Evaluation of Reconnection Options for White Sturgeon in the Snake River Using a Population Viability Model

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Abstract.— This paper describes a simulation study of reconnection options for white sturgeon *Acipenser transmontanus* subpopulations in adjacent river segments above and below CJ Strike Dam on the Snake River, Idaho, USA. In contrast to the downstream river segment, the upstream river segment is long and has areas that are suitable for spawning during normal and wet hydrologic conditions. We evaluated demographic and genetic consequences of upstream and downstream passage using different model assumptions about trashrack spacing and density-dependent effects on the spawning interval. Our genetic results predict that, although reconnection would introduce new alleles to the upstream subpopulation, it would also preserve alleles from the downstream subpopulation by propagating them in the larger subpopulation above the dam. Our demographic results predict that halving the space between trashracks would have large and unequivocal benefits, whereas the predicted effects of reconnection were smaller and more sensitive to model assumptions. Simulated upstream passage tended to benefit both subpopulations only in the absence of density-dependent limitation. In the presence of density dependence, the combination of halved trashrack spacing and upstream and downstream passage produced the best results. Narrower trashracks kept spawning adults in the upstream segment with spawning habitat, while allowing their progeny to migrate downstream. Screening appears to be the best option for such a species in this configuration of a long river segment acting as a demographic source above a short one acting as a demographic sink.

Introduction

This book describes the research and statuses of anadromous sturgeon species worldwide. Loss of habitat threatens many fishes. This is true whether the habitat is actually destroyed or simply lost to the population because barriers prevent access to it. The fact that sturgeons require multiple habitats, potentially separated by long distances, makes this group particularly vulnerable to habitat loss, followed by population decline and extinction. This symposium highlighted two significant habitat threats facing sturgeon: degradation of estuaries and development of large rivers (Munro 2007, this volume). All sturgeons spawn in freshwater (Bemis and Kynard 1997). Consequently, habitat fragmentation by dams is a

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significant concern during movement to freshwater, for these and other anadromous species (Peter 1998). From a population perspective, losing access to a required habitat has the same effect as destroying it.

Our paper focuses on far-inland subpopulations of white sturgeon that inhabit river segments between dams in the Snake River. Historically, these subpopulations were likely potamodromous (migrating within the Columbia and Snake rivers) and semianadromous (migrating to the Columbia River estuary). Today, a primary concern is that dams are having an adverse effect by isolating subpopulations. But, it is not entirely accurate to say that dams isolate subpopulations. Dams have two main effects: first, they restrict access for each subpopulation to a subset of the types of large-river habitat that are available in the river as a whole. Second, as semipermeable barriers, dams cause asymmetric migration, with considerably more downstream than upstream movement. We envision these two effects as pathways leading to higher extinction risk unless efforts are made to avoid them (Figure 1).

Restricted access creates a problem if habitats needed during different seasons or life stages are not available. We believe that free-flowing habitat is important for sturgeon spawning and as refuge from episodes of poor water quality, if and when they occur, in reservoirs. Simulation results suggest that extinction risk for individual subpopulations of sturgeon is high in river segments with too little free-flowing habitat (Jager et al. 2002). However, white sturgeon in reservoirs tend to have higher condition factors (Lepla and Chandler 1995), suggesting that access to both adequate free-flowing habitat for spawning and good-quality reservoir habitat might be an asset.

Although spawning habitat is undoubtedly important, it is entirely possible that sturgeon require other riverine features, not yet identified. According to Humphries and Lake (2000), attention to flow-related habitat for spawning has obscured the larger role of in-
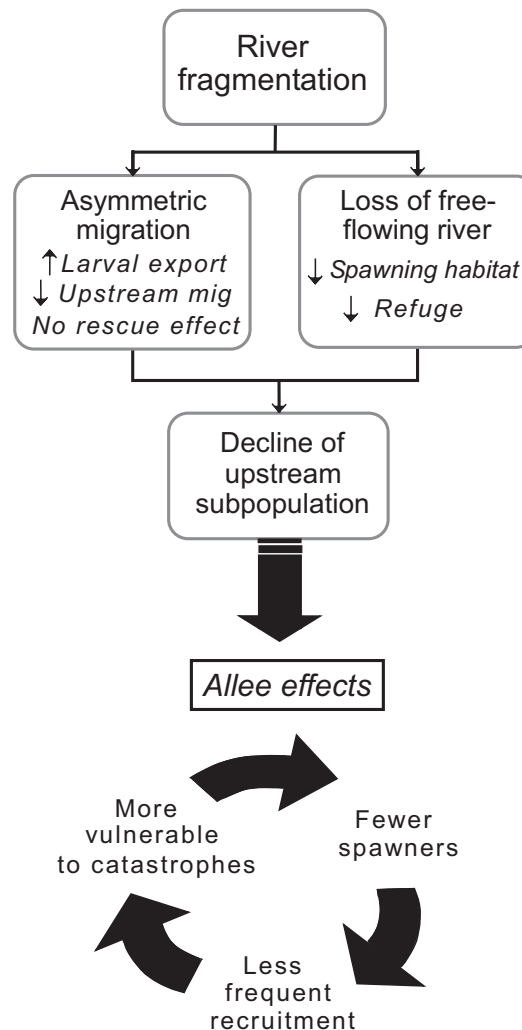

FIGURE 1. Schematic of extinction risks associated with river fragmentation.

cubation habitat for native species in Australian rivers. The larvae of most riverine fish species require shallow, slow-water habitats where productivity of small prey is higher, riparian vegetation provides structure, and predators are excluded (Bowen et al. 2003). It remains unclear to what extent incubation habitat contributes to recruitment in white sturgeon (Coutant 2004). Perrin et al. (2003) proposed that productive areas differ in regulated and unregulated rivers and in confined and unconfined channels. They recovered eggs

and larvae mainly in side channels and confluence areas of the unregulated Fraser River. Habitat diversity alone could be important by offering protection from episodic, local threats and by providing prey habitat. Habitat characteristics (e.g., slackwater, habitat diversity) that ensure a plentiful supply of prey (e.g., salmon or shad carcasses, mussel beds, and other benthic prey) for older sturgeon may be important to enhance overwinter survival and increase the frequency of female spawning (Bevelhimer 2002).

Asymmetric migration (Figure 1) first reduces population sizes and, then, prevents immigration that might "rescue" those that reach local extinction (Jager et al. 2001). Dams that lack upstream passage prevent upstream migration. Downstream migration can easily be too high to sustain the upstream population (Figure 1). Sturgeon small enough to become entrained into the turbines move downstream (whether or not they survive is another matter). In addition, larvae may be exported and lost from upstream subpopulations in shorter river segments with spawning areas too close to the dam. Larval export is a problem shared by other native species of riverine fishes in fragmented rivers (e.g., Plantania and Altenbach 1998). Asymmetric migration is a more important concern for upstream subpopulations than for downstream subpopulations that receive immigrants from upstream.

