, an aggregate model for the eight bull trout patches upstream from Cabinet Gorge Dam predicted only a moderate (59%) likelihood that, collectively, this "metapopulation" was stable or increasing. Management actions that reduced the influence of nonnative trout were predicted to result in the largest comparative improvement in bull trout population status for individual patches and at the aggregate level including all patches upstream of Cabinet Gorge Dam. Increasing the capture and transport of adult bull trout from below Cabinet Gorge Dam to natal habitats upstream appeared to have the second-largest effect. Increasing the capture and transport of out-migrating juvenile bull trout from natal patches in Montana to Lake Pend Oreille, Idaho also had a positive effect, but seemingly only at very high transport rates. Restoration of degraded natal habitat alone was generally not highly effective unless coupled with other management actions, i.e., that reduced nonnative trout or promoted return of adult migratory bull trout to their natal patch. The model is not an accurate representation of the population dynamics of bull trout in the absolute sense, but it is nonetheless a useful tool because it synthesizes current understanding about the ecological system, identifies knowledge gaps, and provides a systematic framework to evaluate these and other management scenarios. The model predicted that much higher levels of management intervention (e.g., nonnative suppression, transport of adults or juveniles) or more targeted actions will be needed to achieve the objective of conserving and enhancing bull trout during the next 15 years.

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INTRODUCTION

Populations of bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in the Lower Clark Fork River system in Montana and Idaho face many of the conservation challenges that plague successful management of native fish species in western North America. The mainstem Clark Fork River between the Thompson River (MT) and Lake Pend Oreille (ID) has three large hydroelectric dams that were impassible to fish moving upstream (Figure 1). The deleterious effects of habitat fragmentation and loss of connectivity for migratory salmonids is well known (e.g., Fausch et al. 2006), and often manifested by differentiation and loss of genetic diversity (Neeras and Spruell 2001; Yamamoto et al. 2004; Neville et al. 2009), constraints on full life history expression because complementary habitats in the riverscape are not accessible (Northcote 1997; Fausch et al. 2002; Schrank and Rahel 2004), and disruption of spatial population structure that may be important for persistence (e.g., Dunham and Rieman 1999; Campbell Grant 2011). Habitat degradation may exacerbate effects of reduced connectivity, as isolated or semi-isolated salmonid populations are less likely to persist (Peterson et al. 2014) or maintain genetic diversity (Neville et al 2006). When present in spawning and rearing habitat, nonnative trout can pose both ecological (Nakano et al. 1998; Rieman et al. 2006) and genetic threats (Leary et al. 1993; Kanda et al. 2002) to native salmonids like bull trout. Also, conversion of free-flowing (lotic) habitats to impoundments or reservoirs – as has occurred in the lower Clark Fork River – can provide an opportunity for establishment of novel predators of native fish (McMahon and Bennett 1996; Schmetterling 2001; Sanderson et al. 2009; Carey et al. 2011; Scarnecchia et al. 2014).

In consideration of these types of conservation concerns, the NSRP for the lower Clark Fork River (LCFR) was produced in 1998 by a working group of fishery biologists and managers during the Federal Energy Regulatory Commission (FERC) relicensing process for the Cabinet Gorge and Noxon Rapids hydroelectric projects (Kleinschmidt and Pratt 1998). The NSRP provides a comprehensive approach and adaptive management process to address fish passage and native salmonid restoration in the LCFR and was formally adopted through the Clark Fork Settlement Agreement (Agreement) in 1999 (Avista Corporation 1999). In general, the NSRP calls for an investigation of factors (e.g., genetics, disease, nonnative species, habitat suitability) that could influence the outcome of restoration actions, develops and implements an

experimental fish passage program to address connectivity problems in the mainstem Clark Fork River caused by large dams, and establishes monitoring programs to evaluate the effectiveness of restoration. Among the NSRP's guiding principles are the examination and refinement of policies and restoration approaches during implementation, and the use of ecological modeling to evaluate monitoring data and provide a rationale for conservation decisions. In addition to the Native Fish Restoration Plan (Appendix C of the Agreement), the Agreement also authorized programs to acquire tributary habitat and enhance fishery resources in Idaho (Appendix A of the Agreement) and Montana (Appendix B of the Agreement).

After nearly 15 years of implementation of the NSRP and Agreement, a large body of monitoring information has been collected in most major tributaries to the Lower Clark Fork River in Montana (e.g., Philip William and Associates, Ltd. 2004; GEI 2005; Kleinschmidt 2007; Moran 2006; Storaasli 2012; Storaasli 2013, 2014; Kreiner and Tholl 2014; Moran and Storaasli 2014;). Significant efforts have been accomplished to trap and transport juvenile and adult bull trout around the dams (e.g., DeHaan et al. 2011; Bernall and Duffy 2012; McCubbins et al. 2012; DeHaan and Bernall 2013), to restore instream habitat in some watersheds (e.g., Horn 2011), and to experimentally suppress nonnative trout in a couple of locations (e.g., Storaasli and Moran 2013). As yet, there not been a systematic effort to evaluate these data in the context of which management actions are providing the greatest conservation benefit for native fishes.

To address this, we conducted a strategic modeling exercise with the objective of guiding and prioritizing future conservation actions for native salmonids in the lower Clark Fork River. We used a participatory modeling process to develop a decision support model that would allow biologists to systematically evaluate management alternatives. This modeling approach was iterative (e.g., Pollino and Henderson 2010), and learning was accomplished through both the process (model building) and the application of the model (e.g, Chen and Pollino 2012; Peterson et al. 2013).

Through a series of workshops, webinars, and individual and group assignments and exercises, we defined the modeling objectives and the spatial extent of the exercise, developed a conceptual model that was translated into a probabilistic model, and finally used that model to evaluate management alternatives. We focused on a single species – bull trout – and the modeling considered how management would affect the population status of the migratory life history

across ten local populations (or patches) in the lower Clark Fork River system. Analyses considered both individual populations (patches) one-at-a time, and sets of populations as per their location in relation to impoundments and dams in the lower Clark Fork River (LCFR), and how management actions in particular locations would contribute to the overall objective of bull trout conservation.

METHODS

The strategic modeling exercise was organized around the principles of structured decision analysis for complex ecological problems that require stakeholder participation and iterative, participatory model building (e.g., Cain 2001; Marcot et al. 2001; Johnson and Weaver 2009; Pollino and Henderson 2010). In short, our approach involved engaging local experts (biologists) and managers involved in the conservation planning process in a series of guided discussions and exercises to explore aspects of the decision problem, such as clarifying the management objectives, characterizing what is known (and not known) about the underlying biology and ecology of the problem, and evaluating the effects of past or ongoing conservation efforts. After the conservation objectives of the modeling problem were identified, subsequent steps involved building a visual representation of those objectives, translating expert knowledge and empirical data into a decision support tool, refining the tool through review and exploratory analyses, and finally using that model to evaluate management alternatives (e.g., Pollino and Henderson 2010).

The modeling team was comprised of local experts and a coordinator/analyst. The experts for this exercise had specific knowledge about the biology, conservation, and management of native fish in the lower Clark Fork River system and/or were researchers familiar with bull trout and westslope cutthroat trout. The experts were biologists and fishery managers from two state agencies (Idaho Department of Fish and Game; Montana Fish, Wildlife and Parks), two federal agencies (US Forest Service, US Fish and Wildlife Service), and a utility company that operates two dams on the lower Clark Fork River (Avista Corporation). Most of the experts also participate in the Aquatic Implementation Team (AIT) that coordinates execution of the NSRP, and are concurrently stakeholders in terms of fish conservation and management in the project

area. The coordinator/analyst (senior author) was an independent (non-stakeholder) scientist who organized meetings and workshops, guided the modeling process, and provided technical expertise in modeling and quantitative analyses.

Refining the modeling objectives and scale of analyses

The modeling team participated in a series of periodic planning meetings, in-person workshops, and webinars over the course of 16 months (Appendix A of this report). The starting point for the process was a 'straw man' conceptual diagram that represented the general objective of the NSRP, the limiting ecological and anthropogenic factors found to have most influenced the objective through the first 13 years of implementation, and management actions that have, and can be, used to address those limiting factors (Figure 2). In short, it was agreed that habitat characteristics in the spawning habitat (patch), connectivity, and biotic interactions with nonnative species had the greatest influence on the successful expression of migratory life histories and persistence of native salmonids. Therefore, actions that improved tributary habitat, increased successful fish passage past dams on the Clark Fork River, and reduced the density of nonnative fishes in spawning and rearing habitat were conservation measures that would be modeled under this exercise.

The first step in the modeling process was to refine the modeling objectives (e.g., Pollino and Henderson 2010), and delimit the spatial and temporal scale of the project area for this analysis. This discussion involved reaching consensus on a number of fundamental questions that were considered during the first workshop, e.g., which species to include in the models, whether to consider occupied or unoccupied habitat, and how far to look into the future in terms of conservation planning. The modeling team decided to focus on bull trout and not to formally consider westslope cutthroat trout. Both species are focal species for the NSRP, but practical concerns – the additional complexity of a two-species model and the fact that bull trout are listed under the US Endangered Species Act – argued for formal analysis of only bull trout in this particular exercise. Additionally, it was recognized that some management actions taken to benefit bull trout – such as habitat restoration or suppression of nonnative trout – very likely

benefit westslope cutthroat trout as well. The refined objectives included components for the model building process as well as the application of the model, and were:

1. *Model building: To use a combination of existing data and expert input to identify measurable outcomes, responses, and indicators for bull trout local populations in the Lower Clark Fork River.*

2. *Application: prioritize conservation actions over the next 15 years that will enhance the bull trout metapopulation to ensure the persistence of bull trout in the Lower Clark Fork River.*

The spatial extent of the modeling project was defined as the tributary, mainstem river, reservoir and lake habitat that encompasses ten local populations of bull trout in the Clark Fork River from the Thompson River downstream to Lake Pend Oreille (Figure 1). The ten local populations were delineated by currently occupied spawning and rearing habitat, which we refer to as patches. Support for the delineation of these local populations is based primarily on genetic differentiation between bull trout from these different patches (DeHaan et al. 2011). We assumed, however, that in the historical condition (no dams, before Euro-American settlement) the patches would function as a metapopulation. We further assumed that some metapopulation structure currently may exist among connected habitats and that adults may stray between patches constrained by the location of mainstem dams. For implementation of the NSRP, the patches are divided in four management regions that correspond to their location relative to dams in the lower Clark Fork River (Figure 1). Management region 1 includes Lightning and Johnson creeks (in Idaho) that are downstream from Cabinet Gorge Dam. Management region 2 includes Bull River and Rock Creek, which are located between Cabinet Gorge and Noxon Rapids dams. Management region 3 includes the Vermilion River, Swamp Creek, Trout Creek, Graves Creek, and Prospect Creek, that are between Noxon Rapids and Thompson Falls dams. Management region 4 includes only the Thompson River, which is upstream from Thompson Falls Dam.

The 15-year time horizon was selected based on biological and practical criteria. Fifteen years encompasses approximately 2-3 generations of bull trout and is half the time remaining in the FERC licenses for Noxon Rapids and Cabinet Gorge dams. Thus, 15 years represents a balance

between the time needed for implementation of management actions and to measure whether bull trout respond to these actions.

A priori patch prioritization exercise

As a preliminary activity, the modeling team was given summary information about each of the ten bull trout patches (e.g., nonnative and native salmonid distribution, physical habitat conditions, redd counts for bull trout; see Appendix B of this report) along with a map showing habitat extent and fish passage barriers, and divided into three groups. Each group was tasked with deciding how best to enhance the metapopulation of bull trout in the LCFR during the next 15 years by prioritizing conservation actions among patches. Results were averaged across groups, but there was consensus that Bull River and Lightning Creek were the most important patches in which to focus conservation efforts whereas Trout Creek was the lowest priority (Table 1). An additional, but unstated, objective of this exercise was to prepare the modeling team participants for subsequent model-building exercises by having them discuss the assumptions and rationale for their rankings.

Conceptual model for migratory bull trout

The next step in the modeling process was to develop a detailed conceptual model to represent the refined modeling objectives, the underlying ecological processes and relationships, and the management interventions to be considered. This process is important because it formalizes knowledge and assumptions, and provides a template to organize thinking and problem solving (Marcot et al. 2006; Uusitalo 2007; Peterson et al. 2013). This was an iterative, many months-long process that occurred in the course of multiple workshops and webinars. The level of detail progressed from a simple depiction of the objective, key ecological factors, and general management interventions (e.g., Figure 2) to increasingly complex diagrams that represented dozens of variables (see Appendix C of this report).

The conceptual model was intended to represent the entire life cycle of migratory bull trout in the lower Clark Fork River system, the major factors influencing habitat quality and survival in

spawning and rearing, foraging, migration and overwintering habitats, and the effect of management interventions. For convenience, the overall conceptual model was divided into two submodels: (1) a within-patch submodel that represents all the life cycle events and interactions that occur within the spawning and rearing habitat, and (2) an outside-the-patch submodel that depicted those processes in the foraging, migration, and overwintering habitats (so-called FMO habitat; see Figure 3). The confluence of a patch and the lower Clark Fork River was selected as the physical delineation between the two submodels. Thus, the two submodels were directly linked by life cycle events that crossed this arbitrary boundary, in this case downstream migration out of the patch by juvenile bull trout and upstream spawning migration into the patch by adult bull trout.

Within the patch, spawning and rearing habitat was a function of intrinsic abiotic factors (temperature, stream size, channel gradient) mediated by any degradation caused by human activities. Realized habitat quality, in concert with other conditions within the patch – such as the presence of nonnative trout, the intensity of electrofishing surveys, recreational angling, juvenile out-migrant capture and transport (all of which could be subject to management) – interacted to influence the reproductive success of spawning bull trout and early life stage survival of bull trout until approximately age 2 or 3, when they out-migrate from the patch. Outside the patch, survival of bull trout is a function of migration strategy, the migration corridor between the patch and Lake Pend Oreille (LPO), the comparative quality of presumed foraging and overwintering habitat, and whether adults can return to their natal patch. For this exercise we assumed that juvenile migrant bull trout from a patch could follow a number of different pathways: they could be transported or move volitionally to LPO, they could move volitionally to a reservoir, or they could stray to another patch. Survival at some or all subsequent life stages would depend on the pathway to which fish were assigned. For juvenile bull trout seeking to migrate to LPO, their survival in the migratory corridor would be negatively related to the number of dams and reservoirs between the patch and LPO. Survival and growth to adulthood varied depending on whether the primary foraging and overwintering habitat was LPO or a reservoir. Adult bull trout that matured in LPO could be precluded from returning to their natal patch by Cabinet Gorge Dam, but this passage barrier could be overcome by the adult capture and transport program. Adult bull trout maturing in reservoir habitats might be unable to enter

the natal patch because of stream dewatering or some other physical migration barrier at the creek mouth, i.e. so-called patch permeability.

The population trajectory for migratory bull trout from a patch was a function of the demographic rates across the entire life cycle. Thus, the within-patch and outside-the-patch submodels are linked to represent a single patch, and sets of patches could be aggregated to depict linkages between patches (metapopulation-like dynamics) and explore the effect of different conservation strategies (Figure 3).

Converting the conceptual model to a decision support model

After completing the conceptual model (Figure 4), the next steps were to select an analytical framework on which to build the decision support model, and then parameterize that model. There are different tools available for creating such a parameterized decision support model. While the conceptual model itself is a useful product in terms of thinking through the decision problem and identifying the important variables and their linkages, the decision support model provides the means to formally evaluate the effect of different management alternatives. We chose Bayesian networks (BN) as a modeling construct because they can incorporate different forms of information, are transparent, and can effectively represent uncertainty (Marcot et al. 2001; Newton et al. 2007; Aguilera et al. 2011). They are often useful in situations – such as the implementation of the NSRP – where management decisions must be made yet information is incomplete. Additionally, we have experience applying this class of models to fishery-related management problems (e.g, Peterson et al. 2013).

Bayesian networks incorporate probabilistic relationships among a set of variables (termed nodes), where causal relationships are shown by directed arrows (Jensen 1996; Marcot et al. 2001; Newton et al. 2007). Thus, there is a direct correspondence between the conceptual model and the structure of the BN. A BN is parameterized by quantifying the conditional relationships among the variables. Each variable or node is assigned a discrete set of states representing possible conditions (e.g., low, moderate, or high) or values (e.g., fecundity or mortality rates) relevant to that variable's definition. A conditional probability table for each variable quantifies the probability of any state given the conditions in any linked, antecedent variables. The

variables can be probabilistic; when the model is 'solved' the probability that a variable is in a particular state is calculated for all child nodes (i.e., those variables with an arrow pointing to them). The strength of the BN approach for this project is that the probability tables can be constructed using many different kinds of 'data', such as results from controlled experiments, observational data from monitoring, output from process-based or statistical models, and even expert opinion. We anticipated that all of these classes of information would be utilized in this exercise.

The conceptual model (Figure 4) and associated BN had dozens of variables, and their names, definitions, states, and data sources are listed in Table 2. A description of the conditional probability tables for each variable is beyond the scope of this report; that information is contained within the BN model and is accessible to the user. To provide a worked example of one portion of the BN and as part of the process for populating the conditional probability tables for other variables in the BN stand-alone analysis, we present results from an exercise to estimate intrinsic habitat potential within the natal patch.

Habitat potential in the natal patch – a spatial analysis using a fragment of the BN

The portion of the conceptual model that addresses habitat conditions in the spawning and rearing habitat (i.e., within the patch), considers intrinsic habitat potential as a function of summer water temperature, stream size, and channel gradient for a given segment, which are then aggrated within a patch. In turn, the realized habitat conditions depend on the intrinsic potential and the degree of human disturbance (Figure 5A). To convert this diagram to a BN (Figure 5B), we defined biological meaningful states for each variable based on our interpretation of relevant literature (Rich et al. 2003; Rieman et al. 2006; Isaak et al. 2009, 2010; Wenger et al. 2011). We then derived a conditional probability table for the potential habitat and realized habitat variables through an elicitation exercise where the members of the modeling team individually estimated the probabilities for each state based on the state combinations for water temperature, stream size, and channel gradient. The responses were summarized by averaging the values to produce the final conditional probability table (e.g., Figure 5C). Differences among respondents about the effect of particular variables were thus expressed as

uncertainty, because the resulting probabilities were more widely distributed among the states in the target variables. We conducted a separate elicitation exercise where the modeling team was asked to characterize the extent of human disruption in each patch as highly altered, moderately altered, or minimally altered/pristine.

The purpose of implementing this portion of the BN was to rank potential and realized habitat conditions for each stream segment within each patch, and then to aggregate those results to the patch scale. First, we conducted a geographic information system (GIS) exercise using ArcMap 10.1 (Esri Inc., Redlands, CA) to derive estimates of temperature, stream size, and channel gradient for each NHD+ stream segment in all patches occupied by bull trout. Stream temperature data came from a regional temperature model for the Northwestern US (www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html), stream size was derived from modeled stream flow (Wenger et al. 2011) converted to stream width (e.g., Peterson et al. 2013), and channel gradient came from the NHD+ stream layer (Horizon Systems Corporation, Herndon, VA, http://www.horizon-systems.com/nhdplus/).

We conducted a pre-processing GIS exercise to remove from further analyses those stream reaches in each patch that do not provide spawning and rearing habitat for bull trout because they are dewatered or inaccessible because of persistent geomorphic or hydrologic features. Dry channels are those that are annually dewatered, though when they are watered they can provide a migratory corridor. Habitat upstream of natural fish passage barriers – typically falls – was excluded as historically inaccessible. Habitat upstream from more transitory (anthropogenic) features – primarily culverts – was not excluded, because we assumed that habitat could be utilized by bull trout (if it was suitable) but for the barrier. A large portion of the Thompson River drainage – especially in the upper part of the watershed – was also excluded as unsuitable for bull trout based on warm water temperatures, which is largely corroborated by lack of occupancy of bull trout in the excluded portions (e.g., GEI Consultants and Steigers 2013). We consolidated information on dry stream channels and natural barrier locations from previous GIS exercises (e.g., GEI 2005), state agency databases, and local knowledge of modeling team biologists. Stream habitat above barriers was removed (clipped) from the dataset by delineating the watershed upstream from the point location of the barrier. Dry channels areas sometimes spanned a portion of an NDH+ segment, so in those cases we split the NDH+ segment into dry or

watered portions. The watered portions were populated with the corresponding NDH+ segment data for temperature, stream size, and channel gradient. We used those data to generate predictions for potential and realized habitat for each stream segment using the BN model fragment in Figure 5B. The BN model fragment was implemented using the 64-bit version of Netica 5.14 (Norsys Software Corp. 2014).

To provide a coarse spatial representation of potential habitat, we reduced the dimensionality of the habitat potential probabilities for each segment to a single index value by weighting low, medium, and high probability categories by 0.2, 0.5, and 1.0 (respectively), and rescaled them so the resulting index scaled from 0 (low potential) to 1 (high potential) within each segment. Results were then mapped, with consideration of dry channels and inaccessible habitat (Figure 6). We emphasize here that our choice of category weights and cut points for the color scheme were arbitrary; the map served simply to illustrate the location of comparatively higher vs. lower potential habitats for bull trout.

To aggregate the segment-by-segment predictions to a summary prediction for each patch, we summarized intrinsic potential for each state (category) within each patch by multiplying the segment-specific (*i*) probability by the segment stream length, summing across all segments (excluding dry channels and habitat above natural barriers), and dividing by the total stream length of wetted and accessible habitats within patch *j*, as:

$$probability\ \ for\ low,\ med,\ or\ high = \frac{\sum_i p_i \times length_i}{\sum_j length}$$

The majority of habitat within each patch and across the project was ranked as low potential, indicating areas of unsuitable stream width (i.e., too much or too little streamflow), high gradient, or warm summer temperatures (Table 3). To provide a comparison of suitable habitat among patches, we calculated the relative amount of habitat that was ranked as high and moderate or high within each patch. When all ten patches are considered, Thompson River, Prospect Creek, Bull River, and Lightning Creek had the greatest intrinsic potential, according to our metric. This stand-alone exercise provided a coarse comparison of modeled habitat suitability among patches. The estimated intrinsic and realized habitat potential from this

exercise were subsequently used in the full decision support model (Bayesian network or BN) to parameterize baseline conditions for those variables within each patch.

Parameterization of the Bayesian Network

In our conceptual model, we were interested in the overall response of migratory bull trout in an individual patch (i.e., local population), and selected the finite rate of population growth (λ) as the indicator variable for bull trout response (Figure 4). We sought to represent the entire life cycle of migratory bull trout while depicting a suite of abiotic, biotic, and anthropogenic factors that could influence specific life stages or ages. Our desire to exert fine control over survival – and to ultimately examine the effect of specific management actions – led to an explicit representation of survival by age in the conceptual model. We used a combination of data analyses, expert opinion, elicitation exercises, literature review, and modeled data to quantify the relationships among variables (i.e., develop the conditional probability tables) for most of the variables in the conceptual model (Table 2). To convert from the age-specific demographic rates to population response (λ), we developed a demographic population model for migratory bull trout. This demographic model was an 8-stage matrix population that was equivalent to our representation of the bull trout life cycle in the conceptual model (Figure 7). Matrix models are useful for species with structured populations, where different ages or life stages survive at different rates and have different reproductive contributions, and they are also helpful to evaluate targeted management decisions that may not affect all age classes or life histories (Morris and Doak 2002). We then parameterized this matrix model and used it to simulate a dataset from which we derived the conditional probability table for λ in the Bayesian network model.

