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Simulating demography, genetics, and spatially explicit processes to inform reintroduction of a threatened char

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Abstract. The success of species reintroductions can depend on a combination of environmental, demographic, and genetic factors. Although the importance of these factors in the success of reintroductions is well-accepted, they are typically evaluated independently, which can miss important interactions. For species that persist in metapopulations, movement through and interaction with the landscape is predicted to be a vital component of persistence. Simulation-based approaches are a promising technique for evaluating the independent and combined effects of these factors on the outcome of various reintroduction and associated management actions. We report results from a simulation study of bull trout (*Salvelinus confluentus*) reintroduction to three watersheds of the Pend Oreille River system in northeastern Washington State, USA. We used an individual-based, spatially explicit simulation model to evaluate how reintroduction strategies, life history variation, and riverscape structure (e.g., network topology) interact to influence the demographic and genetic characteristics of reintroduced bull trout populations in three watersheds. Simulation scenarios included a range of initial genetic stocks (informed by empirical bull trout genetic data), variation in migratory tendency and life history, and two landscape connectivity alternatives representing a connected network (isolation-by-distance) and a fragmented network (isolation-by-barrier, using the known existing barriers). A novel feature of these simulations was the ability to consider the interaction of both demographic and genetic (i.e., demogenetic) factors in riverscapes with implicit asymmetric movement probabilities across the barriers. We found that connectivity (presence or absence of barriers) had the largest effect on demographic and genetic outcomes over 200 yr, with a greater effect than both initial genetic diversity and life history variation. We also identified regions of the study system in which bull trout populations persisted across a wide range of demographic, life history, and environmental connectivity parameters. Finally, we found no evidence that initial neutral genetic diversity influenced genetic diversity and structure after 200 yr; instead, genetic drift due to stray rate and population isolation dominated and erased any initial differences in genetic diversity. Our results highlight the utility of spatially explicit demogenetic approaches in exploring and understanding population dynamics—and their implications for management strategies—in fresh waters.

Key words: bull trout; conservation genetics; demogenetic; freshwater fish; individual-based models; landscape genetics; metapopulation; Pend Oreille River; population genetics; riverscape; *Salvelinus confluentus*; spatially explicit individual-based model.

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INTRODUCTION

Globally, habitat modification, climate change, and invasive species require active management of ecosystems and the species they support (McCarthy and Possingham 2007). Reintroduction of locally extirpated populations is a key strategy of managers and conservation practitioners for combating species imperilment and mitigating population declines and loss (McNeeley and Mainka 2009). However, reintroduction, or repatriation, of populations and species is often costly, resource-intensive, and only occasionally successful (Morell 2008, Cochran-Biederman et al. 2014). Reintroduction failures (i.e., populations fail to establish) are often linked to managers not first addressing the underlying cause(s) of the initial population extirpation (Seddon 1999) or a limited understanding of species' biology and habitat requirements (Godefroid et al. 2011). Additionally, managers often face difficult choices regarding the suitability of donor populations and the long-term viability of both the donor and reintroduced populations of an imperiled species. Therefore, a need exists for approaches and tools to help evaluate the complex interactions between species' biology, the environment, and management actions when considering reintroductions (Jachowski et al. 2016). This is especially true for many freshwater taxa that are among the most imperiled organisms on earth (Dudgeon et al. 2006). Effects of changes in stream temperature, flow regimes, and modification to meet future human water needs are anticipated because of climate change and human population growth (Vörösmarty et al. 2010). Consequently, complex strategies to restore formerly extirpated populations, such as reintroduction, supplementation, and assisted migration, are becoming more important and necessary in the future (Strayer and Dudgeon 2010, Cochran-Biederman et al. 2014, Hayes and Banish 2017, Mcmurray and Roe 2017).

To date, threatened freshwater fishes have been reintroduced with only variable success (e.g., Cochran-Biederman et al. 2014). The importance of two factors, demography and genetic integrity, in the success of reintroductions is well-established, but these factors are traditionally evaluated independently (e.g., Fagan 2002, Jarić et al. 2010). The need to evaluate these factors in concert is further reinforced by our growing understanding of the complex interactions between demographic and genetic effects on population persistence (Mills 2007, Lowe and Allendorf 2010, Luque et al. 2012) over many generations (Seddon 1999).

Factors that influence successful reintroduction of stream fishes are complex, diverse, and often interacting, which require trade-offs that must be carefully considered (McCarthy and Possingham 2007, George et al. 2009, Helmstedt and Possingham 2017). Recent advances in simulation approaches provide a way to evaluate demogenetic responses of stream fishes to multiple interacting factors in a spatially explicit framework. The importance of considering demogenetic factors in understanding species responses (e.g., changes in genetic structure, diversity, and population trends through time) to heterogeneity within stream networks or riverscapes (Fausch et al. 2002) has been highlighted in recent reviews (e.g., Campbell Grant et al. 2007, Frank et al. 2011) and implemented in conceptual frameworks (e.g., Landguth et al. 2014). The value of simulation modeling for assessing genetic vulnerability has been emphasized in a number of recent studies (e.g., Balkenhol et al. 2009, Epperson et al. 2010). As a result, the need to integrate demographic and genetic effects in simulation models (defined herein as "demogenetic modeling"; Labonne et al. 2008, Frank et al. 2011) has become more apparent. Because individual-based simulations provide an opportunity to simultaneously consider demographic and genetic consequences in the coming decades, they provide a powerful tool for management of reintroductions in the face of epistemic uncertainty and complex resource management decisions (Balkenhol and Landguth 2011).

We report results of a spatially explicit demogenetic simulation of the reintroduction of bull trout (*Salvelinus confluentus*) into the lower Pend Oreille River, Washington, USA, and three of its tributaries using CDMetaPOP: a spatially explicit, individual-based eco-evolutionary model (Landguth et al. 2017*a*). The goal of this study was to develop a demogenetic framework within which to evaluate potential reintroduction of aquatic species. To this end, we evaluated the role of spatial, demographic, and genetic factors in the success of reintroduction of bull trout to the lower Pend Oreille River and its tributaries. Specific objectives included (1) quantify temporal trends in population size, occupancy, and age and size distributions of an introduced population of bull trout in the presence and absence of known barriers in the system; (2) identify spatial patterns of occupancy through time; and (3) assess the influence of initial allelic diversity, barriers, and life history diversity on population genetic diversity and structure through time. We evaluated our results in the context of species reintroduction strategies in our study system. More broadly, we evaluate the utility of simulations in providing unique and complementary insights relative to results from empirical studies of the effects of habitat fragmentation and translocation of imperiled organisms with complex life histories and habitat requirements.

METHODS

Study system

Bull trout are a native char that ranges from the Pacific Northwestern United States occurring on both sides of the continental divide and extending through the provinces of British Columbia and north into the Northwest Territories in Canada (Reist et al. 2002, Mochnacz et al. 2013). Bull trout were listed as threatened in the United States in 1999 under the Endangered Species Act due to declining or extirpated populations in the United States. The fragmentation of native habitat via dams and other barriers is likely a major contributor to observed population declines (Neraas and Spruell 2001, U.S. Fish and Wildlife Service 2010), and efforts to recover this species throughout its range involve a combination of habitat restoration, population supplementation, suppression of non-native species, translocation, and reintroduction of formerly extirpated populations (COSEWIC 2012, U.S. Fish and Wildlife Service 2012, Buktenica et al. 2013, Hayes and Banish 2017). Bull trout are cold-water specialists and have complex life histories that involve both resident and migratory forms. Additionally, they can exhibit metapopulation structure, as supported by genetic and demographic evidence (Dunham and Rieman 1999, Costello et al. 2003, Warnock et al. 2010).

Bull trout have been identified as a potential subject for reintroduction and/or supplementation in the lower Pend Oreille River near the United States–Canada border in eastern Washington; although this region does not currently support breeding populations of bull trout, historical populations may have been present (U.S. Fish and Wildlife Service 2012). Concurrently, licensees of major hydropower facilities regulated by the Federal Power Act in the study area have been directed by regulatory authorities to engage in a process identifying and prioritizing actionable alternatives for bull trout reintroduction, supplementation, or translocation (U.S. Fish and Wildlife Service 2012). These investigations are occurring in addition to ongoing and related projects addressing non-native species removal, large-scale barrier removals, habitat restoration, and construction of supplementation facilities (Pend Oreille Public Utility District 2008, Seattle City Light 2010, U.S. Fish and Wildlife Service 2012). Fine-scale environmental data available in the study area, in addition to historical work characterizing the genetics, demographics, and life history of this species and potential donor populations, present an opportunity for a spatially explicit simulation approach to evaluate the range of potential demogenetic outcomes of reintroduction in this system.