Once they become small as a result of factors described above, populations are always at higher risk due to Allee effects—a tendency for small populations to decline (bottom of Figure 1). Mechanisms for extinction attributed to chance events, demographic stochasticity, include years with catastrophes (e.g., fish kills) and years with skewed sex ratios during which spawners fail to mate (Engen et al. 2003). Female sturgeons spawn less frequently than most fishes, and are therefore more likely to experience spawner limitation.

Because upstream movements between river segments are not currently possible in the Snake River, there is a danger that upstream subpopulations will be lost. For this reason, reconnection of subpopulations between dams, via fish ladders, translocation, or stocking, is being considered. The hope is that reconnection would eliminate risks associated with the left pathway in Figure 1.

Connecting subpopulations has potential risks as well as benefits. In the Snake River, there is no clear evidence that a growing subpopulation exists that can withstand removal of individuals to other segments. Human-caused problems that prevent subpopulations in some river segments from growing may act as demographic sinks when connections with other segments are established. Fixing these local problems first may ensure that reconnection options are more successful. Reconnecting subpopulations could also have adverse genetic consequences. Species with a strong stock structure that evolve in isolation become adapted to the local environment and subsequently lose fitness if they interbreed with stocks adapted to conditions in different parts of the river.

Case Study

In this study, we use a subpopulation viability model to quantify the costs and benefits to the white sturgeon metapopulation of reconnecting populations in two river segments in the Snake River: Bliss Dam to CJ Strike Dam and CJ Strike Dam to Swan Falls Dam (Figure 2). The river segment above CJ Strike Dam has conditions more favorable for spawning and incubation than the segment below the dam. Consequently, restoring upstream linkages between these two segments could potentially provide spawning habitat for adults in the downstream segment. We use a simulation approach to evaluate upstream passage as a means of restoring upstream connection between the two subpopulations. The main question we address here is: "What reconnection options (upstream and/or downstream passage) result in larger upstream and downstream subpopulations than those that would exist without reconnection?" In addition, we evaluate the effect of model assumptions on our results.
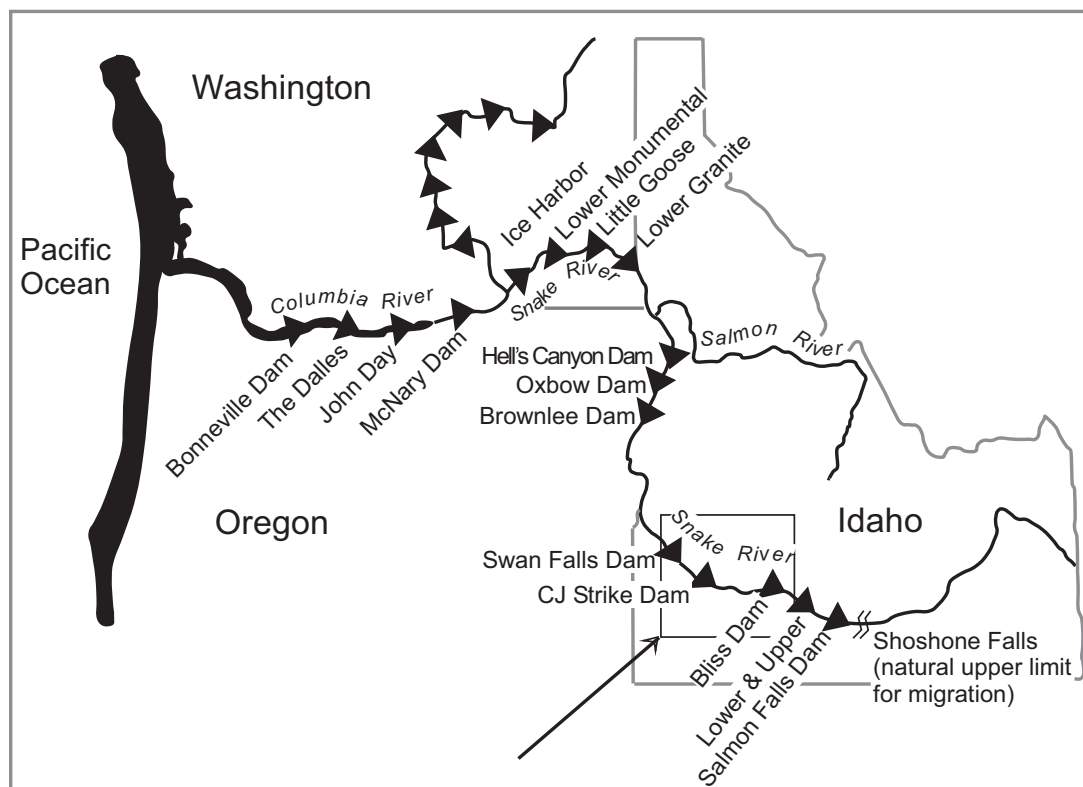
FIGURE 2. These simulations represented the Snake River, Idaho, between Shoshone Falls Dam and Swan Falls Dam. The particular segments of interest here are the downstream segment between Swan Falls Dam and CJ Strike Dam and the upstream segment between CJ Strike Dam and Bliss Dam.

River Segment above CJ Strike Dam

The Snake River below Bliss Dam runs 106 km to CJ Strike Dam (Figure 2). Waters released from Bliss Dam flow through a narrow upper section with large rapids and deep, turbulent run-and-pool habitats. The river transforms into a steep canyon, then meanders slowly through braided channels in a low-gradient section and slows to join the 39-km reservoir pooled behind CJ Strike Dam (Lepla and Chandler 1995). The white sturgeon subpopulation above CJ Strike Dam is the largest subpopulation in the Snake River above Hells Canyon Dam and one of two remaining naturally reproducing subpopulations in the Snake River. Lepla and Chandler (1995) estimated a population size of between 1,938 and 4,445 individuals greater than 80 cm fork length.

River Segment below CJ Strike Dam

The Snake River below CJ Strike Dam extends 57.9 km to Swan Falls Dam (Figure 2). The free-flowing river extends for 17.3 km before entering Swan Falls Reservoir (IPC 2003). This segment, referred to as CJ-SF, has a low gradient and is dominated by shallow runs and island complexes, with few deep pools (Anglin et al. 1992). A 1994–1996 survey estimated a subpopulation of between 473 and 1,565 individuals (>90 cm fork length) below CJ Strike Dam (Lepla and Chandler 1997). In contrast to the subpopulation above the dam, this river segment shows little evidence of recruitment.

Other River Segments

Simulations also include four other river segments (Figure 2):

- Shoshone Falls (the historic upstream limit of white sturgeon distribution in the Snake River) to Upper Salmon Falls Dam,
- Upper Salmon Falls Dam to Lower Salmon Falls Dam,
- Lower Salmon Falls Dam to Bliss Dam, and
- Below Swan Falls Dam.

The segment between Shoshone Falls and upper Salmon Falls Dam contains both free-flowing river and a current population of more than 700 white sturgeon, but the next two downstream are short, reservoir segments with few white sturgeon. The segment below Swan Falls is included in these simulations simply to provide realistic downstream boundary conditions.