<u>Matrix population model for migratory bull trout</u>

Life history of migratory bull trout in the context of capture and transport

A total of 2,481 juvenile bull trout were captured moving downstream in tributary streams during 2000-2013; approximately 64.5% of these were judged age 2 and 20.9% were age 3 (Moran 2012; see also Appendix D of this report), thus these two age classes comprised approximately

85.6% of the catch. Bull trout that migrate at age-0 are assumed to survive at very low rates outside the natal habitat (e.g., Downs et al. 2006), and other age classes (besides ages 0, 2 and 3) collectively represent about 10% of the out-migrating juvenile bull trout (Moran 2012). Bull trout ages 2 and 3 at time of capture and transport comprised more than 94% transported fish that were subsequently captured below Cabinet Gorge Dam as adults (Moran 2012). Given these data, and to achieve a balance between the focus of the transport program and model complexity, we ignored the potential demographic contribution of migrants aged 0, 1 or >3. We thus assumed that the relative contribution of age-2 and age-3 bull trout captured moving downstream was generally representative of the migration strategy for that local population and contributed to the pool of juveniles that were subsequently available for capture and transport as adults. We normalized the contribution of age-2 and age-3 bull trout to correspond to the assumption that these two age classes comprise 100% of the juveniles that migrate from the patch. Thus in any given year, an average of 76% of the age-2 bull trout (normalized from 64.5%) would attempt to migrate, while 24% would remain and migrate the following year as age 3. Total age-specific survival during age 2 and 3 is a function of the habitat occupied (patch conditions and FMO habitat), which itself is a function of the proportion of fish of a given age that experienced a particular migratory pathway (i.e., transport or volitional movement).

Survival during age 3 (for individuals out-migrating as age 2), age 4, and age 5 occurs in FMO habitat. All bull trout are assumed to mature at age 6. Mature adults comprise four groups: (a) those reared in LPO and that are captured below Cabinet Gorge Dam and transported upstream, (b) those reared in LPO but not captured below Cabinet Gorge Dam, (d) those reared in a reservoir within that patch's management region, and (d) strays that immigrate from other patches within a management region or from patches in management region further upstream. The mature bull trout not captured at Cabinet Gorge Dam are assumed to spawn in non-natal habitat below the dam or to resorb their eggs. In either case it is assumed that these fish experience some stress related to the straying or failure to spawn when mature, and do not contribute to the reproductive output for the natal patch in that year. Mature bull trout not captured below Cabinet Gorge Dam at age 6 can be captured and transported in subsequent years. After first spawning, bull trout enter a 'terminal' reproductive stage (age 7 and older). Fish in this terminal stage represent those that returned to LPO after first spawning and were

captured (or recaptured) below Cabinet Gorge Dam, those that make return spawning migrations between the adjacent reservoir, and any immigrants.

Survival rates for migratory bull trout

The model was parameterized with vital rates derived from various sources: information specific to bull trout in the Clark Fork River, data from other bull trout populations, and the expert opinion of biologists that manage bull trout in the project area. Egg survival and age-specific survival rates were not available for bull trout in the project area. For modeling we used hypothesized vital rates based on mark-recapture studies with migratory (fluvial) bull trout in the Walla Walla River system (Al-Chokhachy and Budy 2008; Bowerman 2013) that have been previously used for an individual-based model (IBM) for one local population of bull trout in the project area (Al-Chokhachy and Ebinger 2012). We also referred to hypothesized survival rates used to model migratory bull trout in the Flathead Lake system (Staples et al. 2004). Collectively, these survival rates provided a starting point from which we made adjustments to reflect conditions in the project area and to best depict the management interventions and scenarios of interest.

Survival of eggs, age-0, age-1, and age-6 and older bull trout was assumed identical to the corresponding values in Al-Chokhachy and Ebinger (2012). These latter three vital rates are slightly less than those hypothesized for the adfluvial bull trout in the Flathead Lake system (Staples et al. 2004). In general, we assume that the bull trout habitat in the lower Clark Fork River project area has been more significantly degraded by human activity than it has in the Flathead Lake system.

Survival rates for bull trout ages 4 and 5 depended on whether fish were rearing in LPO or a reservoir. Bull trout that reared in LPO were assumed to survive at the mean age-specific rates from Al-Chokhachy and Ebinger (2012); whereas those in a reservoir were hypothesized to survive at lower rates because the reservoirs have less suitable physical habitat (shallower and warmer) and forage than LPO. Hypothesized survival values for bull trout in reservoirs were derived from an elicitation exercise where biologists on the modeling team were asked to characterize the relative difference in survival of bull trout that reared in LPO compared with

reservoirs (Appendix E of this report). The reservoir survival rates were calculated as a proportion of the LPO value weighted by the relative frequency of responses in the five categories that ranged from >50% decrease to >50% increase relative to a hypothesized baseline value. The resulting values were used for bull trout whose FMO habitat was Noxon Reservoir. Cabinet Gorge Reservoir and Thompson Falls Reservoir and River were considered less suitable than Noxon Reservoir, so the survival rates were adjusted downward by 0.08 (16% decrease).

Variation in survival at ages 2 and 3 were critical elements of the modeling exercise because these age classes are directly influenced by the capture and downstream transport program for juvenile bull trout. Assumptions about survival at these ages may strongly influence the overall modeling results. The assumptions included:

- Survival of age-2 bull trout in reservoirs was taken as the mean age-specific value (0.264) from Bowerman (2013). This value is intermediate between values hypothesized for migratory bull trout in the Flathead Lake system (Staples et al. 2004) and migratory bull trout in the Walla Walla River system (Al-Chokhachy and Budy 2008).
- Survival of age-3 bull trout in reservoirs was the mean age-specific value (0.45) from Al-Chokhachy and Ebinger (2012).
- Survival of age-2 or -3 bull trout transported to LPO or those that migrated volitionally to LPO was based on elicitation results that were scaled using the return rates estimated from a mark-recapture experiment (i.e., the so-called Skalski experiment, McCubbins et al. 2012; Moran 2012)
- Age-3 bull already present in LPO (i.e., those that were transported or moved volitionally at age 2) survived at slightly higher rates than those that were transported or moved volitionally at age 3. These differences were based on the elicitation exercise.
- Survival of age-2 bull trout that remained in the patch and did not migrate at age 2 was hypothesized to be 0.4. We reasoned that these individuals would survive at higher rates than age-1 bull trout because of their greater size and competitive ability.
- The mean capture efficiency of adult bull trout below Cabinet Gorge Dam was 0.4 (40%).
- Return rate of bull trout captured and transported to LPO as putative age 2 was 2.1% (34 adults recaptured from 1605 transported juveniles).

- Return rate of bull trout captured and transported to LPO as putative age 3 was 6.2% (32 adults recaptured from 519 transported juveniles).
- The product of survival from age 2 or age 3 to maturity (includes the age-5 survival interval) for transported bull trout should be roughly equivalent to the above return rates, after accounting for capture efficiency below Cabinet Gorge Dam.
- Survival of bull trout age 4 or older that are present in LPO did not depend on whether they migrated or were transported there at age 2 or age 3.

Maturity and fecundity of migratory bull trout and the effect of immigration

Based on sexual maturity results from LPO (McCubbins 2013), female bull trout were considered to be mature at age 6. Annual growth of adult bull trout that reared in LPO were based on McCubbins (2013) and those that reared in reservoirs were assumed to grow at 75% of this rate; therefore, we assumed that age-6 females that reared in LPO were 500 mm TL, on average, at the time of spawning (cf. McCubbins 2013); those that reared in reservoirs were assumed 450 mm TL. The mean size of female bull trout in the terminal age class was estimated as the median size of ages 6 through 12. The median size of age-7 and older bull trout from LPO was estimated as 610 mm, whereas the size of those from reservoirs was 532 mm. Length-specific fecundity was estimated by nonlinear least-squares regression ('nls' function in R 3.0.01, R Core Team 2013; $p<0.001$ for slope estimate) using data from Prospect Creek and the Bull River (Brunson 1952) as:

$$Fecundity = (5.82 \times 10^{-7}) \times TL^{3.549}$$

We assumed an equal sex ratio for spawning adults, and that the probability of repeat spawning was 0.75. The list of vital rates and initial values for the matrix population model are listed in Table 4.

The parameterized matrix model (Figure 7C) had values that were stand-alone entries (e.g., matrix entries *S0* and *S1*; Figure 7B and Table 4), and those that were functions of other variables. The functions were needed to decompose survival rates and reproductive output to

account for potential differences resulting from capture and transport of bull trout. Matrix model entries with functional equations were:

$$S2 = JM_2[(Jt * S2t_2) + (Jv * S2v_2) + (Jr * S2r_2) + (Js * 0)] + (1 - JM_2) * S2p$$

$$S3 = (1 - JM_3)[(Jt * S3t_2) + (Jv * S3v_2) + (Jr * S3r_2) + (Js * 0)] + JM_3[(Jt * S3t_3) + (Jv * S3v_3) + (Jr * S3r_3)]$$

$$S4 = (Jt * S4t) + (Jv * S4v) + (Jr * S4r)$$

$$S5 = (Jt * S5t) + (Jv * S5v) + (Jr * S5r)$$

$$S6 = \left(CG * S6b * (Jt + Jv)\right) + (Jr * S6b)$$

$$S7 = (CG * S7b * (Jt + Jv)) + (Jr * S7b)$$

$$M6 = \frac{[(Jt + Jv) * F6_{LPO} + (Jr * F6_{RES})] * R * Se}{1 - \frac{Imm}{2}}$$

$$M7 = \frac{[(Jt + Jv) * F7_{LPO} + (Jr * F7_{RES})] * R * Se * repeat}{1 - \frac{Imm}{2}}$$

Matrix entries *S2* through *S5* were age-specific survival probabilities weighted by the proportion of fish that followed a particular pathway to maturation (i.e., transport to LPO - *Jt*, volitional movement to LPO - *Jv*, or reservoir - *Jr*). Matrix elements *S6* and *S7* were similarly weighted by the pathway to maturation but also consider two additional elements. First, the calculations considered the probability that bull trout rearing in LPO were captured below Cabinet Gorge Dam (*CG*). This represented a transition from maturity to spawning for those bull trout with natal patches upstream from Cabinet Gorge Dam (i.e., management regions 2-4); if they were not captured and transported then they could not contribute demographically to their natal patch. Bull trout from Lightning and Johnson creeks were not subject to this capture and transport constraint, as their natal patches were downstream from Cabinet Gorge Dam.

Stage-specific reproductive output (*M6* and *M7*) was generalized as sex ratio × size specific fecundity × egg-to-fry survival × spawning probability, and adjusted to account for any demographic contribution of immigrants (i.e., strays from other patches; patch-specific

immigration rates were derived from elicitation). We assumed that any immigrants were evenly divided between the age-6 and age-7 and older age classes, thus the term for immigrants (*Imm*) is divided by two in the equations for *M6* and *M7*. For example, if *M6* is 500 in the absence of immigration, then it would be about 521 if the effective immigration rate was 0.08 (8%), e.g.

$$M6 = \frac{500}{1 - \frac{0.08}{2}} = \frac{500}{0.96} = 520.83$$

Thus in this example, approximately 4% of the reproductive output of age 6 fish would come from immigrants. The total reproductive output depended on the proportion of fish reared in LPO or a reservoir and their respective sizes, as well as the influence of immigration.

Generic matrix model parameterization

The parameterized matrix model predicted a stable population (Figure 7C), which was consistent with population trends from redd counts for bull trout in the project area (Appendix F of this report). This template or generic parameterization does not represent bull trout in any particular patch; rather, it is intended to represent the average conditions for a local population of bull trout subject to downstream and upstream transport programs at the levels implemented during the preceding decade. In the decision support (BN) model, the demographic will vary to account for conditions within the patch, such as habitat quality or presence of nonnative trout, and those outside the patch, such as number of dams passed to reach Lake Pend Oreille.

Using the matrix model to parameterize the Bayesian network

The next step in the modeling process was to use output from the matrix model to develop the conditional probability table for the population growth rate variable (lambda, λ) in the decision support model (BN model). First, Monte Carlo simulation was used to calculate a large number of λ values based on the matrix model structure and various combinations of the underlying demographic rates. At each repetition, survival rates, immigration rates, and repeat spawning frequency were drawn from a uniform distribution such that the values in the conditional

probability table were approximately the median value in the distribution for each parameter. The proportion of juvenile bull trout that leave the patch and are either transported to LPO (*Jt*), move volitionally to LPO (*Jv*), rear in a reservoir (*Jr*), or immigrate to another patch (*Js*) must sum to one. Consequently, *Js* was drawn from a uniform distribution with specified bounds, and the dependent values (*Jt*, *Jv*, *Jr*) were drawn from a uniform distribution and standardized such that the sum of the four probabilities was one. Fecundity values were based on the average age- and FMO-habitat-specific female body sizes (see Table 4) drawn from a normal distribution assuming 10% coefficient of variation. A total of 10 million replicate matrices were generated, and λ was estimated for each matrix. The Monte Carlo simulations were conducted in the 64-bit version of R 3.0.1 (R Core Team 2013) using the package 'popbio' (Stuben and Milligan 2007).

Next, the Monte Carlo simulation results were used to generate the conditional probability table for λ in the BN model. The Monte Carlo simulation results were entered as cases (observations) for the BN model implemented using Netica, and a counting-learning algorithm was used to generate the conditional probability table for λ. Parent variables for λ (*S0*, *S1*, etc.) were limited to 4-6 states, with the range of values for each state based on the range of values from the Monte Carlo simulations. This was done to reduce the dimensionality of the conditional probability table for λ as there are computational limits to the size the table based on the number of parent variables, states of those variables, and the BN structure.

Analyses

Sensitivity analyses and initial BN performance testing

We conducted sensitivity analyses on both the matrix population model and the BN decision support model. The former explored how λ changed in response to incremental (sensitivity) and proportional changes (elasticity) in the matrix entries. We performed an analogous sensitivity analyses with the corresponding variables in the BN model, but the sensitivity was expressed in terms of a finding (at a variable) that reduced the variance in the expected value of λ. We also conducted one-at-a-time variable testing where we examined the range of λvalues that resulted from switching a variable between its lowest and highest states.

The modeling team also tested the performance of the BN model by using it to explore management scenarios for each patch during the fourth workshop, and by using it during a planning meeting for management of bull trout in the Bull River. Feedback from these exercises was used to fine-tune the model and make it more user friendly.

Patch-level and multi-patch analyses of management actions

We used the BN to explore implementation of management actions at various levels related to the three most relevant management aspects of the NSRP: juvenile and adult fish passage, habitat restoration in the natal patch, and manipulation of nonnative trout. We did this at two scales: patch-by-patch and groups of patches that would be subject to similar management strategies. Patch-level analyses involved searching for the "best" or most important set of management actions that resulted in the largest increase in population growth rate for that local population of bull trout. For this exercise, the modeling team split into pairs and each pair was assigned two patches and tasked with finding the best management actions. The suggested solution for each patch was validated by the coordinator/analyst. We also conducted exploratory sensitivity analyses for one patch (Vermilion River) by contrasting results obtained under different initial conditions or different assumptions about the migratory strategy of juvenile bull trout. For these analyses we typically used systematic changes in the state level of management variables one-at-a-time, but also included a limited number of post-hoc combination scenarios to examine interactions among variables and the effect on λ.

Patches were placed in two groups for the multi-patch analyses: those patches where dams impeded movement and where fish passage was an important management consideration and those where it was not. The eight local populations whose natal habitat was in Montana (management regions 2, 3 and 4) were all upstream from Cabinet Gorge Dam and placed in the first category; the two local populations in management region 1 (Lightning and Johnson creeks) where bull trout do not need to pass a dam to access natal habitat were in the second category.

To aggregate predictions across patches or management regions, we weighted each patch's contribution based on its intrinsic habitat potential. In this scheme, we assumed that patches with a greater extent of habitat ranked medium or high intrinsic potential would support larger

populations and thus contribute more to the overall status of bull trout in the project area. We calculated λ for management region or groups of management regions weighted by the sum of the Med and High intrinsic habitat potential categories in Table 3.

RESULTS AND DISCUSSION

General model assumptions and sensitivity

Inferences about the benefits of particular management interventions depend on a number of assumptions and sensitivity to modeled or elicited variables. A key one is that we have correctly specified the model structure and not omitted any critical variables. If the model structure and parameterization are considered accurate (or at least suitably representative), then it is tempting to make some broad generalization about the different categories of management actions using the subsequent patch-by-patch results (e.g., reducing effects of nonnative trout is very important). While some management strategies – such as focusing on nonnative trout – might appear robust, this strategy and others may be very sensitive to the presumed baseline conditions within each patch.

In the BN, λ is very sensitive to intrinsic habitat potential and human disruption (Figure 8), and collectively these two variables represent the baseline habitat suitability within a patch. Intrinsic habitat potential is thus an overarching filter on the ability of bull trout to respond to management, and no interventions we modeled were capable of changing this underlying potential. We estimated intrinsic habitat potential as a function of modeled variables – stream size, water temperature, and channel gradient – according to an elicited rule set (i.e., conditional probability table, see Figure 5), and recognize that these model-based results could potentially differ from conditions measured in the field. The model predicts high habitat potential in downstream reaches of some patches, but in reality this may overestimate its true potential or underestimate the influence of legacy habitat disturbance. A unique feature of many tributary streams in the project area is a high degree of natural stream intermittency resulting from sediments deposited by Glacial Lake Missoula (e.g., in Rock, Swamp, Trout, and Prospect Creeks; see Figure 6), and early snowmelt runoff at lower elevations (Sando and Blasch, in review). Thus, the actual extent of suitable habitat may be less and the water temperatures

warmer than would be predicted by the BN. This intermittency has also contributed to the mixed life history expression (i.e., resident and migratory) for local bull trout populations in some patches within the project area (Zymonas 2006). Our modeling focused exclusively on the migratory life history and the fish which express a resident, or less migratory, life history, may respond differently to the management interventions that were modeled. Additionally, the model aggregates habitat suitability and the effect of biotic interactions with nonnative trout to the patch level and may not fully capture the spatial heterogeneity in habitat degradation or occurrence of nonnative trout. For example, if bull trout cannot expand their distribution downstream into reaches where nonnative trout have been removed and must do so to respond at the population level (i.e., increased λ), then the benefits of reducing nonnative trout could be overstated. On the other hand, removal of nonnative trout from the migratory corridor may have a positive effect on bull trout independent of habitat suitability for spawning and rearing if, for example, predation on out-migrating juvenile bull trout was reduced.

Complex model behavior, trade-offs between different management actions, and the influence of actual conditions might only become apparent if considerable time is spent exploring different sets of baseline conditions for each patch. An in-depth examination of assumptions about input conditions for all ten patches is beyond the scope of this report; however, a brief review of some of the more pertinent baseline conditions used for the patch-by-patch analyses should be considered both by the reader and future users of this model (see Table 2 for additional details about the information sources for each variable).

In patches where trapping occurred, we assumed initially that 10% of out-migrating juvenile bull trout are captured and transported to LPO, and that the remaining fish were divided between volitional migrants to LPO (40%), volitional migrants to the nearest reservoir (47%) and strays to other patches (3%). Trap efficiency was estimated empirically at 10%, but there is considerably greater uncertainty about the latter three values. Baseline survival age-2 and age-3 bull trout captured and transported to LPO was 32% and 55%, which was higher than those that reared in a reservoir or those that moved volitionally to LPO. Those that moved volitionally to LPO were subject to additional mortality by passing through reservoirs and over dams, but we did not directly model the effect of the migration distance within a patch or variation in the density of nonnative trout encountered in the lower reaches of a patch. Survival of sub-adult bull

trout and fecundity of female bull trout that reared in LPO was greater than those from Noxon Reservoir, and higher still than those from Cabinet Gorge and Thompson Falls reservoirs. This was because of a recognized continuum in the quality of FMO habitat from high (LPO) to low (Cabinet Gorge and Thompson Falls) due to differences in physical conditions (depth and temperature profile) and the abundance of forage fish and predators. The baseline capture and transport efficiency of adult bull trout at Cabinet Gorge Dam was 40%, a value that was generated by a scientific panel convened for an earlier planning exercise (Epifanio et al. 2003). The generic population model used to parameterize the BN model was consistent with population trends from redd counts, but the baseline λ within each patch that was estimated by the BN ultimately depended on the local conditions used to initiate the BN (e.g., Table 6).

These are just a few of important assumptions and baseline conditions used in the modeling exercise; literally thousands of combinations of input conditions are possible when all ten patches are considered. Important patch-specific conditions that might exert a strong influence on model results are highlighted in seriatim in the patch-by-patch analyses. A more comprehensive illustration of sensitivity to input conditions is provided by the example of the Vermilion River at the end of the patch-by-patch results. Finally, the BN model output for any given scenario is interpreted simply as the percent likelihood that a local population is stable or increasing (as opposed to declining) by summing the probabilities for the state values for λ than encompass stable and increasing populations. This was done because the point estimates for λ should not be interpreted literally given the large number of assumptions and uncertainties inherent in the BN model.

Ultimately, the BN should not be considered an accurate representation of reality, but instead as an approximation based on a synthesis of current understanding that can serve as a tool for biologists to evaluate different management alternatives under a common framework. In simpler terms, the model may not be perfect but it was useful.

Patch-by-patch analyses

Lightning Creek

Under baseline conditions λ was 0.995 (SD=0.21) and the sum of the probabilities indicated a high probability of a stable or increasing population (~85% for states with λ>0.9; Figure 9; Appendix G). Reducing the effect of nonnative trout or restoring habitat – alone or in combination – had a nominal influence on the probability that the population was stable or increasing. In all cases the probabilities were high (86-91%).

Johnson Creek

Under baseline conditions λ was 1.06 (SD=0.24) and the sum of the probabilities for state values indicated a high probability of a stable or increasing population (92% for states with λ>0.9; Appendix G). There were no threats to this local population that could be addressed in the context of the BN; the accessible habitat was not degraded, nonnatives were judged rare, monitoring or angling were not thought to result in appreciable mortality, and there was no juvenile transport program because fish could move volitionally to LPO. Therefore, a figure depicting λ response to management scenarios for this patch was not depicted and this patch was not considered further.

Bull River

Most of the bull trout in this patch spawn in the East Fork Bull River (see Appendix A of this report), but this modeling exercise considered the entire patch as defined by its confluence with the Clark Fork River[1]. Under baseline conditions in the Bull River patch, λ was 0.921 (SD=0.2) and the sum of the probabilities for λ>0.9 was 54%, indicating considerable uncertainty about whether the population is stable (Figure 10; Appendix G). The team modeling exercise to determine the best single strategy that would positively influence λ found that reducing the abundance of nonnative trout had a larger effect than the other management actions. Modest increases in juvenile transport (from current 10%) to 20% or 50% transport did little to improve

[1] Potentially, the BN could be used to consider actions within a smaller portions of a drainage (e.g., sub-patches such as East Fork Bull River) within the larger patches defined in this exercise. In that case, the BN would need to be initialized with input conditions appropriate to the delineated sub-patch, and the inferences from the BN would be constrained to the subset of bull trout that spawn and rear within that sub-patch.

the chances of population stability or growth, unless it was coupled with an increase in adult capture efficiency at Cabinet Gorge Dam.

