

Chutes and ladders and other games we play with rivers. I. Simulated effects of upstream passage on white sturgeon

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Abstract: River fragmentation by dams has often preceded declines in sturgeon populations, which suggests that reconnecting populations would contribute to their recovery. This study used a population viability model to quantify the effects of upstream passage at dams on white sturgeon (*Acipenser transmontanus*) metapopulations inhabiting a series of long (source) and short (sink) river segments. Simulated river systems with high interspersed long and short segments and a long segment far upstream supported the healthiest metapopulations, suggesting biological criteria for siting dams. Contrary to expectation, the model predicted that upstream passage, without screening or downstream passage, was harmful to the metapopulation as a whole. However, upstream passage was beneficial when downstream migration was either restricted (by screening larger fish) or made safe (by providing downstream passage). The combination of upstream and downstream passage was most beneficial at dams above a long river segment. Screening, alone or combined with upstream passage, was most beneficial at dams below a long segment. These theoretical results highlight the need for field research to evaluate management options and provide practical guidance for restoring sturgeon metapopulations in large rivers.

Résumé : La fragmentation des rivières par les barrages précède souvent le déclin des populations d'esturgeons, ce qui laisse croire qu'un rétablissement des connexions entre les populations pourrait contribuer à leur restauration. Un modèle de viabilité de la population permet ici de quantifier les effets des passages vers l'amont dans les barrages sur les métapopulations d'esturgeons blancs (*Acipenser transmontanus*) qui habitent dans des segments longs (sources) et courts (pertes) de rivière. Les systèmes de rivière simulés, à forte alternance de segments longs et courts, qui possèdent un long segment dans la partie amont tout à fait supérieure contiennent les métapopulations les plus saines, ce qui indique qu'il y a des critères biologiques pour le positionnement des barrages. Contrairement aux attentes, le modèle prédit qu'un passage vers l'amont, sans triage ni passage vers l'aval, est désavantageux pour la métapopulation dans son ensemble. Cependant, le passage vers l'amont est bénéfique lorsque la migration vers l'aval est restreinte (par la rétention des poissons plus grands) ou rendue plus sécuritaire (par l'établissement de passages vers l'aval). La combinaison des passages vers l'amont et vers l'aval présente le plus d'avantages dans les barrages situés en amont d'un long segment de rivière. Le tri, avec ou sans passage vers l'amont, présente le plus d'avantages dans les barrages situés en aval d'un long segment de rivière. Ces résultats théoriques démontrent la nécessité de faire des études sur le terrain pour évaluer les options de gestion et ils permettent d'élaborer des recommandations pratiques pour la restauration des métapopulations d'esturgeons dans les grandes rivières.

[Traduit par la Rédaction]

Introduction

The landscape of rivers and streams has changed considerably over the past 200 years. Water flow is now stored behind reservoirs at over 75 000 dams that impound nearly all medium and large rivers in the continental USA (Graf 1999). Dams provide the flexibility to use water when it is needed for irrigation, electricity, and other purposes, but have ecological costs. Impoundment has diminished waterfalls, rapids, and floodplain wetland habitat in rivers (Dynesius and Nilsson 1994). Dams act as semipermeable barriers that bias

migration patterns between fish populations by curtailing safe downstream migration of fishes while preventing upstream migration entirely.

Sturgeon species are uniquely adapted to diverse and dynamic large mainstem rivers, ranging widely to take advantage of scattered and seasonally abundant resources (Beamesderfer and Farr 1997). Habitat fragmentation by dams is considered responsible for declines in sturgeon populations by blocking movements and creating homogeneous reservoirs that reduce habitat diversity (Beamesderfer and Farr 1997). Because of their large size, downstream migration past dams is a particularly hazardous undertaking for sturgeons, and upstream movement past dams is impossible without special provisions.

This leads us to conclude that sturgeon populations should benefit from reconnection. In theory, populations in linked river segments are more likely to recolonize their neighbors after local extirpation, an event more common in short river

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segments fragmented by dams. Reconnection should also increase the likelihood that habitat requirements of all life stages are met by the wider diversity of habitat types available among adjacent river segments.

Riverine populations now separated by dams can be reconnected either by providing upstream passage or by translocating fish captured in one segment to another. Upstream passage is usually accomplished by constructing fish ladders at the dams. Fish ladders are designed for surface-oriented anadromous species with strong swimming and leaping ability (e.g., salmon and shad; Cada and Sale 1993). Current fish ladder designs are less effective for bottom-oriented sturgeons, but sturgeon do occasionally use them (Warren and Beckman 1993). Fish elevators, which have been installed for sturgeon in Russia and Holyoke Dam on the Connecticut River, USA, are effective (Kynard 1998) but costly. Preliminary results with spiral loop fish ladders are promising for sturgeon (Kynard et al. 2003), particularly at smaller, low-head dams.

This research, which relies on simulation, was motivated in part by the lack of available field data on population-level effects of upstream passage. The assumption that upstream passage benefits the fish populations involved has not been adequately tested. Gehrke et al. (2002) suggest that multi-year studies are needed to test this assumption. Although hydropower licenses in the USA often require upstream passage facilities, particularly at dams that block migration of anadromous species, long-term monitoring has not been required (Cada and Sale 1993). The usual measure of success for upstream passage is simply that fish are observed using the passage facilities, and even this criterion has been difficult for sturgeons to meet (Knights et al. 2002).

