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ARTICLE

Evaluating trade-offs in bull trout reintroduction strategies using structured decision making

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Abstract: Structured decision making allows reintroduction decisions to be made despite uncertainty by linking reintroduction goals with alternative management actions through predictive models of ecological processes. We developed a decision model to evaluate the trade-offs between six bull trout (*Salvelinus confluentus*) reintroduction decisions with the goal of maximizing the number of adults in the recipient population without reducing the donor population to an unacceptable level. Sensitivity analyses suggested that the decision identity and outcome were most influenced by survival parameters that result in increased adult abundance in the recipient population, increased juvenile survival in the donor and recipient populations, adult fecundity rates, and sex ratio. The decision was least sensitive to survival parameters associated with the captive-reared population, the effect of naivety on released individuals, and juvenile carrying capacity of the reintroduced population. The model and sensitivity analyses can serve as the foundation for formal adaptive management and improved effectiveness, efficiency, and transparency of bull trout reintroduction decisions.

Résumé : Le processus décisionnel structuré permet la prise de décisions de réintroduction même en présence d'incertitude, en reliant les objectifs de réintroduction à différentes mesures de gestion par l'entremise de modèles de prévision de processus écologiques. Nous avons mis au point un modèle décisionnel pour évaluer les compromis entre six décisions de réintroduction d'ombles à tête plate (*Salvelinus confluentus*) dans le but de maximiser le nombre d'adultes dans la population réceptrice sans réduire la population donatrice à un niveau inacceptable. Des analyses de sensibilité portent à croire que des paramètres associés à la survie qui se traduisent par une abondance d'adultes accrue dans la population réceptrice, une survie accrue des juvéniles dans les populations donatrice et réceptrice et les taux de fécondité et les rapports de masculinité des adultes exercent la plus grande influence sur l'identité et les résultats de la décision. La décision était moins sensible à des paramètres de survie associés à la population élevée en captivité, à l'effet de la naïveté sur les individus relâchés et à la capacité de charge de juvéniles de la population réintroduite. Le modèle et les analyses de sensibilité peuvent servir de base pour une gestion adaptative formelle et pour améliorer l'efficacité, l'efficience et la transparence des décisions concernant la réintroduction d'ombles à tête plate. [Traduit par la Rédaction]

Introduction

Bull trout (*Salvelinus confluentus*) require cold water for spawning and early rearing (Buchanan and Gregory 1997), and if climate change predictions are accurate and habitat degradation and fragmentation continue to limit connectivity, then populations are expected to decline even further (Rieman et al. 1997). The Pacific Northwest warmed 0.8 °C in the twentieth century, and this trend is expected to continue and magnify (IPCC 2007; Mote and Salathé 2010). Rieman et al. (2007) evaluated bull trout response to a range of predicted climate warming scenarios for the Columbia River Basin and estimated a loss ranging from 18% of 92% of suitable natal habitat. The range of this estimate suggests substantial uncertainty when considering the effects of climate change on bull trout populations (Wenger et al. 2013). It is thought that warming trends will restrict populations to small isolated patches in headwater streams, further limiting population connectivity (Rieman et al. 2007) and increasing extinction risk (Rieman and McIntyre 1995). Large populations residing in less degraded habitat will increase in importance as source populations for recolonization and reintroduction efforts (Dunham and Rieman 1999).

There are numerous options to deal with the harmful effects of climate change on bull trout populations. Isaak et al. (2010) suggested minimizing disturbances in riparian habitat (i.e., grazing, road building, and timber harvest) to buffer stream temperatures from additional warming. Unoccupied habitat can be made available for natural recolonization or reintroduction (Dunham and Rieman 1999) by removing or reengineering human-made structures that limit habitat connectivity. Connectivity is the mechanism that promotes complex life histories exhibited by bull trout where resident populations supply individuals to migratory populations and vice versa (Rieman and McIntyre 1993). Connectivity between suitable habitats is required to promote these life history strategies and long-term persistence of the population. Connecting multiple small isolated populations that result from a warming climate will create functional metapopulations that provide a greater value to conservation (Dunham and Rieman 1999). In areas where reclaiming and reconnecting suitable habitat does not re-

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sult in natural recolonization, managers may decide to implement a reintroduction program.

The Bull Trout Recovery Plan (USFWS 2015) identifies translocation and controlled propagation as potential tools to produce individuals for reintroduction programs. A translocation strategy consists of capturing individuals from a donor population and directly transporting and releasing them into a recipient habitat. Controlled propagation can be divided into two strategies; captive rearing and artificial production. A captive-rearing strategy involves capturing, transporting, and rearing wild individuals in a controlled environment to be released at a later date when their potential for survival has been improved. Artificial production differs from captive rearing in that wild fish are brought into captivity and spawned. The resulting progeny are reared in captivity to maturity and subsequently spawned or released into the wild as part of a reintroduction program (Hard et al. 1992).

Each strategy comes with its own advantages, disadvantages, and uncertainties. Translocation is the least expensive of the three strategies and comes with a variety of benefits. Natural fish behaviors, genetic diversity, and ecological diversity will not be affected by the captive environment (e.g., Flagg and Nash 1999; Brown and Day 2002; Naish et al. 2007; Fraser 2008). For these reasons, translocation is the first option among many managers and has produced some success with releases of bull trout into the Willamette and Clackamas rivers in Oregon (UWBTWG 2010; Barrows et al. 2016). Disadvantages to translocation include high risk to donor populations due to the number of individuals needed to create a viable population (Shively et al. 2007), the potential for local adaptation of donor populations hindering performance in the recipient system, and limited ability for fish health screening. Relative to translocation, captive rearing and artificial production can provide more individuals for reintroduction while lessening the demographic impact to donor populations (Shively et al. 2007). These strategies also provide a greater opportunity to monitor fish health. However, there is a suite of recent literature summarizing the effects of captivity on salmonids (e.g., Flagg and Nash 1999; Brown and Day 2002; Naish et al. 2007; Fraser 2008). Impacts to stress (Dickens et al. 2010), behavior (Berejikian et al. 2001), and morphology (Taylor 1986) and concerns over genetic diversity (Fraser 2008) are inevitable in captive-rearing and artificial production programs. In general, the costs and benefits of a captive-rearing strategy fall in between a translocation and an artificial production strategy. Managers opt to use artificial production only when natural populations are extremely low, all other options have been exhausted, and the extinction risk outweighs the negative impacts of artificial production (Hard et al. 1992). Selecting the best strategy to benefit bull trout conservation will depend on levels of uncertainty, the understanding of how the biological system works, the amount of risk managers are willing to incur, and the probability of achieving the desired outcome (e.g., increased abundance, distribution, or both).

A better understanding of the trade-offs between alternative bull trout reintroduction decisions is needed and can be accomplished through structured decision making. Structured decision making is a process that promotes informed decision making and transparency by linking explicit quantifiable objectives to management alternatives (i.e., reintroduction strategies) through predictive models (Clemen 1996; Conroy and Peterson 2013). These predictive models can represent competing hypotheses that describe the understanding of how ecological processes may respond to a particular decision and the structure of those processes. However, most decisions in natural resources are confounded by uncertainty. Rather than ignore uncertainty, structured decision making incorporates it into the decision process. Natural resource decisions reoccur in time and space and new information gained through monitoring will minimize uncertainty (i.e., learning, adaptive management). Given the inherent uncertainty, need for transparency, and importance of natural resource conservation and recovery, the Department of the Interior and the US Fish and Wildlife Service have adopted structured decision making to guide habitat and species conservation into the future (i.e., Strategic Habitat Conservation; USFWS 2008; Williams et al. 2009).

Table 1. Matrix of state-dependent penalties applied to the decision utility for reducing the adult bull trout (*Salvelinus confluentus*) abundance of the donor population below a desired state.

Ending abundance	Starting abundance				
	0–50	50–100	100–250	250–500	>500
0–50	0	0	0	0	0
50–100	1	1	0	0	0
100–250	1	1	1	0	0
250–500	1	1	1	1	1
>500	1	1	1	1	1

Note: If the donor population was reduced to an undesirable state, the value of the decision was 0. If the donor population was not reduced to an undesirable state, the value of the decision was the number of adults in the recipient population, up to a maximum of 300.

The process of structured decision making can inform future bull trout reintroductions and would be a useful tool for managers given the threatened status of the species and uncertainty of reintroduction strategies (USFWS 2015). To this end, we employed structured decision making to evaluate the trade-offs of alternative bull trout reintroduction decisions. We identified model objectives and alternative reintroduction decisions and presented the model structure. A series of sensitivity analyses were conducted to determine the relative uncertainty of decision model parameters. We then used the model and stochastic dynamic programming to develop a state-dependent policy that managers can use to guide bull trout reintroductions given any combination of available donor and recipient population sizes (i.e., states). Finally, we used forward simulation to compare the quasi-extinction probability of donor and recipient populations under different management alternatives and environmental stochasticity.

Methods

Valuation of decision outcome

Fundamental objectives of a reintroduction are to build a viable recipient population and do so without endangering the donor population (IUCN/SSC 2013). Accurate estimates of abundance and demographics are needed to determine the probability that a population will persist (Caswell 2001; Morris and Doak 2002). However, obtaining accurate estimates of demography is difficult and expensive, relative to estimation of adult abundance. Redd surveys are widely used to estimate adult bull trout abundance. However, these estimates may be biased by observer experience, sampling effort, and habitat variability. These biases may result in abundance estimates that are typically less than the true population size (Al-Chokhachy et al. 2005; Muhlfeld et al. 2006), which suggests that basing the decision value on abundance estimates derived from readily available redd count data will result in conservative abundance estimates and limit the need for additional monitoring resulting in a user-friendly model. We calculated the value of a decision outcome (i.e., the utility) as the number of adults in the recipient population up to a maximum of 300 adults, with the assumption that the marginal gain from additional adults would not outweigh the cost and effort of additional releases. We assumed that any removal of individuals would reduce adult abundance in the donor population by some level and used a state-based approach to apply a penalty if the donor population was reduced to an unacceptable state (Table 1). The value of the decision (i.e., utility) was multiplied by zero if abundance in the ending donor population state was less than abundance in the starting

Table 2. Six alternative bull trout (*Salvelinus confluentus*) reintroduction decisions evaluated in the decision model.