Methods

We conducted simulation experiments with a model designed for population viability analysis (PVA). The model simulates population dynamics and predicts the future viability of white sturgeon subpopulations in the Snake River. Below, we review the structure of the model and provide references that give more details, we describe aspects of the model that deal with simulating reconnection in detail, and we describe our simulation experiments.

The PVA model is a stochastic model that simulates a sample of replicate subpopulations into the future using an annual time step. Subannual processes are represented statistically. Spatially, the model tracks individuals in each river segment between dams as members of the same subpopulation. The primary demographic prediction of the model presented here is final population size. Two genetic predictions, the final number of original and introduced alleles, are described below. Downstream migration between adjacent segments is influenced by hydrologic year, turbine type, and individual girth, as is described further below.

We simulate future environmental conditions in the Snake River as stochastic sequences of hydrologic-year types (i.e., dry, normal, or wet). A Markov model simulates transition from one type to another, with probabilities estimated from the historical record between 1912 and 1995. We defined normal years as those with annual inflows to Brownlee Reservoir between 4,616 m³/s and 7,730 m³/s. Wet and dry years fall on either end of this range.

In these simulations, age-0 fish were exposed to the following risks: baseline mortality, mortality due to extreme temperatures during incubation, larval export, and mortality due to poor water quality in summer. Sources of mortality applied to older fish included baseline mortality, harvest and hooking, poor water quality in summer, and turbine mortality. Simulation of these factors is described in Jager et al. (2002).

Below, we focus on describing aspects of the model that pertain specifically to these simulation experiments. Other aspects are described in Jager et al. (2002). The first section below explains two alternative assumptions about hydrologic conditions required for spawning below CJ Strike Dam used in the simulations. The next three sections describe aspects of the model specifically related to reconnection: upstream passage, turbine mortality, and screening and downstream passage. Next, we describe initial conditions for the model, followed by a description of the genetic and demographic response variables reported for these simulations. The final section outlines the design of our simulation experiments.

Spawning

High spring flows are considered important for the spawning of white sturgeon (Parsley and Beckman 1994). Although the PVA model is designed to represent recruitment processes mechanistically in response to average spring flows and weighted usable area for spawning and rearing during different hydrologic year types, the simulations performed for this paper use a simpler alternative. For each river segment, we designate which hydrologic year types

(wet, normal, or dry) provide suitable conditions for spawning.

Above CJ Strike Dam, we assume that spawning can occur in wet and normal years. Variation in the percentage of juvenile white sturgeon surveyed between 1979 and 2000 suggest that higher recruitment occurred in years with normal and above-normal spring flows (IPC 2003). Below CJ Strike, we consider two assumptions: (1) habitat for spawning is never present and (2) habitat for spawning is only present in wet years. Although habitat analysis suggests that spawning habitat should be available in wet years below CJ Strike Dam, empirical surveys found little evidence of recruitment during five consecutive high-flow years from 1982 to 1986 or during four consecutive high-flow years from 1996 to 1999 (IPC 2003). The reconnection scenarios listed in Table 1 allow us to consider both cases.

Under favorable hydrologic conditions, the PVA model evaluates reproduction annually for each subpopulation as described by Jager (2001). Eligible spawners form a mating aggregation that participates in broadcast spawning. Each egg produced by females inherits genetic material (alleles) from the female parent and from a male parent selected at random from the aggregation.

We consider two possibilities for determining the spawning interval for females. In half of the scenarios, we simulate a fixed spawning interval of 6 years for females. In the other half, the interval, I, depends on the density of spawners, where D_t is the density of spawners in year t, $D_{opt} = 5$ adults/km, $I_{min} = 3$ years, and $I_{lag} = 10$ years:

$$I(D_t) = I_{min} + \frac{I_{lag}D_t^2}{D_{opt}^2 + D_t^2}$$

Upstream Passage

We simulate upstream passage by setting the rate of upstream movement equal to the maximum downstream rate. In other words, each individual experiences the same annual probability of moving upstream and the number of sturgeon that move upstream increases in proportion to the size of the downstream subpopulation. We assume that sturgeon ages 1 and older are equally likely to move upstream when upstream passage is available.

Turbine Mortality

Each individual sturgeon older than age-0 simulated in the model has a chance of attempting downstream migration each year (Jager et al. 2002). This chance reaches a maximum of 0.02 per year when sturgeon densities exceed the capacity of the river habitat. Once an individual "decides" to move downstream, there are two options: it may spill over the dam or entrain through the turbines. We make the simplifying assumption that the likelihood of entrainment for sturgeon migrating downstream in a particular hydrologic year type is the same as the proportion of flow entrained. Thus, entrainment is less likely in wet years because the proportion of flow spilled over the dam is higher in wet years than in dry years. We assume that individuals spilled over the dam survive.

Individuals that are slated to move downstream, but that do not spill over the dam, may avoid entrainment if they are broader in girth than the distance between bars in the trashrack. As the name implies, trash racks are designed to screen out logs and other large debris that might damage the turbines. In some scenarios, we manipulate the trashrack spacing by reducing the spacing by half. Given that an individual sturgeon is small enough to be entrained, its likelihood of being struck and killed by a turbine depends on the size of the fish (Figure 3). The risk of blade strike increases linearly with increasing sturgeon size, and the slope of this relationship differs for different types of turbines. CJ Strike Dam has three vertical fixed-blade turbines (FERC 2004). Those individuals that survive passage through the turbines are relocated to the next downstream segment. Narrower spacing between trashracks screens out a size range of sturgeon that are currently small enough to pass through trashracks, but large enough to be
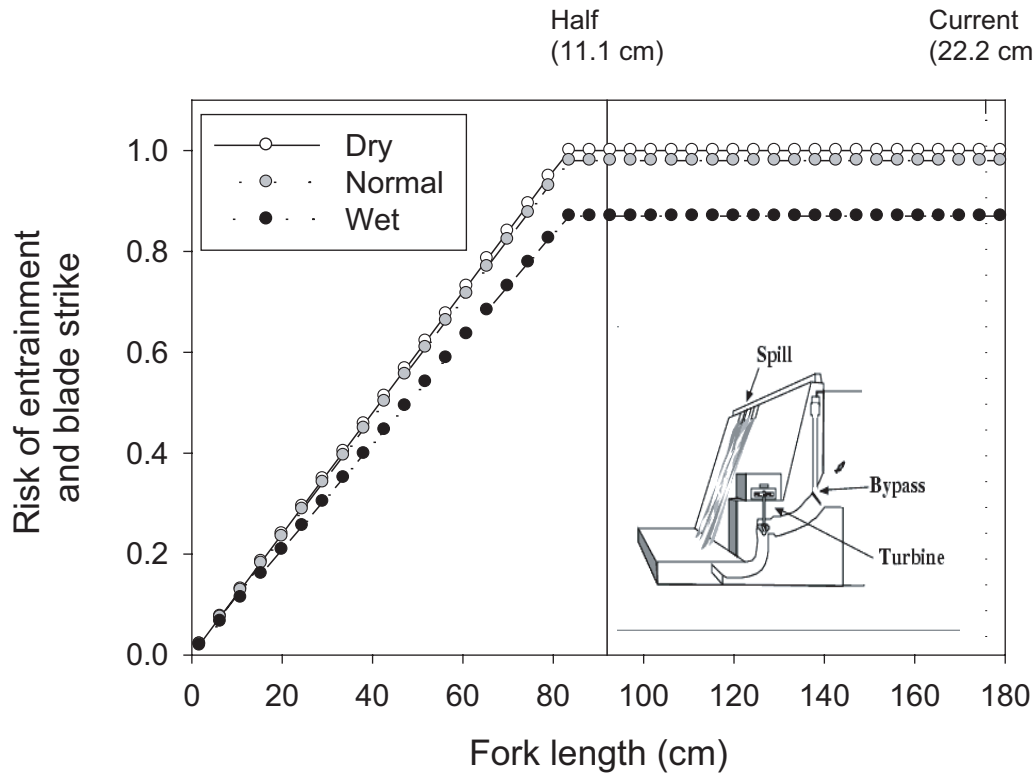
FIGURE 3. The risk of turbine strike for the ~2% of white sturgeon that attempt to migrate downstream annually results from two sequential events: Entrainment of the fish through turbines (more likely in dry years than wet years), and the turbine blade striking the fish (more likely for larger fish). Size thresholds for sturgeon excluded by current and halved trashrack spacing are indicated.