This study uses a simulation approach to quantify the benefits of reconnecting river segments to a metapopulation of white sturgeon (*Acipenser transmontanus*). Unassisted, voluntary upstream movements of white sturgeon are considered here, and a companion paper considers assisted movements (Jager 2006). Demographic effects of providing upstream passage are quantified, with and without mitigation efforts to reduce entrainment or the associated mortality. I simulate rivers composed of different configurations of long (source) and short (sink) segments to examine how river configuration influences the effectiveness of upstream passage.

The following questions are addressed: (i) What is the magnitude of costs and benefits of upstream passage to each population and to the metapopulation as a whole? (ii) Do costs and benefits to individual populations change depending on the length of the river segments above and below the dam? (iii) How do mitigation measures intended to reduce entrainment mortality influence results? Answers to these questions suggest practical guidelines for restoring sturgeons and fish species with similar ecology by providing upstream passage at selected dams.

Model description

I conducted simulation experiments with a population viability analysis (PVA) model designed to simulate the dynamics and future viability of white sturgeon populations. The simulation experiments described here compare populations simulated in a series of river systems with different configurations

of long and short river segments. Simulated populations in long segments tend to increase (source habitat), and those in short segments tend to decrease (sink habitat). By comparing river configurations, the results of this study provide more general conclusions about situations that might benefit from reconnection.

The PVA model simulates the reproduction and mortality of individual white sturgeon inhabiting a series of adjacent river segments and migration between segments. It uses an annual time step and is driven by a Markov sequence of dry, normal, and wet years (see Jager et al. 2002, 2003). Because individual-based models are stochastic, I report the average and standard error of each response variable among replicate simulations.

Those aspects of the PVA model specific to this study are described below. Other aspects of the model are described in Appendix A. Model parameters and values used in these simulations are listed in Tables 1 and 2. Mortality factors simulated include baseline mortality, density-dependent mortality, temperature- and flow-related mortality during incubation, larval export, turbine strike, and hooking mortality.

River configurations

Pulliam (1988) introduced the distinction between source and sink habitat areas. Metapopulation theory suggests that source river segments support populations that recruit enough offspring to grow in size and export surplus individuals (Hanski and Gilpin 1991; Rieman and Dunham 2000). Populations in sink habitats do not produce a surplus; instead they decline when they are isolated from source habitats. River segments between closely spaced dams that consist of mostly reservoir habitat tend to be demographic sinks for sturgeons for a number of reasons. Short segments dominated by reservoir provide less spawning habitat for sturgeons (Beamesderfer and Farr 1997), and larvae that are produced are more likely to be swept into a downstream segment. I chose the lengths of river segments in the river such that long segments represent source habitats and short segments represent sink habitats.

Results from case studies produce results that may apply only to the particular river under study. Simulating a variety of different river configurations allows this study to draw more general conclusions about the effects of segment length and upstream–downstream position on the benefits of upstream passage because these two influences are not confounded. To initialize the model, I divide the total length of river, $L_{\text{tot}} = 270$ km, into a specified number of segments, $N_s = 6$, with three short segments (40 km) and three long segments (80 km). Twenty upstream–downstream configurations of these six segments (three long and three short) exist. All 20 combinations of short (sink) and long (source) segments shown in Fig. 1 are simulated.

Preliminary results suggested that trickle-down effects to the next adjacent segment could be important in determining the net benefit of reconnection. I therefore added a seventh short segment at the downstream end to minimize boundary effects. By including this extra segment, metapopulation indices account for trickle-down effects on the segment downstream.

Once the physical layout of river segments is established, the free-flowing length of river, L_{ff} , in each segment is esti-

Table 1. Parameter values of the white sturgeon (*Acipenser transmontanus*) population viability model.

| Parameter name | Parameter description | Reference | Baseline value |
|--------------------|--|------------------------------|----------------|
| S_y | First year survival rate (year ⁻¹) | Calibrated | 0.0002 |
| S_j | Survival rate of juveniles (year ⁻¹) | Cochnauer 1983 | 0.855 |
| S_a | Survival rate of adults (year ⁻¹) | Cochnauer 1983 | 0.855 |
| t_{larva} | Duration (days) of demersal larval stage | Brannon et al. 1985 | 1.0 |
| L_0, L_1 | Free-flowing length (km) associated with 0% and 100%, respectively, chance of reaching reservoir | Calibrated | 45, 12 |
| \bar{L} | Average size at first maturity for females, males (cm) | Cochnauer 1983 | 156, 134 |
| L_{SD} | Standard deviation of size at maturity for females, males (cm) | Cochnauer 1983 | 15, 15 |
| A_{egg}, B_{egg} | Intercept and exponent, respectively, of relationship between fecundity (no. of eggs) and fork length (cm) | DeVore et al. 1995 | 0.072, 2.94 |
| M_{down} | Maximum annual chance of attempting downstream migration (at high density) | K. Lepla* | 0.05 |
| K_{vb} | Rate of change in fork length (cm) with age (years) | Lepla and Chandler 1995 | -0.045 |
| T_0 | Initial age (years) | Lepla and Chandler 1995 | -0.795 |
| L_∞ | Maximum size (cm) | Lepla and Chandler 1995 | 275 |
| D_{egg} | Optimal egg density (no.·km ⁻¹) | Calibrated | 35 |
| D_{opt} | Optimal adult density (no.·km ⁻¹) | Fixed | 10.0 |
| P_{sweep} | Maximum chance of export | Calibrated | 0.6 |
| S_{sweep} | Survival of larvae swept downstream | Fixed | 0.1 |
| H_{res} | Length (km) of reservoir assumed suitable for spawning | Fixed | 1.0 |
| B_{strike} | Slope of linear relationship between risk of turbine strike and fork length (cm) | Average for Snake River dams | 0.0092 |
| W_{screen} | Trashrack spacing (cm) | Average for Snake River dams | 17.74 |