Alternative	Strategy	Embryos	Juveniles	Subadults	Small adults	Large adults
1	Do nothing	0	0	0	0	0
2	Translocation	0	1000	0	0	0
3	Translocation	0	0	0	30	30
4	Translocation	0	1000	60	20	20
5	Captive-rearing	20 000	0	0	0	0
6	Artificial production	0	0	0	30	30

Note: A decision consisted of two components: a reintroduction strategy and the number of individuals by life stage to remove from a donor population.

donor population state (Table 1). For example, if the recipient population is estimated to be 80 adults after a reintroduction and the donor population is not reduced to an undesirable state, the value of the division is 80 × 1 = 80, whereas if the donor populations is reduced to an undesirable state, the value of the decision is 80 × 0 = 0.

Decision alternatives

A reintroduction decision for bull trout consists of two components. First, a reintroduction strategy (i.e., translocation, captive rearing, and artificial production) is selected. Then, depending on the strategy selected, the life stage(s) and number of individuals needed for the reintroduction effort can be determined. We evaluated six reintroduction decision alternatives (Table 2). The first alternative is to do nothing. Alternatives 2 through 4 are structured similar to the Clackamas River reintroduction in which 30 adults, 30 subadults, and 1000 juveniles were targeted for transfer (USFWS and ODFW 2011). We used these numbers for the basis of alternative 4 in which 1000 juveniles, 60 subadults, and 40 adults were translocated. Also, we evaluated a 1000 juvenile-only translocation (alternative 2) and a 60 adult-only translocation (alternative 3) using similar numbers of fish. The fifth alternative was a captive-rearing strategy to collect 20 000 eyed embryos by hydraulic redd sampling (McNeil 1964; Berejikian et al. 2011) and incubate and rear those individuals for 1 year before releasing them into the recipient habitat (alternative 5). The sixth alternative is an artificial production strategy of collecting 30 small adults and 30 large adults, artificially spawning those individuals in captivity, and releasing the resulting progeny after 1 year of rearing. We assumed that managers would be able to collect the exact number of individuals for the planned reintroduction (i.e., perfect controllability; Conroy and Peterson 2013) and each decision represents what is feasible from either a logistical perspective (e.g., collection, rearing) and (or) reasonable risk to a donor population.

Each decision alternative consisted of five annual collections and subsequent releases of individuals. Do-nothing and translocation strategies encompassed 5 years, whereas the captive-rearing strategy and artificial production strategy encompassed 6 or 7 years, respectively. These timesteps were a function of the additional time it takes to incubate and rear animals in captivity before release. A 5–7 year timestep coincides with the age at maturity in bull trout (4–7 years; McPhail and Murray 1979; Fraley and Shepard 1989; Johnston 2005) and allows the youngest life stages an opportunity to become mature adults at the end of the time horizon. The Final Bull Trout Recovery Plan is to be updated approximately every 5 years to reflect current information (USFWS 2015) and this time horizon allows new information gained from monitoring efforts to be incorporated into recovery plan revisions.

Model structure and parameters

The foundation of the model were three stage-based, post-breeding, Leslie matrix models (Caswell 2001) that represent the donor, captive, and recipient populations. Once a decision is made, individuals are collected, moved between populations, and released before future populations are projected. Populations were projected for 7 years using matrix multiplication (Caswell 2001). A 7 year projection provided all individuals collected for an artificial production strategy to be released before evaluating a decision outcome. We incorporated demographic stochasticity after matrix population projections where the number of individuals surviving was drawn from a binomial distribution where n_i is the number of individuals in life stage i and p is the stage base survival parameter. Similarly, fecundity was drawn from a Poisson distribution where λ was equal to F_i (Conroy and Peterson 2013).

The donor model consisted of five life stages adopted from Schaller et al. (2014): embryos, juveniles, subadults, small adults, and large adults. The transition matrix of the donor population (d) takes the form

$$\mathbf{A}_{\mathrm{d}} = \begin{pmatrix} 0 & 0 & 0 & F_4 & F_5 \\ G_1 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{pmatrix}$$

where F_i is the fecundity of stage i, G_i is the probability of surviving and transitioning to stage $i + 1$, and P_i is the probability of surviving and staying in stage i. Small adult fecundity (F_4) is calculated as

$$F_4 = m_4 \times sexr \times B_4 \times (G_4 + P_4)$$

and large adult fecundity (F_5) is calculated as

$$F_5 = m_5 \times sexr \times B_5 \times P_5$$

where m_i is the number of eggs produced by a female in stage i, *sexr* is the sex ratio of the adult population, and B_i is the probability of a female in stage i spawning. We chose to incorporate sex ratio in the population models rather than build a female-only matrix model (Caswell 2001) to evaluate the uncertainty associated with sex ratio of a reintroduction program. We incorporated density dependence in survival at the juvenile stage (G_1) of the population as

$$G_1 = egg.max.s \times \left(1 - \exp\left[\frac{-juvi.CC}{egg.max.s \times N.juvi}\right]\right)$$

where *egg.max.s* is the maximum embryo survival rate at low densities, *juvi.CC* is the juvenile carrying capacity, and *N.juvi* is the number of juveniles in the population (Lee and Rieman 1997).

Animals released into new environments, captive or natural, take time to acclimate and individuals that fail to do so may exhibit reduced survival (Dickens et al. 2010). Therefore, the transition matrix for the captive population consisted of 10 life stages: a naive (n) component of five life stages that transition into the experienced (e) component of the population. Animals that are collected and transferred into captivity remained in the naive group for one timestep before transitioning into the experienced group. The transition matrix of the captive population (c) takes the form

$$\mathbf{A}_c = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & nF_4 & nF_5 & 0 & 0 & 0 & eF_4 & eF_5 \\ nG_1 & 0 & 0 & 0 & 0 & eG_1 & 0 & 0 & 0 & 0 \\ nR_1 & nG_2 & nP_3 & 0 & 0 & eR_1 & eG_2 & eP_3 & 0 & 0 \\ 0 & 0 & nG_3 & nP_4 & 0 & 0 & 0 & eG_3 & eP_4 & 0 \\ 0 & 0 & 0 & nG_4 & nP_5 & 0 & 0 & 0 & eG_4 & eP_5 \end{pmatrix}$$

where stage-based fecundity (F_i), growth (G_i), and survival probabilities (P_i) are as described for the donor population. However, each parameter in the naive component (n) of the population matrix was multiplied by an additional variable to account for the reduced survival of a naive individual (*naive*). For example, if the probability of survival for an experienced fish is 0.80 and *naive* is 0.50, then the probability of survival for a naive fish is equal to 0.80 × 0.50, or 0.40. In addition, we added a rapid growth parameter (R_1) that represents the probability that an embryo may survive and advance to the subadult life stage when provided a controlled captive environment and consistent feed availability (Fredenberg et al. 1995; Fredenberg 1998). We assumed that space and resources in captivity were not limiting and therefore density dependence would not affect the captive population.

The transition matrix of the recipient population (r) was similar to that of the captive population in that we included a naive (n) and experienced (e) component. The transition matrix takes the form

$$\mathbf{A}_r = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & nF_4 & nF_5 & 0 & 0 & 0 & eF_4 & eF_5 \\ nG_1 & 0 & 0 & 0 & 0 & eG_1 & 0 & 0 & 0 & 0 \\ 0 & nG_2 & nP_3 & 0 & 0 & 0 & eG_2 & eP_3 & 0 & 0 \\ 0 & 0 & nG_3 & nP_4 & 0 & 0 & 0 & eG_3 & eP_4 & 0 \\ 0 & 0 & 0 & nG_4 & nP_5 & 0 & 0 & 0 & eG_4 & eP_5 \end{pmatrix}$$

where stage-based fecundity (F_i), growth (G_i), survival probabilities (P_i), and reduced survival for naive individuals (*naive*) are as described for the donor and captive populations. We again accounted for density dependence using the equation from Lee and Rieman (1997) with the carrying capacity (*juvi.CC*) and maximum embryo survival (*egg.max.s*) parameters that are specific to the recipient population and where the *N.juvi* parameter was equal to the summation of juvenile individuals in both the naive and experienced components of the population. In addition to applying a survival reduction for a fish's naivety, we also applied a survival reduction at the first timestep depending on which reintroduction strategy was used. This reduction represented the negative effects of handing and captivity and we assumed that survival of a translocated fish (*trans.reduc*) would be greater than that of a captive-reared (*cap.reduc*) fish, which would be greater than that of an artificially produced fish (*artprod.reduc*).

Until recently, a comprehensive set of demographic parameters for all bull trout life stages was unavailable. To fill this data gap, Schaller et al. (2014) estimated survival rates for a bull trout metapopulation using 10 years of mark–recapture data. We used similar values to parameterize the Leslie matrixes (Table 3). Estimates of the survival reduction for naive fish and reintroduction strategy reduction do not exist. As such, we set the survival reduction for naive fish at 0.50 with the understanding that the variable would range from 0.10 to 0.99 during sensitivity analysis, which would provide a better understanding of the effect of this variable on the decision outcome. After conversations with biologists working with bull trout, we assumed that handling stress during capture, transport, and release would result in delayed mortality and reduce the survival of translocated fish by 0.70. In addition to the effect of capture, transport, and release, we assumed that the deleterious effect of captivity would result in a reduced survival of captive-reared fish by 0.30. We applied a survival reduction of 0.20 to artificially produced fish due to the combined effects of capture, transport, release, captivity, and artificial spawning practices that lack natural mate selection processes (Table 3).