Rock Creek

Under baseline conditions the λ was 0.938 (SD=0.2) and the sum of the probabilities for λ>0.9 was 59.1%, indicating it was slightly more likely that the population was stable or increasing (Figure 11; Appendix G). The single-best management strategy was to capture and transport all juvenile bull trout to LPO (λ = 1.0, sum of probabilities of λ>0.9 = 84.1%. The second-best strategy was reduce nonnative trout from moderate to low (λ = 0.985, sum of probabilities of λ>0.9 = 78.1%). In Rock Creek there is little overlap between bull trout spawning and rearing areas and the current distribution of nonnative trout (see Appendix B of this report), so the predicted response of bull trout to fewer nonnative trout presumes that bull trout can expand their distribution downstream (into habitat formerly occupied by nonnative trout) and/or juvenile bull trout would experience less predation when the move through the migratory corridor within the patch. The relative benefit from changing adult capture rates at Cabinet Gorge Dam or juvenile transport rates depended on the extent to which transport/capture rate was increased. Increasing capture rates at Cabinet Gorge Dam from the baseline of 40% to 60% (0.951, 65.1%) or 75% (0.963, 70.2%) benefitted the population more than increasing juvenile transport from the baseline of 10% to 20% (0.947, 63.0%) whereas increasing juvenile transport to 50% (0.97, 73.0%) was similar to increasing adult capture rate to 90% (0.973, 74.3%).

Swamp Creek

Under baseline conditions the λ was 0.94 (SD=0.2) and the sum of the probabilities for λ>0.9 was 61.5%, indicating it was likely that the population was stable or increasing (Figure 12; Appendix G). Human disruption was judged minimal. Reducing the influence of nonnative trout had a large effect on the probability of a stable or increasing population, with state values exceeding 77% (nonnatives to moderate) and 87% (nonnatives to low). Swamp Creek does not currently have a juvenile bull trout transport program but results suggested that unless other

variables were also manipulated (e.g., nonnative trout, adult capture rate), there was little benefit from instituting one unless nearly all juveniles were captured and transported. Increasing adult captures below Cabinet Gorge Dam had a positive effect that was intermediate between reducing nonnative trout and transporting more juveniles.

Trout Creek

Under baseline conditions the λ was 0.997 (SD=0.21) and the sum of the probabilities λ>0.9 was 75.5%, indicating a moderate-to-high likelihood that the population was stable or increasing (Figure 13; Appendix G). Human disruption was judged minimal, and currently there is no juvenile capture and transport program in Trout Creek. Reducing nonnative trout from moderate to low had a larger effect on increasing the probability of a stable or increasing population (λ=1.04, probabilities 86.5%) than did increasing adult capture rates at Cabinet Gorge Dam or instituting a juvenile transport program (unless all juveniles were transported). As in Rock Creek, bull trout spawning and rearing within Trout Creek occurs in the upper drainage and nonnative trout are present primarily in the lower drainage, so the mechanism of population response by bull trout would be to expand their distribution downstream and/or that juveniles experience less predation and competition with nonnative trout during out-migration.

Vermilion River

Under baseline conditions, the λ was 0.953 (SD=0.21) and the sum of the probabilities for λ>0.9 was 70.9%, indicating a moderate-to-high likelihood that the population was stable or increasing (Figure 14; Appendix G). During the modeling process, nonnative trout and habitat disruption were both identified as significant concerns in the Vermilion River. Reducing the effect of nonnative trout had a stronger positive effect on the probability of a stable or increasing population than did reducing habitat disruption. The effect of increasing adult capture efficiency at Cabinet Gorge Dam to 60% and 75% had a slightly greater effect than that achieved by reducing human disruption to moderate or minimal. The effect of increasing juvenile transport was counterintuitive when the other variables were in their baseline states; increasing juvenile

transport to 50% actually caused a slight decline in population status. This appeared to be caused by an interaction between the effect of juvenile transport and other factors. For example, increasing juvenile transport to 50% in concert with either a reduction in nonnative trout or increased adult capture rates at Cabinet Gorge Dam had a positive effect greater than that estimated for either factor alone.

Graves Creek

Under baseline conditions, the λ was 1.02 (SD=0.21) and the sum of the probabilities for $\lambda>0.9$ was 90.5%, indicating a very high likelihood that the population was stable or increasing (Figure 15; Appendix G). Altering single-factor management scenarios did little to change the population status of bull trout in Graves Creek, including even dropping the juvenile capture and transport program in that stream. Seemingly, the additional management interventions did little because the baseline conditions within the patch were comparatively favorable for spawning and rearing of bull trout. Increasing adult capture rate at Cabinet Gorge did increase the effective survival rate of age 6 and older bull trout, but there was little effect at the population level because λ was relatively insensitive to survival of these age classes (e.g., Table 5). Baseline conditions assume high permeability, and upstream transport of adults would have a much larger (positive) effect on λ if permeability was low. Increasing juvenile capture and transport from 10% to 20% or 50% had only a very small positive effect. The BN predictions should not be interpreted as formal test of density dependence, but the general results for Graves Creek may also be consistent with a population at or near carrying capacity

Prospect Creek

Under baseline conditions, λ was 0.906 (SD=0.18) and the sum of the probabilities for $\lambda>0.9$ was 48.5%, indicating a high degree of uncertainty for whether the population is stable (Figure 16). Reducing the influence of nonnative trout had a larger effect on the population status of bull trout in Prospect Creek than did any other single management intervention. For example, changing the status of nonnatives from high to moderate increased λ to 0.96 and the likelihood of a stable

or increasing population to more than 71%. Prospect Creek, like Trout and Prospect creeks, is a situation where nonnative trout currently occupy the lower reaches of the drainage whereas much of the bull trout spawning and rearing farther upstream (see Appendix B of this report). The effect of reducing human disruption of natal habitat to moderate and minimal and increasing capture rates of adult bull trout below Cabinet Gorge Dam to 60% and 75% were roughly equivalent. Combining either of these two in concert with a reduction of nonnatives resulted in a similar response. The positive effect of increasing the capture and transport of juvenile bull trout increased in proportion to the percentage transported.

Thompson River (WFk & Fishtrap)

Under baseline conditions in the Thompson River area of interest (WFk and Fishtrap) λ was 0.906 (SD=0.2) and the sum of the probabilities for $\lambda>0.9$ was 48%, indicating uncertainty about whether the population is stable (Figure 17; Appendix G). Reducing the influence of nonnative trout had a larger effect on the population status of bull trout than did any other single management intervention. For example, changing the status of nonnatives from high to moderate increased λ to 0.952 and the likelihood of a stable or increasing population to more than 68%. However within the Thompson River drainage, nonnative trout densities are greatest outside the current spawning and rearing locations for bull trout. The effect of increasing capture rates of adult bull trout below Cabinet Gorge Dam from 40% to 60% or 75% was slightly more positive than the effect of reducing human disruption of natal habitat to moderate and minimal. Combining either of these two in concert with a reduction of nonnatives resulted in a similar response. Instituting a juvenile transport program had little effect unless nearly all the out-migrating juveniles were captured.

Sensitivity to input conditions and complex model behavior for individual patches: Vermilion River example

Under the best guess baseline conditions (modeled above), management actions targeting nonnative trout were judged to have the largest effect on the population status of bull trout in

Vermilion River. A counter-intuitive result was that – in the absence of additional management actions – increasing juvenile transport from 10% to 20% had little effect on population status and was similar in effect to discontinuing transport or transporting all the juveniles, whereas increasing transport to 50% actually resulted in a slight *decrease* in population status (Figure 14). The results appear to be affected by assumptions about the quality of the reservoir FMO habitat and the per-dam mortality rate. For example, changing the reservoir FMO habitat from moderate (Noxon Reservoir) to a lower-quality state (equivalent to Cabinet Gorge/Thompson Falls) results in a reversal of the response to changes in juvenile transport (Figure 18; Appendix G). Under this different set of conditions, discontinuing juvenile transport reduced the population status, increasing juvenile transport from 10% to 20% resulted in a small increase in population status, and transporting all juveniles had a large, positive effect (Figure 18). Increasing juvenile transport to 50% had no discernable effect. If, concurrently, the per-dam mortality rate also increased from a baseline 10% to at least 30%, then increasing juvenile transport from 10% to 50% slightly increased the population status (e.g., Figure 18).

Variation in vital rates

The modeled baseline population status in all patches including the Vermilion River will depend on our confidence in the baseline conditions which represent what the modeling team determined were most likely the current conditions that were subsequently input into the BN to generate the baseline estimates. For these analyses, we used a 10% coefficient in variation (CV) in survival rates to model the aggregate effect of process variation and parameter uncertainty. Increasing the CV resulted in a more pessimistic population baseline in the Vermilion River. For example, at 10% CV in Vermilion River, λ was 0.953 (SD = 0.19) and the percent likelihood of a stable or increasing population was 71% (Figure 19; Appendix G). With a 40% CV, the estimated λ was 0.941 (SD=0.25) and the percent likelihood of a stable or increasing population decreased by 10% (to 61%). However, the effects of management interventions were generally consistent for both 10% and 40% CV, except possibly for juvenile transport where there was greater uniformity in response at 40% CV (Figure 19). The primary difference between the two CV levels appeared to be the response at 50% juvenile transport; a decrease in population status was predicted at 10% CV while there was no change at 40% CV (Figure 19). We applied a conservative CV

(10%) uniformly across all patches. If additional demographic data indicated greater variation vital rates within specific patches, then a higher CV could be used in subsequent analyses.

Assumptions: migration strategies and FMO habitat for juvenile bull trout

The assumptions about the migration strategies of juvenile bull trout from each patch can have a very strong influence on the outcome of management interventions. We assumed that in bull trout patches having juvenile transport programs the mean capture and transport rate was 10%, whereas the remaining out-migrants were divided into 40% volitional to LPO, 47% volitional to the nearest reservoir, and 3% strays. Modeled increases or decreases in the capture and transport rate lead to decreases or increases that were equally divided between the volitional to LPO and volitional to reservoir migratory strategies (stray rate was assumed constant at 3%). For example, a modeling scenario that increased doubled the juvenile transport rate to 20% resulted in 5% decrease for both volitional to LPO and volitional to nearest reservoir strategies.

Under the default assumptions about migration strategy (52% Noxon and 45% LPO), stopping juvenile transport in Vermilion River resulted in λ 0.954 (SD=0.19) and the likelihood of a stable or increasing bull trout population was 71% (Figure 20; Appendix G). If we assume – in the absence of transport – that all juvenile bull trout migrate volitionally to LPO, the population was slightly less secure ($\lambda = 0.95 \pm 0.22$, 67%). In contrast, if we assume that all the juvenile bull trout migrate to Noxon Reservoir for their FMO habitat, then the population was predicted to be slightly more robust ($\lambda = 0.974 \pm 0.26$, 75.5%).

In some cases, there were substantial differences in the strength of the population response when additional management actions were implemented. Reducing the influence of nonnative trout or reducing the effect of human disturbance on natal habitat had a stronger positive effect on the population if one assumed all or 45% of the juveniles went to LPO, then when they all went to Noxon Reservoir (Figure 20). If 45% of the juveniles went to LPO, then increasing adult captures produced a linear increase in population status, whereas if all the juveniles went to LPO then the benefits of increased adult capture rate appeared to plateau at 75% percent or greater capture rate (Figure 20).

While this example is patch-specific, the result highlights that a detailed exploration of baseline conditions and assumptions can reveal potential management trade-offs and identify key assumptions where additional data collection or targeted studies are warranted. In Vermilion River, a strategy that focuses on reducing impacts of nonnative trout in natal habitat appears more robust compared to the assumptions about the quality of FMO habitat, dam mortality, juvenile migration strategy, and uncertainty in survival rates. In contrast, the effect of changing juvenile transport or adult capture rates depended more strongly on assumptions about baseline conditions and juvenile migration strategy. Each bull trout patch has a unique set of baseline conditions which implies the results in Vermilion River are context-dependent. A "best practice" when using the patch-specific BNs for conservation planning will be to conduct a reasonably thorough investigation of sensitivity to baseline conditions and assumptions, as demonstrated above for the Vermilion River.

Multi-patch analyses: metapopulation-scale exploration of management alternatives

Results of the patch-by-patch analyses are useful for understanding how best to improve the status of bull trout in particular tributary streams. The objective of the NSRP is to conserve and enhance bull trout (and cutthroat trout) populations at the scale of the lower Clark Fork River; therefore, this modeling exercise was intended to help biologists think through possible alternatives or management scenarios that could be used to reach that objective. The patch-by-patch results could be informally aggregated such that the "best" strategy for each patch is selected, with the assumption that collectively they would represent the best management strategy for the collection of local populations of bull trout in the project area. However, this may not necessarily lead to a single comprehensive strategy given the different set of conditions in each patch.

An alternative way to explore management consequences at the larger spatial scale is to more formally link the patches. We did this by weighting the patch-level predictions and applying consistent management strategies across all patches. In effect, we sought to answer the question: "If all the patches were considered a single conservation unit and additional conservation actions were to be implemented, which strategy would most benefit bull trout?" For analyses, we

separated out the two local populations of bull trout from Idaho because there are no permanent physical barriers between their natal habitat and Lake Pend Oreille and there are no ongoing or planned capture and transport programs for adults or juveniles, in contrast to what is occurring in some of the local bull trout populations in Montana. Under the habitat-weighting scheme we used to aggregate predictions, the results from the Region 1 (Idaho) conservation unit (collectively, Lightning and Johnson creeks) offer little insight beyond the patch-by-patch analyses because the weighted predictions are dominated by Lightning Creek, which was estimated to have more than 98% of the accessible habitat with high intrinsic potential. Consequently, we focus here on the eight local populations of bull trout that comprise the bull trout conservation unit in Regions 2, 3, and 4 (Montana).

For a comprehensive single-scenario strategy, reducing the negative effects of nonnative trout had the largest positive effect on bull trout population status in management regions 2-4 (Table 7). For example, reducing the status of nonnative trout from high to moderate in five patches – Bull R., Swamp Cr., Vermilion R., Prospect Cr., and Thompson R. – increased the predicted likelihood of a stable or increasing "metapopulation" (collectively, the eight Montana patches) from about 59% to 78%. Reducing the status of nonnative trout to low – which assumes that that nonnative trout have virtually no effect on bull trout – required intervention in two additional patches (Rock and Trout creeks) but increased the predicted likelihood to nearly 88%. The overall effect of reducing nonnative trout assumes that in patches with minimal overlap between nonnative trout and spawning and rearing by bull trout, that bull trout can still respond by increasing their distribution into the habitat formerly dominated by nonnatives and/or by experiencing greater survival as juveniles when they are moving downstream within the patch prior to entering the Clark Fork River.

Generally, increasing the capture rate of adult bull trout at Cabinet Gorge Dam (above the baseline 40%) and transporting them upstream was the second most-effective strategy (Table 7). At the baseline adult capture rate at Cabinet Gorge Dam, increasing the amount of juvenile capture and downstream transport had a comparatively smaller effect unless nearly all the out-migrating juveniles were captured leaving their natal streams and then released in Lake Pend Oreille. The only instance where juvenile transport alone approached the predicted effectiveness of reducing nonnative trout in five streams (Table 7, Scenario 2) was when the

juvenile transport program was extended to all eight patches *and* the capture efficiency was increased to 97% (predicted likelihood 77%; see Table 7, Scenario 18).

Examination of the management scenarios that incorporated mixed management strategies (i.e., changes to more than one category of management intervention) or those that considered reductions in management effort also tended to support that moderate increases in juvenile capture and transport rates provided only marginal benefits relative to adult transport. Dramatically reducing the adult capture and transport program was predicted to make a population decline more likely than not (Table 7, Scenario 14), whereas altogether discontinuing the juvenile transport program had little effect (Scenario 6). A similar pattern held for mixed conservation strategies. For example, when a reduction in nonnative trout (to moderate) was coupled with an increase in adult capture in transport (from 40% to 60%), then dropping juvenile transport had little effect (Table 7, cf. Scenarios 19 and 22). With the same nonnative and adult transport treatments, an increase in juvenile transport to 50% in streams with an existing program was needed before even marginal positive effects were evident (Table 7; cf. scenarios 22 and 23; 79.2% and 83.0%, respectively).

Model application and next steps: caveats and uncertainty

Caveats

The BN model for bull trout in the Lower Clark Fork River was developed using an interactive and iterative model-building process with theoretical underpinnings in decision analysis and practical application in natural resource management (e.g., Cain 2001; Marcot et al. 2001; Newton et al. 2007; Pollino and Henderson 2010; Aguilera et al. 2011). Stakeholder participation is critical for this type of model building to provide diverse knowledge and perspectives and to facilitate acceptance (Cain 2001; Pollino and Henderson 2010), as well as to implement resulting management recommendations (e.g., Allen and Gunderson 2011). The BN produced in this exercise admittedly is not a perfect representation of reality, but it is still useful and represents an advancement in the systematic evaluation of management alternatives under the NSRP.

Predictions for the patch-by-patch and multi-patch analyses depend on the baseline conditions within each patch (especially assumptions about intrinsic habitat potential) and the BN model structure and parameterization. A different set of baseline conditions, combination of management actions, or patch weighting scheme (e.g., patch sizes generated using a different methodology – Dunham et al., US Geological Survey, Unpublished data; genetic diversity within patches – DeHaan et al. 2011) might produce results and suggest a different management strategy. Thus, these results here are illustrative and are not formal management recommendations. Biologists can use the BNs to explore different conditions and management remedies, and should do so to provide a more complete understanding of the decision space.

Ultimately, management decisions will be based not only on the predicted outcome, but also on the perceived costs and feasibility of implementing such actions. We have not addressed or quantified those costs in this modeling exercise. For example, without additional thought or analyses it is not possible to state whether it would be less expensive (or even realistic) to suppress nonnative trout in five streams relative to increasing the capture and transport rates at Cabinet Gorge Dam or capturing and transporting nearly all the out-migrating juvenile bull trout from all eight tributaries. The BN model predictions simply identify that this topic merits formal discussion and assessment.

Uncertainty

Scientifically, the BN and the processes it represents are best characterized as working hypotheses, and the predictions generated by the scenario analyses are thus testable hypotheses. The modeling exercise and the resulting BN can also be considered the initial steps in a more formal structured decision making process, such as adaptive management, because this exercise has framed the problem and objectives and developed a predictive model to evaluate alternatives (Runge 2011; Lahoz-Monfort et al. 2014). The model was constructed using all readily available data and expert opinion, but considerable uncertainty in model structure and parameterization – and hence in predictions – exists. A logical next step would be to reduce those key uncertainties (or evaluate testable hypotheses) though targeted studies or management experiments focusing on assumptions which have a strong influence on the model outcomes or for which data are

lacking, and those scenarios predicted to have the greatest positive effect on bull trout population status. Some of the seemingly important data gaps identified in this exercise include the direct measurement of movement and survival of juvenile bull trout through the dams and within reservoirs, and a clear demonstration of the effects of management interventions, such as a large increase in adult bull trout capture and transport or nonnative suppression, on population status.

Assumptions about the relative survival of juvenile bull trout in different FMO habitat, the disposition of out-migrating juveniles (i.e., proportion migrating to LPO or a reservoir, or to which reservoir) and instantaneous mortality of juvenile bull trout that pass downstream through dams were fundamental aspects of the model structure, but their parameterization here is best characterized as a reasoned guess supported by limited data. Direct measurement would obviously provide a more rigorous test of these assumptions; and, existing technologies such as acoustic, sonic, or PIT tags in conjunction with strategically-placed detection and interrogation systems (e.g., at tributary junctions of occupied streams, within or adjacent to the main stem dams on the Clark Fork River) could provide these data. The large-scale tagging of juvenile salmon and detection at dams in the Columbia River basin provides an apt analogy.

In the BN model, population status of bull trout within and among the eight bull trout patches upstream of Cabinet Gorge Dam was sensitive to the capture and transport rates of adult bull trout at Cabinet Gorge Dam (Figures 10-17, Table 7). Transported adult bull trout have been demonstrated to spawn in natal tributaries (DeHaan and Bernall 2013), but at current transport rates there is little evidence of an increase in bull trout redd counts (Appendix F). A possible exception were the comparatively high redd counts in East Fork Bull River during 2001-2003 when adults captured at Cabinet Gorge Dam were almost all released in Management Region 2 (Bernall and Duffy 2012; Appendix F). In subsequent years, genetic assignment tests were used to distribute captured fish among the management regions that contained their inferred natal streams (DeHaan et al. 2011). One possible inference from these transport and redd count data is that higher transport rates, or equivalently more adult bull trout, are needed to see any effect given current population monitoring protocols.

Nonnative trout had a strong effect on bull trout populations in the BN model, and management actions that reduced this effect had a larger positive effect on bull trout population status than any other single management intervention (e.g., Figures 10-17, Table 7). Hybridization with

brook trout and redd superimposition by brown trout are recognized threats to bull trout within its range in western North America (e.g., US Fish and Wildlife Service 2014), and in the LCFR (Kleinshmidt and Pratt 1998, 2001); furthermore, these direct impacts have been documented in LCFR tributaries (Moran 2003; DeHaan and Hawkins 2009). Biotic interactions with brook trout can also affect the survival and distribution of bull trout (McMahon et al. 2007), and brown trout could have a similar effect, especially given that adult brown trout are typically piscivorous. Experimental suppression of nonnative brook trout and brown trout in the Bull River increased the relative abundance of native fishes, including bull trout, in the experimental sections (e.g., Moran and Storaasli 2010). However, evidence for a numerical response was equivocal; there appeared to be an increase in juvenile bull trout following successive years of suppression (Moran and Storaasli 2010), but favorable hydrologic and thermal conditions could not be discounted as important factors influencing that response. Long-term suppression efforts that clearly document a population response by bull trout are few, in part because of the substantial effort required to implement these projects even for small remnant populations (e.g., Buktenica et al. 2013). Additional management experiments that alter the distribution and density of nonnative trout in the project area seem appropriate given the large relative importance of this model variable. A more robust cause-and-effect relationship might be achieved through increased effort and an experimental design that account for confounding environmental variables, includes replication, or one that incorporates a cross-over between treatment and control sites. Additionally, it seems important to consider suppression of nonnative trout in reaches not currently occupied by bull trout to test whether such action increases lower distribution limit of spawning and rearing by bull trout or increases survival of out-migrating juvenile bull trout. Such management experiments might also provide a more realistic measure of the actual cost of implementing such actions over the long term.

Walters and Holling (1990) noted that for some fisheries management cases "there is little prospect of resolving the uncertainties through continued monitoring and modest policy change". A fundamental impetus for adaptive management programs is there exists important uncertainty about the response to management and that uncertainty can impede decision making (Runge 2011); yet the resource or ecological system is judged to require management intervention (Allen and Gunderson 2011) and action may even be mandated (e.g., for ESA-listed species). Unfortunately, adaptive management has generally not met expectation because implementation

is often hampered by a suite of social, political, and institutional limitations (Walters 1997, 2007; Allen and Gunderson 2011). A common characteristic of the uncertainty about the effect of management actions on bull trout in the Lower Clark Fork River is that the level of intervention predicted to have a positive effect exceeds the current level. To have the greatest likelihood of meeting the objective of conserving or enhancing bull trout in the lower Clark Fork River during the next 15 years, the model suggests that the following actions or a combination of these actions need to be implemented including: suppression of nonnative trout multiple patches, increasing capture and transport rates at Cabinet Gorge Dam must be increased from 40% to at least 60-75%, and/or capturing nearly all out-migrating juvenile bull trout from some patches and transporting them to Lake Pend Oreille. Not all of these actions may be possible or even realistic. Nonetheless, the modeling exercise indicates it will be important to implement one or more of the management strategies at greater than the current level of intervention; at a minimum, this may provide a proof of concept and reduce uncertainties or fill data gaps identified in the modeling exercise.