excluded by the new spacing, and prevents them from becoming entrained into turbines and risking exposure to blade-strike mortality

Screening and Downstream Passage

Because fish that move upstream are subsequently subject to entrainment and turbine mortality at CJ Strike Dam, our simulation experiments evaluate the effects of trashrack spacing and downstream passage to see whether they influence the efficacy of upstream passage.

If a particular individual chooses the downstream segment as its desired destination, it may or may not succeed. The sturgeon may attempt to move downstream via the spillway (i.e., over the dam, particularly in wet years),

via entrainment with flow through the turbines, or through a downstream passage facility (Figure 3). We estimated the sturgeon's diameter from empirical data from fork length [FL] as $0.2765/\pi \, FL^{1.07}$. If the sturgeon is too large to pass through screens, we assume that it is unable to move downstream unless there is a downstream bypass facility. Simulations with downstream passage differ from others in two respects: (1) larger (excluded) sturgeon may move downstream without turbine mortality, and (2) the size-structure of down-migrating fish more-closely mirrors that of the upstream subpopulation.

We simulated a number of scenarios with downstream passage (Table 1). To simulate downsteam passage, we assume that sturgeon

T<small>ABLE</small> 1. The 24 options simulated for CJ Strike Dam vary model assumptions (columns two and three) and reconnection scenarios (columns four and five). Model assumptions varied concern the potential for spawning below CJ Strike Dam, whether or not density influences spawning interval. Alternating regular and italic fonts are used below to indicate changes in model assumptions.

| | Model assumptions | | Reconnection scenario | |
Option	Spawning below CJ Strike Dam	Density-dependent spawning?	Trashrack spacing	Passage, up and downstream
1	Never	No	Current	None
2	Never	No	Current	Up
3	Never	No	Current	Both
4	Never	No	Half	None
5	Never	No	Half	Up
6	Never	No	Half	Both
7	*Never*	*Yes*	*Current*	*None*
8	*Never*	*Yes*	*Current*	*Up*
9	*Never*	*Yes*	*Current*	*Both*
10	*Never*	*Yes*	*Half*	*None*
11	*Never*	*Yes*	*Half*	*Up*
12	*Never*	*Yes*	*Half*	*Both*
13	Wet years	No	Current	None
14	Wet years	No	Current	Up
15	Wet years	No	Current	Both
16	Wet years	No	Half	None
17	Wet years	No	Half	Up
18	Wet years	No	Half	Both
19	*Wet years*	*Yes*	*Current*	*None*
20	*Wet years*	*Yes*	*Current*	*Up*
21	*Wet years*	*Yes*	*Current*	*Both*
22	*Wet years*	*Yes*	*Half*	*None*
23	*Wet years*	*Yes*	*Half*	*Up*
24	*Wet years*	*Yes*	*Half*	*Both*

large enough to be excluded by trashracks find the bypass facility and travel downstream with no risk of mortality. This is a reasonable assumption for sturgeon, which grow quickly and, upon entering the downstream segment, might experience a much lower level of predation risk than salmon would.

Initial Conditions and Calibration

Simulations were initialized with recent estimates of the initial densities of sturgeon greater than 43 cm. For example, in one replicate simulation, this resulted in 772 fish below Shoshone Falls, 0 in Upper and 38 in Lower Salmon Falls reservoirs, 2,662 below Bliss Dam, and 726 below CJ Strike Dam. We also specified initial size distributions (percent of individuals less than 95 cm, between 95 and 170.5 cm, and greater than 170.5 cm) based on recent stock assessments in these river segments (Lepla and Chandler 1995, 1997; Lepla et al. 2002, 2004).

We used a previously calibrated value of age-0 survival, $S_y = 0.0002$. This value was obtained using simulations with current trashrack spacing, no passage, and a density dependent spawning interval and gave reasonable agreement to current stock assessments in historical simulations from presumed conditions taken

from those below Hell's Canyon Dam to present.

Genetic Responses

We quantify the potential for genetic introgression by simulating private alleles, defined as alleles present in one subpopulation but not the other. In the simulations described here, we simulated a single locus with four private alleles and four shared alleles initially present in each subpopulation. We report the final number of original alleles preserved in each subpopulation, where the maximum number is eight (neglecting mutation). We also report the final number of introduced alleles (private alleles that originated in the other river segment) found in each subpopulation. Because we also simulated three subpopulations in river segments upstream of the two segments of interest, the number of alleles can be as high as 24 (four private alleles per segment times five segments plus four shared alleles).

Demographic Responses

We consider upstream and/or downstream passage most beneficial in win–win situations: those for which passage increases average final population sizes (Nf) both above and below CJ Strike Dam compared with those of the corresponding baseline scenario without passage. However, alternative definitions of a successful reconnection are possible. Because the downstream population is smaller and at greater risk of extinction, we might be interested in reconnection strategies that increase the population below CJ Strike without too much negative impact on the population above CJ Strike. Success along these lines is measured by the index NT500, defined as the sum of final population sizes capped at an arbitrary size of 500 individuals, which prevents the sum from being dominated by one healthy population at the expense of others.

Model Scenarios

Reconnection scenarios.—To evaluate the potential benefits of providing upstream passage at CJ Strike Dam, we simulated 24 scenarios (Table 1). These represent all eight combinations of assumptions about hydrologic conditions for recruitment below the dam (only in wet years versus never), density dependence (or not), and screening (current versus halved trashrack spacing). For each set of assumptions, we simulate three passage options: none, downstream passage, and both upstream and downstream passage. The above simulations assume that spawning is possible during wet and normal years in the segment above CJ Strike Dam. These scenarios address the left risk pathway in Figure 1.

Predam scenarios.—In addition, we simulated two predam scenarios with no dam between Bliss and Swan Falls dams, one with and one without density dependence. We included these scenarios because the other reconnection options (those described above) do not change the relative amounts of free-flowing river and reservoir habitat available, whereas removing the dam increases the length of free-flowing river by 46%. These scenarios remove the right risk pathway depicted in Figure 1.