Table 3. Lower-level vital rates of populations used in Leslie projection matrices and in sensitivity analyses for the bull trout (*Salvelinus confluentus*) reintroduction decision model.

Population	Parameter	Value	CV	Minimum	Maximum
All	m_4	1 250	0.5	427	2 423
	m_5	2 500	0.5	854	4 846
	B_4	0.45	0.3	0.23	0.68
	B_5	0.9	0.1	0.72	0.99
	sexr	0.5	0.3	0.25	0.75
Donor (d)	*juvi.CC*	15 000	0.5	5124	29 076
	egg.max.s	0.3	0.5	0.08	0.57
	G_2	0.12	0.5	0.04	0.23
	G_3	0.15	0.5	0.05	0.29
	G_4	0.15	0.5	0.05	0.33
	P_3	0.05	0.5	0.02	0.10
	P_4	0.1	0.5	0.03	0.19
	P_5	0.35	0.5	0.09	0.66
Captive (c)	G_1	0.4	0.5	0.10	0.75
	G_2	0.4	0.5	0.10	0.75
	G_3	0.2	0.5	0.06	0.39
	G_4	0.15	0.5	0.05	0.29
	P_3	0.2	0.5	0.06	0.39
	P_4	0.5	0.5	0.10	0.90
	P_5	0.75	0.5	0.00	1.00
	R_1	0.1	0.5	0.03	0.19
	naive	0.5	0.7	0.01	0.99
Recipient (r)	*juvi.CC*	15 000	0.5	5124	29 076
	egg.max.s	0.3	0.5	0.08	0.57
	G_2	0.12	0.5	0.05	0.29
	G_3	0.15	0.5	0.06	0.39
	G_4	0.15	0.5	0.06	0.39
	P_3	0.05	0.5	0.03	0.19
	P_4	0.1	0.5	0.05	0.29
	P_5	0.35	0.5	0.10	0.83
	naive	0.5	0.7	0.01	0.99
	trans.reduc	0.7	0.5	0.45	0.90
	cap.reduc	0.3	0.5	0.21	0.40
	artprod.reduc	0.2	0.5	0.14	0.27

Note: m_i, number of eggs per female at stage i; B_i, proportion of females spawning; *sexr*, sex ratio; *juvi.CC*, juvenile carrying capacity; *egg.max.s*, maximum egg survival; G_i, probability of surviving and growing from stage i to i + 1; P_i, probability of surviving and persisting in stage i; R_1, probability of growth from embryo to subadult in captive population; *naïve*, reduction in survival during the first year in captivity or after release; *trans.reduc*, reduction in survival of translocated fish; *cap.reduc*, reduction in survival of captive-reared fish; *artprod.reduc*, reduction in survival of artificially produced fish. The mean value was varied by a coefficient of variation (CV) to determine the minimum and maximum range of that value for sensitivity analyses.

Table 4. Bull trout (*Salvelinus confluentus*) abundances by life stage used to create every possible combination of donor and recipient populations that may be observed at the beginning of a decision timestep in real-world reintroduction scenarios.

Embryos	Juveniles	Subadults	Small adults	Large adults
0	0	0	0	0
3 409	449	118	19	5
6 136	809	212	35	9
6 817	899	236	39	10
9 544	1258	330	54	14
12 271	1618	424	70	18
13 635	1797	471	78	20
19 771	2606	683	113	29
25 224	3325	872	144	37
27 951	3684	966	159	41
33 405	4403	1154	190	49
38 859	5122	1343	221	57
41 586	5482	1437	237	61
54 539	7189	1884	311	80
66 811	8807	2308	380	98
69 538	9166	2403	396	102
87 263	11 502	3015	497	128
104 988	13 839	3627	598	154
111 806	14 737	3863	637	164
118 623	15 636	4099	676	174
125 440	16 535	4334	714	184
139 757	18 422	4829	796	205
174 526	23 005	6030	994	256
209 295	27 588	7231	1192	307

Note: This resulted in 576 potential combinations of donor and recipient populations. These numbers were calculated with large adult abundance ranging from 0 to 307 individuals. The stable age distribution from the donor transition matrix was used to determine the abundance of all younger life stages, with 1499 adults in the largest population.

Decision model sensitivity analysis

Before determining the optimal decision, we evaluated the characteristics of the decision model with sensitivity analyses, response profiles, and indifference curves (Clemen 1996; Conroy and Peterson 2013). These analyses were used to identify model parameters that have the greatest effect on the value of the decision and the resulting decision alternative as well as ensure that the model is functioning as expected. One-way sensitivity analysis was conducted by holding all model parameters, including starting donor population abundance, at a mean value and incrementally varying each parameter between a minimum and maximum range (Tables 3 and 4). The output of the one-way sensitivity analysis was used to create a tornado diagram of all parameters (Fig. 1) and indifference curves for each parameter (Fig. 2). To evaluate interactions between parameters, we conducted a two-way sensitivity analysis in which two model parameters were varied simultaneously while the others were kept at mean values. We then created contour plots of the expected outcome and response profiles of the identity of the optimal decision (Fig. 2) (Conroy and Peterson 2013). We ran 1000 simulations for all sensitivity analyses and used the mean utility value.

Optimal state-based decisions

The goal of optimization is to identify the decision alternative that maximizes or minimizes the outcome as quantified by the utility. We applied stochastic dynamic programing (SDP) to determine the optimal management decision (Lubow 1996; Rout et al. 2009; Chadès et al. 2014) across a combination of donor and reintroduced population states. SDP is used to solve Markov decision problems and uses backward induction to identify the best decision under uncertainty by maximizing the sum of future expected rewards, in this case recipient adult abundance. This technique is appropriate for management decisions that are confounded with uncertainty and stochasticity and consist of a finite set of potential states where sequential decisions are being made (Bellman 1957; Rout et al. 2009). SDP has been applied to maximize harvest of ducks (Anderson 1975) and sandhill cranes (Gerber 2015), exploitation of fisheries (Walters 1975; Walters and Hilborn 1976), and to optimize the translocation of threatened species (Lubow 1996; Rout et al. 2009).

We generated 24 starting populations of bull trout with large adult abundances ranging from 0 to 307 individuals. The stable age distribution from the donor transition matrix was used to determine the abundance of all younger life stages. This resulted in a maximum of 1499 mature adults (small and large adults) in the largest starting population (Table 4). Using these populations as starting abundances for the donor and recipient populations, we created every possible combination of populations that may be observed in real world reintroduction scenarios, resulting in 576 (24 × 24) potential starting population sizes. These populations were replicated 100 times to account for demographic stochasticity during the optimization. For each of these starting populations, the utility and ending population size of the donor and recipient populations were calculated for all six reintroduction decisions using the mean parameter values (Table 3). We conducted 10 000 simulations of this process and the utility and ending populations used to create a transition probability matrix for each decision that describes the probability of transitioning from a starting population state to an ending population state and the associated return (i.e., the decision outcome or utility). The transition probability tables and return values were put in the Markov decision process policy iteration algorithm implemented in R package *MDPtoolbox* (Chadès et al. 2014) with a discount factor of 0.9999. The algorithm uses backward induction and outputs a table of state dependent management policies for all possible starting donor or recipient population states. The adult populations were discretized into five abundance states: 0–50, 50–100, 100–250, 250–500, and greater than 500 individuals (Table 5).

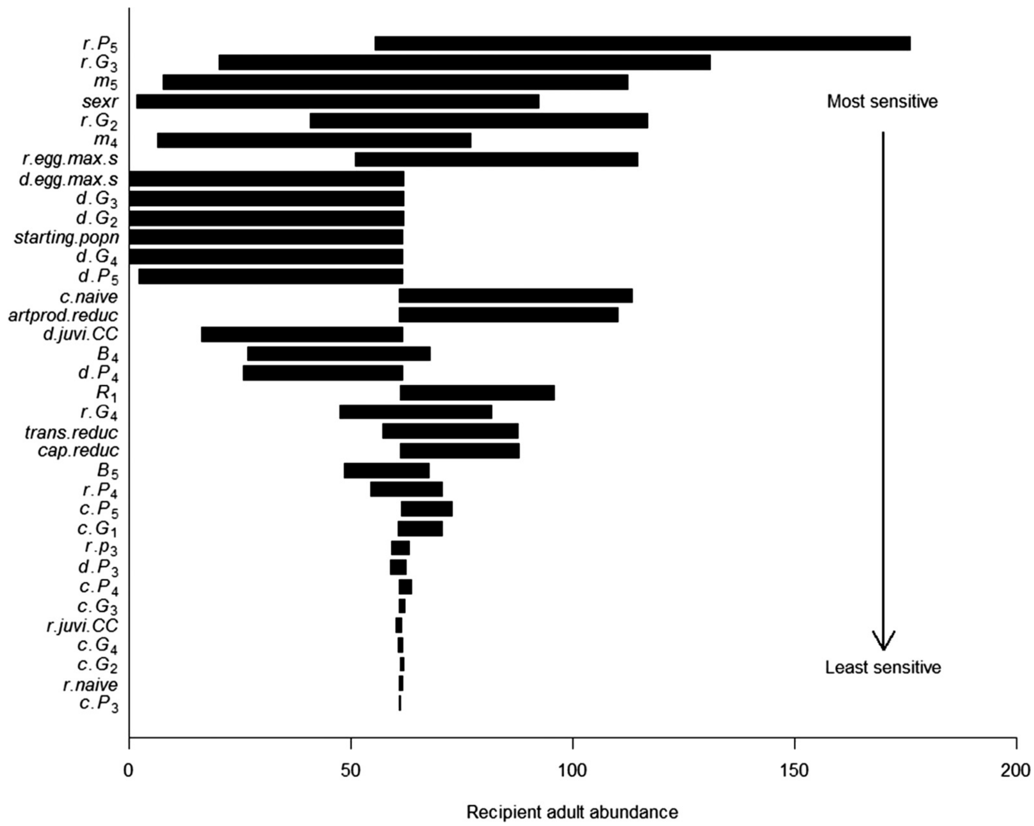
Leslie matrix sensitivity and elasticity

We considered the implications of demography with sensitivity and elasticity analyses of the population growth rate (λ) to changes in transition matrix elements (Caswell 2001; Wilson 2003) for the donor, recipient, and captive populations. Sensitivity and elasticity estimates were calculated with the *vitalsens* function in the popbio package in R, which calculates sensitivities and elasticities of λ to lower-level vital rates (e.g., *sexr*, B_i, m_i, *d.juvi.CC*; Stubben and Milligan 2007). All parameters were set at mean values (Table 3) for these analyses and juvenile abundance (*N.juvi*) was set at 15 000 individuals to determine the sensitivity and elasticity of lower-level vital rates contained in the density-dependent equation (i.e., *egg.max.s*, *juvi.CC*) of G_1 for the donor and recipient populations.