*Ken Lepla, Idaho Power Company, P.O. Box 70, Boise, Idaho 83707, USA, unpublished data.

Table 2. Parameter values and initial conditions listed below applied to all segments of the hypothetical rivers.

| Parameter name | Parameter description | Dry years | Normal years | Wet years |
|----------------|------------------------------------|-----------|--------------|-----------|
| $P_{entrain}$ | Probability of entrainment | 0.9956 | 0.9567 | 0.8322 |
| S_{temp} | Age-0 temperature-related survival | 0.8839 | 0.8574 | 0.8080 |

mated from a regression relationship with L_{tot} . Parameter values were estimated from segment length data for nine river segments in the Middle Snake River in the western USA (hereafter referred to as Snake River) ($R^2 = 0.98$) as follows:

$$(1) \quad L_{ff} = 0.724 L_{tot} - 9.486$$

According to this relationship, the short segments contain approximately 50% free-flowing habitat and 50% reservoir habitat, and the long segments contain approximately 60% free-flowing habitat and 40% reservoir habitat.

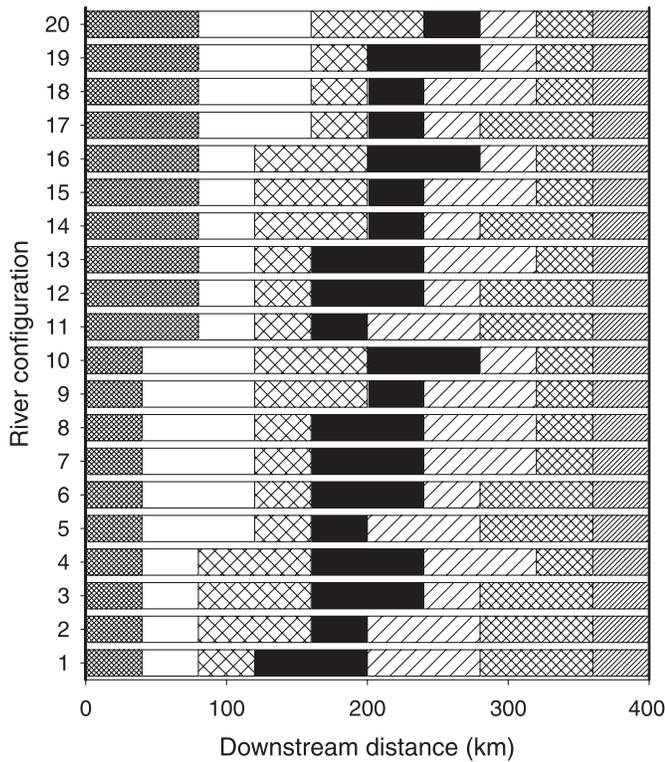
Several other site-specific parameters were needed (Tables 1 and 2). For parameters that would be expected to show neither a longitudinal trend nor a relationship to river segment length, I used average values from the Snake River segments. For parameters that might be expected to show such relationships, I developed empirical relationships based on data for the nine Snake River segments. In some cases, different values were used for wet, normal, and dry hydrologic years (Table 2). Temperature-related age-0 survival, S_{temp} (Appendix A) did not show trends with either distance downstream or segment length. Reservoir retention time, t_R , which influences survival of larval export, S_{larva} , increased with reser-

voir length. I fitted a power relationship between t_R and reservoir length for each hydrologic year type (Fig. 2a; $R^2 = 0.90$ for all three). Average flow during spawning and incubation, Q_{spawn} , showed an increasing trend with distance downstream because of tributary inputs. I fitted a linear relationship (Fig. 2b) for each hydrologic year type ($0.82 \leq R^2 \leq 0.92$). Likewise, Q_{high} , the threshold flow above which flow is adequate for spawning, increased with distance downstream (Fig. 2b; $R^2 = 0.81$).

Simulation of downstream movement

Each year, simulated individuals ages 1 and older have an opportunity to move downstream. The probability that individual i will decide to move downstream, P_d , increases from zero to a maximum value of M_{down} at high densities, with an inflection point at the optimal white sturgeon density, D_{opt} . Let u_i be a random variate drawn for individual i from a uniform distribution on the interval [0,1] (i.e., $u_i \in U[0,1]$). The simulated fish decides to move if $u_i \leq P_d$. The realized downstream migration rate is usually a smaller proportion of the population size than the individual probability because not all individuals succeed in moving downstream, as described below.

Fig. 1. Hypothetical river systems constructed of three long and three short segments, plus one short segment at the bottom. Twenty possible combinations of long and short segments are shown.