ACKNOWLEDGEMENTS

D. Peterson was supported by Avista Corporation and PPL Montana (Avista Contract # R-39307) and US Fish and Wildlife Service's Abernathy Fish Technology Center. Avista Corporation and the USFWS Montana ES Office provided logistical and financial support for meetings and workshops. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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Table 1. Summary of preliminary modeling exercise to rank the relative importance of ten bull trout patches to the overall persistence of bull trout in the lower Clark Fork Project modeling area. The modeling team was divided into three groups, given summary biological and physical data for each patch, and then asked to independently rank the importance of each patch in terms of where restoration should be prioritized. Values are the mean of the three responses, where patches with rank 1 were considered most important.

Patch name	Mean rank (high to low)
Bull River	1
Lightning Creek	1
Thompson River	1.3
Vermilion River	1.3
Graves Creek	1.7
Prospect Creek	2
Rock Creek	2.3
Johnson Creek	2.7
Swamp Creek	2.7
Trout Creek	3

Table 2. Variable names, definitions, state values and data sources of the BN decision support model for migratory bull trout in the lower Clark Fork River – Lake Pend Oreille system. Data sources for conditional probability tables (CPT) or input conditions are categorized as: modeled data, empirical data, expert opinion, elicitation, equation, literature review, or arbitrary.

Variable name	Definition	States and description	Data source for CPT or input conditions
Stream width	Mean wetted width in an NDH+ segment during summer base flow	<2 m: Generally too small for spawning and rearing by bull trout 2–4 m: Bull trout may be present, but at low redd and juvenile densities 4-10m: Ideal for spawning and rearing for bull trout; associated with highest density of redds and juveniles >10m: Generally too large for spawning and rearing by bull trout	Modeled data: estimated by regression from Variable Infiltration Capacity model predictions for stream flow
Summer water temperature	Mean water temperature in an NDH+ stream segment from mid-July through mid-September.	≤10°C: Ideal for bull trout 10-15°C: Thermally suitable, but less than ideal; bull trout likely present but at lower densities than in colder habitats 15-18°C: Marginal thermal habitat for bull trout; low probability of occurrence and low density if present >18°C: Poor - too warm for bull trout; zero probability of occurrence	Modeled data: water temperature estimates from the NorWEST dataset
Channel gradient	Channel gradient in the NDH+ stream segment	<2%: ideal for bull trout 2-5%: moderate-ideal for bull trout >5-10%: moderate for bull trout >10-20%: poor for bull trout >20%: very poor for bull trout	Modeled data: digital elevation model within NDH+ stream layer
Potential habitat by segment	Intrinsic potential for spawning and rearing by bull trout in each NDH+ stream segment based on the combination of temperature, stream size, and channel gradient.	Low; Medium; High	Elicitation

Variable name	Definition	States and description	Data source for CPT or input conditions
Human Disruption	Legacy and ongoing human disturbances across the patch that alters the structure and function of current bull trout habitat.	Highly Altered and Degraded: Activities that disrupt watersheds, such as logging, road construction, mining, water development, utility corridors, 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 dramatically reduced. Moderately Altered: Activities that disrupt watersheds, such as logging, road construction, mining, water development, utility corridors, 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 moderately 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.	Elicitation: states for each bull trout patch based on consensus expert opinion
Realized habitat (by segment)	Realized habitat quality for spawning and rearing by bull trout in a NDH+ segment based on how human disturbance affects the segments habitat potential.	Low: Bull trout absent or rare (e.g., density ≤ 1.7 juvenile bull trout per $100m^2$) Moderate: Bull trout present at low-moderate density (1.7-3.8 per $100m^2$) High: Bull trout present at high density (≥3.8 per 100 m^2) Range values come from distribution of juvenile bull trout densities from the lower Clark Fork River, Flathead River, and elsewhere in western Montana	Elicitation

Variable name	Definition	States and description	Data source for CPT or input conditions
Intrinsic habitat potential	Intrinsic habitat potential for bull trout within an entire patch based on persistent abiotic or geomorphic features (temperature, gradient, stream size).	Low; Medium; High	Model predictions: parameterized for each patch from BN predictions driven by modeled GIS layers for temperature, gradient, and stream size.
Realized habitat by patch	Actual habitat conditions across the patch based on intrinsic potential modified by patch-level human disruption.	Low; medium; high	Elicitation
Proportion nonnative trout	The strength of interspecific competition and predation and the effect of redd superimposition and gametic wastage on the number of bull trout redds from nonnative trout species.	High: one-quarter or more of the sites are dominated by nonnatives (NPP>0.5) Moderate : between one tenth and one quarter of the sites are dominated by nonnatives (NPP>0.5) Low: fewer than one tenth of the of the sites are dominated by nonnatives (NPP>0.5) NPP metric is calculated using density estimates as: $NPP = \frac{(brown\ trout + brook\ trout)}{(bull\ trout + brown\ trout + brook\ trout)}$	Empirical: Patch-level values based on single-year survey data deemed most representative in terms of spatial coverage and sampling intensity.
Electrofishing mortality	Whether the intensity and extent of population monitoring by electrofishing is high enough to result in additional mortality to juvenile bull trout when they are present in the patch.	Yes: Electrofishing intensity is moderate-to-high (i.e., annual surveys) and a majority of juvenile bull trout present are susceptible to capture. Additive mortality estimated at 1% of the susceptible population. No: Electrofishing is infrequent or only a small portion of the population is susceptible to capture such that there is no measurable additional mortality.	Elicitation

Variable name	Definition	States and description	Data source for CPT or input conditions
Angling effect	Whether the intensity and extent of recreational angling is high enough to result in additional mortality to adult bull trout present in the patch and juvenile bull trout that are emigrating from the patch. The effect includes intentional poaching, incidental capture, and post-release mortality from incidental capture.	Yes: Angling intensity results in 2.5% additional mortality. No: Little or no angling pressure with no measurable additive mortality for the bull trout population present in the patch. Assumes that only larger bull trout (age-2+ or >125 mm) are susceptible to angling. Juvenile bull trout are only susceptible to angling when they are leaving the patch at age-2 or -3. Adults are susceptible when in the stream to spawn.	Elicitation: consensus expert opinion
Per "dam" additional mortality	Discrete mortality rate for juvenile or sub-adult bull trout that move downstream through a dam.	0-0.5 (7 states)	Expert opinion: Actual values for each dam are unknown, but default value of 0.1 is based on expert opinion of modeling team and interpretation of data from the Columbia River basin
Total instantaneous mortality from volitional migration	Total instantaneous mortality experienced by juvenile bull trout during their migration to Lake Pend Oreille.	Calculation node that estimates instantaneous mortality as a function of the number of dams and the per-dam mortality rate	Equation
Total discrete mortality from migration to LPO	Total discrete mortality experienced by juvenile bull trout during their migration to Lake Pend Oreille.	Calculation node that converts instantaneous to discrete mortality	Equation
Status of FMO-reservoir habitats sub-adult	Condition of foraging, migration, and overwinter (FMO) habitat for sub-adult bull trout that use reservoirs.	Deteriorate by 20%, Deteriorate by 10%, Current condition, Improve by 10%, Improve by 20% Effect is modeled as a direct function of the percent change (e.g., 20% improvement means that the dependent demographic rates increase by 20%)	Arbitrary: State levels are arbitrary

Variable name	Definition	States and description	Data source for CPT or input conditions
Status of FMO-LPO habitat sub-adults	Condition of foraging, migration, and overwinter (FMO) habitat for sub-adult bull trout that use Lake Pend Oreille (LPO).	Deteriorate by 20%, Deteriorate by 10%, Current condition, Improve by 10%, Improve by 20% Effect is modeled as a direct function of the percent change (e.g., 20% improvement means that the dependent demographic rates increase by 20%)	Arbitrary: State levels are arbitrary
Status of FMO-reservoir habitat adults	Condition of FMO habitat for adult bull trout that use reservoirs.	Deteriorate by 20%, Deteriorate by 10%, Current condition, Improve by 10%, Improve by 20% Effect is modeled as a direct function of the percent change (e.g., 20% improvement means that the dependent demographic rates increase by 20%)	Arbitrary: State levels are arbitrary
Status of FMO-LPO habitat adults	Condition of foraging, migration, and overwintering (FMO) habitat for adult bull trout that use Lake Pend Oreille (LPO).	Deteriorate by 20%, Deteriorate by 10%, Current condition, Improve by 10%, Improve by 20% Effect is modeled as a direct function of the percent change (e.g., 20% improvement means that the dependent demographic rates increase by 20%)	Arbitrary: State levels are arbitrary
CV in survival	Coefficient of variation [CV = (SD/mean) × 100%] in survival rates.	10% 20% 40%	Abitrary: State levels are arbitrary but selected to encompass the variation in survival rates from representative studies with bull trout (e.g., Al-Chokhachy & Ebinger 2012; Bowerman 2013).
Capture rate at Cabinet Gorge Dam	Mean capture efficiency for adult bull trout below Cabinet Gorge Dam.	0-1 (6 states)	Expert opinion Mean value of 0.4 (40%) based from scientific panel convened for a previous conservation planning exercise in the Lower Clark Fork River system (see Epifanio et al. 2003)
Patch permeability	Probability that adult bull trout can enter the patch. Values are best interpreted as the average condition over ~10-15 yr.	0-1 (10 states), values range from impermeable (full blockage = 0) to open (=1).	Elicitation

Variable name	Definition	States and description	Data source for CPT or input conditions
Reproductive contribution of strays	Proportion of the migratory spawners comprised of strays (immigrants) from other patches.	0-0.16 (5 states)	Elicitation
Frequency of repeat spawning	Proportion of repeat spawning or annual frequency of spawning after first spawning	0.45-0.95 (4 states)	Literature review
LengthAge6res	Total length (mm) of age-6 female bull trout reared in Lake Pend Oreille.	425-575 (5 states). Default mean size is 500 mm.	Literature review: McCubbins (2013)
LengthAge6res	Total length (mm) of age-6 female bull trout reared in a reservoir.	375-525 (5 states). Default mean size is 450 mm.	Arbitrary: Assumes that bull trout growth in reservoirs is approximately 75% of that experienced by same-aged bull trout rearing in Lake Pend Oreille.
LengthAge7plusLPO	Total length (mm) of age-7 and older female bull trout reared in Lake Pend Oreille. Default mean size is 610 mm.	510-710 (5 states). Default mean size is 610 mm.	Literature review: McCubbins (2013)
LengthAge7plusres	Total length (mm) of age-7 and older female bull trout reared in reservoir.	435-630 (5 states). Default mean size is 532 mm.	Arbitrary: Assumes that bull trout growth in reservoirs is approximately 75% of that experienced by same-aged bull trout rearing in Lake Pend Oreille.
Transport to LPO	Proportion of age-2 and age-3 bull trout that are captured leaving a patch and transported to Lake Pend Oreille.	0 0.1 0.2 0.5 0.97	Arbitrary: state levels Empirical: mean value of 0.1 for patches with a juvenile trapping and transport program based on estimates of capture efficiency at weirs and rotary screw traps; value of 0 for those that do not have a juvenile transport program
Volitional to LPO	Proportion of age-2 and age-3 bull trout that leave the patch and move volitionally to Lake Pend Oreille.	0 0.2 0.35 0.4 0.45 0.97	Arbitrary: state levels Expert opinion: mean value of 0.4 for patches with a juvenile trapping and transport program; 0.5 for those that do not have a juvenile transport program

Variable name	Definition	States and description	Data source for CPT or input conditions
Reservoir	Proportion of age-2 and age-3 bull trout that leave the patch and move volitionally to the nearest reservoir.	0 0.27 0.42 0.47 0.52 0.97	Arbitrary: state levels Expert opinion: mean value of 0.47
Migration strategy consistent?	Boolean node to ensure the different migration strategies are selected properly	Node ensures that the probabilities for the four different migration strategies of strays, transport to LPO, volitional to LPO, and reservoir sum to 1. The assumed stray rate is 0.03 (3%). Yes: migration strategies have been properly selected No: migration strategies are not properly selected and must be adjusted so that the node returns "yes".	Equation
Proportion migrating at age 2	Proportion of juvenile bull trout migrating from the patch at age 2. Any that do not migrate at age 2 are assumed to migrate the following year as age 3.	0.6-0.7 0.7-0.8 0.8-0.9	Empirical: Size at capture and inferred age for 2,481 juvenile bull trout captured in tributary streams and transported to Lake Pend Oreille.
Presumed reservoir habitat	Presumed foraging, migration, and overwintering (FMO) habitat for those bull trout that DO NOT migrate to Lake Pend Oreille.	Low: Cabinet Gorge Reservoir and Thompson Falls Reservoir/River have less suitable habitat for bull trout based on depth, temperature, forage, and predators. Medium: Noxon Reservoir has more suitable habitat for bull trout than Cabinet Gorge or Thompson Falls Reservoir, but much less than Lake Pend Oreille.	Expert opinion: reservoir rankings. A key assumption is that bull trout that do not migrate to Lake Pend Oreille use the accessible reservoir that is closest their natal patch.
Migration distance to LPO	Number of dams that a juvenile bull trout from a given patch must pass to reach Lake Pend Oreille. The number of dams is also a surrogate for migration distance.	No dams 1 dam 2 dams 3 dams	Empirical: location of dams relative to the natal patch
Se	Survival of eggs from spawning to emergence as a function of realized habitat conditions and nonnative trout.	0.22-0.66 (4 states)	Elicitation and literature review: Mean value derived from the literature (e.g., Al-Chokhachy & Ebinger 2012; Bowerman 2013) and CPT based on elicitation of modeling team.

Variable name	Definition	States and description	Data source for CPT or input conditions
S0	Annual survival of age-0 bull trout	0.11-0.32 (4 states)	Elicitation and literature review: Mean value derived from the literature (e.g., Al-Chochachy & Ebinger 2012; Bowerman 2013) and CPT based on elicitation of modeling team.
S1	Annual survival of age-1 bull trout based on realized habitat conditions, nonnative trout, and electrofishing.	0.11-0.32 (4 states)	Elicitation and literature review: Mean value derived from the literature (e.g., Al-Chochachy & Ebinger 2012; Bowerman 2013) and CPT based on elicitation of modeling team.
Age 2 remain in patch	Survival of age-2 bull trout that remain inside the natal patch (i.e., do not migrate at age-2).	0.2-0.6 (4 states)	Expert opinion: Conditional probability table based on elicited CPT for age-1 bull trout, but with different state values. Mean value (0.4) based on assumption that survival of age-2 bull trout that remain in the patch will be greater than those that migrate and are exposed to additional sources of mortality (novel predators, dams, angling, etc.).
Age 2 transport mean	Mean survival age-2 bull trout that are transported to Lake Pend Oreille.	0.16-0.48 (10 states)	Elicitation: Mean value (0.32) based on interpretation of juvenile transport and adult return data from the Lower Clark Fork River, and expert elicitation exercise on the effect of transport vs. volitional movement conducted with the modeling team.
Age 2 reservoir (in reservoir)	Mean survival of age-2 bull trout that use a reservoir for FMO habitat.	0.1-0.4 (6 states)	Expert opinion: Conditional probability table based on mean survival of 0.26 in Noxon Reservoir and 0.22 in Thompson River/Reservoir & Cabinet Gorge Reservoir.
Age 2 volitional mean (in patch)	Mean survival age-2 bull trout within the natal patch that ultimately move volitionally to Lake Pend Oreille.	0.16-0.48 (10 states)	Expert opinion: Mean value (0.32) is based on the assumption that fish in this group should experience a similar in-patch survival rate as age 2 bull trout that are subsequently transported. This group incurs additional mortality after leaving the patch that is accounted for in subsequent variables (e.g., S2v).

Variable name	Definition	States and description	Data source for CPT or input conditions
S2t_a	Intermediate node for survival of age-2 juvenile bull trout transported to Lake Pend Oreille, and that integrates the effects of realized habitat quality, nonnative trout, and electrofishing.	0.16-0.48 (4 states)	Elicitation and expert opinion: The CPT for this node is identical to that for age 1 bull trout, with the exception that the mean survival rate is greater so the states cover a different range of values.
S2r_a	Intermediate node for survival of age-2 juvenile bull trout in reservoirs that integrates the effects of realized habitat quality, nonnative trout, and angling.	0.16-0.48 (4 states)	Elicitation and expert opinion: The CPT for this node is identical to that for age-1 bull trout, with the exception that the mean survival rate is greater so the states cover a different range of values.
S2v_a	Intermediate node for survival of age-2 juvenile bull trout that migrate volitionally to Lake Pend Oreille, and that integrates the effects of realized habitat quality, nonnative trout, and electrofishing.	0.16-0.48 (4 states)	Elicitation and expert opinion: The CPT for this node is identical to that for age 1 bull trout, with the exception that the mean survival rate is greater so the states cover a different range of values.
S2t	Estimated survival of age-2 juvenile bull trout that are captured and transported to Lake Pend Oreille. The estimate accounts for the effect of any angling and capture mortality.	0-0.48 (6 states)	Equation: the CPT is a function of the parent variables, and converts between instantaneous and discrete mortality.
S2r	Mean survival of age-2 juvenile bull trout that move to and reside in the reservoir nearest to the natal patch.	0.1-0.44 (6 states)	Equation and expert opinion: the CPT is calculated as the mean of survival in the patch and reservoir because the fish spends time in both.
S2v	Survival of age-2 juvenile bull trout that move volitionally from the natal patch to Lake Pend Oreille.	0-0.48 (6 states)	Equation: the CPT is a function of the parent variables, and converts between instantaneous and discrete mortality.

Variable name	Definition	States and description	Data source for CPT or input conditions
S2	Annual survival of age-2 bull trout	0.13-0.51 (5 states)	Equation: Conditional probability table based on weighted average of survival of age-2 bull trout that either stayed in the patch, moved volitionally to LPO, was transported to LPO, or that moved to the nearest reservoir for rearing.
Age 3 transport mean	Mean survival of age-3 bull trout rearing in Lake Pend Oreille that were transported at age 3.	0.28-0.83 (5 states)	Elicitation and expert opinion: Mean value (0.55) based on interpretation of juvenile bull trout transport and adult return data from the Lower Clark Fork River. The CPT is based on elicitation exercise on the effect of transport vs. volitional movement conducted with the modeling team.
Age 3 volitional mean	Survival of age-3 bull trout rearing in Lake Pend Oreille that moved volitionally at age 3.	0.28-0.83 (5 states)	Elicitation and expert opinion: Mean value (0.51) based on interpretation of juvenile bull trout transport and adult return data from the Lower Clark Fork River. The CPT is based on elicitation exercise on the effect of transport vs. volitional movement conducted with the modeling team.
meanStv2	Mean survival of age-3 bull trout rearing in Lake Pend Oreille that were either transported or moved volitionally to that lake when they were age 2.	0.57 (1 state)	Elicitation and expert opinion: Point value (0.57) based on interpretation of juvenile bull trout transport and adult return data from the Lower Clark Fork River.
S3r23	Survival of age-3 bull trout in reservoirs that migrated as either age 2 or 3.	0.23-0.68 (5 states)	Expert opinion: Conditional probability table based on mean survival of 0.45 in Noxon Reservoir and 0.40 in Thompson River/Reservoir & Cabinet Gorge Reservoir.
St_a	Survival of age-3 juvenile bull trout that remained within the natal patch as age 2, and that integrates effects of habitat quality, nonnative trout, and electrofishing.	0.28-0.83 (4 states)	Elicitation and expert opinion: The CPT for this node is identical to that for age-1 bull trout, with the exception that the mean survival rate is greater so the states cover a different range of values.

Variable name	Definition	States and description	Data source for CPT or input conditions
S3t	Survival of age-3 bull trout rearing in Lake Pend Oreille that were transported at age 3, and that accounts for additional mortality from angling and capture.	0.2-0.83 (5 states)	Equation: Conditional probability table is a deterministic function of the parent variables, and converts between instantaneous and discrete mortality.
S3v	Survival of age-3 bull trout rearing in Lake Pend Oreille that moved volitionally at age 3, and that accounts for additional mortality from angling (if applicable).	0-0.83 (6 states)	Equation: Conditional probability table is a deterministic function of the parent variables, and converts between instantaneous and discrete mortality.
S3tv2	Survival of age-3 bull trout rearing in Lake Pend Oreille that were either transported or moved volitionally to that lake when they were age 2.	0.28-0.86 (5 states)	Equation: Conditional probability table is a deterministic function of the parent variables.
S3	Annual survival of age-3 bull trout	0.22-0.84 (5 states)	Equation: Conditional probability table based on weighted average of survival of age-2 bull trout that either stayed in the patch (as age 2), moved volitionally to LPO (as age 2 or 3), was transported to LPO (as age 2 or 3), or that moved (as age 2 or 3) to the nearest reservoir for rearing.
Age 4 reservoir	Mean survival of age-4 bull trout in a reservoir.	0.23-0.69 (5 states)	Expert opinion: Conditional probability table based on mean survival of 0.48 in Noxon Reservoir and 0.40 in Thompson River/Reservoir & Cabinet Gorge Reservoir.
mean4LPO	Survival of age-4 bull trout rearing in LPO; rate is the same for fish that moved volitionally or were transported.	0.52 (1 state)	Expert opinion: Point value (0.52) based on interpretation of juvenile transport and adult return data from the Lower Clark Fork River.

Variable name	Definition	States and description	Data source for CPT or input conditions
Age 4 transport & volitional	Survival of age-4 bull trout rearing in Lake Pend Oreille that were either transported or moved volitionally to that lake as age 2 or 3.	0.25-0.75 (5 states)	Equation: CPT is a function of parent variables.
S4	Annual survival of age-4 bull trout	0.22-0.74 (5 states)	Equation: Conditional probability table based on weighted average of bull trout that experience different migration pathways as juveniles and that use different FMO habitats.
Age 5 reservoir	Mean survival of age-5 bull trout in a reservoir.	0.25-0.75 (5 states)	Expert opinion: Conditional probability table based on mean survival of 0.50 in Noxon Reservoir and 0.42 in Thompson River/Reservoir & Cabinet Gorge Reservoir.
mean5LPO	Survival of age-5 bull trout rearing in LPO; rate is the same for fish that moved volitionally or were transported.	0.55 (1 state)	Expert opinion: Point value (0.55) based on interpretation of juvenile transport and adult return data from the Lower Clark Fork River.
Age 5 transport & volitional	Survival of age-5 bull trout rearing in Lake Pend Oreille that were either transported or moved volitionally to that lake.	0.28-0.83 (5 states)	Equation: CPT is a function of parent variables.
S5	Annual survival of age-5 bull trout.	0.24-0.82 (5 states)	Equation: Conditional probability table based on weighted average of bull trout that experience different migration pathways as juveniles and that use different FMO habitats.
Mean6	Survival of age-6 bull trout.	0.45 (1 state)	Literature review: Al-Chohachy & Ebinger (2012); Bowerman (2013).
Age 6 survival reservoir	Mean survival of age-6 bull trout in a reservoir.	0-0.9 (5 states)	Equation: CPT is a function of parent variables.
Age 6 survival LPO	Mean survival of age-6 bull trout in Lake Pend Oreille (LPO).	0-0.9 (5 states)	Equation: CPT is a function of parent variables.