Management scenarios

A viable population is one that has a low probability of going extinct within a specific timeframe (i.e., quasi-extinction probability; Morris and Doak 2002). To better understand the viability of populations after a management action, we used forward simulation to compare quasi-extinction probabilities of the donor and recipient populations under seven different management scenarios. Six of the scenarios consisted of simulating each reintroduction decision in the set (Table 2) for one decision timestep (i.e., 7 years) and using forward simulation to estimate the donor and recipient population abundances after 50 years (i.e., one-and-done scenario). The final scenario consisted of using the optimal state-dependent policy (Table 5) to simulate recurring reintroduction decisions over a 50 year time period (i.e., the SDP scenario). With this scenario, current adult abundances of the donor and recipi-

Fig. 1. Tornado diagram from one-way sensitivity analysis with decision model parameters listed from most influential (top) to least influential (bottom) for a bull trout (*Salvelinus confluentus*) reintroduction decision. Donor (*d*), captive (*c*), and recipient (*r*) population-specific parameters are represented by a prefix and parameter definitions are listed in the text and Table 2. The *x*-axis represents the number of adults in the recipient population after one timestep.



ent populations are estimated via monitoring, and the state-dependent policy (Table 5) identifies the optimal management decision to be implemented for the next timestep (i.e., 7 years). Once a timestep is complete, the state-dependent policy informs the subsequent management action, and so on for a total of 50 years, or seven consecutive management decisions.

All scenarios were run with four starting adult abundance states for the donor population: 100, 150, 300, and 500 adults. Similarly, we also ran all scenarios with an annual disturbance probability of 0.05 to evaluate the resiliency of the populations under environmental stochasticity. If a disturbance did occur, the population abundance of each life stage was reduced by 25%. Populations were simulated 1000 times for each decision, starting donor population state, and with and without environmental stochasticity, and the mean adult abundances were plotted (see Figs. 4 and 5) and used to determine the quasi-extinction probability of the average population. Quasi-extinction probabilities were determined with the count-based extinction time cumulative distribution function in R package *popbio* (Table 6) (Morris and Doak 2002; Stubben and Milligan 2007). Estimated mean population size (*mu*) and sample variance (*sig2*) were calculated from year 8 to year 50, current population size (N_c) was equal to adult population abundance at year 8, the quasi-extinction threshold (N_e) was set at 50 adults, and the latest time to calculate extinction probability (*tmax*) was equal to 50 years. Beginning the quasi-extinction estimates at year 8 allows all scenarios to complete one decision timestep.

Results

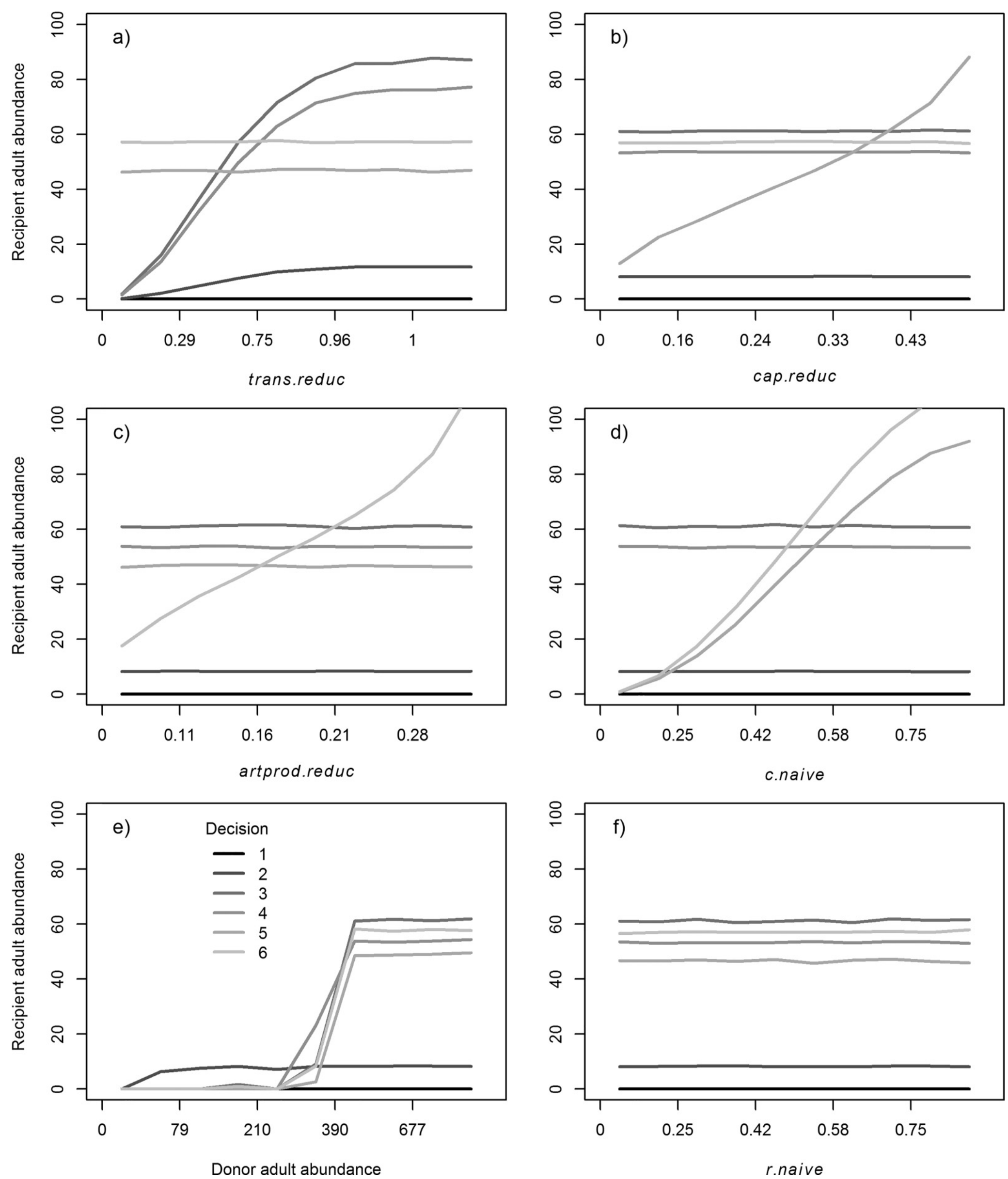
Optimal state-based decisions

The state-dependent policy included four of the six decision sets that were evaluated. All translocation decisions (alternatives 2, 3, and 4) and the do-nothing decision (alternative 1) were included in the state-dependent policy table (Table 5). Captive rearing of embryos (alternative 5) and artificial production (alternative 6) decisions were never the optimal alternative. In situations where adult abundance in the donor population was below 100 individuals or the recipient population was above 500 individuals, the optimal strategy was to do nothing (alternative 1). Any scenario where the recipient adult abundance was less than 50 individuals, like one would expect to encounter at the first timestep of a reintroduction program, the optimal decision changed four times depending on donor population abundance. When donor abundance was greater than 100 individuals, the optimal decision shifted from doing nothing (alternative 1) to translocating 1000 juveniles (alternative 2), and between 300 and 500 donor adults, the optimal decision shifted to translocation of all life stages (alternative 4). When the donor population was large (i.e., greater than 500 adults), translocating adults only (alternative 3) became the optimal decision. As a reintroduction program continues, the decisions prescribed in the policy table reflect the value in continued supplementation of the recipient population to reduce extirpation risks while balancing the risk of crashing the donor population. This trade-off process continued until the recipient population was above 300 individuals at which point the marginal gain of additional adults was negligible, as defined by the structure of the utility function, resulting in the optimal decision of doing nothing.

Decision model sensitivity analysis

The tornado diagram created from the one-way sensitivity analysis (Fig. 1) suggested that the decision outcome was most influenced by survival parameters that resulted in increased adult

Fig. 2. Response profiles of adult bull trout (*Salvelinus confluentus*) abundance in the recipient population to varying levels of (*a*) the effect of translocation on post-release survival (*trans.reduc*), (*b*) the effect of captive-rearing on post-release survival (*cap.reduc*), (*c*) the effect of artificial production on post-release survival (*artprod.reduc*), (*d*) the effect of naivety to survival in the captive population (*c.naive*), (*e*) the adult abundance of the donor population at the beginning of the decision timestep, and (*f*) the effect of naivety to survival in the recipient population (*r.naive*).



abundance in the recipient population ($r.P_5$, $r.G_2$, $r.G_3$) and maximum egg survival in the donor and recipient populations (*d.egg.max.s*, *r.egg.max.s*). The decision outcome was also sensitive to small and large adult fecundity rates and sex ratio (m_i, *sexr*). The outcome was least sensitive to survival parameters associated with the captive population ($c.P_3$, $c.P_4$, $c.G_2$, $c.G_3$, $c.G_4$), the survival reduction of naive reintroduced individuals (*r.naive*), and juvenile carrying capacity of the reintroduced population (*r.juvi.CC*).