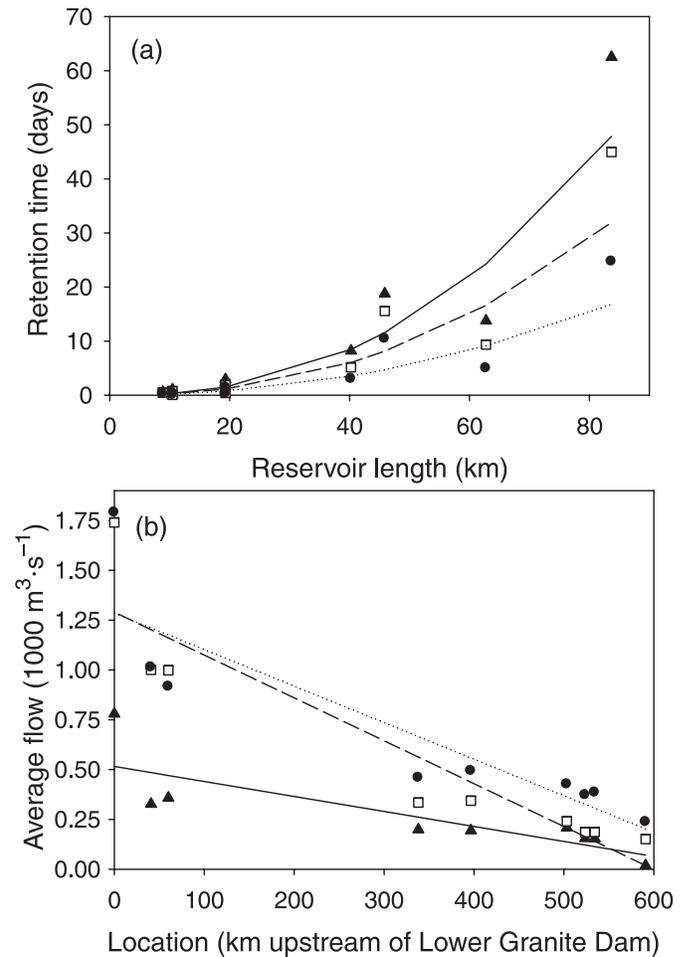


Once a particular individual chooses to move downstream, it is either entrained through the turbines or spilled over the dam. The model assumes that the probability of moving downstream with spilled flow is equal to the proportion of flow spilled, P_{spill} . A particular fish i is spilled if $u_i \leq P_{\text{spill}}$, $u_i \in U[0,1]$. This common assumption that fish “go with the flow” overestimated entrainment rates for juvenile salmon into diversions of the Sacramento River (Hanson 2001), but it nevertheless represents the best guess in the absence of data for white sturgeon. P_{spill} is higher in wet hydrologic years because flows exceed the capacity of the turbines more often. Simulated individuals that pass over the dam in spilled flow avoid any risk of mortality during downstream movement.

White sturgeon can avoid entrainment and the risk of turbine mortality if either a screening device or a downstream fish passage device is in place. The most common screening devices are racks with bars set at a fixed spacing to exclude large objects that might damage the turbines (Cada and Sale 1993). Screening reduces the downstream migration rate by preventing larger fish from moving downstream, except during high flows when water spills over the dam.

The model simulates screening by setting a screening width, W_{screen} , which is multiplied by proportion P_{screen} (Table 1). First, the model determines whether the fish is small enough to pass through the screen, a decision represented by an indicator function, $I_{i \in \text{entrained}}$ (eq. 2). The white sturgeon remains in the upstream segment if its diameter exceeds the screening width (the model does not currently represent the risk of impingement against screening devices). The diame-

Fig. 2. Relationships from segments in the Middle Snake River used to parameterize hypothetical river configurations. (a) Power relationships for each hydrologic year type fitted between reservoir retention time, t_R , and reservoir length in the Middle Snake River ($R^2 = 0.90$ for all three). (b) Linear relationships for each hydrologic year type between average flow, Q_{spawn} ($1000 \text{ m}^3 \cdot \text{s}^{-1}$), and distance upstream ($0.82 \leq R^2 \leq 0.92$) for dry years (circles, dotted lines), normal years (squares, broken lines), and wet years (triangles, solid lines).



ter of cylindrical fish i , W_i , is calculated as $(0.2765 L^{1.07})/\pi$, with parameter values relating diameter to fork length, L , estimated from white sturgeon collected in the Snake River (K. Lepla, ID Power Company, P.O. Box 70, Boise, Idaho 83707, USA, unpublished data).

$$(2) \quad I_{i \in \text{entrained}} = \begin{cases} 1, & W_i \leq W \cdot P_{\text{screen}} \\ 0, & \text{otherwise} \end{cases}$$

Fish using downstream passage facilities, such as bypass channels, are able to migrate downstream safely by avoiding the turbines. To simulate downstream passage, the model permits white sturgeon to migrate to the segment downstream without excluding larger sizes and without risk of turbine mortality. Downstream passage, as simulated here, is probably safer than it is in reality because smaller juveniles

following this alternative route might encounter higher-than-usual predation risk.