Riverscape demogenetic simulation program

We used CDMetaPOP v1.0 (Landguth et al. 2017*a*) to simulate reintroduction strategies of

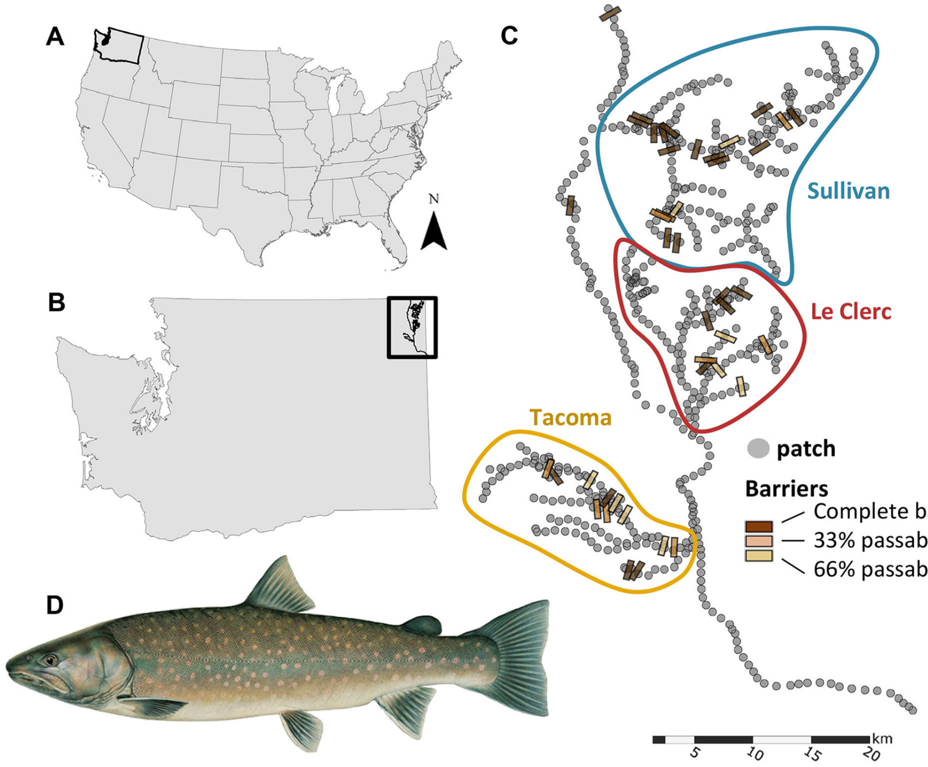

Fig. 1. Location (A, B) of Pend Oreille River and tributaries assessed in this study as a spatial network of habitat patches and barriers (C) for which reintroduction of bull trout (*Salvelinus confluentus*) (D) was simulated. Bull trout illustration by Joseph R. Tomelleri.

bull trout in the lower Pend Oreille River system (Fig. 1). CDMetaPOP is a spatially explicit, individual-based, demogenetic model (SIBM) of metapopulation dynamics. CDMetaPOP simulates demographic and genetic processes as interactions between individuals located across a number of patches (e.g., Landguth et al. 2017*b*, Nathan et al. 2017, Rice and Clark 2017, Day et al. 2018). Individuals within a patch share a common environment that is defined by spatially explicit parameterization of relevant variables representing habitat characteristics. Within each patch, a class (age/stage/size) structure is used to simulate stochastic demographic processes, while movement of individuals between patches is controlled as a function of any number of spatially explicit resistance (or permeability) surfaces. More simply, a landscape is populated with patches, which are in turn populated with individuals. Within a patch, individuals undergo growth, reproduction, migration, and mortality. The resulting genetic processes are simulated over time at the individual level. Metapopulation structure is emergent in CDMetaPOP when individuals in proximate patches begin to share demogenetic characteristics to the extent that they are distinguishable from other local populations, via spatial separation and/or genetic differentiation driven in turn by underlying mechanisms related to riverscape and environment. A more detailed breakdown of each process can be found in Landguth et al. (2017*a*) and the user manual (https://github.com/ComputationalEcologyLab/CDMetaPOP). Following, we highlight specific processes with respect to our bull trout system model. All parameter values and references can also be found in Appendix S1.

Patch attributes

The bull trout simulation extent consists of 554 patches defined as spatially delineated stream reaches ranging between 200 and 1000 m each along the lower Pend Oreille River system in northeastern Washington, USA (Fig. 1). Patches were delineated by gradient that exceeded 7.45% (Bowerman 2013), and patches along areas of continuous river without gradient delineations were divided into approximately 1-km river sections. Carrying capacity for bull trout in our system is not well known. Therefore, for each patch we calculated two carrying capacities as a function of habitat size with two individuals (Low *K*) or four individuals (High *K*) per 100-m^2 stream surface area within a patch (Fraley and Shepard 1989, Dunham and Chandler 2001, Hagen and Decker 2011). Habitat size was estimated for each patch from the product of reach length and approximate baseflow stream width estimated using regional hydraulic geometry equations developed by Castro and Jackson (2001).

For our simulation, stream temperature metrics were extracted for each patch using gridded datasets described by Day et al. (2018). Stream temperatures are used in the model to govern local growth rates (see CDMetaPOP user manual for additional details). We used average temperatures for the spawning period (August 1st–October 15th), as well as the overwintering period (October 16th–July 31st).

Population demographic parameters and vital rates

Simulations were initiated with a single reintroduction event assuming age 1 fingerlings of mean size 137 mm (±5 mm SD; Appendix S1: Table S1). Individuals occupied patches during two distinct seasons: spawning and overwintering. Growth was based on the von Bertalanffy equation (von Bertalanffy 1938) and adjusted based on spatially explicit temperature values (Appendix S1). As individuals grew over time, they were grouped into eight size classes following reported values in the literature (Fraley and Shepard 1989, Zymonas 2006). Size classes (mm) from ages 0 to 7 were 75, 137, 204, 273, 339, 402, 460, and >514 and regulated probability of mortality, straying, and migration. See Appendix S1 for details on class-dependent parameters.

Reproduction considered both maturation and fecundity of individuals. Probability of maturation was modeled as a function of individual fish length and determined by a logistic probability curve derived following Bowerman (2013; Appendix S1: Fig. S1; see also Benjamin et al. 2017: Table 3). To provide an overriding control on maturation of very slowly growing animals, individuals become mature at age 6 regardless of their size. Fecundity was modeled as an exponential function of size (Appendix S1; Bowerman 2013), and number of eggs was drawn from a Poisson deviate. Spawning patches were deemed suitable for spawning if the average daily temperature was between 7° and 12°C from August 1 to October 15 (the spawning period) and the average slope of the patch was <7.45% (Bowerman 2013). Overwintering grounds for migrants included any suitable patches downstream from spawning locations.

Mortality was governed by density dependence and age-based processes. In CDMetaPOP, individuals can migrate to new patches or maintain residency in their present patch. Recruits are added into their natal patches. At each time step in the model, the number of individuals within each patch can potentially exceed resource capacity. The resulting level of mortality, reflecting competition for limited resources, was implemented via a density-dependent function with a hierarchical specification of patch- and size-structured carrying capacities (e.g., Ray and Hastings 1996; see user manual for more details). Egg mortality was density-independent and set at 0.6 for all patches, although model output was insensitive to this parameter. An additional density-independent, age-based mortality was used to calibrate the age distribution to approximate empirical observations and prevent unrealistically old individuals from persisting in the model. Fish age seven and above had 50% probability of mortality each year.

Population genetics and initial allele frequencies

We initialized the model with allele frequencies generated from empirical bull trout data (DeHaan et al. 2011 and unpublished data; Appendix S1: Table S2). The empirical dataset included 817 individuals from 13 locations genotyped for 18 microsatellite markers (Appendix S1: Table S2). Locations (or populations) were selected from available empirical data according to those deemed most desirable or most likely to be used for source populations according to numerical abundance and other factors such as life history (A. Bearlin and P. DeHaan, *personal communication*). Any individuals with >30% missing genotype data were excluded from subsequent analyses. Allele lengths were automatically binned using the program Tandem (Matschiner and Salzburger 2009), and individuals with more than two outlier alleles were removed from the dataset. Extreme outlier alleles (>50 base pair gap) were coded as missing. Loci were evaluated for Hardy-Weinberg equilibrium and presence of null alleles using Microsatellite Analyzer (MSA) 4.05 (Dieringer and Schlötterer 2003). Evidence of linkage disequilibrium between markers was evaluated using GenePop (Raymond and Rousset 1995). Allelic richness, expected heterozygosity, and observed heterozygosity were calculated using MSA (Dieringer and Schlötterer 2003) for each population. Effective population size (Ne) for each sampling location was estimated using the linkage disequilibrium method (LDNe; Waples and Do 2008) as implemented in NeEstimator V2 (Do et al. 2014). LDNe has been shown to perform well in simulations, even in the presence of migration (Gilbert and Whitlock 2015).