The response profiles from the one-way sensitivity analysis showed that the optimal decision changed as a function of the strategy-specific survival reduction (Figs. 2*a*, 2*b*, and 2*c*). For example, if a translocated fish survived at 60% or less than a nontranslocated fish, then the optimal decision was artificial production (alternative 6), whereas above a 60% survival reduction, the optimal decision was to translocate adults only (alternative 3). When the survival reduction for the translocation strategy (*trans.reduc*) was at 60%, the decision maker would be indifferent to artificial production or adult translocation because either option was expected to produce the same outcome (Fig. 2*a*). Similarly, the optimal decision was to captive-rear embryos (alternative 5) when the captive-rearing survival reduction (*cap.reduc*) was above 40% (Fig. 2*b*), and artificial production (alternative 6) was the optimal decision when the survival reduction for artificial production (*artprod.reduc*) was greater than 20% (Fig. 2*c*). The survival reduction for fish that are naive to captivity (*c.naive*) also influenced which decision was optimal. As more fish survived in captivity, more fish are available for release into the recipient habitat, thereby resulting in more recipient adults, the primary component of the decision utility. When naive captive fish survived at a rate of 50% or more than an experienced captive fish, artificial production and then captive-rearing of embryos became the optimal and second best decision, respectively (Fig. 2*d*).

Response profiles suggested that the optimal reintroduction decision changed four times as a function of the adult abundance

Table 5. State-dependent policy identifying the optimal bull trout (*Salvelinus confluentus*) reintroduction decision as a function of adult abundance (i.e., the summation of large adult and small adult abundances) in donor and recipient populations.

	Recipient abundance							
Donor abundance	<50	50–100	100–200	200–300	300–500	500–800	800–1000	>1000
<50	1	1	1	1	1	1	1	1
50–100	1	1	1	1	1	1	1	1
100–200	2	1	1	1	1	1	1	1
200–300	2	1	1	1	1	1	1	1
300–500	4	2	2	2	1	1	1	1
500–800	3	3	3	3	4	1	1	1
800–1000	3	3	3	3	3	1	1	1
>1000	3	3	3	3	3	1	1	1

Note: Alternative 1 is to do nothing, alternative 2 is to translocate 1000 juveniles, alternative 3 is to translocate 60 adults, alternative 4 is to translocate 1000 juveniles and 40 adults, and alternatives 5 and 6 are not represented. This state-dependent policy represents the optimal decision calculated from the mean value of lower-level vital rates.

Table 6. Quasi-extinction probability of donor and recipient bull trout (*Salvelinus confluentus*) populations under seven simulated management alternatives.

		Starting donor adult abundance			
Population	Decision	100	150	300	500
Donor	1	0	0	0	0
	2	0	0	0	0
	3	1	1	0	0
	4	1	1	0	0
	5	1	1	0	0
	6	1	1	0	0
	SDP	0.02	0.05	0	0
Recipient	1	1	1	1	1
	2	1	1	1	1
	3	1	1	0.01	0.04
	4	1	1	0.09	0.17
	5	1	1	1	1
	6	1	1	0.12	0.11
	SDP	1	1	1	0.08

Note: Six alternatives consisted of simulating each reintroduction decision in the decision set for one timestep and then forward simulating to estimate the donor and recipient population abundances after 50 years (i.e., one-and-done alternatives). The final alternative consisted of using the state-dependent policy (SDP) to determine recurring reintroduction decisions for a 50 year time period. Quasi-extinction probabilities are reported for four starting adult abundance states of the donor population: 100, 150, 300, and 500 adults.

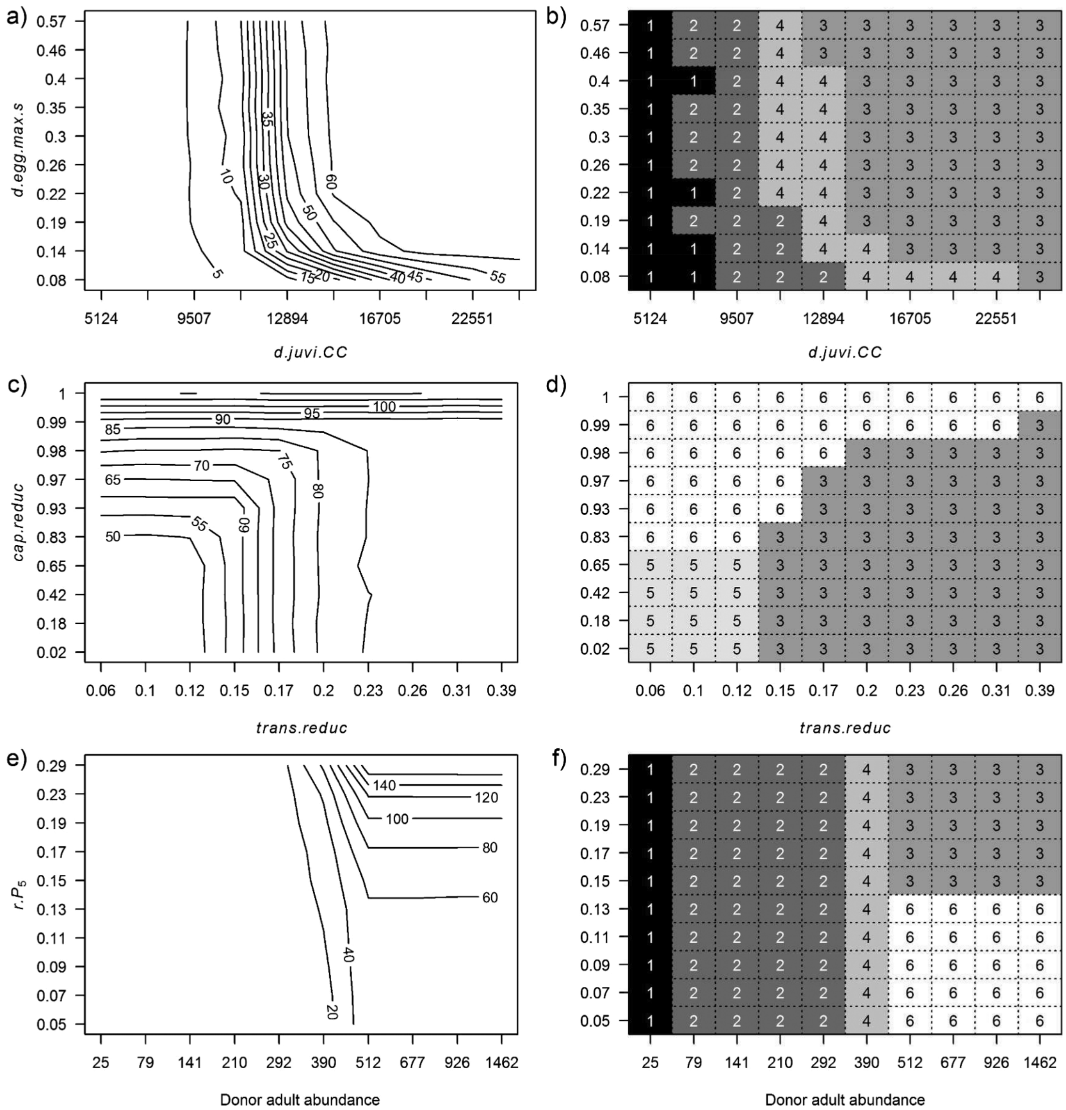
in the donor population: below 25 adults, the optimal decision was to do nothing (alternative 1), between 25 and 250 adults, the optimal decision was to translocate only juveniles (alternative 2), between 250 and 400 adults, translocating all life stages (alternative 4) was the optimal decision, and above 400 adults, translocating adults only (alternative 3) is the optimal decision (Fig. 2*e*). Understandably so, parameters that drive donor adult abundance (*d.egg.max.s*, *d.juci.CC*, *d.G$_i$*, *d.P$_i$*) exhibited very similar patterns as Fig. 2*e*. There were other parameters that when varied over their estimated range did not change the optimal decision. The optimal decision was static to changes in growth and survival of captive individuals (*c.G$_i$*, *c.P$_i$*), probability of large adults spawning (B_5), juvenile carrying capacity in the recipient population (*r.juvi.CC*), and the survival reduction of naive reintroduced fish (*r.naive*) (Fig. 2*f*).

Two-way sensitivity analysis with all combinations of model parameters resulted in more than 1000 contour and response profile plots. We present contour and response profile plots of three parameter combinations that were influential in the decision context and represent the types of results one can expect from two-way sensitivity analyses (Fig. 3). A comparison of the juvenile density-dependent parameters (*d.egg.max.s*, *d.juvi.CC*) for the donor population indicated that when above a maximum egg survival of 0.14, the juvenile carrying capacity had a greater influence on the expected value of the decision; this was indicated by the expected value of the decision changing more across the range of carrying capacity values identified by the close contour lines (Fig. 3*a*). There were four alternatives that resulted in the optimal outcome, depending on the value of the juvenile carrying capacity and maximum egg survival of the donor population (Fig. 3*b*). When juvenile carrying capacity in the donor population was less than approximately 5500 individuals, the optimal strategy was to do nothing (alternative 1), which most likely avoided an unacceptable reduction in donor population abundance, whereas translocating adults (alternative 3) was the optimal decision when both density-dependent parameters were in the upper end of the ranges that were evaluated (Fig. 3*b*) and resulted in a decision outcome of greater than 60 adults in the recipient population at the end of one decision timestep (i.e., 7 years) (Fig. 3*a*).