For each scenario, we ran 100 replicate simulations over 500 years. Statistics reported include final subpopulation size, the number of introduced alleles acquired, and the number of original alleles remaining. For each of three response variable, we report subpopulation averages and standard errors for the replicate simulations. We compare baseline responses with those of each reconnection option (Table 1).

Results

Demographic

Upstream passage increased the simulated final sizes of both subpopulations relative to the no-passage baseline only in scenarios that assumed no density dependence (Appendix A). These win–win scenarios are illustrated by ratios that exceed one in Figure 4. Upstream passage was beneficial to both subpopulations in two scenarios with current trashrack spacing
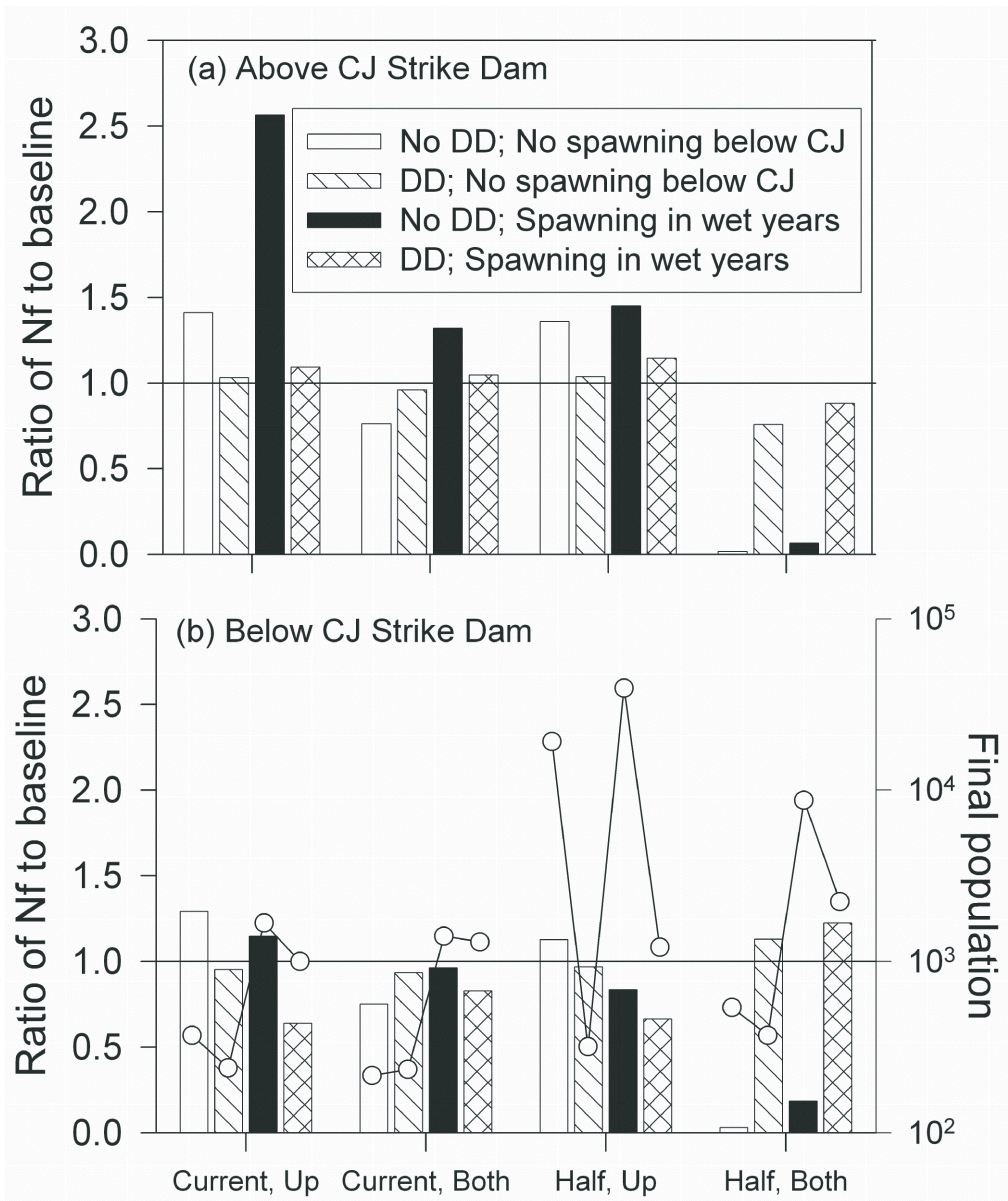
FIGURE 4. Bar height indicates the ratio of final population size, Nf, for the reconnection scenario indicated on the *x*-axis to that of the corresponding baseline scenario with no passage. Scenarios combine current (Current) or half trashrack spacing (Half) with upstream passage (Up) or both upstream and downstream passage (Both). The horizontal line at one is the line of no net effect. The four bars represent different model assumptions about density dependence (DD) and the potential for spawning below CJ Strike Dam. Simulated results are shown for the populations (a) above, and (b) below CJ Strike Dam. The final population size, Nf, is predicted to be more than 6,000 above CJ Strike Dam for all scenarios (not shown), but Nf below CJ Strike Dam varies, as shown by the line graph in (b).

(solid white and black bars in Figure 4, "Current, Up"), and in the scenario with halved trashrack spacing that assumed spawning was not possible below CJ Strike (white bar in Figure 4, "Half, Up"). Adding downstream passage was not beneficial in scenarios that assumed no density dependence (solid bars in "Current, Both" and "Half, Both" in Figure 4).

When we assumed that spawning intervals would increase at high density (striped and crosshatched bars in Figure 4), there were no win–win scenarios that increased subpopulations both above and below the dam. However, halved trashrack spacing with both upstream and downstream passage resulted in significant increases in the downstream population, with the upstream subpopulation remaining large (Figure 4). The NT500 index also favors this option (Appendix). Thus, adding downstream to upstream passage benefited the downstream subpopulation only when density dependence was simulated (Figure 4b), and at the expense of the subpopulation above the dam.

Halved trashrack spacing increased the two subpopulations in all scenarios, sometimes substantially, by increasing the subpopulation above the dam and providing trickle-down benefits downstream. This was true with or without upstream passage. Returning sturgeon upstream via upstream passage was beneficial if the possibility of spawning downstream was nil and no density dependent impacts were simulated upstream (open bar in Figure 4b, "Half, Up" scenario).

We expected the reference scenarios without CJ Strike Dam, and therefore more free-flowing habitat, to grow a larger single population than the two combined subpopulations of other reconnection options. As expected, the predam scenario produced a larger average final population than the combined sizes of the two segments in other reconnection scenarios in simulations with density dependence, (solid bars in Figure 5). In the absence of density dependence, the combined population size produced by scenarios with halved trashrack spacing and no downstream passage exceeded that of the corresponding predam scenario (striped bars in Figure 5).