We developed five allele frequency scenarios for the model to simulate a range of reintroduction strategies. First, we created the full scenario with all individuals and populations included. Next, to more closely approximate realistic management scenarios, we simulated a series of scenarios with individuals from a limited number of populations, including a single population with the highest allelic diversity (High1), a single population with the lowest allelic diversity (Low1), three populations with the highest allelic diversity (High3), and three populations with the lowest allelic diversity (Low3).

Individual movement and riverscape surfaces

Riverscape structure can govern movement of individuals between patches, and this concept is implemented through resistance (or permeability) surfaces whose values represent the stepwise cost of moving between patches (e.g., Spear et al. 2015). The model simulated movement as probabilistic functions of cumulative cost across these resistance surfaces (e.g., Landguth and Cushman 2010). In this study, we developed two riverscape surfaces that govern probability of fish movement: one based on distance along the river network alone (isolation-by-distance, or Riverine only), and one incorporating current barriers within the river network (Riverscape and Barriers). As movement costs are notoriously difficult to evaluate, the two resistance surfaces we modeled represent necessary simplifications of the true suite of factors that affect movement costs for bull trout. The first riverscape surface provides a null model of how individuals move through the riverscape, that is, isolation-by-distance (IBD). In IBD, fish have an equal probability of moving to any two locations on the riverscape that are an equal distance from the fish. In other words, no variables other than riverine distance are considered as contributing to the likelihood of a fish successfully moving to a new patch. The second riverscape included IBD and known dams and culverts throughout the study system (Fig. 1, Table 1). This barrier riverscape considered asymmetrical movement probabilities with multiple probabilities of passage that varied by barrier and also by direction (e.g., Timm et al. 2016; Fig. 1) to test one-way movement (Appendix S1; Meeuwig et al. 2010). Here, we note that these two cost surfaces are simplified versions of true movement costs for bull trout. Each movement process was associated with a matrix of patch-to-patch movement probabilities informed by riverine distance. In the riverscape scenario which included known dams and culverts as complete and partial barriers to movement, additional steps were needed to compute movement probabilities. First, a riverscape

Table 1. Barrier summary descriptions, where “None” for passability indicates a complete barrier.

Major tributary	Barrier type	Passability (%)	N
Pend Oreille River	Dam	None	2
Sullivan Creek	Culvert	None	11
Sullivan Creek	Culvert	33	3
Sullivan Creek	Culvert	66	1
Sullivan Creek	Dam	None	3
Sullivan Creek	Non-culvert crossing	66	1
Le Clerc Creek	Culvert	None	5
Le Clerc Creek	Culvert	33	2
Le Clerc Creek	Culvert	66	2
Le Clerc Creek	Dam	None	2
Le Clerc Creek	Non-culvert crossing	66	1
Tacoma Creek	Culvert	None	4
Tacoma Creek	Culvert	33	3
Tacoma Creek	Culvert	66	4
Tacoma Creek	Non-culvert crossing	33	1
Tacoma Creek	Other	66	1

surface was created (Washington State Plane, USA, m) in which each cell (30 × 30 m resolution) was assigned a resistance value of one. The point locations of patches (N = 544) were then used to calculate a riverine distance matrix with the landscape connectivity program UNICOR (Landguth et al. 2012). The resulting 544 × 544 riverine distance matrix was then transformed to a permeability matrix by converting riverine distance probabilities to movement probabilities based on the relationship:

$$P(\text{movement}) = 1 - \text{resist}/\max(\text{resist}), \qquad (1)$$

where resist is the riverine resistance between two patches. UNICOR was then used to generate an asymmetrical probability matrix based on locations of barriers/culverts in the system; values of zero in the probability matrix reflected zero movement probability and thus complete barriers to movement, values of one reflected complete passability, intermediate values (0–1) reflected partial passability, and differential or asymmetric (down vs. upstream) passability was incorporated. Finally, the two matrices (permeability matrix and barrier asymmetrical probability matrix) were multiplied together. The resulting probability matrix included one-way and two-way partial and complete barriers to movement reflective of the dams and culverts within our study system. Thus, fish movement accounted for riverine distance and the asymmetrical effect of barriers to movement (Appendix S1: Section S2 and Fig. S2).

CDMetaPOP considers four different movement processes (mating, migration out, migration back, and straying), as well as thresholds to limit the maximum distance available to a fish for each movement process. Each movement process is governed by the same riverscape surface in each scenario that was simulated. For example, mating movement is governed by the same riverscape surface as migration and straying, but is restricted to a maximum of 2 km (Table 2).

Migration, wherein fish move annually between feeding grounds and spawning grounds, takes place as two separate events during the

Table 2. Key parameters and references used in the simulation of a bull trout reintroduction to the Pend Oreille River watershed in northeastern Washington State.

Input parameter	Values	References
Monte Carlo replicate runs	10	–
Runtime (years)	200	–
Carrying capacity†	2 scenarios: 2 or 4 individuals per 100 m^2	Hagen and Decker (2011), Dunham and Chandler (2001), Fraley and Shepard (1989)
Movement resistance surfaces†	Isolation-by-distance and isolation-by-distance + physical barriers (i.e., dams and culverts). Max mating movement = 200 m. Max migration/straying movement = anywhere on the landscape	UNICOR (Landguth et al. 2012)
Straying probability†	0.01, 0.001, 0.0001	–
Initial allele frequency†	Five stocking scenarios based on alternate source populations: 1 pop. with lowest allelic diversity (AD) (Low1), 3 pops. with lowest (Low3), 1 pop. with highest AD (High1), 3 pops. with highest AD (High3), and all populations (All)	DeHaan et al. (2011)
Number of loci/alleles	14 loci, 34 alleles per locus	DeHaan et al. (2011)
Probability that individual becomes migrant at each size class	Early migration scenario: 0, 0.075, 0.208125, 0.12, 0.0675, 0.0375, 0.031875, 0.031875 Standard migration scenario: 0, 0, 0.075, 0.208125, 0.12, 0.0675, 0.0375, 0.031875	–
Probability of maturation	$P(\text{mature}) = \exp(-6.04431 + 0.01704 \times \text{Length})/(1 + \exp(-6.04431 + 0.01704 \times \text{Length}))$	Seattle City Light, *unpublished data*; Downs et al. (1997)
Fecundity	Number of eggs = 126.07 × exp (0.0061 × Length)	Seattle City Light, *unpublished data*

Note: For more uncertain parameters, we simulated multiple values to understand how those parameters affected demographic and genetic responses. En dash indicates no reference available.

† Indicates parameters included in focal scenarios.

simulation. After spawning in its natal patch, an individual is assigned a probability of migration as a function of size. We examined two suites of size-based migration probability: a standard migration scenario in which size classes 2 and up have a non-zero probability of migration, and an early migration scenario in which size classes 1 and up have a non-zero probability of migration. We focused on the early migration scenario for which the probability of migration was 0, 0.075, 0.21, 0.12, 0.068, and 0.038 for size classes 0–5, respectively, and 0.032 for size classes 6 and 7. Estimates of the proportion of migratory bull trout vary in the literature (Zymonas 2006, Prince 2010); our generic suite of migration probabilities allows 75% of fish to become migratory at some point in their lives. The migration probabilities used in our simulations were not obtained from empirical field data, but assumed. Probabilities for the standard migration scenario are described in Appendix S1: Table S1.

Migrants, as determined by binomial draw with the assigned probability, were then assigned a new patch based on a combination of IBD and physical barriers (i.e., dams and culverts) such that individuals had a higher probability of assignment to closer, accessible patches. After overwintering, barring a straying event or barrier (described in the following paragraph), migrants returned to their natal patch. If individuals encountered a barrier, then they were given the opportunity to stray to a new natal patch nearest to their original natal patch (Neraas and Spruell 2001, DeHaan et al. 2011, DeHaan and Bernall 2013).

Annual stray rates (i.e., local dispersal) are generally unknown for most salmonid species but are thought to be low for bull trout given high genetic structure between populations (Spruell et al. 1999, Ardren et al. 2011). Because of the uncertainty around this parameter, and the potentially large effect it could have on genetic and demographic outcomes of simulations, we explored a range of parameter values to determine the effect of stray rates on the demogenetic outcomes of this study. We tested annual stray rates of 0.01, 0.001, and 0.0001. All individuals in the model had some probability of straying to a new patch, away from their natal grounds, at the end of the overwintering period. Stray events can result in assignment to a new patch anywhere on the landscape, with individual movements governed by riverscape scenario (Table 2).