The survival reductions of captive-reared (*cap.reduc*) and translocated (*trans.reduc*) fish were parameters of interest given the limited information regarding the effects of captive-rearing and direct translocation of bull trout. Two-way sensitivity analysis suggested a strong interaction between these parameters when *cap.reduc* ranged from 0.83 to 0.99 and *trans.reduc* ranged from 0.13 to 0.23; this was evident in the lack of parallel contours between these ranges (Fig. 3*c*). The optimal decision was to captive-rear embryos (alternative 5) when both parameters were at the lower limits of their range, whereas the optimal decision was to translocate adults (alternative 3) when *cap.reduc* was less than 0.75 and *trans.reduc* was greater than 0.14. As *cap.reduc* nears 1.00, which indicated little to no effects of captivity on a fish's survival after release, artificial production (alternative 6) was the optimal decision regardless of the value of *trans.reduc* (Fig. 3*d*).

The final combination of variables presented for the two-way sensitivity analysis is survival of large adults in the recipient population (*r.P$_5$*) and adult abundance in the donor population. One-way sensitivity analyses suggested that the decision outcome (i.e., utility) (Fig. 1) and the decision identity (Fig. 2*e*) were sensitive to these variables, and collectively, these parameters are major components of the model in that the utility was a function of recipient and donor adult abundances. When *r.P$_5$* was below 0.14, the parameter had little influence on the value (Fig. 3*e*) or identity (Fig. 3*f*) of the decision. When adults in the donor population were less than 450 individuals, the value of the decision, regardless of the optimal strategy, resulted in 40 or less adults in the recipient population. Doing nothing (alternative 1) was the optimal strategy when donor adult abundance was less than 25 individuals and

Fig. 3. (*a*, *c*, and *e*) Contour plots of recipient adult bull trout (*Salvelinus confluentus*) abundance and (*b*, *d*, and *f*) response profiles of the identity of the optimal decision at varying levels of the parameters in the density-dependent equation for (*a* and *b*) the donor population (*d.egg.max.s*, *d.juvi.CC*), (*c* and *d*) the effect of captivity and translocation on post-release survival (*cap.reduc*, *trans.reduc*), and (*e* and *f*) large adult survival in the recipient population ($r.P_5$) and donor adult abundance at the first decision timestep.



translocating 1000 juveniles (alternative 2) was the optimal strategy until donor adult abundance was greater than 300 individuals (Fig. 3*f*). When donor adult abundance was approximately 390 individuals, the model indicated that translocation of all life stages (alternative 4) was the optimal decision, suggesting that at this abundance level, the donor population could sustain the removal of adults without falling below a point at which the donor penalty would be applied. When donor adult abundance was above 400 and $r.P_5$ was less than 0.14, artificial production (alternative 6) produced the greatest value resulting in between 40 and 60 adults in the recipient population. However, if $r.P_5$ was greater than 0.14, the value of the decision increased at a much faster rate, indicative of the narrow spaces between contour lines on this portion of the plot. This suggests that accurate estimates of adult survival in the recipient population ($r.P_5$) are important and any conservation actions that improve $r.P_5$ could result in a more than doubling of the decision value.

Matrix model sensitivity and elasticity analysis

Setting the vital rates for the donor and recipient populations at similar levels resulted in the sensitivities and elasticities for these Leslie matrices being similar (Table 7). The sensitivity and elasticity analysis of matrix model elements suggest that small changes in G_2, G_3, G_4, P_5, *sexr*, and *egg.max.s* will have the greatest effect on λ of the donor and recipient populations, and small changes in G_3, G_4, R_1, and *sexr* will have the greatest effect on λ in the captive population. Surviving and persisting in the subadult life stages (P_3) had a minimal effect on λ for all populations. The juvenile carrying capacity (*juvi.CC*) and number of juveniles (*N.juvi*) in the density dependence equation had a minimal effect on λ of the donor and recipient populations, with an increase in *N.juvi* resulting in a reduction in λ. Nether the survival reduction of naive individuals (*naive*) nor the survival reduction associated with a reintroduction strategy (*strat.reduc*) had any effect on λ.

Management scenarios

The simulation of management scenarios suggests that regardless of the starting adult abundance in the donor population, the state-dependent policy (SDP) scenario is better at balancing the risk to the donor population and the benefit to the recipient population. This is evident in that under the SDP scenario, the adult donor population never drops below the quasi-extinction thresh-

Table 7. Estimates of sensitivity and elasticity of lower-level vital rates used to populate the Leslie matrices representing the donor, captive, and recipient populations in the bull trout (*Salvelinus confluentus*) reintroduction decision model.

	Sensitivity			Elasticity		
Parameter	Donor	Captive	Recipient	Donor	Captive	Recipient
G_1	—	—	0.506	—	—	0.120
G_2	1.649	1.649	0.506	0.199	0.199	0.120
G_3	1.319	1.319	2.085	0.199	0.199	0.246
G_4	1.090	1.090	2.096	0.164	0.164	0.186
P_3	0.209	0.209	0.254	0.010	0.010	0.007
P_4	0.565	0.565	1.288	0.057	0.057	0.076
P_5	0.492	0.492	0.577	0.173	0.173	0.119
R_1	—	—	2.145	—	—	0.127
m_4	0	0	0	0.086	0.086	0.151
m_5	0	0	0	0.112	0.112	0.095
B_4	0.191	0.191	0.570	0.086	0.086	0.151
B_5	0.124	0.124	0.178	0.112	0.112	0.095
sexr	0.396	0.396	0.834	0.199	0.199	0.246
egg.max.s	0.578	0.578	—	0.174	0.174	—
juvi.CC	0	0	—	0.024	0.024	—
N.juvi	0	0	—	−0.024	−0.024	—
naive	—	0	0	—	0	0
strat.reduc	—	0	—	—	0	—

Note: Parameters that were not included in a matrix model for a particular population are represented with a dash. G_i, probability of surviving and growing from stage i to i + 1; P_i, probability of surviving and persisting in stage i to i + 1; R_1, probability of rapid growth from embryo to subadult stage in a captive population; m_i, number of eggs per female at stage i; B_i, proportion of females spawning; *sexr*, sex ratio; *egg.max.s*, maximum egg survival; *juvi.CC*, juvenile carrying capacity; *N.juvi*, number of juveniles in the population; *naive*, reduction in survival during the first year in captivity or after release; *strat.reduc*, reduction in survival that represents the reintroduction strategy.

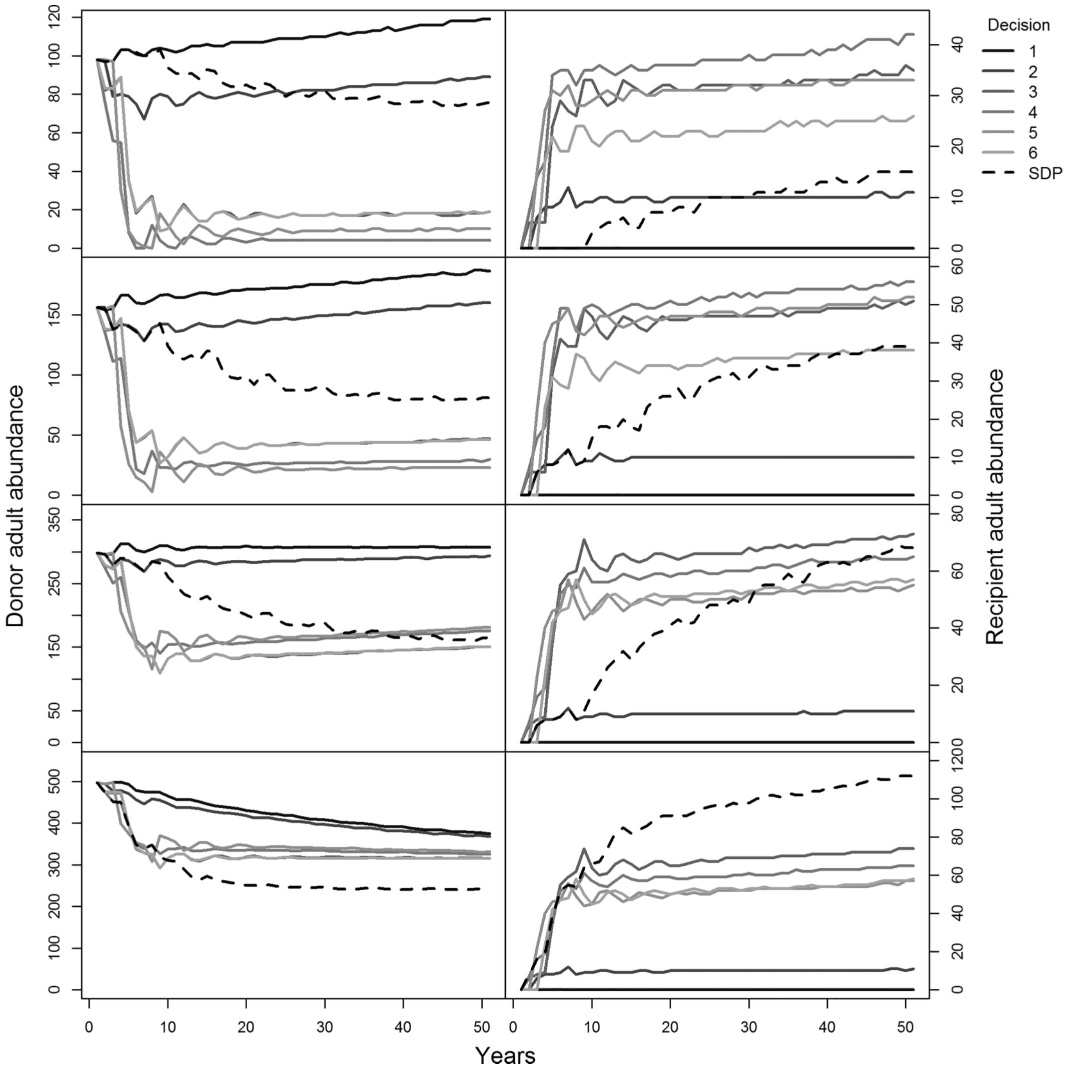
old (N_e) of 50 individuals (Fig. 4) and the probability of quasi-extinction is less than 0.05, regardless of the starting donor adult abundance (Table 6). Similar results are seen with the one-and-done scenario of decisions 1 and 2, but these decisions fail to generate a recipient population of adults as large as or greater than the SDP scenario. Each of these three scenarios fail to generate a recipient population with a quasi-extinction probability of less than 1.00, with the exception of the SDP scenario and a large starting donor population of 500 individuals, which has a quasi-extinction probability of 0.08 (Table 6). The one-and-done scenario with decisions 3 through 6 consistently produce recipient populations as large as or larger than the SDP scenario. However, these one-and-done scenarios also result in quasi-extinction of the donor population when the adult donor population is small (Fig. 4; Table 6). When simulating a 5% chance of environmental stochasticity that reduced the population abundance by 25%, all management scenarios resulted in quasi-extinction of the donor and recipient population. However, despite the pending quasi-extinction after 50 years, the SDP scenario continues to balance the risk to the donor population while attempting to create a recipient population (Fig. 5).