Genetic

Providing upstream and/or downstream passage increased the retention of original alleles below the dam (Figure 6). This was particularly true when spawning was possible during wet years. The pattern for introduced alleles acquired and maintained in the population above the dam was more complex. Recall that these alleles could have originated in one of the three populations above Bliss Dam, or they might have been acquired from the population below CJ Strike via upstream passage.

First consider the baseline scenarios with no passage (Figure 6). The number of introduced alleles acquired from upstream was very low in baseline simulations with current spacing but higher in simulations with both halved trashrack spacing and no density dependence. In the former case, few of the 12 alleles private to the three upstream populations migrated to the Bliss–CJ Strike population, or if they did, nearly all were lost to genetic drift. In contrast, the frequencies of alleles acquired from upstream increased in simulations with halved trashrack spacing and no density dependence (Figure 6). We attribute this result to fact that the population above the dam reached much larger final sizes (~9,000 individuals) in these scenarios.

Next, we consider the effect of passage on the acquisition and retention of introduced alleles. In all scenarios, upstream passage increased the final number of introduced alleles (Figure 7). The final number of introduced alleles was especially high in scenarios that assumed no density dependent effects on the spawning interval and those with halved trashrack spacing—the same scenarios that resulted in large final populations. Scenarios with both upstream and downstream passage also maintained higher numbers of introduced alleles, but not quite as many as scenarios with upstream passage alone (Figure 7).
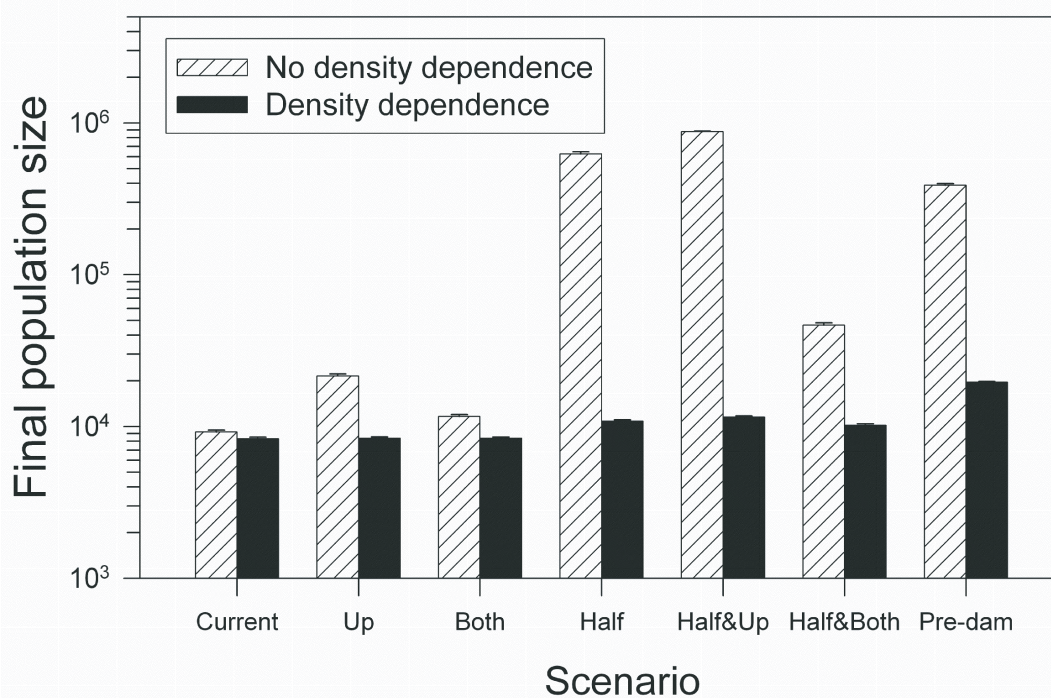
FIGURE 5. For postdam reconnection scenarios we assumed recruitment was possible below the dam in wet years. Bar height indicates the sum of average final population sizes above and below the dam. For the predam scenario, bar height is the final population size of the single population. Results are shown for simulations that assumed density dependence (black bars) and those that did not (striped bars). Scenarios (*x*-axis) combine current (Current) or half trashrack spacing (Half) with upstream passage (Up) or both upstream and downstream passage (Both).

Discussion

The simulated benefits of reconnection depend on model assumptions, whereas those of reduced trashrack spacing appear to be robust. Our simulation results suggest that upstream passage is more likely to benefit both populations when density dependence is weak and downstream passage is not provided. If density dependence is strong, the best we can hope for is that reconnection will permit the upstream population to bolster the downstream subpopulation, at the cost of a smaller, but self-sustaining, upstream subpopulation. The scenarios that accomplished this result required halved trashrack spacing and downstream passage, in addition to upstream passage. Density dependence played an

important role in this situation[1] because the potential for increasing the larger, upstream population is much higher when it is absent. However, the population sizes attained by the upstream population in the absence of density dependence in some scenarios appear unrealistically high to us, suggesting that density dependence is not completely absent in the real world.

Given this uncertainty, perhaps the best course of action would be to implement upstream translocation as a means of determining the responses of the two subpopulations, before in-

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[1] This situation is a river configuration with a larger sturgeon subpopulation in a longer river segment above a smaller subpopulation that has little or no potential for recruitment in a shorter segment.
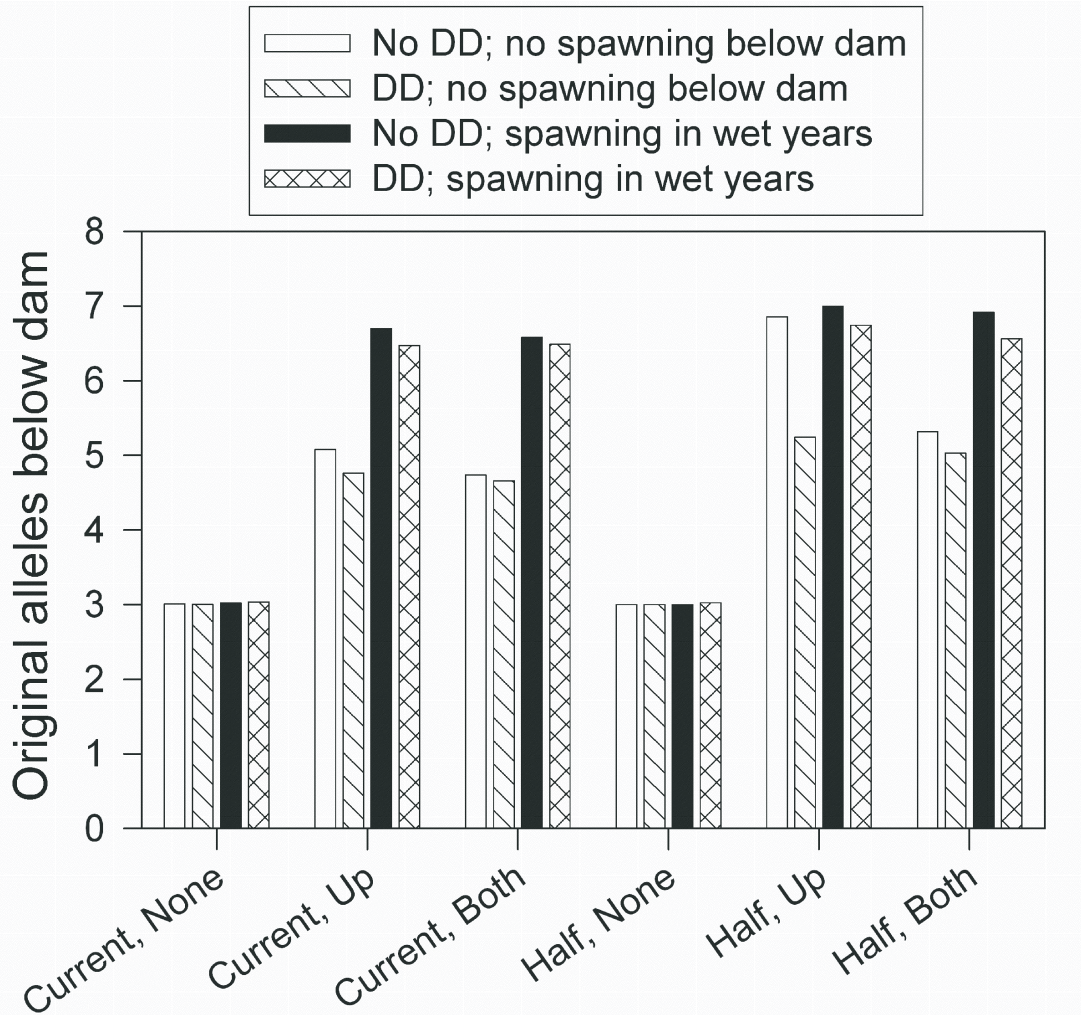
FIGURE 6. Bar height indicates the number of original alleles in the final population simulated below CJ Strike Dam for the reconnection scenario indicated on the *x*-axis. Scenarios combine current or half trashrack spacing with three passage options (none, upstream passage, or both upstream and downstream passage). The four bars represent different model assumptions about density dependence (DD) and the potential for spawning below CJ Strike Dam. Simulated values above the dam are all equal to seven.