Analyses

Our analyses explored demographic and genetic outcomes of the scenarios tested. First, we examined total population size across years for key focal scenarios (described in *Results*). We also examined and characterized size and age distribution across scenarios, including the mean, median, maximum, and first and third quartile age and size values for each scenario. We calculated the percent time each patch was occupied on the landscape to identify spatial patterns of persistence or extinction.

Genetic diversity and structure were analyzed using the F-statistic in which F is defined as the ratio of the difference between the expected (He) and observed (Ho) heterozygosities to He (i.e., F_{IS} following Nei 1977). F was calculated at 0, 50, 100, 150, and 200 yr. The effects of watershed and barriers (both all barriers and complete barriers only) on genetic structure were tested using an analysis of molecular variance (AMOVA) for the focal scenarios. The AMOVA estimated the proportion of genetic variance explained at three hierarchical levels: genetic variation among the (1) major groups of patches in the study system (watershed, all barriers, or complete barriers only), (2) patches within a group, and (3) individuals within patches. For each focal scenario ($n = 8$), AMOVAs were run for each replicate (10 runs per scenario). To summarize the AMOVA output across replicates for the eight focal scenarios, a three-way analysis of variance (three-way ANOVA) was used to compare the mean percent variance explained at the highest level of variance partitioning (i.e., variation among the major groups of patches, or Patch Groups [below], in the study system—watershed, all barriers, or complete barriers only) from the AMOVA output. Three factors were used to explain the mean percent variance among groups. The first factor labeled Riverscape describes the structural landscape which includes two levels (Riverine and Barriers). The second factor labeled Demographics (nested within the riverscape factor) has four levels that represent different combinations of stray rate and carrying capacity (K). The third factor labeled Patch Group has three levels each representing how patches were grouped across the study system when running the AMOVA (patches assigned to Patch Groups as delineated by watershed, all barriers (dams + culverts), or complete barriers only; Table 1). Additionally, in the three-way ANOVA, an interaction term was specified between Riverscape and Demographics to evaluate genetic variance partitioning in response to barriers in the landscape for different stray rate and *K* values. AMOVAs/ANOVAs and the data manipulation for them were conducted in R v3.3.2 (R Core Team 2016) using packages gStudio (Dyer 2014), adegenet (Jombart 2008), and poppr (Kamvar et al. 2014). Original code and input data are available at: https://github.com/ComputationalEcologyLab/bulltrout-riverscapegenetics.

RESULTS

Temporal demographic trends

Across all simulation scenarios, which included a wide range of carrying capacities, stray rates, and initial allele frequencies, we found evidence supporting the critical role of connectivity in the study system as well as the importance of spatial strongholds for bull trout establishment and persistence. Among focal scenarios, we found a strong effect of carrying capacity (*K*) and stray rate on population size (Fig. 2). However, all other parameters being equal, population size for populations that persisted to year 200 was, on average, between five-fold and 10-fold higher in scenarios without barriers (Riverine) vs. scenarios that incorporated all known barriers as of 2015 (Barriers; Fig. 2). In the absence of barriers (Riverine), all populations exceeded 10,000 individuals by year 200 with the exception of the lowest annual stray rates at the lowest carrying capacity, in which only small populations persisted (Fig. 2). In contrast, the presence of barriers at the lower carrying capacity (Low *K*) resulted in extinction early in all simulations, including those with a high stray rate (approximately year 25).

In general, mean and median age and size of bull trout did not differ substantially among scenarios (Table 3). However, the presence of barriers resulted in lower maximum age and smaller maximum size of fish at the conclusion of simulations (year 200) and higher variation in the maximum age and maximum size between replicates of a given scenario (Table 3). Among Riverine scenarios, higher stray rate (0.01 vs. 0.0001 probability of straying) was associated with slightly larger mean and median bull trout size, as well as larger first and third quantile sizes. However, the relationship between stray rate

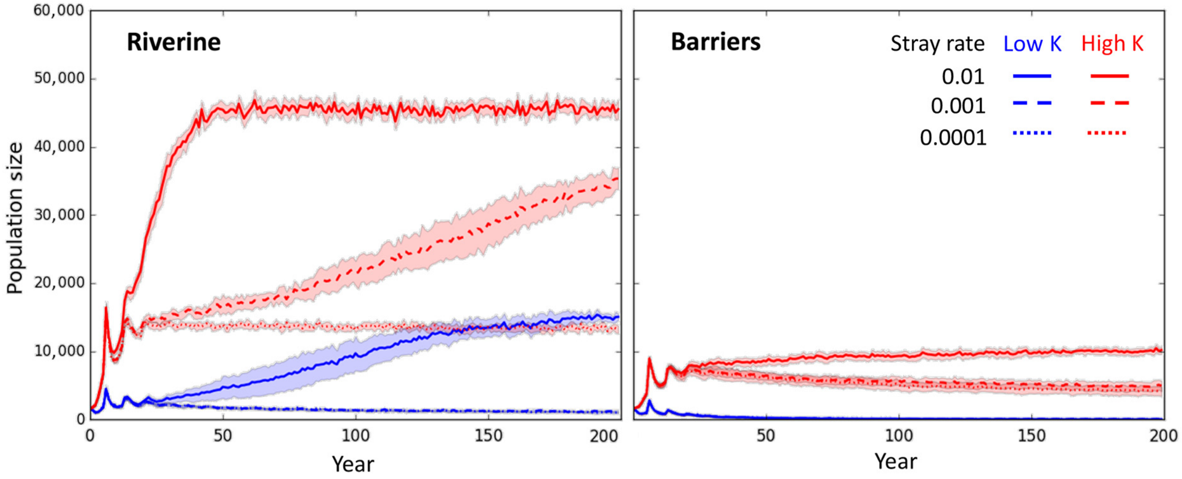

Fig. 2. Population size (measured as total number of individuals) through time for six simulation scenarios spanning a range of stray rates and carrying capacities (*K*) in river networks with and without barriers. Stray rates indicate the probability of straying to a new patch, away from an individual's natal grounds, at the end of the overwintering period.

Table 3. Age and size distributions for focal simulations.

			Mean	Age summary					Size summary				
K	Stray	N_{MCs}	and SD	Mean	Max	Med	Q1	Q3	Mean	Max	Med	Q1	Q3
Riverine													
Low	0.0001	10	μ	1.94	11.50	1.00	1.00	2.10	127.17	397.24	106.20	99.72	132.89
			σ	0.15	1.27	0.00	0.00	0.32	2.96	21.73	1.44	1.23	4.71
Low	0.01	10	μ	1.82	14.70	1.00	1.00	2.00	135.38	451.38	112.87	106.31	147.23
			σ	0.04	1.42	0.00	0.00	0.00	1.22	17.78	0.35	0.43	1.72
High	0.0001	10	μ	1.89	14.90	1.00	1.00	2.00	122.82	431.97	104.35	96.41	128.95
			σ	0.06	1.10	0.00	0.00	0.00	1.67	11.39	0.75	0.67	4.03
High	0.01	10	μ	1.82	15.70	1.00	1.00	2.00	134.21	460.24	112.36	105.23	146.42
			σ	0.04	1.64	0.00	0.00	0.00	1.52	11.48	0.51	0.46	2.35
Barriers													
Low	0.0001	5	μ	1.73	9.60	1.00	1.00	2.20	128.89	317.66	110.77	105.09	142.53
			σ	0.12	4.39	0.00	0.00	0.45	8.97	91.33	4.94	5.69	5.75
Low	0.01	4	μ	2.52	5.75	1.75	1.75	3.00	143.74	203.70	131.99	124.97	158.83
			σ	0.93	2.50	0.96	0.96	0.82	20.86	24.03	25.50	28.05	14.01
High	0.0001	10	μ	1.96	12.80	1.00	1.00	2.10	134.78	411.87	114.76	106.60	151.30
			σ	0.08	1.48	0.00	0.00	0.32	2.94	33.53	1.39	1.74	3.72
High	0.01	10	μ	1.85	14.80	1.00	1.00	2.00	136.98	429.28	114.50	108.26	152.30
			σ	0.02	2.10	0.00	0.00	0.00	0.92	21.16	0.38	0.34	1.07

Note: Includes Riverine or Barrier scenarios (left; main headings); carrying capacity (*K*: Low or High); stray rate (Stray: 0.01 or 0.0001); the number of Monte Carlo replicates (N_{MCs}); and mean (μ) and standard deviation (σ) of the mean, maximum, median (Med), and first and third quantiles for age and size across all replicates for each scenario at year 200.

and median, mean, Q1, and Q3 bull trout size is far less pronounced among Barrier scenarios—particularly at High K (Table 3; Appendix S1: Table S3).