Discussion

Structured decision making is a process that links alternative management actions to quantifiable objectives through predictive models (Conroy and Peterson 2013). We have presented an example of how the structured decision making process can be used to evaluate the trade-offs of alternative reintroduction decisions with the objective of maximizing the number of adults in the recipient population without reducing the donor population to an unacceptable level. The structure and inputs of this model are intended to be flexible and can be adjusted to suit the reintroduction strategy, numbers of animals for removal, and population-specific vital rates for any bull trout donor population or suitable recipient habitat throughout the historical range of the species. As the outcomes of ongoing and future reintroductions are realized through effective monitoring programs, the structural and demographic uncertainty of the model can be reduced, resulting in a better understanding of system dynamics (i.e., learning). The process of incorporating new information into subsequent decisions is adaptive management, which is a special case of structured decision making (Williams et al. 2009; Conroy and Peterson 2013).

Monitoring may consist of a combination of state variables (e.g., population abundance, patch occupancy) and vital rates (e.g., fecundity, survival, emigration). State variables describe the health and status of the system and are necessary when using a state-dependent policy to guide management decisions. Vital rates describe the parameter rates that result in changes to the state variables (Nichols and Armstrong 2012) and monitoring of vital rates is necessary for the learning component of adaptive resource management. Even though demography is difficult and expensive to collect, it should not be ignored (Caswell 2001). The only comprehensive set of vital rates that we found for all bull trout life stages was provided by Schaller et al. (2014). These estimates provided helpful starting values for the model although model parameters can be updated as monitoring informs future reintroductions. The bull trout decision model consisted of 34 demographic parameters making up three discrete populations (i.e., donor, captive, and recipient) and it is unlikely that resources would be available to monitor all demographic rates for each population. The results of the decision model sensitivity analysis suggest that additional resources available for monitoring the reintroduction effort are best focused on survival and growth parameters of the adult component in the recipient population. This will provide the greatest benefit in reducing uncertainty and better estimating the effect of these parameters on the decision outcome (Williams et al. 2009; Conroy and Peterson 2013). Monitoring the state of the donor and recipient populations ensures that they are not reduced to an undesirable state, is necessary if recurrent decisions are to be made, and if managers intend to identify the optimal decision given the state-dependent policy (Table 5). Also, monitoring of vital rates and state variables is implicit in fish culture

Fig. 4. Bull trout (*Salvelinus confluentus*) population projections of the mean donor and recipient populations under seven simulated management alternatives. Six alternatives consisted of simulating each reintroduction decision in the set for one decision timestep and then forward simulating to estimate the donor and recipient population abundances after 50 years (i.e., one-and-done alternatives). The final alternative consisted of using the state-dependent policy (SDP) to determine recurring reintroduction decisions for a 50 year time period. Projections are presented for four starting adult abundance states of the donor population, from top to bottom: 100, 150, 300, and 500 adults.



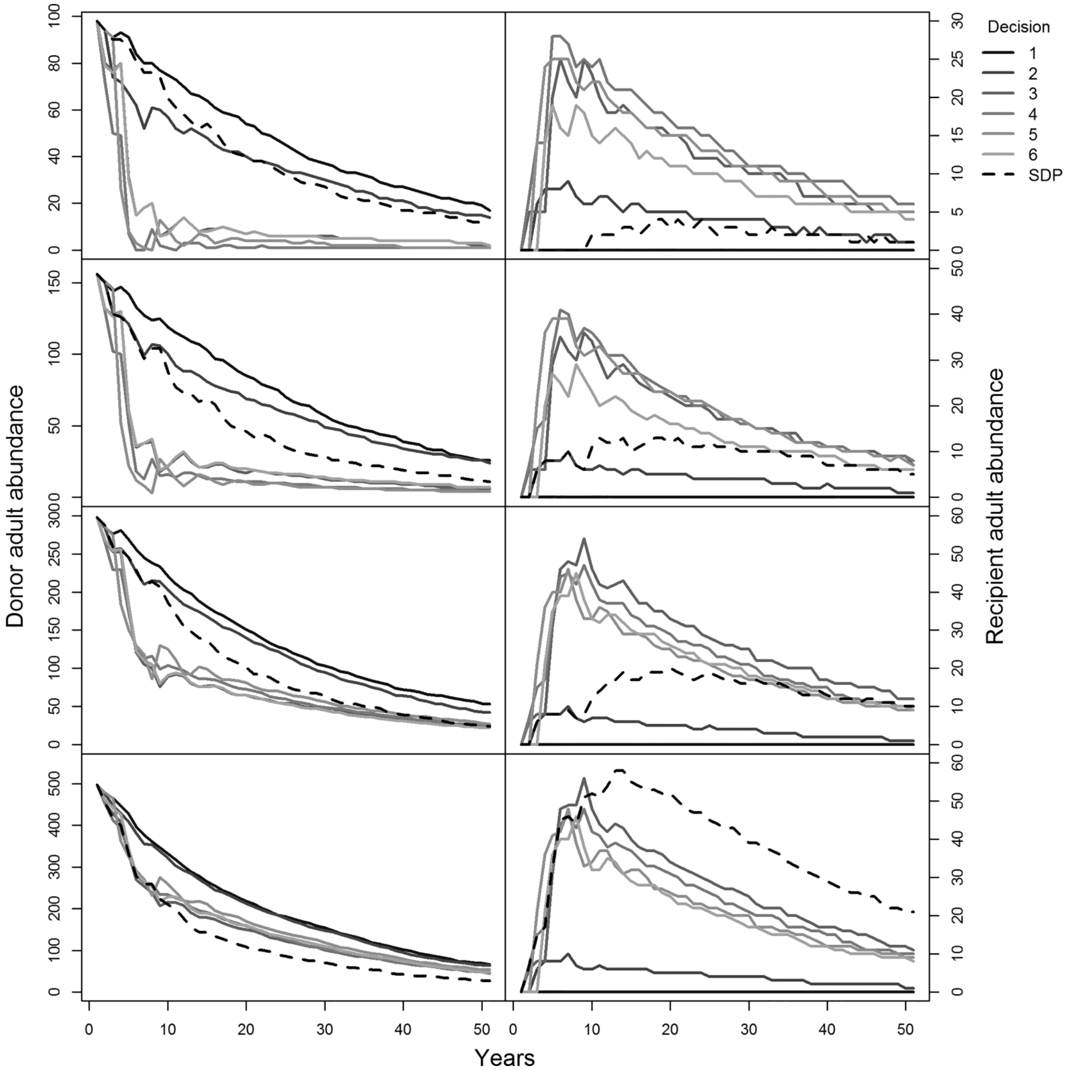
programs with fish size, mortality, behavior, and population size being documented as a part of basic animal husbandry.

Parameters of the captive population (i.e., *c.P3*, *c.P4*, *c.G2*, *c.G3*, *c.G4*), survival reduction of naive reintroduced individuals (*r.naive*), and juvenile carrying capacity of the reintroduced population (*r.juvi.CC*) were identified by the one-way sensitivity analysis as having had the least influence on the decision outcome. This can be explained in that these parameters do not directly affect abundances in the recipient or donor population, the influential components of the utility function. These parameters are only one component of an equation, combined with other lower-level vital rates (e.g., *cap.reduc*, *c.naive*, B_i, *sexr*, m_i, *egg.max.s*, *N.juvi*), that was used to calculate stage-specific matrix elements. While one-way sensitivity analysis indicated that these parameters have little influence on the decision outcome, two-way sensitivity analysis suggests that the influence of these parameters is contingent on level of other lower-level vital rates (e.g., *cap.reduc*, *c.naive*, B_i, *sexr*, m_i, *egg.max.s*, *N.juvi*) used to calculate the stage-specific matrix elements.