Three equations summarize the decision process above for individuals in river segment j . Equation 3 describes individual i 's chance of downstream movement in year t , and eq. 4 describes the corresponding binomial decision to move or not to move downstream. The number of downstream migrants in year t is given by eq. 5, where $N_j(t)$ is the number of age-1 and older white sturgeon in river segment j at the start of year t .

$$(3) \quad P_{\text{down},i}(t) = \begin{cases} P_d, & \text{with downstream passage} \\ P_d[P_{\text{spill}}(t) + [1 - P_{\text{spill}}(t)]I_{i \in \text{entrained}}], & \text{otherwise} \end{cases}$$

$$(4) \quad I_{i \in \text{down}} = \begin{cases} 1, & \text{if } u_i \leq P_{\text{down},i}, u_i \in U[0,1] \\ 0, & \text{otherwise} \end{cases}$$

$$(5) \quad \text{Migrants}(t) = \sum_{i=1}^{N_j(t)} I_{i \in \text{down}}$$

In three sets of simulation experiments, I compared three options for downstream movement past the dam with upstream passage. The first scenario simulated migration using wider screens at the dam. The screen spacing was set to the average for dams in the Snake River, which excluded white sturgeon with fork lengths greater than 143 cm. In the second scenario, this spacing was halved (narrow spacing scenario), but only at the dam with upstream passage. In the third scenario, I simulated downstream passage again, but only at the dam with upstream passage.

Entrainment mortality

Given that an individual white sturgeon has been entrained, its likelihood of being killed by turbine blade strike depends on the fish's length and the type of turbine (Fig. 3). The model estimates the risk at each dam using two parameters: (i) B_{strike} , the slope of a linear relationship between strike probability and sturgeon size and (ii) W_{screen} , the size of the largest fish that can pass through the downstream screening device (Table 1). If the fish survives passage through the turbines, it moves to the downstream segment.

Simulation of upstream passage

In baseline simulations, migration probabilities are zero for nonadjacent segments and upstream segments. Voluntary upstream passage is simulated in scenarios with upstream passage using an individual probability of upstream movement equal to the maximum downstream probability, with no bias in ages or sizes of white sturgeon moving (i.e., strictly in proportion to abundance).

Preliminary simulations

Source-sink dynamics

To assess which segments were sources or sinks, I compared population dynamics in simulations of populations in river configuration 15, with and without downstream migration. Results were similar for other river configurations. When the segments were isolated (Fig. 4a), populations in

long segments increased and the populations in short segments declined, usually reaching extinction within a 300-year time span. When simulating downstream migration (Fig. 4b), populations in long river segments attained stable sizes (usually greater than 500 individuals). Thus, the three short segments acted as demographic sinks. The long segments acted as demographic sources, which, if situated upstream of a short segments, may subsidize short segments through downstream migration.

Effects of river configuration

In baseline simulations (no upstream passage and wide screening), populations in the long segments were larger at the end of the simulation than populations in short segments. Among the 20 river configurations, configurations with a long segment positioned farther upstream and with high interspersions of long and short segments had a higher metapopulation status, as measured by NT_{500} (the sum of final population sizes including all seven populations, where the maximum counted in any population is 500), at the end of the simulations (Fig. 5).

Effects of screening width

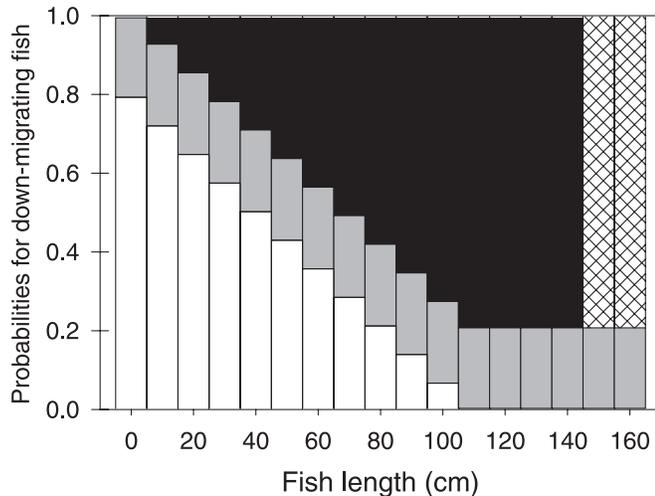
To understand the effects of screening smaller and smaller fishes, a series of simulations varied the screening widths at the dam below segment two. The screening width was reduced by multiplying the wider screening width by a fraction, P_{screen} . This series compared results for P_{screen} values of 0.0, 0.2, 0.4, 0.6, 0.8, and 1 for river configuration 15 (see Fig. 1). The case of 0.0, although unrealistic, was included to simulate the limiting case of no downstream migration. The results presented are final population sizes below and above the dam and cumulative values including emigration from above the dam, immigration below the dam, and turbine mortality.

Decreasing the size of fish able to pass through the screen increased the size of the final population simulated above the dam (open circles in Fig. 6) and decreased turbine mortality (hatched bars in Fig. 6) as expected. Interestingly, the downstream population reached the largest size at an intermediate width because very close spacing reduced immigration of juveniles from the upstream population (closed circles in Fig. 6). The narrow screening scenario (50% of wide screening) increased the size of the population above the dam in 99% of cases and increased the population below the dam in 94% of cases (river configurations and dams).