Variable name	Definition	States and description	Data source for CPT or input conditions
S6	Annual 'survival' of age-6 bull trout that accounts for patch permeability, juvenile migratory pathway, FMO habitat, and adult transport (if applicable).	0-0.67 (5 states)	Equation: CPT is a function of parent variables.
Mean7	Survival rate of age-7 and older bull trout.	0.53 (1 state)	Literature review: Al-Chohachy & Ebinger (2012); Bowerman (2013).
Age 7 survival reservoir	Mean survival of age-7 and older bull trout in a reservoir.	0-0.9 (5 states)	Equation: CPT is a function of parent variables.
Age 7 survival LPO	Mean survival of age-7 and older bull trout in Lake Pend Oreille (LPO).	0-0.9 (5 states)	Equation: CPT is a function of parent variables.
S7	Annual 'survival' of age-7 and older bull trout that accounts for patch permeability, juvenile migratory pathway, FMO habitat, and adult transport (if applicable).	0-0.8 (5 states)	Equation: CPT is a function of parent variables.
M6	Net reproductive output of age-6 bull trout that accounts for female size at age, FMO habitat, fecundity, egg survival, and the reproductive contribution of strays.	150-860 (4 states)	Equation: Conditional probability table based on equation that takes into account female size at age, fecundity based on data from the lower Clark Fork River (Brunson 1952), egg survival (Se), and the reproductive contribution of immigrants.
M7	Net reproductive output of age-7 and older bull trout that accounts for female size at age, FMO habitat, fecundity, egg survival, and the reproductive contribution of strays.	180-1510 (5 states)	Equation: Conditional probability table based on equation that takes into account female size at age, fecundity based on data from the lower Clark Fork River (Brunson 1952), egg survival (Se), and the reproductive contribution of immigrants.

Variable name	Definition	States and description	Data source for CPT or input conditions
Lambda (λ)	Estimated long-term (~10 yr) average population growth rate for migratory bull trout.	0-1.8 (5 states)	Simulation: Conditional probability table 'learned' (via counting algorithm) with results of 10 million Monte Carlo simulations of a matrix population model with matrix entries corresponding to the parent variables S0, S1, S2, S3, S4, S5, S7, S7, M6 and M7.

Table 3. Modeled intrinsic habitat (habitat potential) across the ten patches in the project area, and the percent (and rank) of each habitat class for each patch relative to the total habitat extent. Values are based on aggregation of segment-scale estimates generated by the BN model fragment in Figure 5B. Stream length in habitat patch based on NDH+ stream layer with dry channels and habitat above natural barriers excluded. Total percent of habitat in the high potential categories – and relative among-patch ranks – are summarized for all ten patches, and also for those eight patches in Montana which comprise management regions 2, 3 and 4 of the Native Salmonid Restoration Plan for the lower Clark Fork River.

Region	Patch	Total stream length (km)	Potential habitat by category (km)			Probabilities by category			Percent of total habitat in High category (relative rank) [1]	
			Low	Med	High	Low	Med	High	All patches	Montana
1	Lightning Cr.	145.20	98.55	25.26	21.39	0.679	0.174	0.147	10.9% (4)	-
	Johnson Cr.	3.24	2.39	0.45	0.40	0.738	0.140	0.122	0.2% (10)	-
2	Bull R.	225.21	167.18	33.79	24.24	0.742	0.150	0.108	12.3% (3)	13.9% (3)
	Rock Cr.	38.73	28.98	5.02	4.74	0.748	0.130	0.122	2.41% (8)	2.71% (7)
3	Swamp Cr.	48.90	30.86	8.80	9.25	0.631	0.180	0.189	4.71% (7)	5.30% (6)
	Trout Cr.	53.71	29.69	10.54	13.48	0.553	0.196	0.251	6.86% (5)	7.72% (4)
	Vermillion R.	60.69	42.53	8.83	9.33	0.701	0.145	0.154	5.51% (6)	5.35% (5)
	Graves Cr.	18.32	12.78	3.55	1.99	0.698	0.194	0.109	1.01% (9)	1.14% (8)
	Prospect Cr.	205.93	119.79	38.54	47.61	0.582	0.187	0.231	24.2% (2)	27.3% (2)
4	Thompson R.[2]	358.69	248.82	45.89	63.98	0.694	0.128	0.178	32.6% (1)	36.6% (1)
	SUM	1,158.63	781.56	180.67	196.39					
	SUM (Montana)	1,010.20	680.62	154.96	174.61					

[1] Relative rankings based on the sum of Med and High categories are identical and values were highly correlated (Pearson's $r = 0.99$).

[2] The Thompson River patch is an "area of interest" that includes Fishtrap Creek and West Fork Thompson River, which comprises the majority of occupied bull trout habitat in the Thompson River watershed.

Table 4. Baseline demographic parameters for migratory bull trout that can follow three different pathways to maturation: transport to Lake Pend Oreille (LPO), volitional movement to LPO, and rearing in an adjacent reservoir. These parameters were used in the matrix model simulations.

Description	Abbreviation	Value
Egg survival	*Se*	0.44
Age 0 survival	*S0*	0.21
Age 1 survival	*S1*	0.21
Age 2 survival for transports that migrated at age 2	*S2t*	0.32
Age 2 survival for volitional to LPO that migrated at age 2	*S2v*	0.26
Age 2 survival for reservoir that migrated at age 2	*S2r*	0.26
Age-2 survival for those that remained in patch	*S2p*	0.40
Age 3 survival for transports/volitional to LPO that originally migrated as age 2	$S3tv_2$	0.57
Age 3 survival for transports captured as age 3	*S3t*	0.55
Age 3 survival for volitional to LPO that migrated at age 3	*S3v*	0.51
Age 3 survival for reservoir that originally migrated as age 2 or 3	$S3r_{23}$	0.45
Age 4 survival for those transported as age 2 or 3	*S4t*	0.52
Age 4 survival for volitional to LPO that migrated at age 2 or 3	*S4v*	0.52
Age 4 survival for reservoir that migrated at age 2 or 3	*S4r*	0.48 (0.42)
Age 5 survival for transports that migrated at age 2 or 3	*S5t*	0.55
Age 5 survival for volitional to LPO that migrated at age 2 or 3	*S5v*	0.55
Age 5 survival for reservoir that migrated at age 2 or 3	*S5r*	0.50 (0.42)
Age 6 survival	*S6b*	0.45
Age 7 and older survival	*S7b*	0.53
Proportion age 2 and 3 transported	*Jt*	0.1
Proportion age 2 and 3 volitional to LPO	*Jv*	0.4
Proportion of age 2 and 3 to nearest reservoir	*Jr*	0.47
Proportion age 2 and 3 straying from patch	*Js*	0.03
Capture rate of adults below Cabinet Gorge Dam	*CG*	0.4
Size of age-6 females reared in LPO (mm)	$L6_{LPO}$	500
Proportion of juvenile migrants in a given year that are age 2	JM_2	0.76
Proportion of juvenile migrants in a given year that are age 3	JM_3	0.24
Median size of age-7 and older females reared in LPO (mm)	$L7+_{LPO}$	610

Description	Abbreviation	Value
Size of age-6 females reared in reservoir (mm)	$L6_{RES}$	450
Median size of age-7 and older females reared in reservoir (mm)	$L7+_{RES}$	532
Fecundity of age-6 females reared in LPO	$F6_{LPO}$	2,206
Fecundity of age-7 and older females reared in LPO	$F7+_{LPO}$	4,467
Fecundity of age-6 females reared in reservoir	$F6_{RES}$	1,518
Fecundity of age-7 and older females reared in reservoir	$F7+_{RES}$	2,749
Proportion of reproductive output resulting from strays (immigrants)	*Imm*	0.03
Sex ratio	*R*	0.5
Proportion of repeat spawning	*repeat*	0.75

Table 5. Results of sensitivity and elasticity analyses for a matrix model and a Bayesian network of migratory bull trout population. Sensitivity values reflect that change in population growth rate (lambda) that would occur from a small change in the matrix element, assuming all other elements were fixed at their present value. Elasticity values reflect the proportional change in population growth rate (lambda) that results from a proportional change in the matrix element. Variance reduction represents the expected reduction in variance of the expected value of population growth rate (lambda) due to a finding at a node. For example…(at least in text)?

	Matrix model		Bayesian network
Matrix element or variable in Bayesian network	Sensitivity	Elasticity	Variance reduction (%)
S0	0.63	0.13	11.0
S1	0.63	0.13	10.8
S2	0.45	0.13	9.98
S3	0.27	0.13	0.87
S4	0.27	0.13	0.25
S5	0.26	0.13	0.2
S6	0.18	0.05	0.09
S7	0.08	0.03	0.03
M6	1.96×10^{-4}	0.08	9.94
M7	9.01×10^{-5}	0.05	10.2

Table 6. Initial conditions for the BN model to predict population growth rate of bull trout in ten local populations of bull trout (patches) in the lower Clark Fork River. See Table 3 for intrinsic habitat potential for each patch. State or mean values for variables that are constant across all patches include: mean capture and handling mortality (0.1 ± 0.011) for those patches with juvenile capture and transport programs, frequency of repeat spawning (0.7-0.75), and proportion migrating at age 2 (0.7-0.8).

	Bull trout patches by management region									
	Region 1		Region 2		Region 3					Region 4
Variable name	Lightning	Johnson	Bull	Rock	Swamp	Trout	Vermilion	Graves	Prospect	Thompson
Human disruption	high	min	mod	mod	min	min	high	mod	high	high
Angling mort.	Yes	No	Yes	No	No	No	Yes	No	Yes	Yes
E-fishing mortality	No	No	No	No	No	No	No	No	No	No
Proportion nonnative trout	Med	Low	High	Med	High	Med	High	Low	High	High
Juv. trapping	No	No	Yes	Yes	No	No	Yes	Yes	Yes	No
juv_transport	0	0	0.1	0.1	0	0	0.1	0.1	0.1	0
juv_vLPO	0.97	0.97	0.4	0.4	0.5	0.5	0.4	0.4	0.4	0.5
juv_reservoir	0	0	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47
Permeability	0.62 ± 0.30	0.95 ± 0.06	0.99 ± 0.04	0.53 ± 0.27	0.63 ± 0.28	0.42 ± 0.18	0.99 ± 0.01	0.96 ± 0.06	0.50 ± 0.21	0.99 ± 0.02
Strays	0.026 ± 0.018	0.022 ± 0.014	0.077 ± 0.034	0.087 ± 0.038	0.02 ± 0.012	0.02 ± 0.012	0.057 ± 0.034	0.053 ± 0.041	0.102 ± 0.024	0.023 ± 0.016
Per dam additional mortality	-	-	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Capture rate at CG dam	-	-	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4
Presumed reservoir	-	-	CG	CG	Noxon	Noxon	Noxon	Noxon	Noxon	Thomp.
Migration distance to LPO (# dams)	0	0	1	1	2	2	2	2	2	3

Table 7. Likelihood that the collective set of eight bull trout local populations that spawn in Montana (Management Regions 2-4) is stable or increasing as a function of baseline conditions and potential management interventions. Table values for population growth rate (λ_w±SD) and likelihood of a stable or increasing set of local populations are weighted by the percentage of potential habitat ranked high within each patch (see Table 3). Other weighting schemes are possible so these results are illustrative of a management objective seeking larger population sizes. The likelihood values are the sum of the state probabilities for the weighted population growth rate (λ_w) that are 0.9 or greater (i.e., stable or increasing). Relative ranks for single-factor scenarios (S1-S18) are in the far right column. Combinations are post-hoc scenarios that consider multiple categories of management interventions based on results of single-factor scenarios.

#	Category	Scenario	Growth rate (λ_w)	Likelihood stable or increasing (%)	Rank
1		Baseline	0.917±0.17	59.3	15
2	NON-NATIVES	Reduce nonnatives to moderate (all moderate or better)	0.964±0.16	77.7	2
3		Reduce nonnatives to low (all low)	0.998±0.16	87.5	1
4	NATAL HABITAT DISTURBANCE	Reduce human disturb. to moderate (all moderate or better)	0.927±0.17	63.1	10
5		Reduce human disturb. to minimal (all minimal/pristine)	0.937±0.17	67.2	7
6	JUVENILE TRANSPORT	Discontinue existing transport programs	0.914±0.17	58.1	16
7		Increase juvenile transport to 20% in patches w/ existing transport programs	0.919±0.16	60.2	14
8		Increase juvenile transport to 50% in patches w/ existing transport programs	0.925±0.17	62.7	11
9		Increase juvenile transport to 97% in patches w/ existing transport programs	0.944±0.18	70.5	5
10		Start juvenile transport (10%) in patches w/o existing transport program	0.92±0.16	60.5	13
11		Increase juvenile transport to 20% in all 8 patches	0.923±0.16	61.9	12
12		Increase juvenile transport to 50% in all 8 patches	0.93±0.16	65.0	9
13		Increase juvenile transport to 97% in all 8 patches	0.964±0.18	77.1	3
14	ADULT	Reduce adult capture and transport to 10%	0.881±0.17	44.1	18

15	CAPTURE AND TRANSPORT AT CABINET CORGE	Reduce adult capture and transport to 25%	0.9±0.17	52.2	17
16		Increase adult capture and transport to 60%	0.932±0.17	65.4	8
17		Increase adult capture and transport to 75%	0.945±0.18	70.5	6
18		Increase adult capture and transport to 90%	0.962±0.19	75.6	4
19	COMBINATIONS	Reduce nonnatives + increase CG captures to 60% (S2 + S16)	0.972±0.16	80.4	-
20		reduce nonnatives + juv transport to 50% existing (S2 + S8)	0.97±0.16	80.2	-
21		Increase juv passage + 50% existing + increase CG captures 60% (S8 + S16)	0.946±0.17	71.0	-
22		Reduce nonnatives + CG captures 60% + drop juv trans (S2 + S6 + S16)	0.969±0.17	79.2	-
23		Reduce nonnatives + CG captures 60% + juv trans 50% existing (S2 + S8 + S16)	0.981±0.17	83.0	-
24		Reduce nonnatives + CG captures 75% + drop juv trans (S2 + S6 + S17)	0.975±0.18	80.4	-
25		Reduce nonnatives + CG captures 90% + drop juv trans (S2 + S6 + S18)	0.982±0.19	81.2	-
26		Reduce nonnatives + CG captures 90%, juv trans 50% existing (S2 + S8 + S18)	0.992±0.19	83.0	-

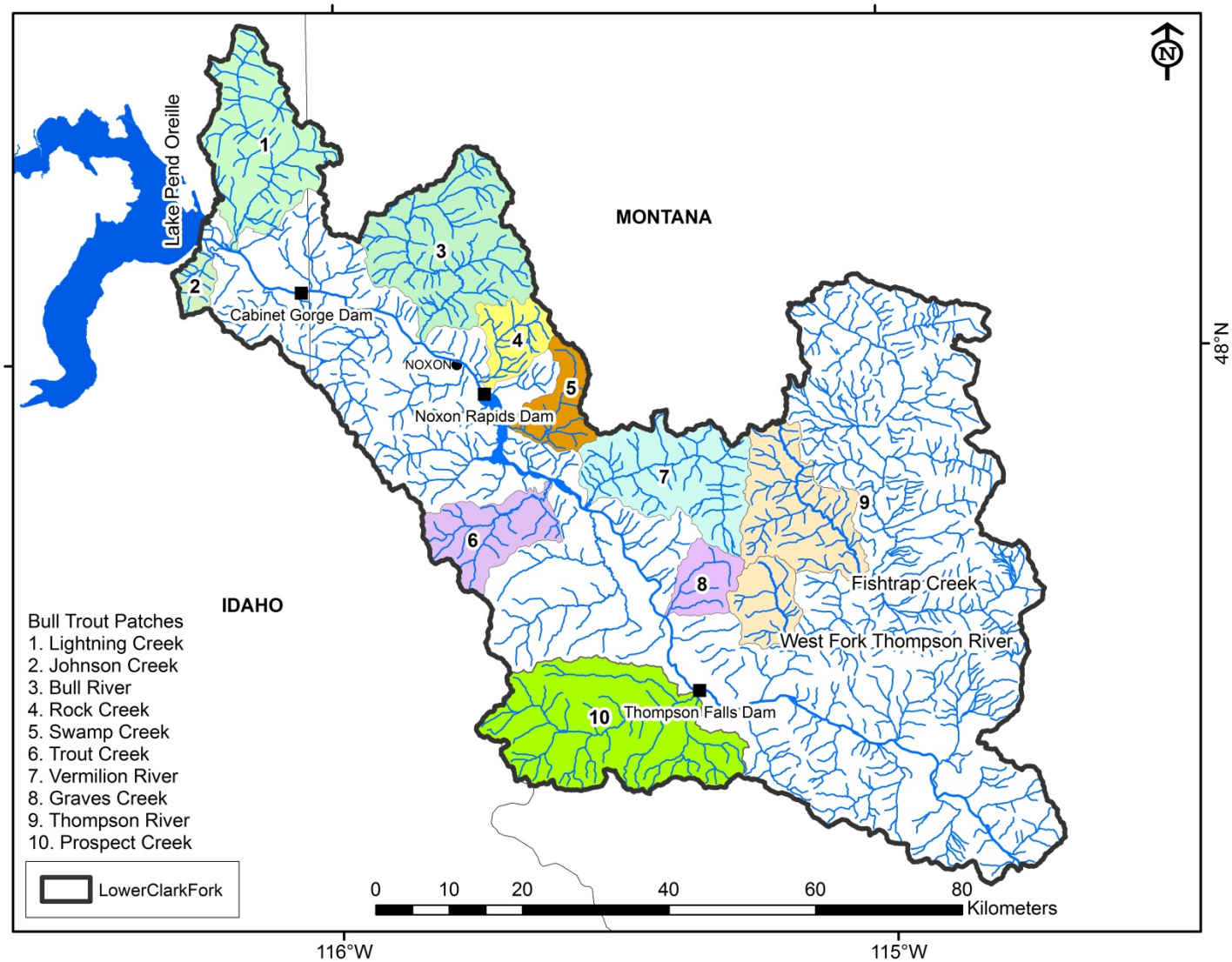


Figure 1. Lower Clark Fork River watershed showing the modeling project area (dark black outline) and the occupied bull trout patches (colored shaded areas) considered in the modeling analyses.

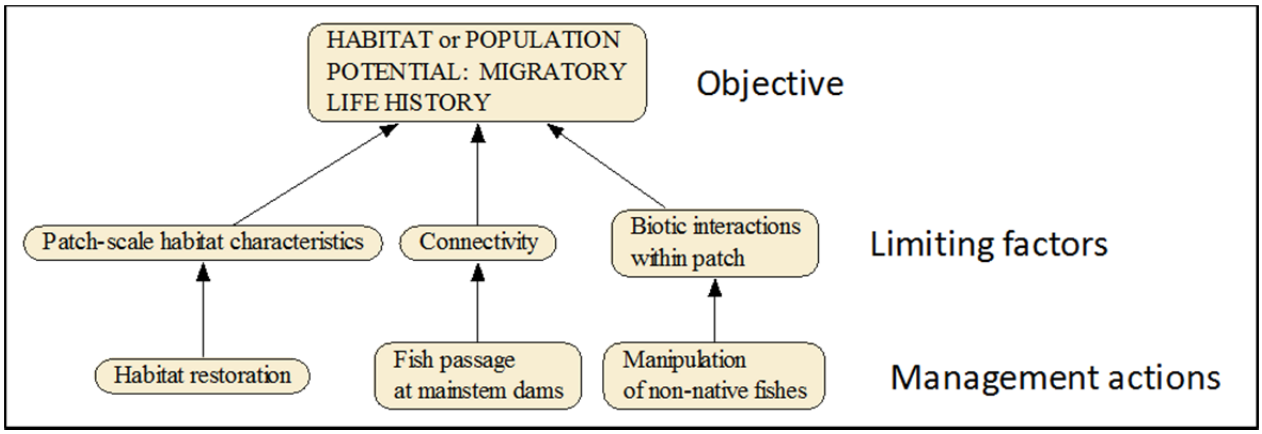


Figure 2. Example of a template conceptual model for the management paradigm of the Native Salmonid Restoration Plan.

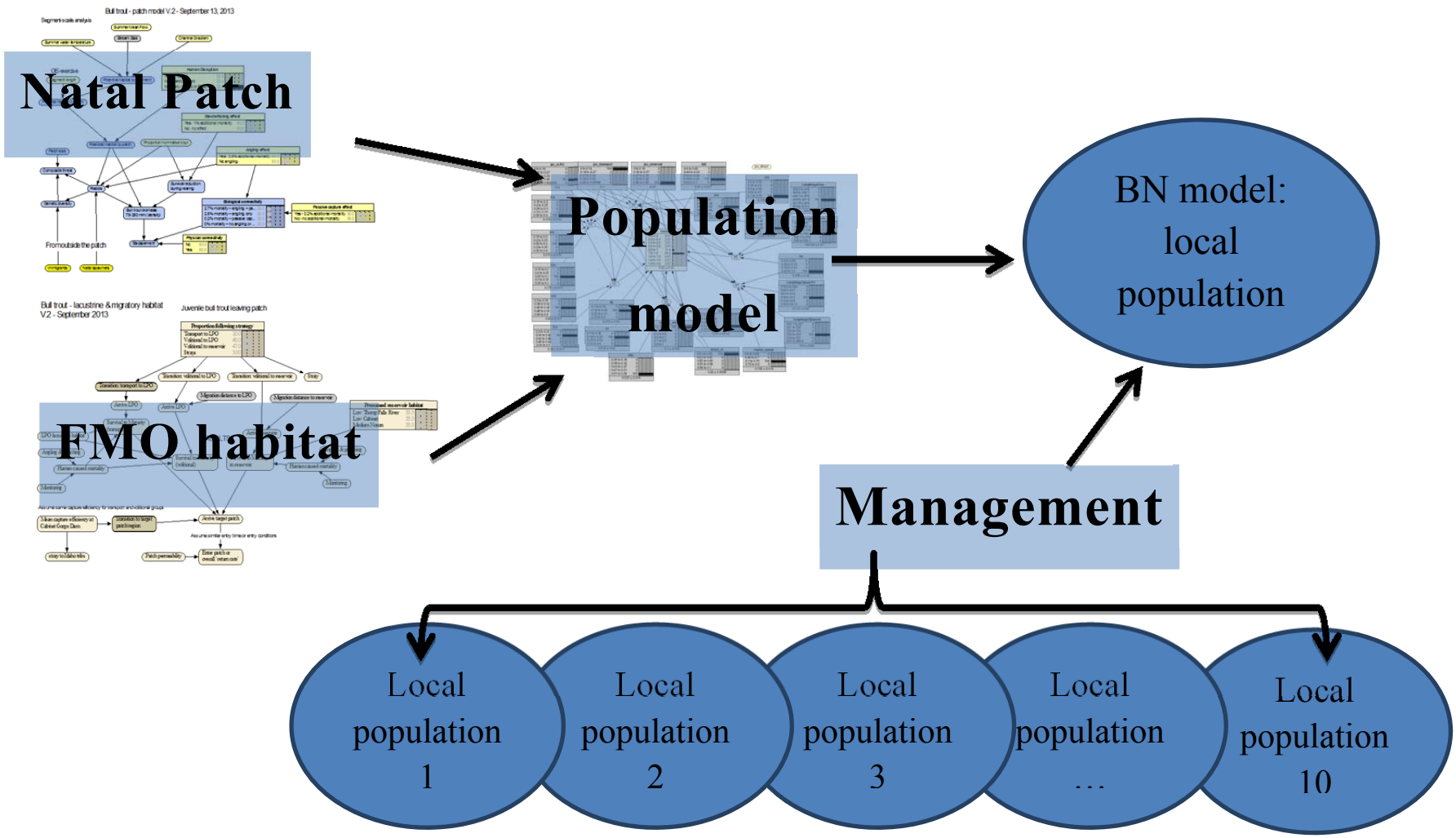


Figure 3. Schematic of the modeling work-flow illustrating how conceptual models for natal and FMO habitat that will be integrated with a population model to produce a Bayesian network (BN) for a local population of bull trout. Management interventions can be explored using the BN for a particular population, or scenarios can be applied across a set of local populations.