There are few examples of bull trout being reared or artificially spawned in captivity and survival of animals in these programs is highly variable, resulting in uncertainty. Survival and productivity in captivity will be a function of rearing temperature, life stage, nutrition, disease, and probability of successful fertilization (Fredenberg et al. 1995; Fredenberg 1998; N. Zymonas, Oregon Department of Fish and Wildlife, personal communication, 2015). This uncertainty is compounded by the unknown survival of artificially produced, captive-reared, and translocated bull trout upon release into the recipient habitat. We examined these uncertainties by applying a reduction in survival as a function of the reintroduction strategy (i.e., *trans.reduc*, *cap.reduc*, *artprod.reduc*) and naivety (Table 3). The response profiles and two-way sensitivity analysis suggest that the optimal decision is sensitive to these parameters and future bull trout reintroduction programs would benefit from a better understanding of the effects of reintroduction strategy and the concept of naivety on the survival of animals at release (McCarthy et al. 2012) and ultimately the utility and identity of optimal reintroduction decisions.

We evaluated six alternative management actions or decisions that could be taken to reintroduce bull trout. These decisions reflect past and ongoing reintroduction decisions (Buchanan et al. 1997; Soorae 2011; USFWS and ODFW 2011). Because a reintroduc-

Fig. 5. Bull trout (*Salvelinus confluentus*) population projections of the mean donor and recipient populations under seven simulated management alternatives and with environmental stochasticity. Six alternatives consisted of simulating each reintroduction decision in the set for one decision timestep and then forward simulating to estimate the donor and recipient population abundances after 50 years (i.e., one-and-done alternatives). The final alternative consisted of using the state-dependent policy (SDP) to determine recurring reintroduction decisions for a 50 year time period. Projections are presented for four starting adult abundance states of the donor population, from top to bottom: 100, 150, 300, and 500 adults. The effect of environmental stochasticity was included with a 0.05 probability of a disturbance occurring in any year. If a disturbance did occur, the population abundance of each life stage was reduced by 25%.



tion decision is a combination of a reintroduction strategy, life stage(s), and number of animals, there are endless combinations of alternative decisions that can be evaluated. The model was developed to be flexible and the inputs for life stage and numbers of animals to be removed can easily be adjusted to evaluate the trade-offs of alternative translocation, captive-rearing, or artificial production decisions for site- and population-specific reintroduction scenarios. The risk of incorporating flexibility in the model is that determining the optimal decision could become an exercise in "dredging" or "fishing" until the desired result is reached. Ideally, the decision set will be developed with stakeholder input and represent what is feasible and reasonable from a biological, logistic, and financial point of view.

Optimization techniques require multiple objectives to be combined into one value with an objective or utility function; however, the relative weights or values of each attribute may differ between stakeholders. It is likely in reintroduction decisions that donor populations and recipient habitats are managed by different stakeholder groups. Some groups may be more risk adverse where other groups are more liberal regarding risk. In these situations, the penalty for reducing the donor population (Table 1) is a composite of the risk aversion of the stakeholder group. Incorporating stakeholder input in identifying the fundamental objectives improves buy-in with the decision process and helps transparently convey how and why decisions are made.

A state-dependent policy (Table 5) is a useful tool for reintroduction programs. A reintroduction program is only considered a reintroduction in the first timestep of the decision when abundance in the recipient population is zero. Managers and decision makers can use the state-dependent policy to identify the optimal decision at subsequent timesteps given the current state of the donor and recipient populations. Ideally, a reintroduction program would accomplish its goals after one timestep; however, this is an unlikely outcome. Forward simulating a reintroduced population using one-and-done management scenarios suggested that, in the best case, the recipient population would consist of less than 80 adults after 50 years in the absence of environmental stochasticity (Fig. 4), whereas simulation of a reintroduction with the state-dependent policy resulted in more than 100 adults after 50 years. This is a function of selecting the optimal decision given the current state of the donor and recipient populations that balanced the risk to the donor population and the benefit to the recipient population. In doing so, the quasi-extinction probability of the donor and recipient populations is minimized while allowing for some level of reintroduction to occur (Table 6). The effective population size of bull trout to minimize inbreeding depression is 50 adults and more than 500 adults are needed to maintain adaptive genetic variation (Rieman and Allendorf 2001). Also, the goal of the ongoing Clackamas River reintroduction is to reestablish a viable population of 300–500 adults within 20 years (USFWS and ODFW 2011). Collectively, this suggests that any reintroduction program for bull trout will require more than one decision timestep to avoid the genetic effects of small population sizes and to build a viable population that is resistant to demographic and environmental stochasticity.

Before beginning a reintroduction, a feasibility assessment should be completed to determine the suitability of recipient habitat and donor populations (Dunham et al. 2011). Components of a habitat assessment may explore historical occupancy, current species presence, availability of spawning and rearing areas, mitigation of past, present, and future threats, and the likelihood of natural recolonization. In terms of the donor population, an assessment may consider the potential for an evolutionary match to the recipient habitat and strength of the donor population to withstand removal of individuals (see Dunham et al. (2011) for example applied to bull trout). In our model we assumed that suitable recipient habitat was identified and we considered the impact to the donor population via a penalty applied to the decision utility when the donor population was reduced below an unacceptable level. Two forms of uncertainty that are prevalent in natural resource decisions are partial observability and partial controllability. Partial observability is uncertainty associated with the ability to perfectly "see" nature and can be incorporated into the decision process as statistical distributions (Conroy and Peterson 2013). For example, partial observability may influence bull trout reintroduction decisions when redd surveys are used to estimate adult abundance. Partial controllability is uncertainty in that the intended management action is not completely under control. For example, it would be more likely to collect the number of individuals intended for a reintroduction when the donor population is large. We chose not to include partial observability in the model because redd surveys typically underestimate the number of adults in a population (Al-Chokhachy et al. 2005; Muhlfeld et al. 2006), resulting in more conservative estimates of adult abundance. Also, it is difficult to include partial observability and partial controllability when using SDP to determine the optimal decision and there are no software programs that can be used to solve a partially observable Markov decision process (Conroy and Peterson 2013). As reintroductions are implemented and initial estimates of partial controllability and partial observability are generated via monitoring, consideration of these forms of uncertainty can be incorporated into the model to inform future decisions (i.e., adaptive management).

Three features must be present for the formal process of adaptive resource management to occur: (1) recurrent decisions that allow for learning to influence subsequent timesteps, (2) alternative models representing hypotheses of ecological dynamics that identify the optimal decision based on prediction of the outcome at a future state, and (3) a monitoring program that generates data describing the outcome, which is used to update subsequent decisions (i.e., learning; Williams et al. 2009; Conroy and Peterson 2013). One of the first attempts at bull trout reintroduction occurred in the McCloud River, California, and was conducted as a practice in trial and error. An artificial production program began in 1989 and over 60 adults were collected from the Klamath basin. High mortality in captivity resulted in less than 300 fingerling bull trout for the reintroduction, and after 5 years of monitoring, the reintroduction was considered a failure. There was only one release of individuals due to a reduction in abundance and distribution of the donor stock (Buchanan et al. 1997). More recent reintroductions consist of an "ad hoc" adaptive management approach. Between 1997 and 2005, more than 10 000 fry were translocated from the McKenzie River, Oregon, to the Willamette River, Oregon, resulting in less than 15 redds observed. Due to the limited success of the program, translocation of fry was discontinued and the reintroduction program has shifted to using a captive-rearing strategy since 2007. The wild fry are now reared in captivity for up to 8 months in the hope that larger fish will exhibit better survival to spawning (UWBTWG 2010; Soorae 2011). A reintroduction to the Clackamas River has been ongoing since 2011 with 5 years of releases consisting of more than 1700 juveniles, 250 subadults, and 75 adults being translocated from the Metolius River Basin, Oregon. Monitoring has identified mature adults attempting to spawn; however, natural production has yet to be documented (Barrows et al. 2016). The implementation plan for the reintroduction suggests that in 2017, the monitoring data will be reviewed and a change in life stages or release locations to more favorable scenarios may occur (USFWS and ODFW 2011). These "ad hoc" approaches to adaptive management are better than trial and error but lack predictive models that are a key component of formal adaptive management, which is a special case of structure decision making (Fischman and Ruhl 2015).

In 1995, the Director of the US Fish and Wildlife Service approved a plan to use structured decision making with adaptive resource management to guide hunting regulations of the 6–11 million mallards (*Anas platyrhynchos*) breeding in North America (Nichols et al. 2015). Similarities between the decision context for mallard harvest and bull trout reintroduction include species that inhabit multiple federal, state, and agency jurisdictions, are of interest to user groups and conservationists, and actively migrate between areas of overlapping jurisdiction. Anytime management decisions include multiple stakeholders, there can, and most often will, be disagreement about what is the optimal decision. Disagreements are typically a function of institutional inertia, the belief in process complexity, competing value systems, and hidden objectives (Conroy and Peterson 2013; Nichols et al. 2015). Over the last 20 years of using adaptive resource management to set hunting regulations, mallard populations have fluctuated near the desired abundance levels, optimal harvest opportunities have been provided, and the model has been updated and refined with new information. Maybe most important, there has been a reduction in the contention between stakeholders because they can see their belief in system dynamics incorporated in the decision process each year (Nichols et al. 2015), all characteristics of adaptive management that could benefit future bull trout reintroduction efforts.

The US Fish and Wildlife Service adopted the process of adaptive resource management to guide effective conservation actions into the future (i.e., Strategic Habitat Conservation; USFWS 2008) recognizing the success of the mallard harvest program and that natural resource decisions will become more complex as human populations grow and continue to impact animals and their habitats. Effective and efficient conservation will be promoted with a clear connection between management actions and goals and a combination of institutional memory and ongoing research. The bull trout recovery plan (USFWS 2015) represents the current understanding of abundance and distribution of the species and outlines the management goals and recovery actions to delist the species. Linking recovery plan objectives to management actions with predictive models, similar to the one presented here, will build the foundation for formal adaptive management and improved effectiveness, efficiency, and transparency of management decisions. Ongoing bull trout reintroductions and research will reduce uncertainty and new information can be incorporated into this decision model to guide future reintroduction decisions and maximize the benefit from limited resources available for bull trout recovery.

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