Spatiotemporal occupancy dynamics

Patch occupancy through time varied by riverscape and demographics (Fig. 3). At Low K scenarios, the presence of barriers resulted in low occupancy through time, reflecting extinction relatively early in the simulation (Fig. 3). The stray rate was correlated with the overall spatial extent of the population persistence in the absence of barriers. Low stray rate (0.0001) resulted in populations persisting in the upper Sullivan Drainage (Fig. 3A). High stray rate (0.01) resulted in much higher occupancy through time for the Le Clerc and Tacoma Drainages (Fig. 3C). In the presence of barriers, populations went extinct regardless of stray rate. Populations persisted longest in the upper Sullivan Drainage prior to extinction. At High *K*, populations persisted throughout the study system in the absence of barriers and were generally concentrated near the headwaters (Fig. 4A, C). However, in the presence of barriers, populations occupied patches farther downstream in the drainage networks due to asymmetrical barrier passage (e.g., ability to migrate downstream but unable to migrate back to natal patch, thus being forced to stray to a nearby suitable patch; Fig. 4B, D, arrows). In some cases, this effect was particularly pronounced in patches that had high occupancy through time directly below barriers but virtually no occupancy in the absence of barriers (Fig. 4, arrows).

Demogenetic trends and outcomes

Genetic diversity was strongly influenced by the presence of barriers (Tables 4 and 5, Fig. 5). At both Low and High *K* Riverine scenarios, stray rate had a marked influence on the *F*-statistic through time, with low stray rates steadily increasing in *F* over time and with small differences between replicates of the same scenarios. High stray rates resulted in an initial peak in *F* at roughly year 50 with *F* then slowly decreasing over time. This pattern was consistent across all scenarios except Low *K* with low stray, in which *F* behaved unpredictably through time in Barrier scenarios, with large differences between replicates of the same scenarios and no discernible influence of stray rate. Initial allelic diversity had negligible influence on *F* in any of the focal scenarios (Table 5, Fig. 5).

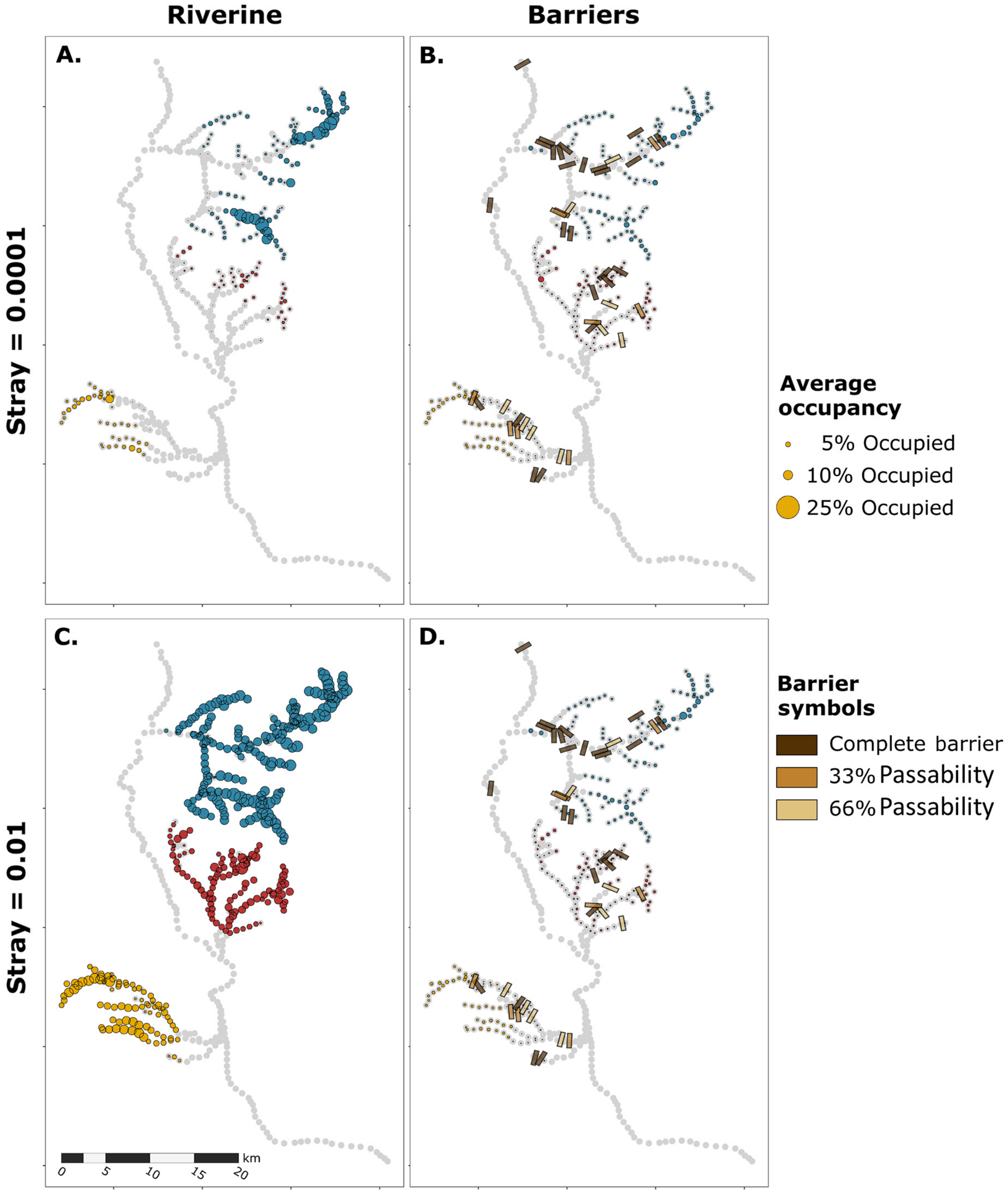

Fig. 3. Patch occupancy through time (reported as % years occupied) for Low *K* scenarios. Unoccupied patches in gray. Colors indicate watersheds (Sullivan, blue; Le Clerc, red; Tacoma, yellow). Stray rates indicate the probability of straying to a new patch, away from an individual's natal grounds, at the end of the overwintering period.