vesting in passage structures. Translocation (capturing sturgeon below the dam and moving them above the dam) is one alternative method for providing upstream passage. In a preliminary analysis[2], we compared upstream passage with

upstream translocation (both with halved trashrack spacing). We found that simulated upstream translocation was generally more beneficial than upstream passage because we assumed all sizes of sturgeon could take advantage of upstream passage, whereas the size-selectivity of gear caused translocation to focus on larger individuals (i.e., those closer to breeding age).

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[2] These simulations assumed a density dependent increase in spawning interval.
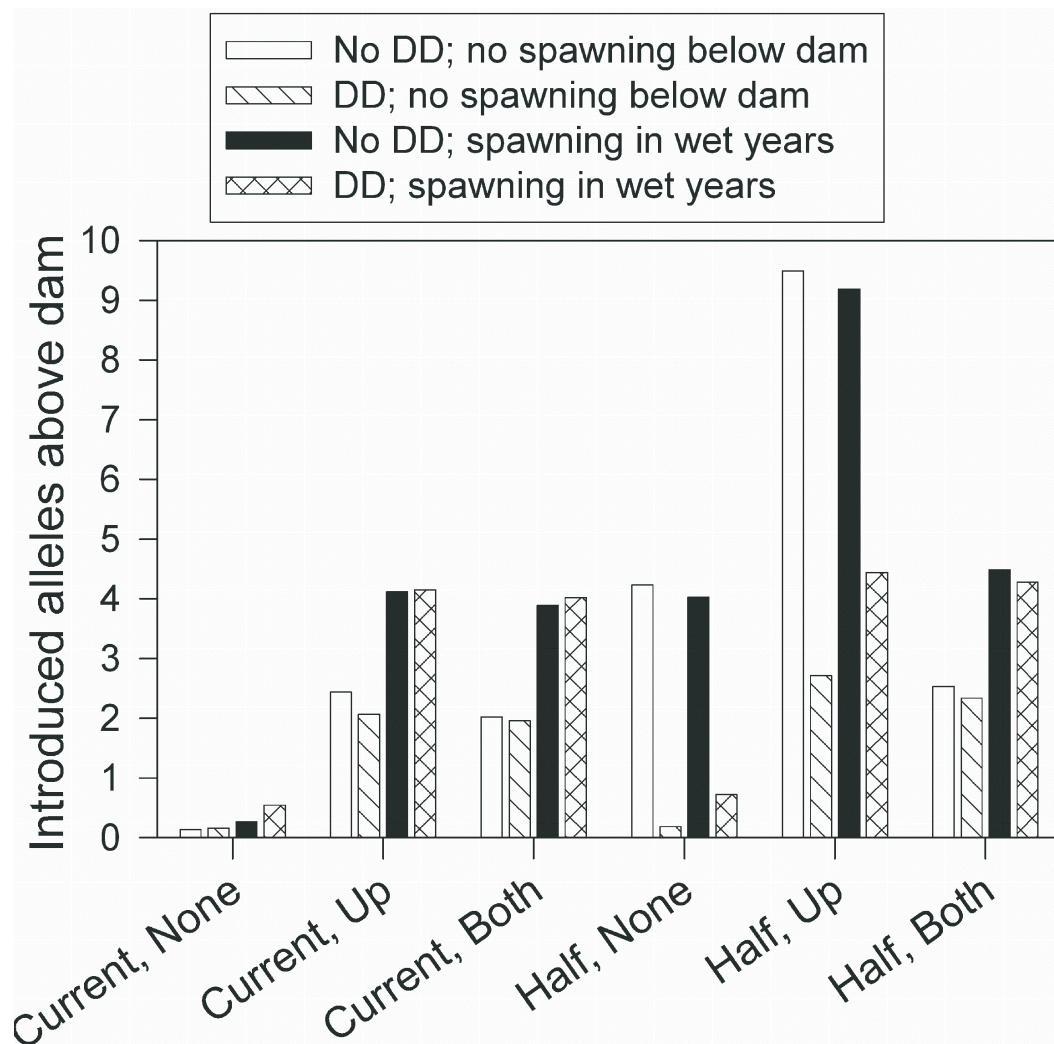
FIGURE 7. Bar height indicates the number of introduced alleles in the final population simulated above CJ Strike Dam for the reconnection scenario indicated on the *x*-axis. Scenarios combine current or half trashrack spacing with three passage options (none, upstream passage, or both upstream and downstream passage). The four bars represent different model assumptions about density dependence (DD) and the potential for spawning below CJ Strike Dam. Simulated values below the dam did not vary much, with a range between 4.0 and 5.5 alleles.

Unlike those of passage, the simulated benefits of halved trashrack spacing were unequivocal: Halved trashrack spacing always increased both the upstream and downstream subpopulations. We imagine that intermediate-sized sturgeon that are excluded by trash bars continued to spawn in the upstream reach, and that some fraction of their offspring move downstream to support the population below the dam. Returning sturgeon upstream via upstream passage was beneficial only when there was no opportunity for spawning downstream and when increased upstream densities did not lead to longer female spawning intervals.