Passage simulations

Because individual-based models are stochastic, 30 replicate metapopulations are simulated for 300 years. The average and standard error (SE) over 30 replicates is presented for NT_{500} . NT_{500} is the sum of final population sizes including all seven populations, where the maximum counted in any population is 500. This makes the index more sensitive to increases in small population and less sensitive to increases in populations that are already large. Six scenarios simulated are as follows: (i) baseline: wide screening alone, (ii) narrow screening alone, (iii) downstream passage alone, (iv) upstream passage with wide screening, (v) upstream pas-

Fig. 3. Simulated probabilities of four possible outcomes for individual white sturgeon (*Acipenser transmontanus*) selected to attempt downstream migration during a wet year: sturgeon remains upstream (crosshatch), survives spilling over the dam (shaded), survives entrainment (open), or is struck by a turbine during entrainment (solid). Sturgeon length influences whether an individual is entrained and, if so, its risk of being struck by turbine blades.



sage with narrow screening, and (vi) upstream passage with downstream passage. Below, the three options without upstream passage are described in one section and the three corresponding options with upstream passage are described in the following section.

No upstream passage with three options for downstream movement

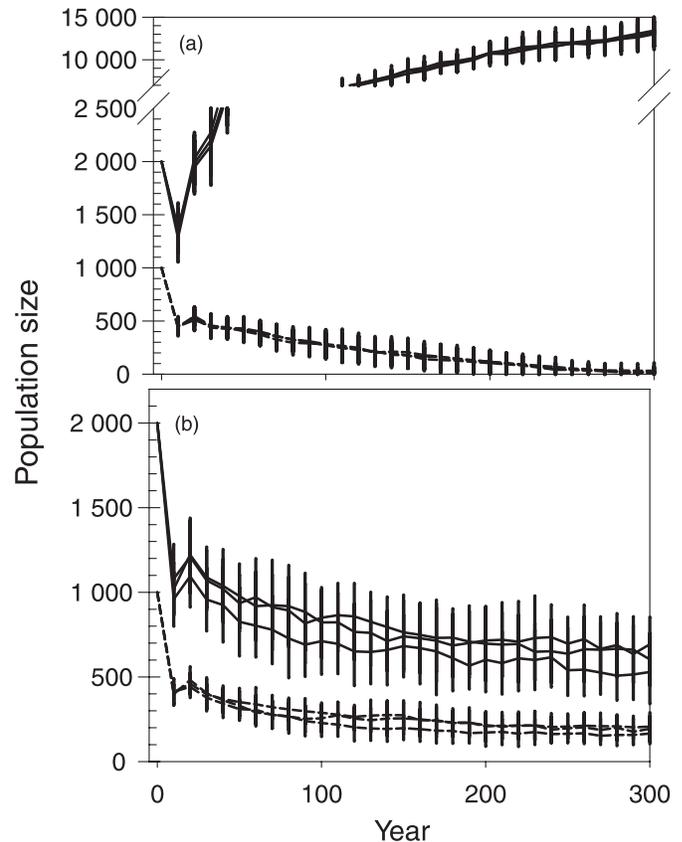
For each river configuration, simulations without upstream passage were run for each of three options for downstream movement: (i) wide screening, (ii) narrow screening, and (iii) downstream passage. There was only one simulation for the baseline scenario with no upstream passage and wide screening at all dams. In contrast, there were six simulations each for narrow screening and downstream passage because these options were applied at each dam, one at a time (the other dams have wide screening). Results from these scenarios were used to separate the effects of upstream passage from the mitigation simulated for downstream movement.

Upstream passage with three options for downstream movement

To evaluate the costs or benefits of providing upstream passage, I simulated upstream passage at each of six dams in each river configuration. These simulations assumed wide screening at all dams. In addition, I simulated upstream passage combined with two different options for reducing turbine mortality only at the dam with upstream passage: narrow screening and downstream passage. These three options were described earlier in the section on Simulation of downstream movement.

First, I present individual population results above and below one dam in a particular configuration to illustrate the effects of upstream passage within river configurations. Next, I present patterns in metapopulation responses as a function of

Fig. 4. Long-term simulations of configuration 15 compare the fates of long (upper, solid lines) and short (lower, broken lines) river segments (a) when they are isolated and (b) when they are connected by downstream migration. Lines connect the mean population size predicted by 30 replicate simulations. Error bars show the standard deviation of the predictions.



the length of the segments above or below the dam with upstream passage and the longitudinal position of the dam.

Results

Upstream passage with wide screening

Within-river configuration

Configuration 15 was used to illustrate the effects of upstream passage within a river. In general, simulating upstream passage at a dam resulted in higher final numbers in the population above the dam (compare solid bars in Figs. 7b–7f with shaded bars directly above in Fig. 7a) and smaller final numbers in the population below the dam (compare open bars in Figs. 7b–7f with Fig. 7a). In most cases, the net effect on the metapopulation was negative. The net demographic benefit of upstream passage was greater when provided at a dam below a long segment (Figs. 7b, 7d, 7f). In these cases, declines in the downstream population appeared to be offset by increased downstream migration from the larger upstream population.