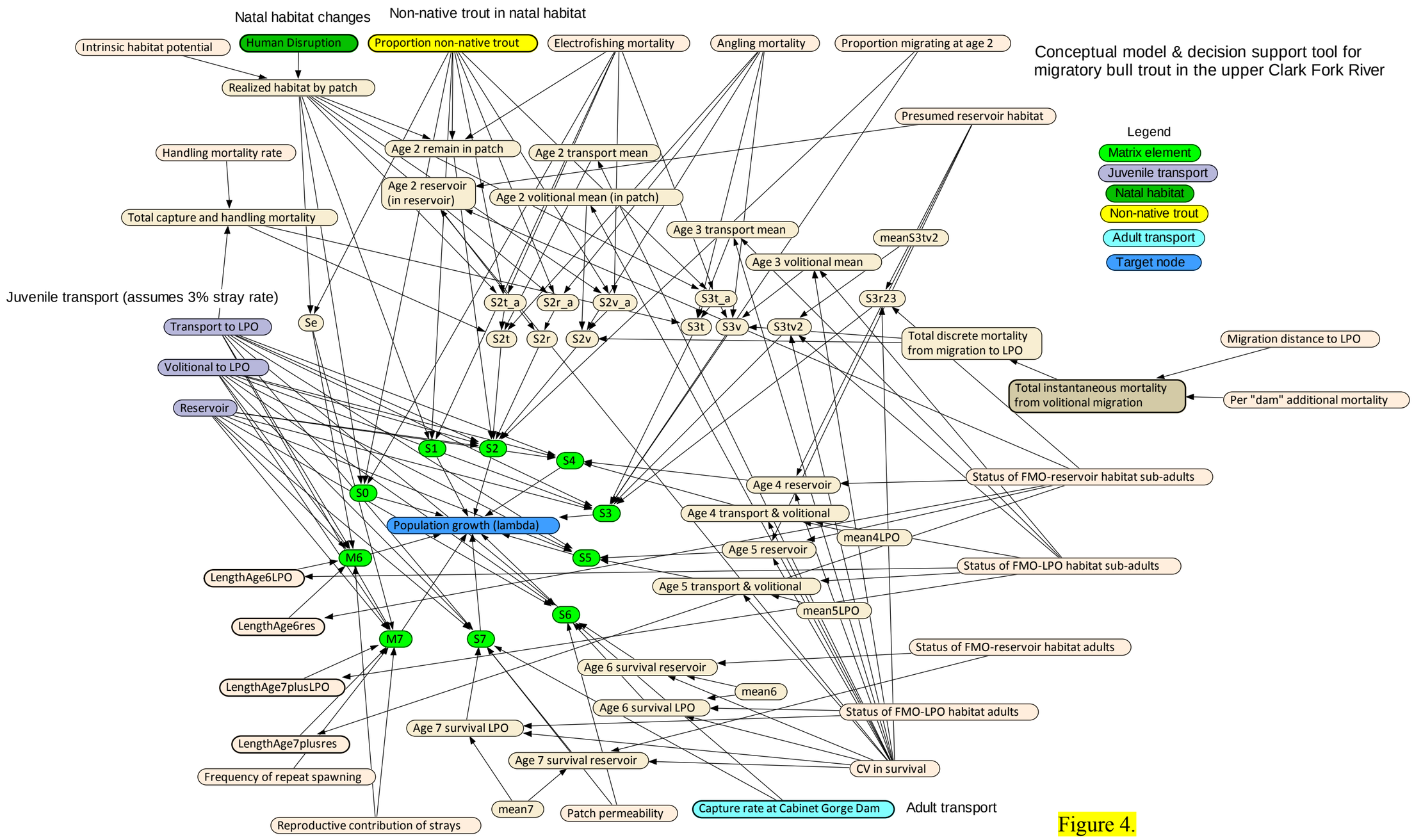
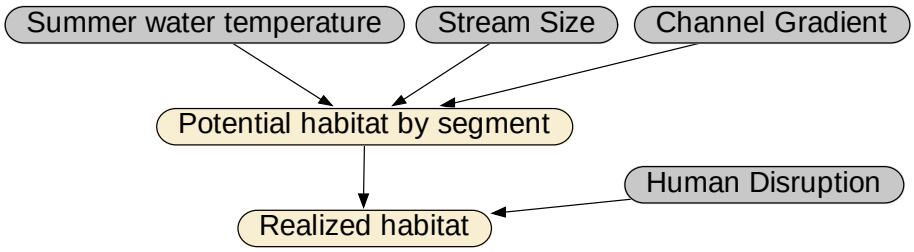

Conceptual model & decision support tool for migratory bull trout in the upper Clark Fork River
Natal habitat changes
Non-native trout in natal habitat
Intrinsic habitat potential
Human Disruption
Proportion non-native trout
Electrofishing mortality
Angling mortality
Proportion migrating at age 2
Realized habitat by patch
Presumed reservoir habitat
Handling mortality rate
Age 2 remain in patch
Age 2 transport mean
Age 2 reservoir (in reservoir)
Age 2 volitional mean (in patch)
Total capture and handling mortality
Age 3 transport mean
meanS3tv2
Age 3 volitional mean
Juvenile transport (assumes 3% stray rate)
S2t_a
S2r_a
S2v_a
S3t_a
S3r23
Transport to LPO
Se
S2t
S2r
S2v
S3t
S3v
S3tv2
Total discrete mortality from migration to LPO
Migration distance to LPO
Volitional to LPO
Total instantaneous mortality from volitional migration
Per "dam" additional mortality
Reservoir
S1
S2
S4
S0
S3
Status of FMO-reservoir habitat sub-adults
Age 4 reservoir
Age 4 transport & volitional
Population growth (lambda)
mean4LPO
Age 5 reservoir
M6
S5
Status of FMO-LPO habitat sub-adults
LengthAge6LPO
Age 5 transport & volitional
mean5LPO
S6
LengthAge6res
M7
S7
Status of FMO-reservoir habitat adults
Age 6 survival reservoir
LengthAge7plusLPO
mean6
Age 6 survival LPO
Status of FMO-LPO habitat adults
Age 7 survival LPO
LengthAge7plusres
Age 7 survival reservoir
CV in survival
Frequency of repeat spawning
mean7
Patch permeability
Capture rate at Cabinet Gorge Dam
Adult transport
Reproductive contribution of strays
Legend
Matrix element
Juvenile transport
Natal habitat
Non-native trout
Adult transport
Target node

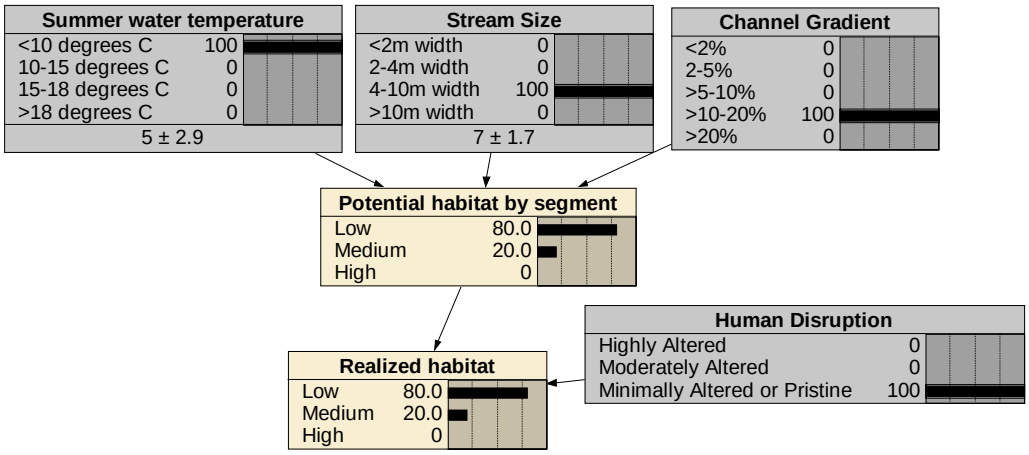
Figure 4.

Figure 4. Detailed conceptual diagram and associated Bayesian network (BN) decision support model for a local population of migratory bull trout in the lower Clark Fork River – Lake Pend Oreille system. Model variables associated with the primary management interventions of interest for the Native Salmonid Restoration Plan or the underlying population growth model are color coded for emphasis. See Table 2 for detailed variable definitions. Versions of this model were parameterized for each of the ten local populations of bull trout (patches) in the project area.

A



B



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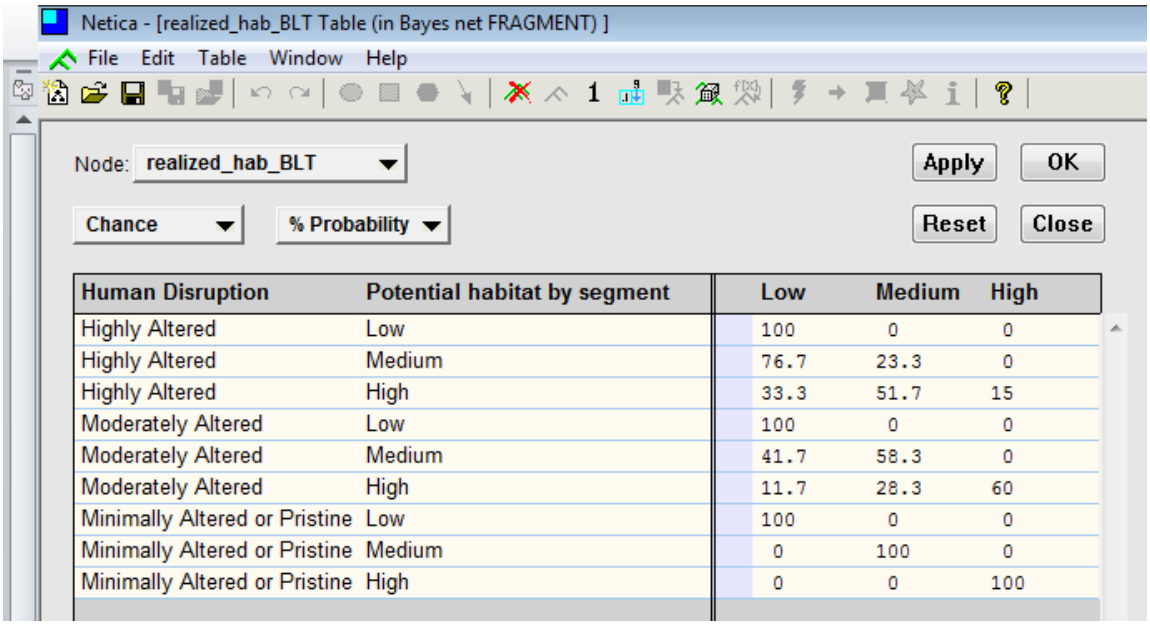


Human Disruption	Potential habitat by segment	Low	Medium	High
Highly Altered	Low	100	0	0
Highly Altered	Medium	76.7	23.3	0
Highly Altered	High	33.3	51.7	15
Moderately Altered	Low	100	0	0
Moderately Altered	Medium	41.7	58.3	0
Moderately Altered	High	11.7	28.3	60
Minimally Altered or Pristine	Low	100	0	0
Minimally Altered or Pristine	Medium	0	100	0
Minimally Altered or Pristine	High	0	0	100

Figure 5. Conceptual model (A), Bayesian network (B), and representative conditional probability table (C) for the fragment of the decision support model that estimates segment-scale potential and realized habitat conditions for migratory bull trout in the lower Clark Fork River.

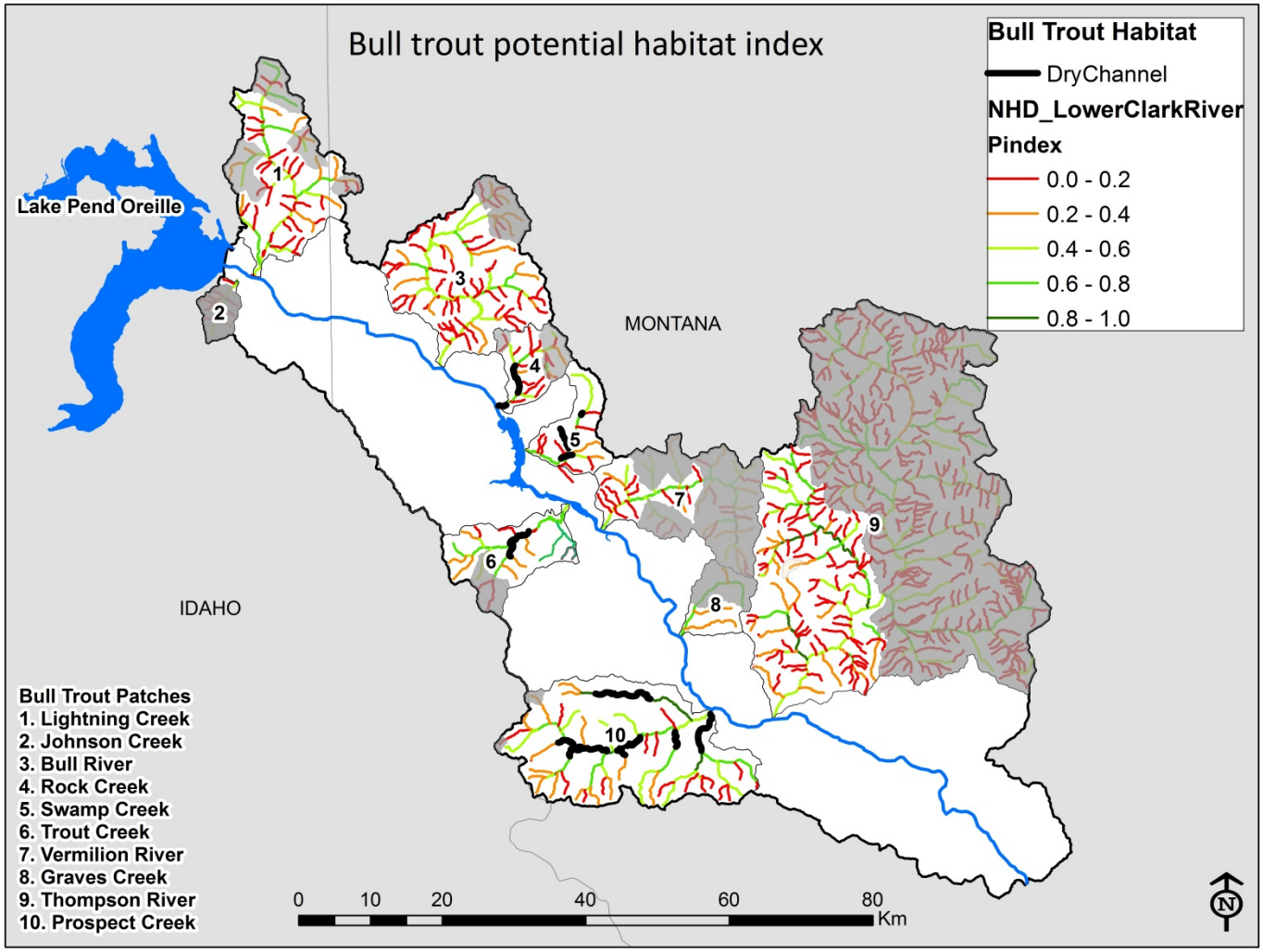
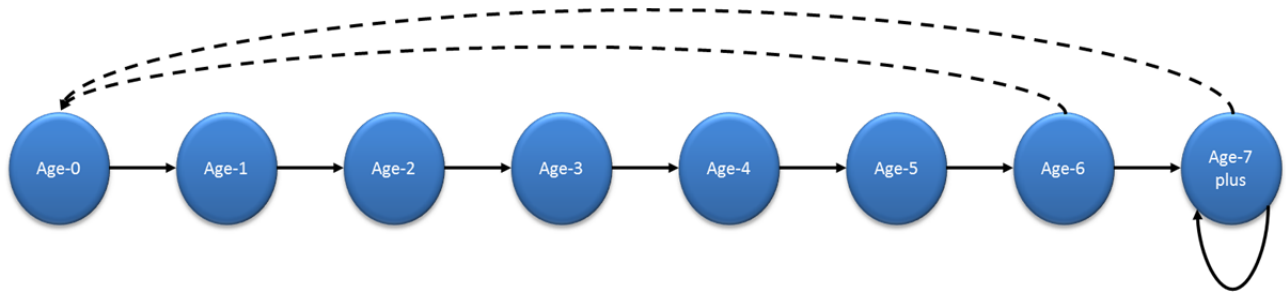


Figure 6. Illustration of the potential habitat for bull trout rescaled to a single index value ranging from 0 (low potential) to 1 (high potential) for each segment. Shaded areas are above natural barriers to fish passage, or in the case of the upper Thompson River drainage, areas where bull trout are rare or absent because of thermally unsuitable habitat. Thick black lines are stream reaches that are annually dewatered. The color scheme for the index value is arbitrary.

A



B

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & M6 & M7 \\ S0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S6 & S7 \end{bmatrix}$$

C

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 405.7 & 590.6 \\ 0.210 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.210 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.295 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.490 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.485 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.510 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.302 & 0.355 \end{bmatrix} \xrightarrow{\text{yields}} \lambda = 1.01$$

Figure 7. Life cycle representation (A) and corresponding generic (B) and parameterized (C) matrix representation of the population model for migratory bull trout in the lower Clark Fork River. In A, solid arrows represent survival or transition probabilities and dotted lines are reproductive output. The life stages and matrix elements correspond to variables in the conceptual model (see Figure 4).

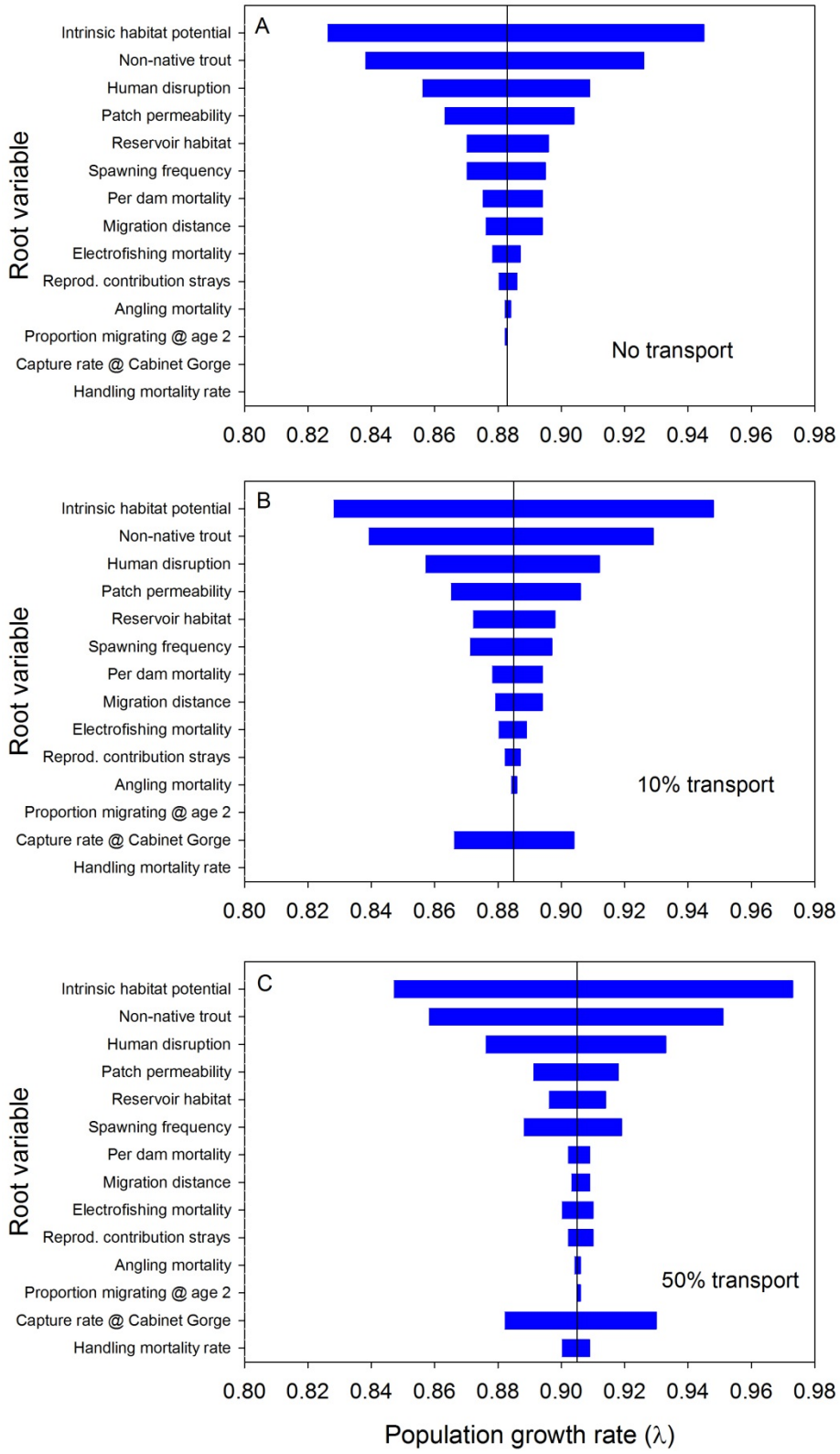


Figure 8. Variation in population growth rate (λ) to BN variables for three juvenile transport levels: (A) no transport, (B) 10% transport, and (C) 50% transport.