Not surprisingly, predam simulations, (i.e., those with one large population, no dam, and more free-flowing habitat) usually produced better results than simulations with artificial reconnection. This confirms the idea that the amount of free-flowing habitat can be as important as reconnection for species that require free-flowing river habitat. Scenarios with reduced trashrack spacing were the only exception: these produced final populations almost as large, or larger than, the corresponding predam scenarios.

This case study confirms the results of a more-general examination of connection in different river configurations that also used this model (Jager 2006a). In that study, reduced trashrack spacing without upstream passage was found to be the best option for the metapopulation as a whole in configurations with a long river segment above a short river segment (Jager 2006a), but not for short segments above long segments. In the case of translocation, closer trashrack spacing caused the recipient segment to benefit from subsidy by a long upstream segment (Jager 2006b).

The genetic results of this study showed that the number of alleles introduced from other subpopulations increased with upstream reconnection, but the number of original alleles preserved in the downstream segment also increased. By sharing its private alleles with the demographically stronger upstream subpopulation, alleles that originally occurred only in the smaller downstream subpopulation were effectively protected. On the other hand, we observed that introduced alleles were also more likely to be maintained when introduced to a growing upstream population. Given the proximity of the two subpopulations and the benefit of retained alleles that is suggested by this study, reconnection in the situation described here would be more likely to have a positive than a negative genetic impact on these subpopulations.

We conclude that designing a reconnection strategy to help restore subpopulations is not necessarily as simple as one might think. This study highlights the importance of unknown factors, such as density dependence, that are predicted to influence the response. Another study found that response to reconnection depends on river configuration (Jager 2006a). In a third analysis, we evaluated the effects of reconnecting subpopulations in the larger system that adds three river segments above Bliss Dam, none of which is believed to be self-sustaining, to the two segments considered here. We found that connecting pairs of subpopulations in short upstream river segments via upstream passage was not beneficial. Only options that linked series of smaller segments to a self-sustaining downstream source population between Bliss and CJ Strike dams were beneficial. Together, these studies are forming a picture of the benefits and costs of passage for sturgeon, and the uncertainties that need to be resolved.

Providing fish passage through dams is often required during relicensing of hydropower facilities. The goal of these policies is to increase fish populations, particularly those that have experienced declines following impoundment. Because passage structures are costly, it is remarkable how few studies have been done to determine under what conditions recon-nection has actually restored populations. We suggest a need for field studies designed with enough power (enough dams and years/dam) to detect changes in population size before and after implementation of passage options. Such studies would provide a scientific basis for policy decisions, which would help the hydropower industry to allocate resources in a way that is most likely to benefit the fish populations involved.

Acknowledgments

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APPENDIX A. Simulation results for six options representing all combinations of reconnection scenarios and model assumptions. Average and SE final population size (Nf) is reported for subpopulations upstream and downstream of CJ Strike Dam. *T*-test statistics compare Nf with the appropriate no-passage scenario. The last two columns report the sum of average Nf and the NT500 index, the sum of min(Nf, 500) for the two subpopulations combined. Alternating regular and italic fonts are used below to indicate changes in model assumptions.

| Model assumption | | Reconnection scenario | | Bliss Dam to CJ Strike Dam | | CJ Strike Dam to Swan Falls Dam | | *T*-statistic compared to Passage = none | | | |
Spawning below CJ Strike Dam	Density dependence	Trash-rack spacing	Passage	Avg. Nf	SE Nf	Avg. Nf	SE Nf	Above	Below	Combined Nf avg.	NT500 index
never	no	current	none	7,759.4	160.9	287.3	5.5	0.0	0.0	8,046.7	787.3
never	no	current	up	10,942.9	339.1	370.9	10.5	12.7	10.5	11,313.8	870.9
never	no	current	both	5,906.1	115.2	216.2	3.7	–13.4	–15.5	6,122.3	716.2
never	no	half	none	594,778.0	18,702.7	17,028.1	478.0	0.0	0.0	611,806.1	1,000.0
never	no	half	up	808,365.0	13,159.8	19,207.6	524.6	13.4	4.3	827,572.6	1,000.0
never	no	half	both	10,168.9	274.7	538.5	12.6	–61.6	–67.2	10,707.4	1,000.0
never	*yes*	*current*	*none*	*6,675.8*	*99.8*	*250.9*	*2.7*	*0.0*	*0.0*	*6,926.7*	*750.9*
never	*yes*	*current*	*up*	*6,881.7*	*97.9*	*239.1*	*3.0*	*2.1*	*–4.1*	*7,120.8*	*739.1*
never	*yes*	*current*	*both*	*6,404.1*	*96.1*	*234.2*	*2.6*	*–2.8*	*–6.2*	*6,638.3*	*734.2*
never	*yes*	*half*	*none*	*9,089.4*	*142.2*	*328.6*	*3.8*	*0.0*	*0.0*	*9,418.0*	*828.6*
never	*yes*	*half*	*up*	*9,426.4*	*134.0*	*318.2*	*3.6*	*2.4*	*–2.8*	*9,744.6*	*818.2*
never	*yes*	*half*	*both*	*6,889.4*	*96.8*	*371.3*	*3.3*	*–18.4*	*12.0*	*7,260.7*	*871.3*
wet years	no	current	none	7,748.5	185.6	1,461.6	79.9	0.0	0.0	9,210.1	1,000.0
wet years	no	current	up	19,862.5	613.6	1,677.2	78.6	30.3	2.7	21,539.7	1,000.0
wet years	no	current	both	10,223.9	260.9	1,407.6	79.2	11.1	–0.7	11,631.5	1,000.0
wet years	no	half	none	577,999.0	17,769.4	47,025.8	2,252.3	0.0	0.0	625,024.8	1,000.0
wet years	no	half	up	837,400.0	6,314.9	39,322.4	1,618.1	21.5	–4.0	876,722.4	1,000.0
wet years	no	half	both	37,890.2	1,131.7	8,707.4	533.8	–57.2	–27.5	46,597.6	1,000.0
wet years	*yes*	*current*	*none*	*6,758.6*	*91.6*	*1,567.8*	*81.9*	*0.0*	*0.0*	*8,326.4*	*1,000.0*
wet years	*yes*	*current*	*up*	*7,384.8*	*106.8*	*999.8*	*52.2*	*6.3*	*–8.5*	*8,384.6*	*1,000.0*
wet years	*yes*	*current*	*both*	*7,072.8*	*99.8*	*1,300.8*	*68.1*	*3.3*	*–3.6*	*8,373.6*	*1,000.0*
wet years	*yes*	*half*	*none*	*9,028.3*	*132.1*	*1,824.1*	*93.2*	*0.0*	*0.0*	*10,852.4*	*1,000.0*
wet years	*yes*	*half*	*up*	*10,338.4*	*147.0*	*1,210.5*	*56.4*	*9.4*	*–8.2*	*11,548.9*	*1,000.0*
wet years	*yes*	*half*	*both*	*7,951.0*	*116.0*	*2,233.6*	*119.1*	*–8.7*	*3.9*	*10,184.5*	*1,000.0*