Across-river configurations

This section addresses the question, “Under what conditions does reconnecting white sturgeon populations by upstream passage benefit the metapopulation?” Upstream

Fig. 5. Metapopulation status, NT_{500} , is higher for simulated river configurations with high interspersions and a long segment upstream. The following linear relationship has adjusted $R^2 = 0.72$: $NT_{500} = 1980 + 30.7 \cdot \text{interspersions} - 120.7 \cdot \text{long position}$.

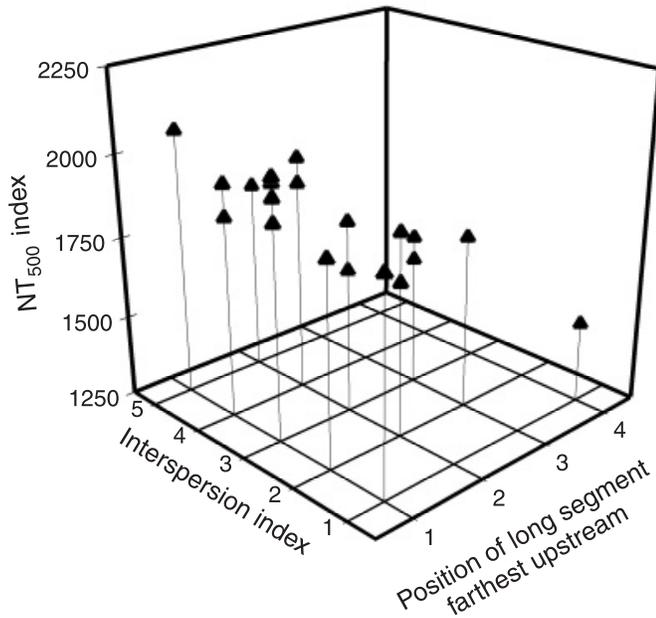
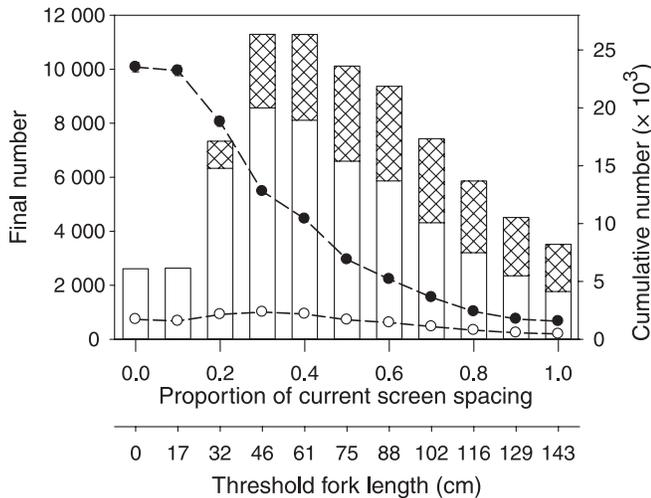
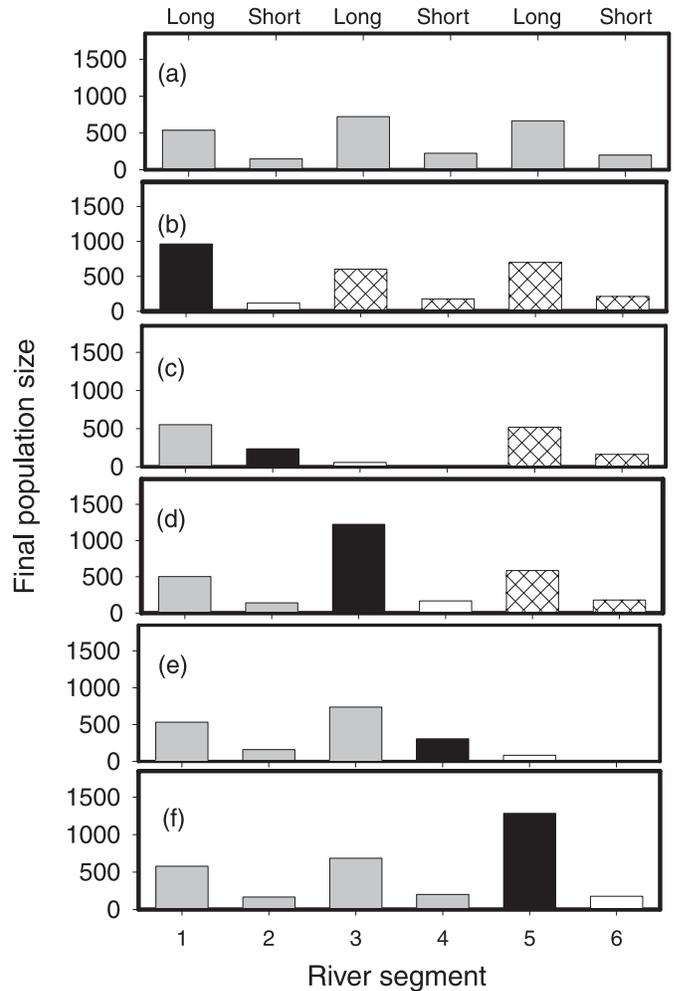


Fig. 6. Two lines show simulated final population sizes above dam (open circles) and below dam (solid circles) below segment two in configuration 15 in response to a proportional reduction in screening width. Stacked bars show cumulative (over time) immigration (open bars) and number of fish killed by turbine strike (crosshatched bars). The threshold fork length of sturgeon that can pass through the screen is indicated on the lower x axis.