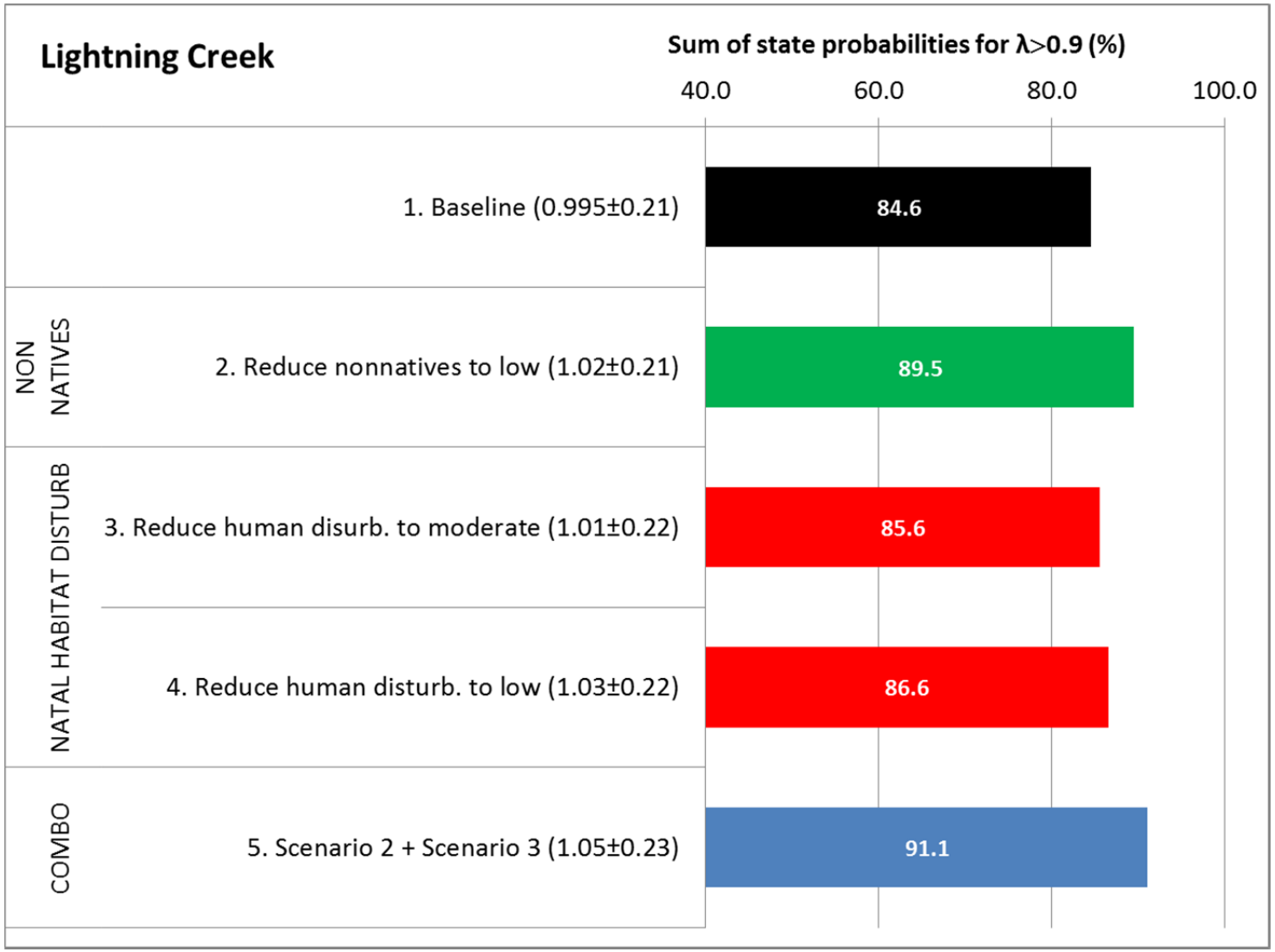


Figure 9. Likelihood that the local population of bull trout in Lightning Creek is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

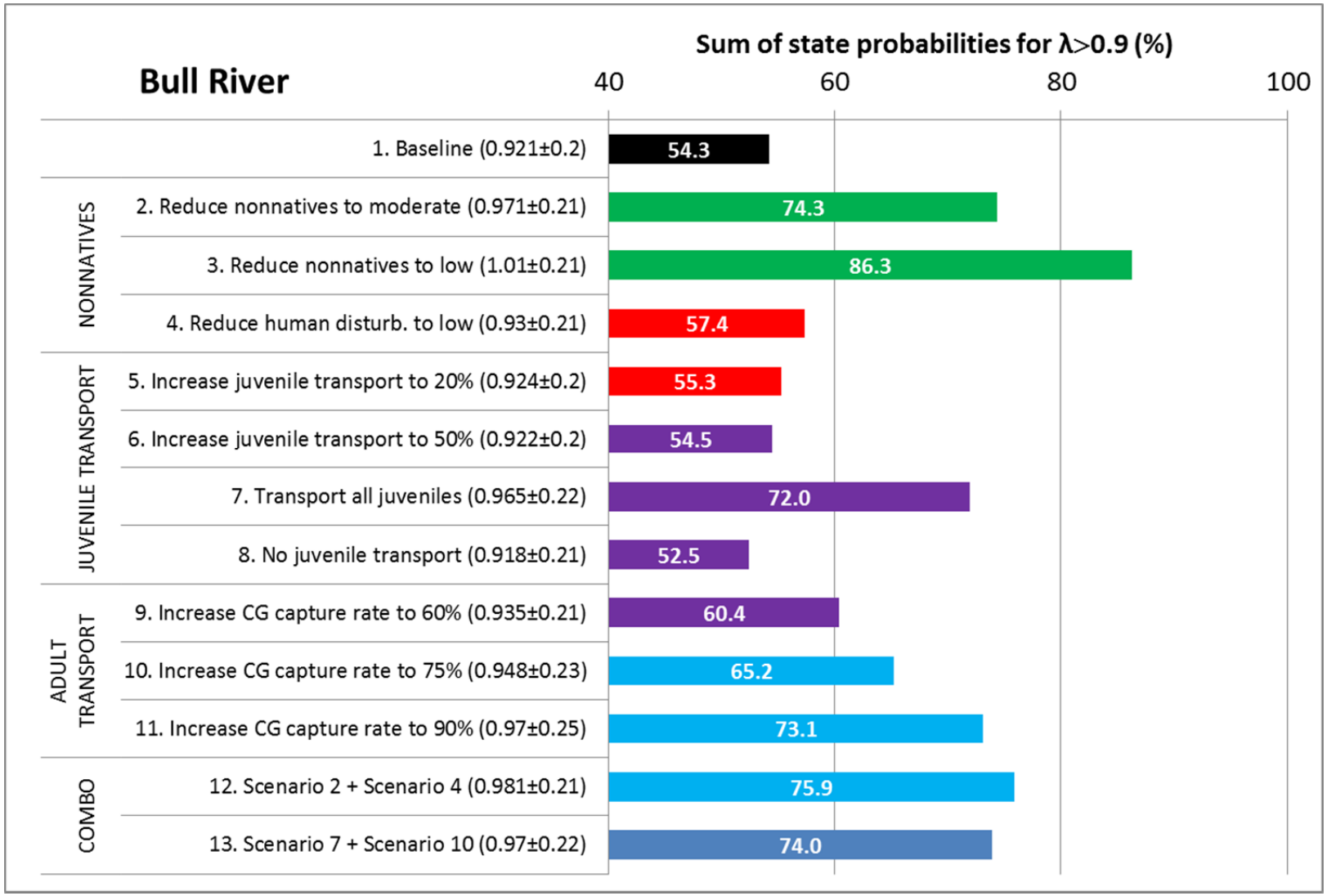


Figure 10. Likelihood that the local population of bull trout in Bull River is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

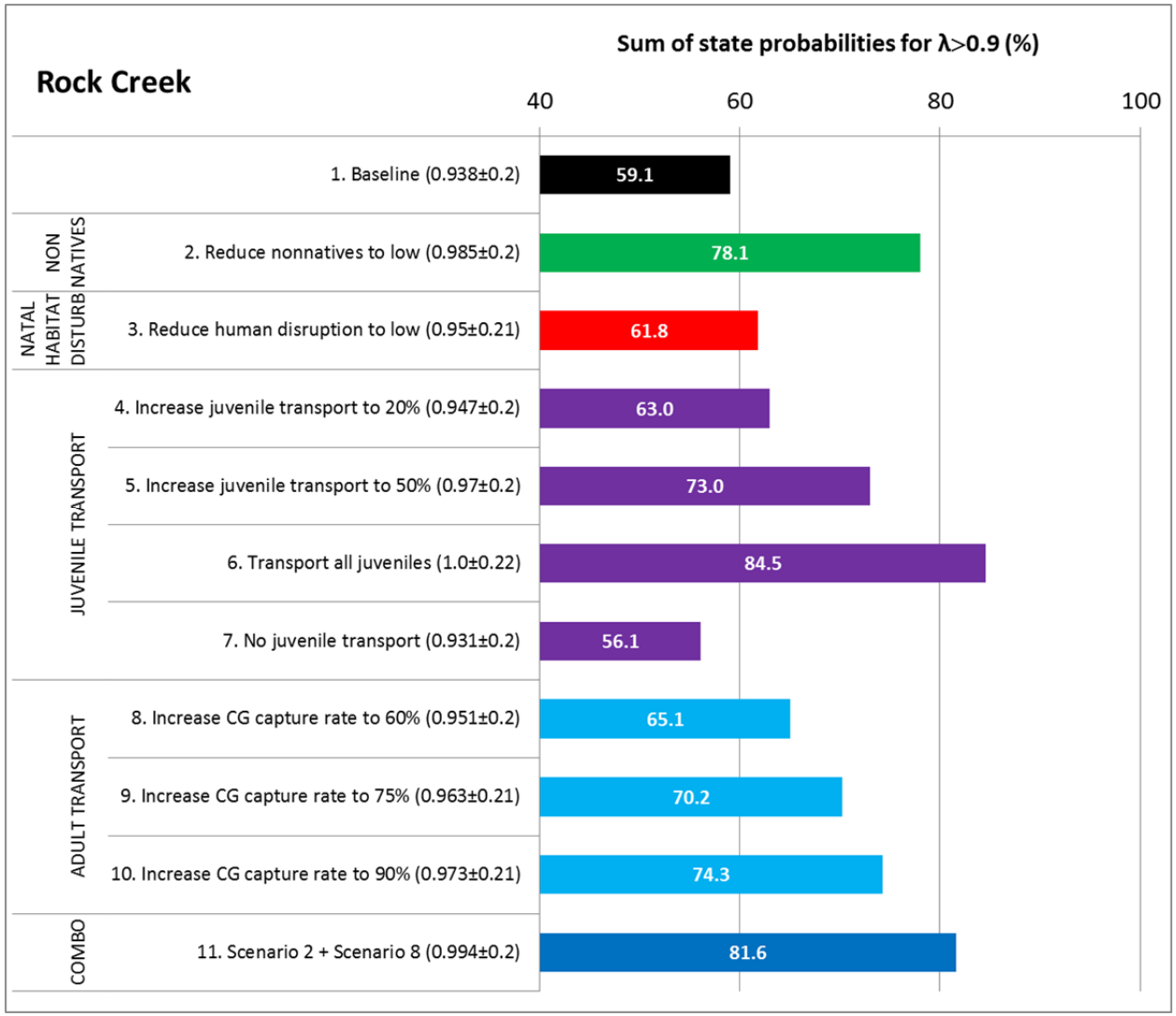


Figure 11. Likelihood that the local population of bull trout in Rock Creek is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

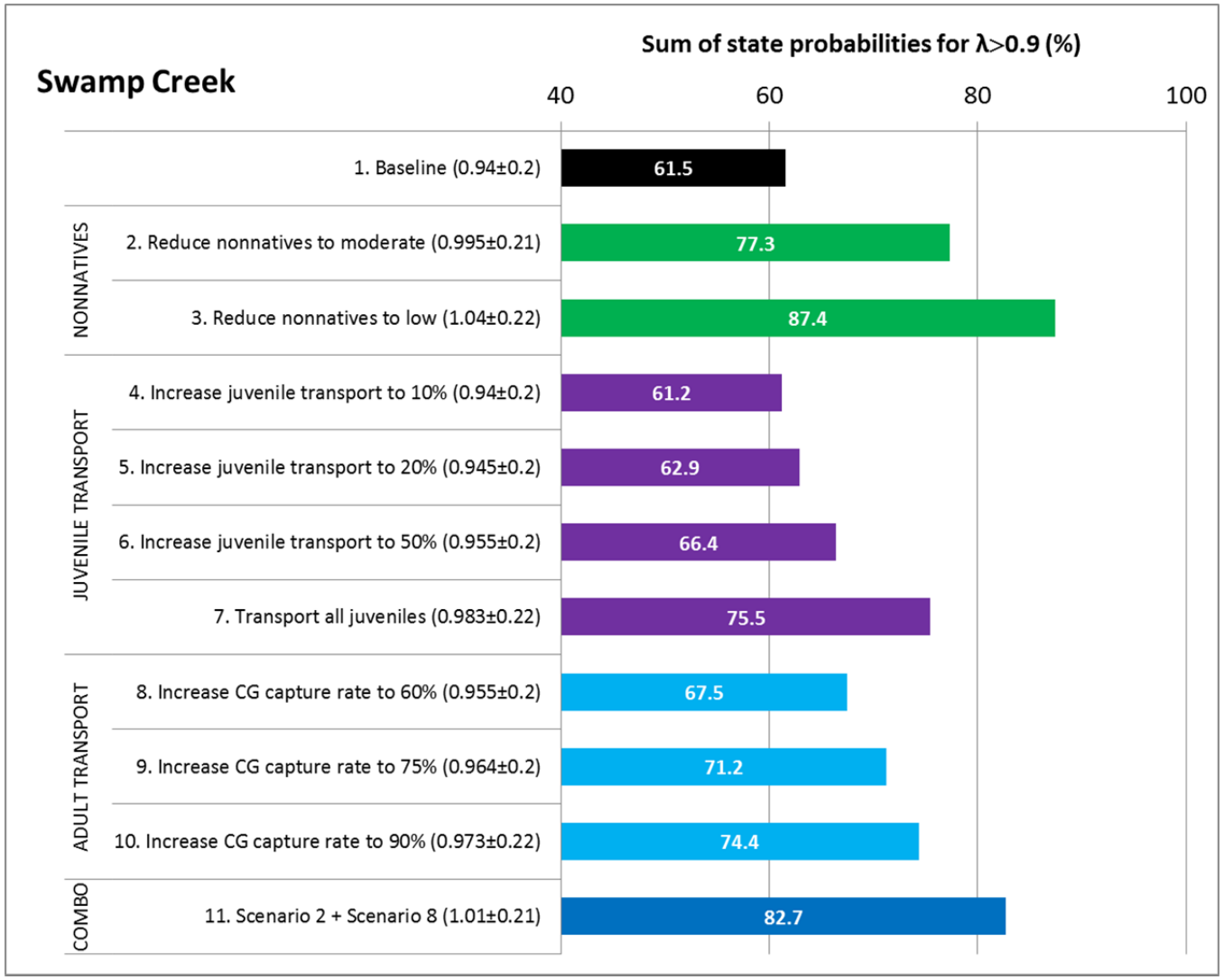


Figure 12. Likelihood that the local population of bull trout in Swamp Creek is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

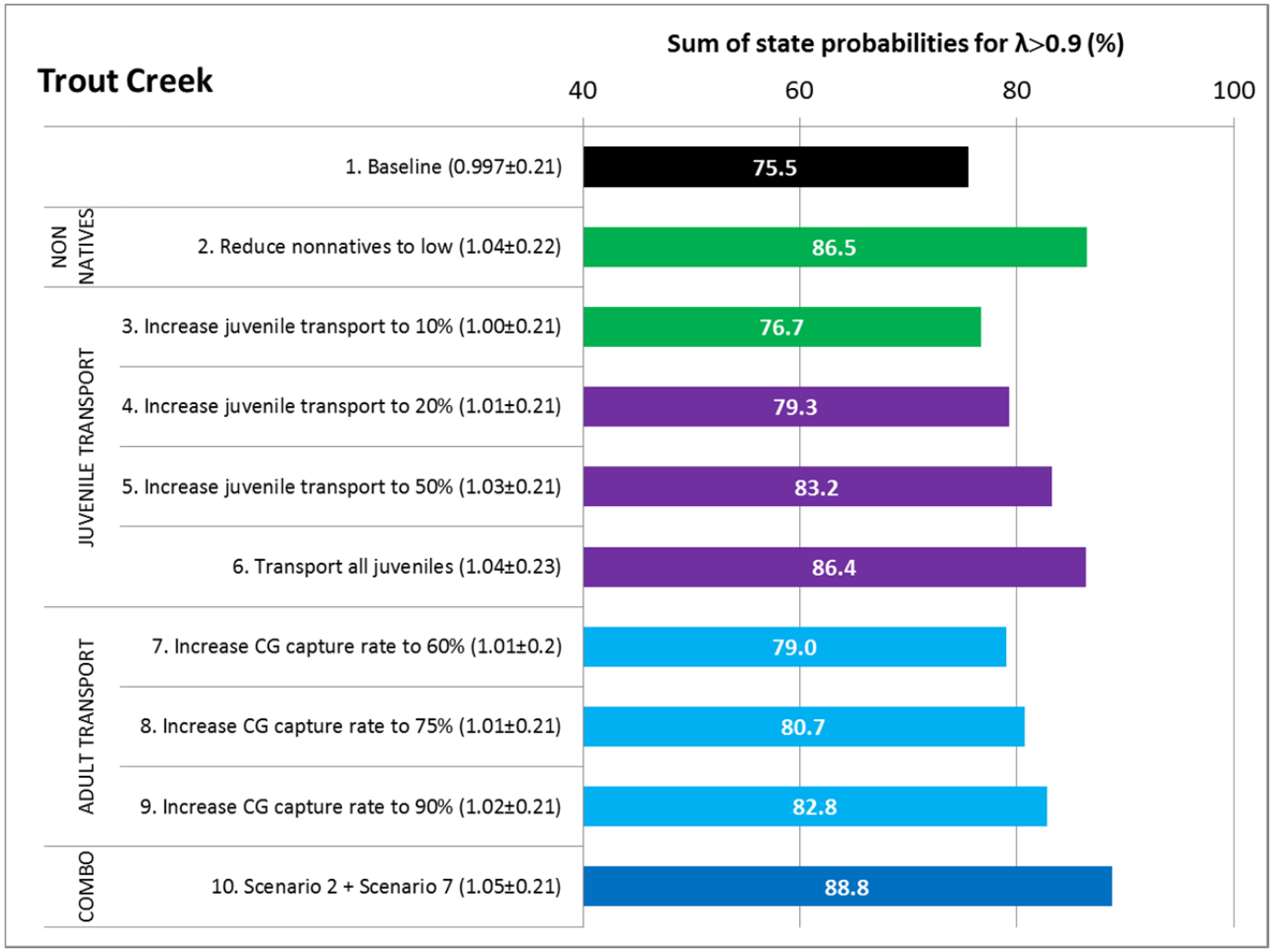


Figure 13. Likelihood that the local population of bull trout in Trout Creek is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

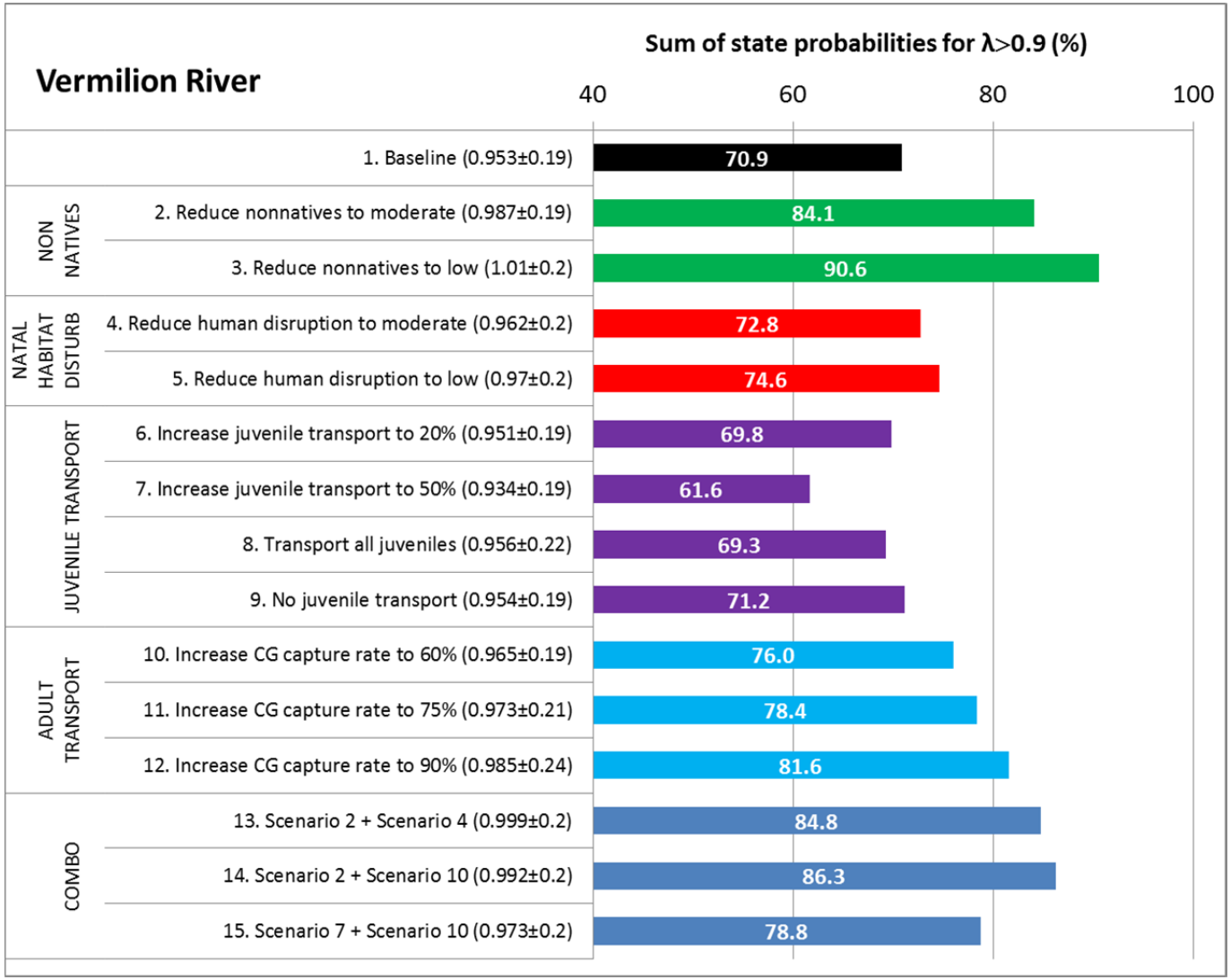


Figure 14. Likelihood that the local population of bull trout in Vermilion River is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