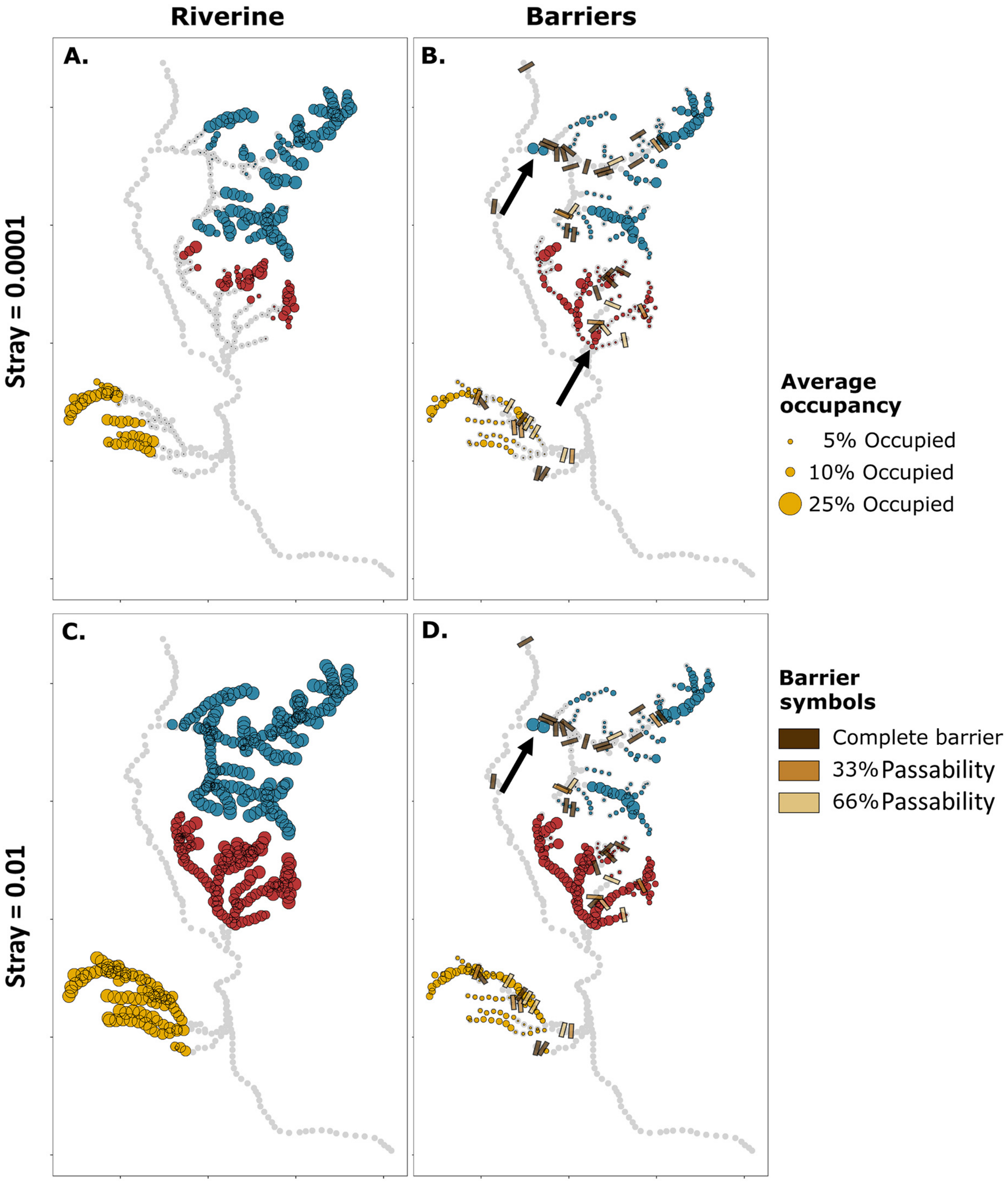

Fig. 4. Patch occupancy through time (reported as % years occupied) for High *K* scenarios. Unoccupied patches in gray. Colors indicate watersheds (Sullivan, blue; Le Clerc, red; Tacoma, yellow). Stray rates indicate the probability of straying to a new patch, away from an individual's natal grounds, at the end of the overwintering period. Arrows identify patches with higher occupancy just below dams as compared to the barrier-free scenarios (Riverine).

Table 4. Genetic diversity outcomes for focal simulations.

K	Stray	N_{MCs}	Mean and SD	$H_{\text{E-Low1}}$	$H_{\text{E-Low3}}$	$H_{\text{E-High1}}$	$H_{\text{E-High3}}$	$H_{\text{E-All}}$	$H_{\text{O-Low1}}$	$H_{\text{O-Low3}}$	$H_{\text{O-High1}}$	$H_{\text{O-High3}}$	$H_{\text{O-All}}$
Riverine													
Low	0.0001	10	μ	0.37	0.56	0.55	0.59	0.64	0.22	0.33	0.31	0.3	0.38
			σ	0.02	0.03	0.04	0.04	0.04	0.03	0.06	0.07	0.05	0.09
Low	0.01	10	μ	0.37	0.6	0.61	0.66	0.69	0.33	0.54	0.55	0.59	0.62
			σ	0.02	0.03	0.02	0.03	0.03	0.02	0.02	0.02	0.03	0.02
High	0.0001	10	μ	0.41	0.66	0.65	0.71	0.76	0.28	0.44	0.42	0.46	0.51
			σ	0	0.01	0.01	0.01	0	0.01	0.01	0.01	0.02	0.01
High	0.01	10	μ	0.41	0.67	0.65	0.7	0.74	0.38	0.62	0.61	0.65	0.7
			σ	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Barriers													
Low	0.0001	5	μ	0.05	0.09	0.06	0.06	0.07	0.06	0.09	0.06	0.07	0.08
			σ	0.04	0.05	0.06	0.06	0.09	0.04	0.06	0.06	0.06	0.09
Low	0.01	4	μ	0.1	0.05	0.05	0.17	0.08	0.01	0.04	0.05	0.08	0.09
			σ	0.14	0.03	0.06	0.16	0.03	0.02	0.04	0.05	0.05	0.04
High	0.0001	10	μ	0.39	0.65	0.62	0.67	0.73	0.21	0.33	0.34	0.36	0.37
			σ	0.01	0.01	0.02	0.02	0.02	0.02	0.05	0.04	0.03	0.07
High	0.01	10	μ	0.4	0.65	0.64	0.69	0.72	0.33	0.54	0.53	0.57	0.59
			σ	0.01	0.01	0.01	0.02	0.02	0.01	0.01	0.01	0.01	0.02

Note: Includes Riverine or Barrier scenarios (left; main headings); carrying capacity (K: L = Low or H = High); stray rate (Stray: H = high, 0.01; or L = low, 0.0001); the number of Monte Carlo replicates (N_{MCs}); and mean (μ) and standard deviation (σ) of expected heterozygosity (H_{E}) and observed heterozygosity (H_{O}) for each allelic diversity scenario (N = 5).

Table 5. Genetic structure outcomes for focal simulations.

K	Stray	N_{MCs}	Mean and SD	F_{Low1}	F_{Low3}	F_{High1}	F_{High3}	F_{All}
Riverine								
Low	0.0001	10	μ	0.38	0.41	0.44	0.48	0.41
			σ	0.1	0.1	0.13	0.09	0.14
Low	0.01	10	μ	0.11	0.1	0.1	0.1	0.1
			σ	0.02	0.01	0.01	0.01	0.01
High	0.0001	10	μ	0.33	0.34	0.35	0.35	0.33
			σ	0.02	0.02	0.02	0.02	0.01
High	0.01	10	μ	0.07	0.07	0.06	0.07	0.07
			σ	0	0.01	0	0	0
Barriers								
Low	0.0001	5	μ	*−0.07*	*−0.02*	*0.02*	*−0.06*	*−0.1*
			σ	*0.19*	*0.08*	*0.07*	*0.09*	*0.13*
Low	0.01	4	μ	*0.44*	*0.1*	*−0.08*	*0.17*	*−0.23*
			σ	*0.62*	*0.18*	*0.15*	*0.45*	*0.15*
High	0.0001	10	μ	0.47	0.49	0.45	0.47	0.49
			σ	0.05	0.08	0.05	0.04	0.08
High	0.01	10	μ	0.19	0.17	0.17	0.18	0.18
			σ	0.02	0.01	0.01	0.01	0.01

Notes: Includes Riverine or Barrier scenarios (left; main headings); carrying capacity (K: L = Low or H = High); stray rate (Stray: H = high, 0.01; or L = low, 0.0001); the number of Monte Carlo replicates (N_{MCs}); and mean (μ) and standard deviation (σ) of the F-statistic (F) for each allelic diversity scenario (N = 5). Italics indicate simulations for which some (10-N_{MCs}) or all replicates resulted in extinct populations.

In the three-way ANOVA, all three factors (Riverscape, Demographics, and Patch Level) and the interaction term (Riverscape:Demographics) were highly significant ($P \ll 0.001$) predictors of the genetic variance explained in the AMOVAs at the highest partition. Post-hoc tests indicated that more genetic variance is explained by Patch Groups (e.g., patches groups by Watershed, All

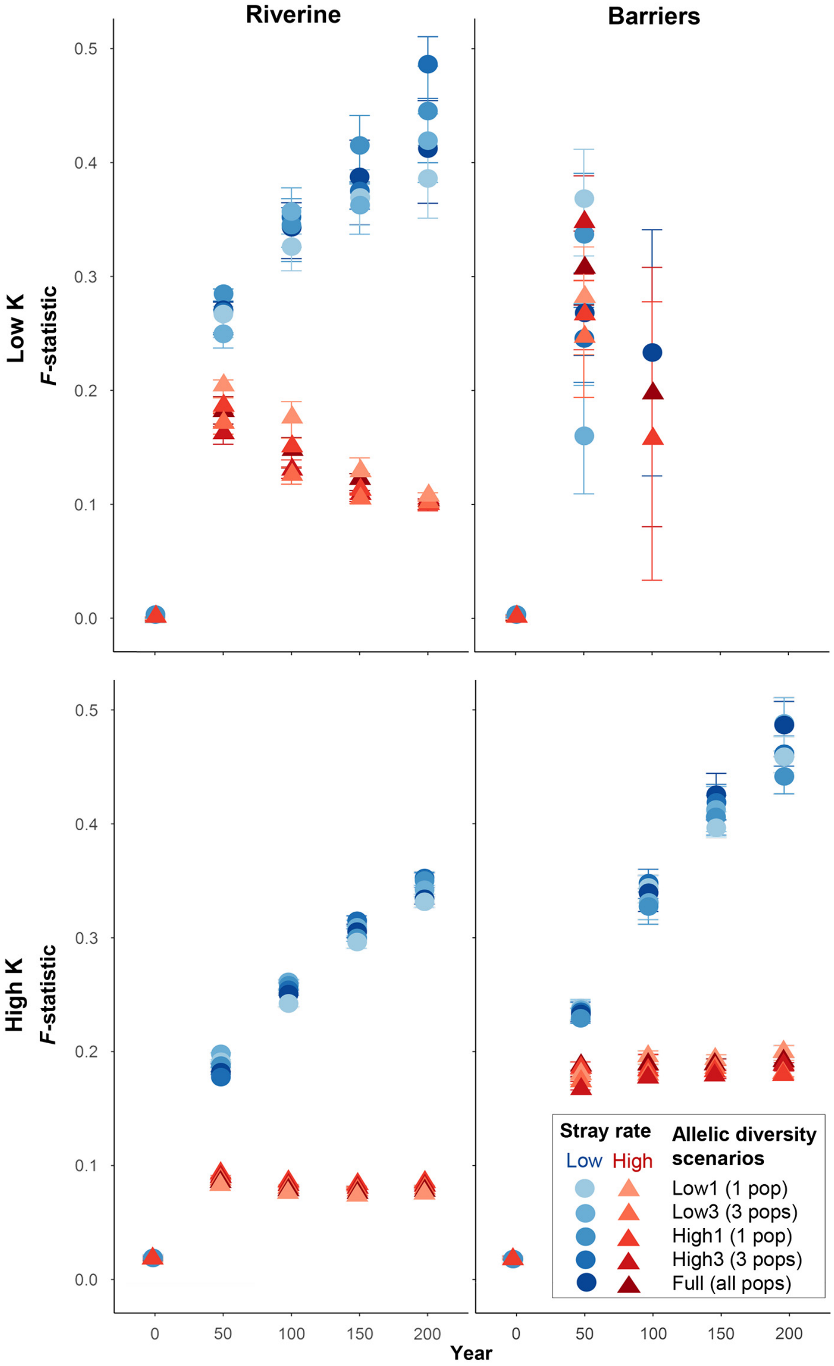

Fig. 5. Genetic structure (*F*-statistic, defined as the ratio of the difference between the expected [He] and observed [Ho] heterozygosities to He [i.e., F_{IS} following Nei 1977]) across years for low (0.0001) and high stray rates (0.01), Low *K* and High *K*, and among allelic diversity scenarios. Stray rates indicate the probability of straying to a new patch, away from an individual's natal grounds, at the end of the overwintering period.

Barriers, and Complete Barriers only) in Barrier scenarios than in Riverine scenarios (Tukey honestly significant difference test, $P \ll 0.001$). The highest percent variation was explained for low stray rate scenarios (Table 6; Appendix S1: Fig. S3). The lowest mean percent variation explained was for scenarios with high stray rates and high carrying capacity (K). All contrasts among the Demographics factor (e.g., scenarios with different stray rates and/or K) were significant at the alpha = 0.05 level. All Barriers and Complete Barriers only explained more genetic variation than Watersheds. However, the two Barrier Patch Groups (All Barriers and Complete Barriers only) were indistinguishable. All contrasts for the interaction term between Riverscape and Demographics were significant (TukeyHSD, $P \ll 0.001$) except for three: (1) Riverine:High K/High Stray – Riverine:Low K/High Stray, (2) Barriers:High K/High Stray – Barriers:High K/Low Stray, and (3) Barriers:High K/High Stray – Riverine:High K/Low Stray (TukeyHSD, $P \geq 0.5$; Table 6; Appendix S1: Fig. S3).

Discussion

A complex suite of factors including biology, environment, and management practices influences the dynamics and success of species

Table 6. Mean and standard deviation (SD) of % variance explained (AMOVA) were calculated over all replicates (N = 10) for each scenario with the exception of Riverine, Low K, low stray rate.

Variation components	Among groups			Among patches			Among individuals		
Scenarios and patch groups	Wshd^{a}	AllB^{b}	Comp^{b}	Wshd^{a}	AllB^{b}	Comp^{ab}	Wshd	AllB	Comp
Low K, Stray = 0.0001									
Riverine†									
Mean % Variance	25.84	29.02	29.02	40.61	36.23	36.23	33.55	34.74	34.74
SD	21.23	10.21	10.21	16.07	17.7	17.7	6.27	9.73	9.73
Barriers									
Mean % Variance	–	–	–	–	–	–	–	–	–
SD	–	–	–	–	–	–	–	–	–
Low K, Stray = 0.01									
Riverine									
Mean % Variance	0.97	2.23	1.18	28.18	26.84	27.84	70.85	70.93	70.98
SD	0.33	0.51	0.57	1.23	1.11	1.36	1.48	1.43	1.41
Barriers									
Mean % Variance	–	–	–	–	–	–	–	–	–
SD	–	–	–	–	–	–	–	–	–
High K, Stray = 0.0001									
Riverine									
Mean % Variance	5.01	14.3	7.6	46.15	36.93	43.17	48.83	48.76	49.22
SD	0.66	1.39	0.94	1.26	1.86	1.48	1.12	1.15	1.16
Barriers									
Mean % Variance	11.04	16.72	13.13	53.71	48.05	52.1	35.24	35.22	34.77
SD	3.55	4.43	3.76	8.38	8.7	8.39	5.96	6.06	5.84
High K, Stray = 0.01									
Riverine									
Mean % Variance	0.74	1.87	1.01	22.98	21.8	22.68	76.28	76.33	76.31
SD	0.04	0.1	0.05	1.28	1.22	1.27	4.26	4.26	4.26
Barriers									
Mean % Variance	8	10.91	15.49	30.4	27.28	27.81	61.6	61.8	56.7
SD	1.25	1.63	1.62	1.46	2.1	1.69	1.96	1.75	1.51

Notes: Variation components include among groups within the study system (Among Groups), among patches within a group (Among Patches), and among individuals within a patch (Among Individuals); groups include watershed (Wshd), all barriers (AllB), and complete (Comp). Letter superscripts ($^{a/b}$) indicate significant difference (Tukey honestly significant difference test) in mean genetic variance explained by AMOVA from the three-way ANOVA. En dash indicates no data available for populations that did not persist to year 200.

† The population persisted to year 200 in only three replicates.

reintroductions (McCarthy and Possingham 2007, McNeeley and Mainka 2009, Jachowski et al. 2016). We demonstrate the utility of a demogenetic modeling approach in evaluating the role of multiple interacting, spatially explicit factors in the probability of a successful reintroduction of bull trout into the lower Pend Oreille River and its tributaries. Even with a wide range of uncertainty surrounding key parameters in the simulation (i.e., carrying capacity, stray rates, and migration timing), we found evidence of the importance of connectivity between habitat patches with barriers (dams and culverts) driving demogenetic outcomes of the simulations. Empirical research and our understanding of the biology of bull trout also support the conclusion that habitat fragmentation and reduced connectivity contribute to declines, and vulnerability, of bull trout populations throughout their range (Dunham and Rieman 1999, Neraas and Spruell 2001). Fine-scale population structure is a defining characteristic of this species (Spruell et al. 2003, Bettles et al. 2005, Warnock et al. 2010, DeHaan et al. 2011, Kanda and Allendorf 2011). We also found strong evidence of the role of genetic drift, attributed to riverscape topology and stray rate, in driving neutral genetic diversity and structure, overwhelming any effects of initial allelic diversity of the reintroduced populations. Finally, our simulations demonstrate the sensitivity of reintroduction outcomes to both landscape and biological characteristics of the species, particularly carrying capacity and stray rate. Continued efforts to understand these parameters, their variability across populations, space, and time, and how they interact with a changing landscape and climate, will inform the potential success of future reintroduction efforts, particularly under variable landscape scenarios (e.g., removal of barriers and land management).

We found compelling evidence that fragmentation in the lower Pend Oreille River and its tributaries is a primary driver of reintroduction success in the region, with strong effects on bull trout population persistence, spatial distribution, and neutral genetic diversity. The life history parameters of stray rate and migration timing, as well as habitat parameters such as carrying capacity, are likely highly variable for this species (Rieman and Mclntyre 1993, Budy et al. 2017) and are difficult to quantify. Predictably, these parameters are influential to simulation outcomes; however, we found riverscape topology ultimately modulates the demogenetic outcomes of simulated reintroduction. Empirical evidence from numerous studies of stream-living trout has shown that instream barriers such as dams and culverts result in reduced population distribution and abundance (Morita and Yamamoto 2002, Peterson et al. 2014, Chelgren and Dunham 2015), demographic viability (Morita and Yokota 2002, Carim et al. 2017), and reduced genetic variability (Morita et al. 2009, Neville et al. 2009). We simulated an idealized, barrier-free landscape to provide a best case scenario. Future efforts could explore management-relevant barrier-removal scenarios. For example, across the study extent two dams and several culverts are slated for removal or for the addition of volitional fish passage in the coming years (Seattle City Light 2010). Demogenetic simulation approaches such as this may offer an important tool for cost–benefit analysis and prioritization of barrier removal, and for the optimization of resources for improving connectivity in the system (Neeson et al. 2015, Moody et al. 2017).