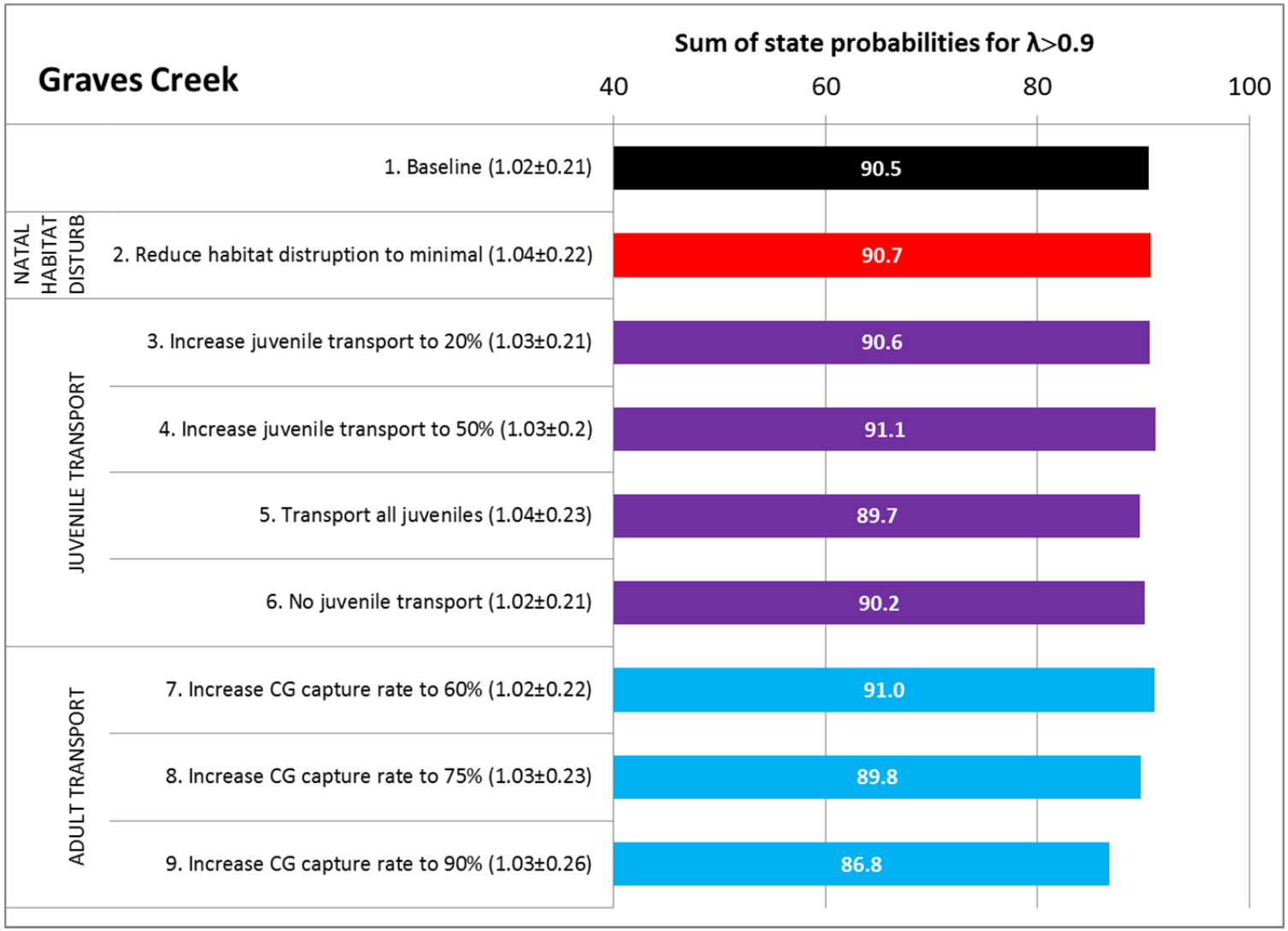


Figure 15. Likelihood that the local population of bull trout in Graves Creek is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

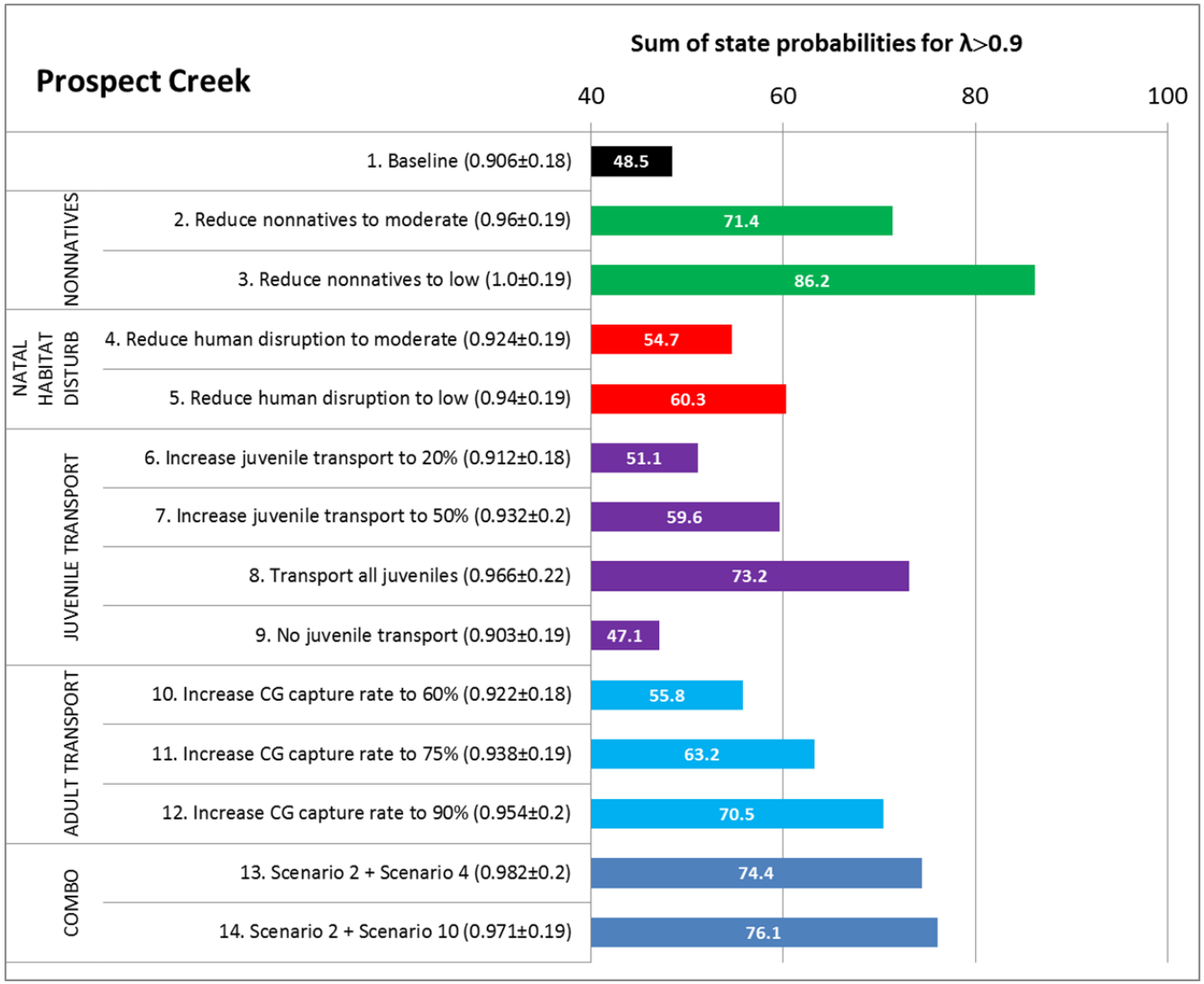


Figure 16. Likelihood that the local population of bull trout in Prospect Creek is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

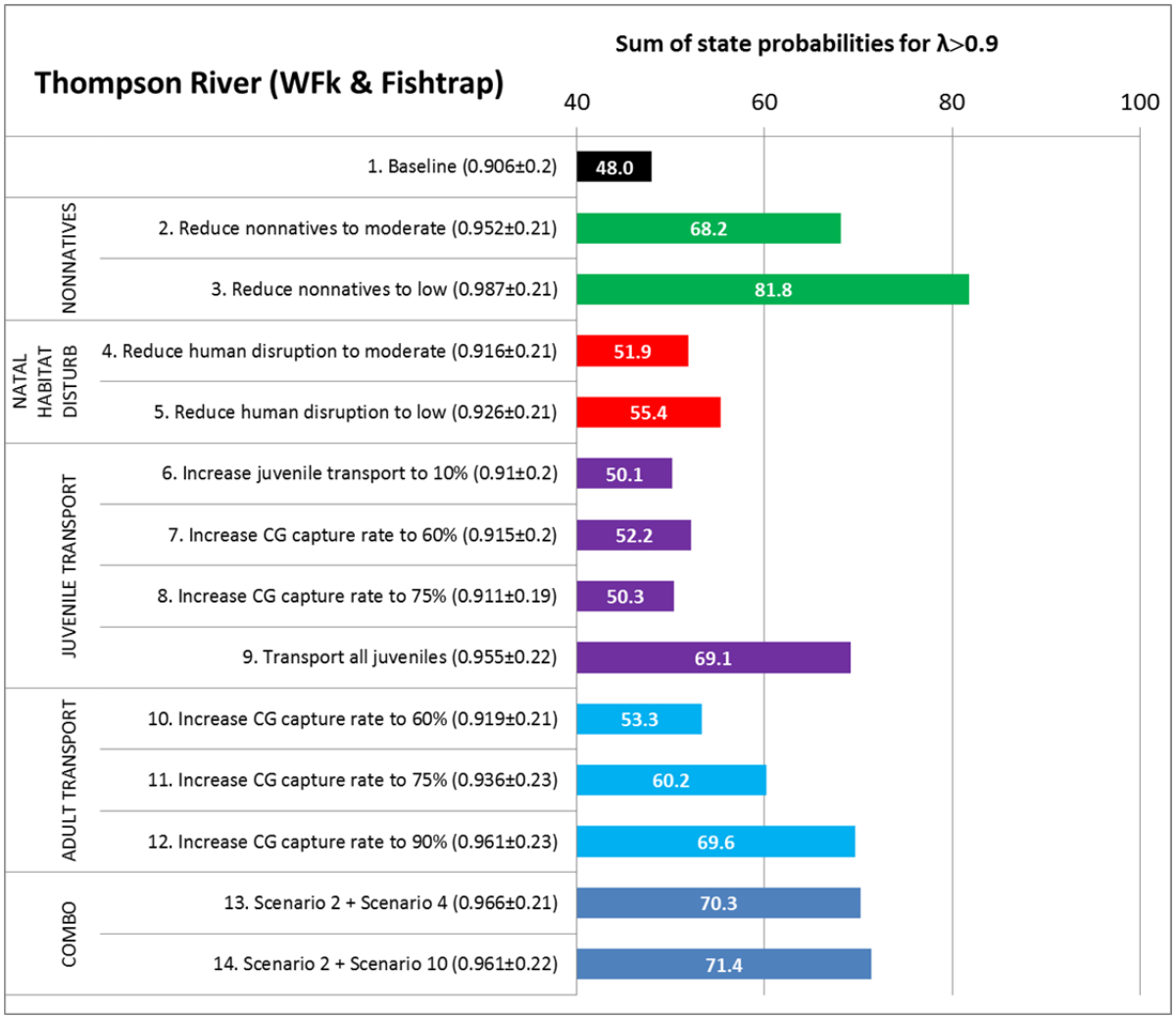


Figure 17. Likelihood that the local population of bull trout in the Thompson River drainage (West Fork Thompson River and Fishtrap Creek) is stable or increasing as a function of current baseline conditions and potential management interventions. Bars are the sum of the state probabilities for population growth rate (λ) that are 0.9 or greater (i.e., stable or increasing), and population growth rate (λ±SD) is listed after each scenario.

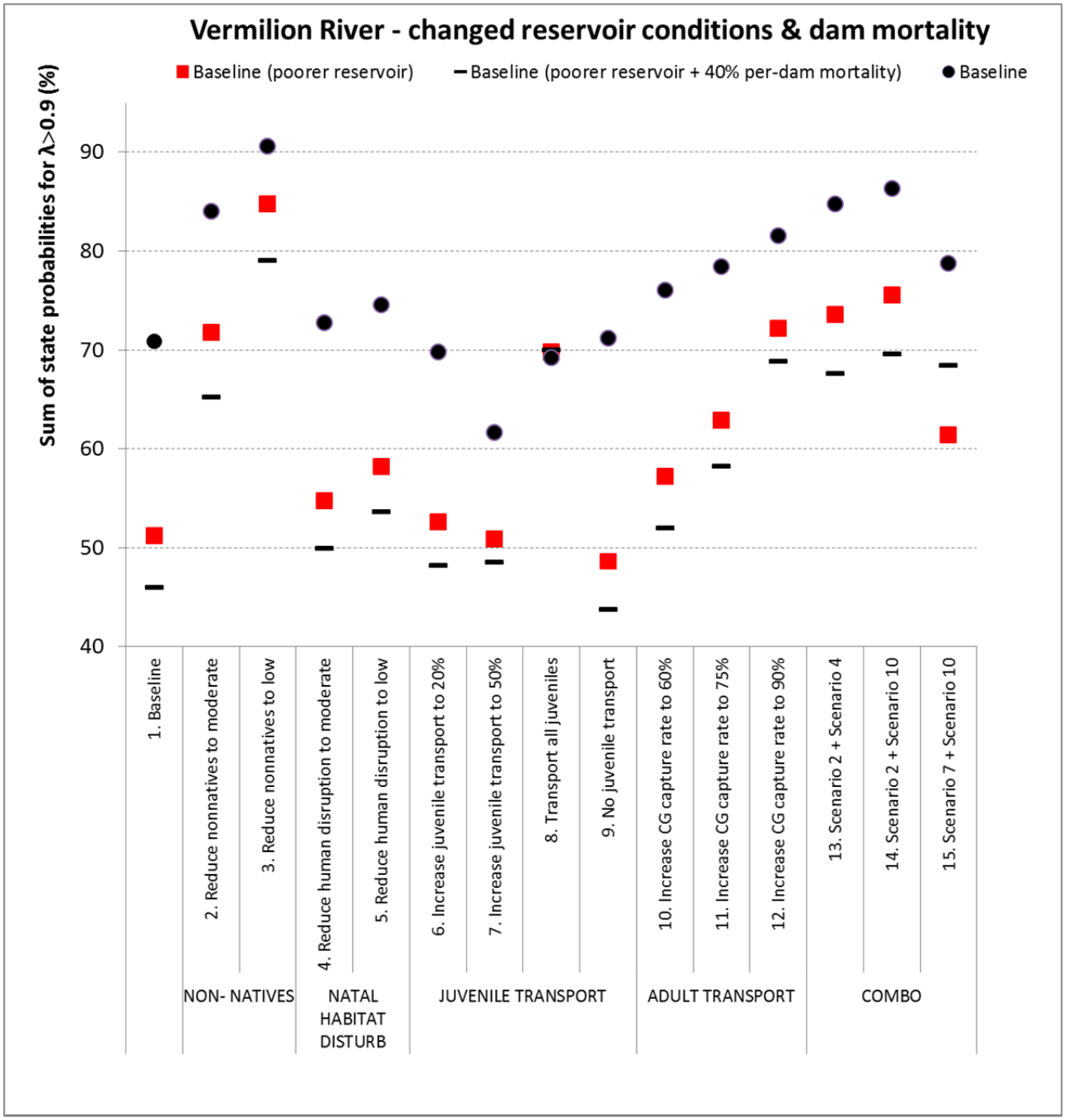


Figure 18. Effect of changing baseline conditions on population status of bull trout in the Vermilion River. Plots show the % likelihood of stable or increasing population under three sets of conditions: best-guess baseline conditions (filled circle, same data as Figure 14), FMO reservoir conditions are poorer (filled square), and FMO reservoir conditions are poorer + per-dam downstream migration mortality is increased from 10% to 40% (horizontal dash). Comparison of scenarios 1, 6, 7 and 8 show that the predicted effect of moderate increases in juvenile fish passage changes from neutral-negative to neutral-positive when initial conditions are changed.

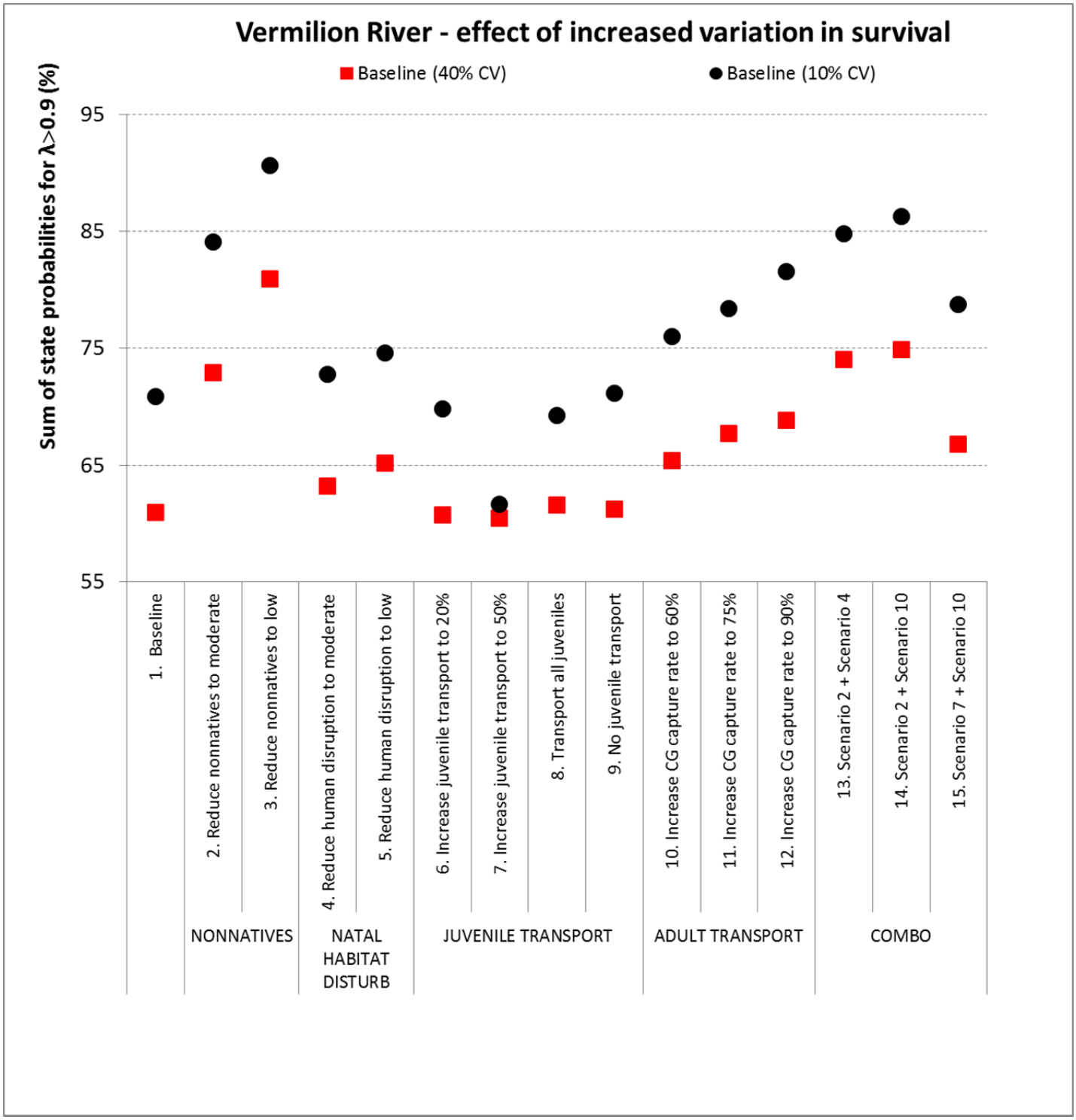


Figure 19. Effect of increased coefficient of variation (CV) in survival on population status of bull trout in the Vermilion River. Plots show the % likelihood of stable or increasing population under best-guess baseline conditions with 10% CV (filled circle, same data as Figure 14) or with a baseline having 40% CV (filled squares).

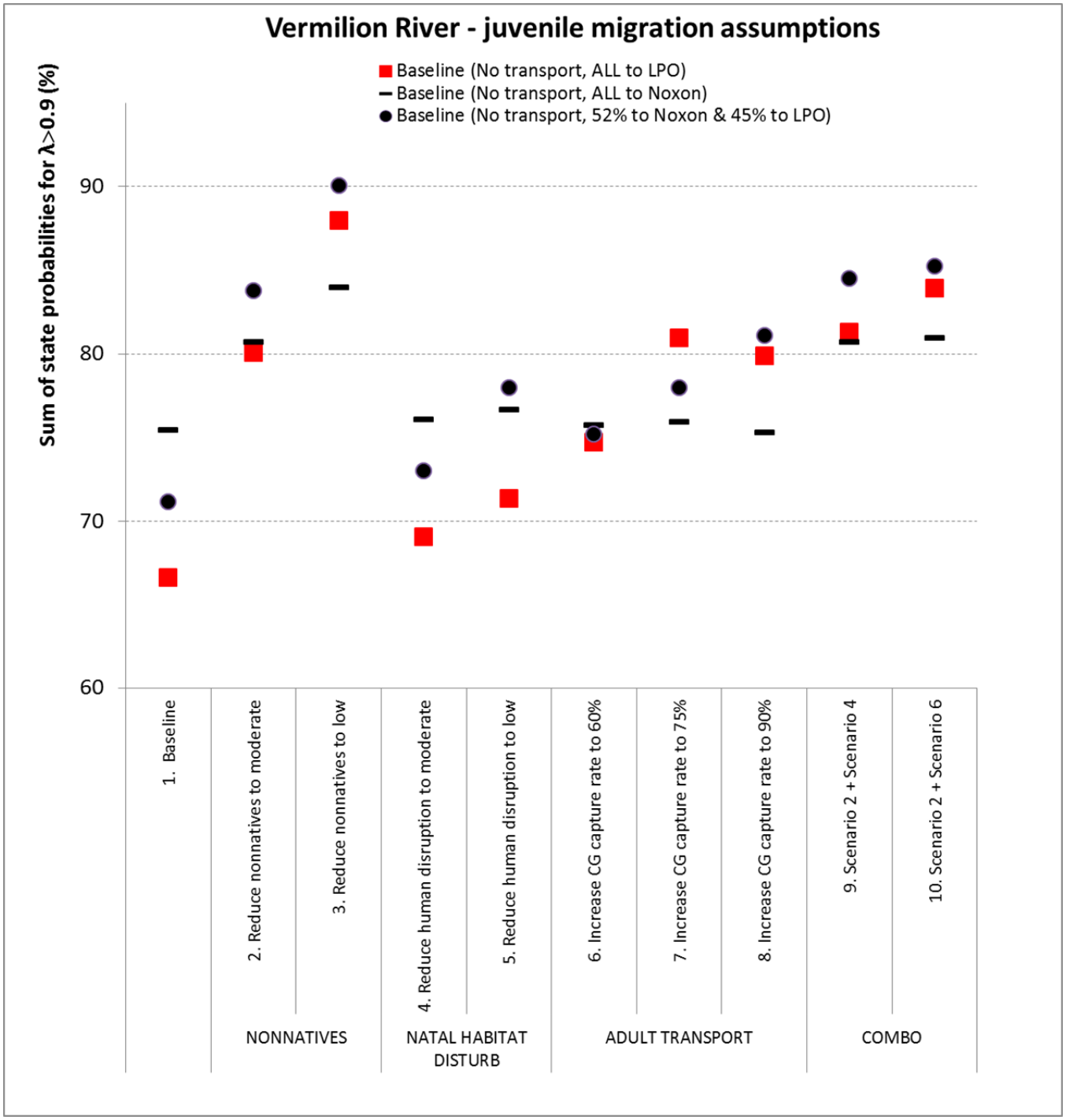


Figure 20. Effect of assumptions about juvenile migration strategy on population status of bull trout in the Vermilion River. Plots show the % likelihood of a stable or increasing population under the assumption of no juvenile capture and transport *and*: (a) the best-guess assumption that 52% use Noxon Reservoir and 45% use Lake Pend Oreille (LPO) for FMO habitat (filled circle), (b) all juveniles migrate to LPO (filled squares), or (c) all juveniles migrate to Noxon Reservoir (thick horizontal dash).

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U.S. Fish & Wildlife Service
Abernathy Fish Technology Center
Longview, Washington, 98632
Phone: 360-425-6072
http://www.fws.gov/aftc/index.html