In the case of high carrying capacity, bull trout persisted for 200 yr in simulations despite the presence of barriers. However, populations were notably shifted downstream in watersheds due to blocked passage back to natal patches upon moving downstream over a barrier. This pattern was starkly different from spatial patterns of occupancy in barrier-free (Riverine) simulations, in which patches near the headwaters saw the highest occupancy through time. Although we did not simulate the effects of climate change in this study, these results provide relevant context for climate change vulnerability of bull trout populations reintroduced into this system. Bull trout in lower elevation streams are likely the most vulnerable to climate change (Eby et al. 2014), and like many other cold-water specialists, bull trout are likely to find refuge in high-elevation, headwater streams as stream temperatures increase in response to warming climate (Dunham et al. 2014, Isaak et al. 2016). Furthermore, vulnerability of bull trout in lower elevation habitats may not be tied to incremental warming but to the effects of episodic events such as wildfire (Falke et al. 2015) or droughts (Schultz et al. 2017) that are more likely in warmer years. Thus, the effects of habitat fragmentation may interact with climate and other human impacts on habitat availability to influence the success of a potential reintroduction in this system (e.g., Dunham et al. 2003, Perkin et al. 2017).

Spatial demographic processes that may influence bull trout populations present a challenge when attempting to generalize risk, vulnerability, and chance of persistence across different systems (Rieman and Mclntyre 1993, Rieman and Dunham 2000). A demogenetic simulation approach, particularly one that is spatially explicit, can help evaluate dynamic patterns of occupancy and emulate spatial processes in ways that cannot be described by simple metapopulation models or conceptual frameworks. Demogenetic simulations can also help identifying strongholds and sinks for populations in specific systems. The concept of strongholds is intuitively appealing in native trout conservation (Haak and Williams 2013) but defining what constitutes a stronghold can be difficult due to lack of empirical data, an understanding of dynamic spatial processes, and a host of other limitations (Dunham et al. 2003). Demogenetic models cannot provide this empirical information, which would take years if not decades to collect, but they can provide crucial demographic insights that are impossible by any other means. Overall, across simulated reintroduction scenarios considered here, one locality, upper Sullivan Creek, consistently supported a local population of bull trout when movement barriers were not a constraint, and as such could be defined as a stronghold in our study system.

In addition to defining strongholds, a major source of uncertainty for understanding spatial population processes for stream fishes and salmonids in particular is the importance of dispersal or straying (Neville et al. 2006, Keefer and Caudill 2014). A review of historical patterns of gene flow in the lower Pend Oreille River suggested that in some cases this process could drive persistence of local populations, but provided only limited insights into demography (Dunham et al. 2014). Results of this study provide much more detailed insights into the demographic processes that can drive straying and ultimately local persistence of bull trout. In simulation scenarios where barriers did not pose movement constraints, we saw a strong interaction between key life history parameters such as stray rate and carrying capacity and the distribution of bull trout in the system. At higher carrying capacity and higher stray rates, populations occupied patches in the Le Clerc and Tacoma Watersheds, in addition to upper Sullivan Creek, for much longer periods of time. Barriers also played a major role in the overall extent of successful reintroduction and whether bull trout persisted in the Le Clerc and Tacoma Watersheds.

Linked to patterns of spatial demography are the strong observed effects of genetic drift. Despite a wide range of initial allele frequencies over five different simulation scenarios, we found no compelling evidence that initial allele frequency predictably influenced genetic diversity or structure over time. We found instead that genetic drift, driven by stray rate and population size, was among the most important factors driving the neutral genetic diversity and structure of populations in our simulations. This finding is congruent with empirical evidence that genetic drift is a primary driver of neutral population genetic characteristics in bull trout (Ardren et al. 2011, Kanda and Allendorf 2011). Furthermore, this result is unlikely to emerge without simultaneous consideration of demographics and genetics, as in our approach here. Although prior empirical work has demonstrated the importance of source populations in driving genetic diversity in recipient (reintroduced) populations, our simulations allowed us to look further into the future in terms of how genetic drift over very long periods influenced outcomes. Recent calls for evaluation of factors influencing the costs/benefits of reintroduction strategies for threatened species include the need to consider demogenetic effects of source populations (Jachowski et al. 2016, Helmstedt and Possingham 2017). For example, Dunham and Minckley (1998) found no associations between genetic diversity of translocated populations of desert pupfish and the genetic diversity of the donor population, instead of finding that the number of fish introduced was most important. In contrast, genetic diversity of donor populations may be the most important factor in determining genetic diversity of introduced populations on a shorter timescale, as found for Oregon chub (*Oregonichthys crameri*) from 3 to 24 yr following introduction (DeHaan et al. 2016, but note that *O. crameri* have limited movement potential compared to bull trout). In general, simulations that allow for evaluation of potential effects over very long periods of time provide an important complement to empirical studies in which effect size, sample size, or simply an insufficient temporal duration may confound results.

Our findings support a multifaceted approach that considers factors other than simply genetic diversity when selecting source populations (George et al. 2009). However, it is important to note that our simulations model neutral genetic diversity and structure only. We did not include adaptive genetic variance, which would directly influence demography and may be linked to higher probabilities of reintroduction success and persistence when individuals are sourced from nearby populations (Weeks et al. 2011; but see Neraas and Spruell 2001, DeHaan and Bernall 2013) or those with similar environments (Wang and Bradburd 2014). Future reintroduction efforts will likely incorporate more powerful genomic or transcriptomic approaches in selecting and evaluating source populations for reintroduction (He et al. 2016). Thus, genetic diversity is an important component of reintroduction strategies and selection of source populations; however, our results indicate that the use of neutral genetic variation alone to select source populations may not ultimately influence the genetic diversity and structure of bull trout populations due to genetic drift.

Our results revealed several management-relevant outcomes. In general, patches in the upper Sullivan Watershed were among the most consistently occupied, providing support for targeting the Sullivan Watershed for reintroduction of bull trout in the lower Pend Oreille system (see also Dunham et al. 2014). Current management has focused on this watershed as a candidate for reintroduction. Efforts targeting the Sullivan Watershed include barrier removal, such as deconstruction of the 17 m high Mill Pond Dam in 2017, extensive habitat improvements, nonnative fish removal, and development of a local supplementation facility (hatchery; Seattle City Light 2010). Le Clerc and Tacoma were occupied only in the most favorable of simulations (high stray rate, High *K*) and saw low occupancy in Low *K*, low stray simulations—even in the absence of barriers. Therefore, under the scenarios tested in this model, these watersheds were not as favorable as Sullivan. In general, a combination of management practices (e.g., barrier removal) and improved empirical understanding of life histories and biological attributes of these populations will help determine whether, and under which conditions, Le Clerc and Tacoma offer viable habitats in which bull trout will persist. Finally, in many simulations (particularly High *K* and high stray rates), population sizes were unrealistically large compared to observed densities in the wild. Therefore, simulation results should be interpreted relative to each other rather than as absolute estimates of population size. It is worth noting that if a reintroduction is implemented, evaluation of genetic responses would provide an important means of evaluating reintroduction success, as well as the validity of assumptions we used in generating model-based evaluations of reintroduction scenarios.

Spatially explicit, individual-based simulations offer many advantages in evaluating system-specific dynamics, including uncovering complex mechanisms, intrinsic properties of a system, and evaluating, to the best of our ability, possible outcomes of management practices (Armstrong and Seddon 2008, Landguth et al. 2014, Day et al. 2018). Our study demonstrates the utility of a demogenetic simulation approach in evaluating multiple complex and interacting factors, including genetics, life history, and the landscape, in influencing a range of potential outcomes from the reintroduction of a threatened species. For species that persist in metapopulations, for which movement through and interaction with the landscape is predicted to be a vital component of persistence, SIBMs provide a unique and powerful method for exploring spatial processes and their role in persistence of these populations and species (Jager and DeAngelis 2018). For example, there is a growing body of research evaluating the effect of climate change on bull trout and many cold-water specialists (Eby et al. 2014, Jones et al. 2014, Falke et al. 2015, Kovach et al. 2015). SIBMs allow explicit incorporation of climate projections and their interactions with other factors at the landscape level to simulate a dynamic landscape—and species response to it. Second, removal of dams and instream barriers is growing in practice (Bellmore et al. 2017), and specific scenarios of barrier removal in the watershed in this study could be simulated to evaluate their demogenetic effects of reintroduced bull trout. In summary, CDMetaPOP and a range of other SIBM platforms (e.g., HexSim: Schumaker and Brookes 2018) offer an important complement to population viability analyses that often more comprehensively evaluate the response of demographic processes to specific parameters (e.g., Benjamin et al. 2017, Brignon et al. 2017) but that often do not evaluate the landscape in a dynamic, spatially explicit way. Generalizations are often difficult for species with complex life histories, specific habitat needs, and migratory behavior (Rieman and Dunham 2000, Dunham et al. 2011, Hand et al. 2016). The role of system-specific demogenetic simulations will likely only grow as the need for evaluation of reintroduction and management strategies continues (Scribner et al. 2016), and as the fields of landscape and metapopulation ecology continue to converge (Howell et al. 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2589/full