passage increased the population above the dam in all but one of 120 cases (20 river configurations × 6 dams). Upstream passage decreased the population below the dam in 116 cases. In 94% of cases, the population two segments downstream of the dam also decreased in response to providing upstream passage. When averaged across all river configurations, simulated upstream passage had a negative

Fig. 7. Example of upstream passage for river configuration 15. The top graph (a) shows baseline results, where the x axis indicates the river segment (left is upstream) and the y axis indicates final population size in the segment. Panels b–f show the results of upstream passage at the dam below segment 1 (b), segment 2 (c), segment 3 (d), segment 4 (e), and segment 5 (f). In each graph, the solid bar is the upstream segment, the open bar is the segment immediately downstream, and other downstream segments are crosshatched. Shaded bars denote river segments not affected by passage.



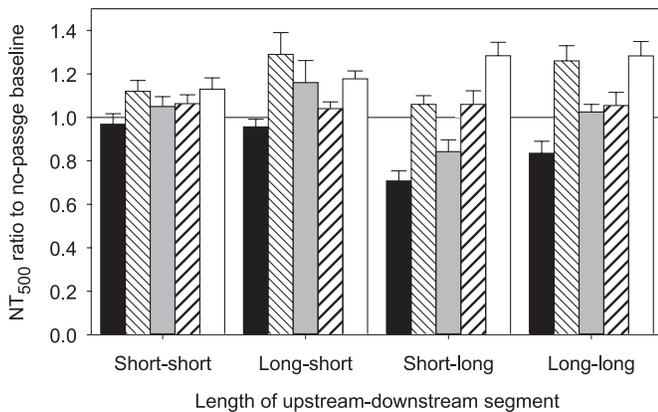
demographic effect on metapopulations, as measured by NT_{500} .

As there were no cases of an appreciable increase in NT_{500} resulting from upstream passage, there was little point in exploring patterns in the index related to properties of the river configuration or of the dams involved in upstream passage. However, upstream passage was most detrimental when the downstream segment was long (compare solid bars in Fig. 8 with horizontal line), especially with a short upstream segment. In this case, white sturgeon inhabiting source habitats can move upstream into sink habitat.

Upstream passage combined with narrow screening

NT_{500} increased when narrow screening was simulated at dams that allowed upstream passage (Fig. 8). However, narrow screening at a given dam alone (i.e., without upstream

Fig. 8. Ratio of NT_{500} for each of five scenarios to NT_{500} for the baseline scenario (no passage and wide screening) for different combinations of long and short segments above and below the dam. The five scenarios are (i) upstream passage with wide screening (solid bars), (ii) narrow screening (narrow striped bars), (iii) upstream passage with narrow screening (shaded bars), (iv) downstream passage alone (wide striped bars), and (v) upstream and downstream passage (open bars). Scenarios with values above the horizontal line increased NT_{500} relative to the baseline and vice-versa. Error bars show one standard deviation.



passage at the dam) increased NT_{500} even more (open bars in Fig. 8).

Narrow screening was more beneficial without upstream passage because it had a positive effect downstream; as the upstream population grows, more small fish are exported downstream. Both upstream passage and narrow screening had a positive effect on the population upstream of the dam, but they had different effects on the population below the dam. Whereas upstream passage usually caused the final size of the population below the dam to decrease (116 of 120 cases), narrow screening usually caused an increase (113 cases). Trickle-down benefits were experienced two segments below the dam in 86% of cases with narrow screening alone, in 6% of cases with upstream passage only, and in 58% of cases with both.

I compared the ratio of NT_{500} for each treatment to that in the baseline situation for all combinations of long and short segments above and below the dam with upstream passage. This analysis suggests that upstream passage combined with narrow screening is harmful when the segment above the dam is short and the segment below the dam is long (Fig. 8). Narrow screening was more beneficial when the upstream segment was long (Fig. 8). The upstream-downstream position of the dam with passage did not have a significant effect on NT_{500} (minimum $p = 0.834$, $T = -1.009$, $df = 18$).

Upstream passage combined with downstream passage

Combining downstream and upstream passage at the same dam increased the average demographic status of metapopulations (open bars in Fig. 8). The simulated increase was greatest when the downstream segment was long. The demographic benefits of downstream passage were smaller without upstream passage (wide striped bars in Fig. 8). Average NT_{500} did not show a trend with the longitudinal position of the dam with passage.

As might be expected, downstream passage alone usually had the opposite effect of upstream passage; final population sizes usually decreased above the dam (94 cases) and increased below the dam (114 cases). When upstream passage was combined with downstream passage, all 120 cases showed an increase above the dam, but decreases below the dam occurred in only 27 cases. Trickle-down benefits were experienced two segments below the dam in 78% of cases. The trickle-down benefits for configuration 15 were substantially higher for upstream and downstream passage (Fig. 9) than for upstream passage alone (Fig. 7) when the upstream segment was long. For example, observe the increase in the simulated final population sizes of segments 2 and 3 in Fig. 9b compared with those of the same segments in Fig. 9a resulting from upstream passage at the first dam. Likewise, final populations increased in segments 5 and 6 (Fig. 9d) relative to baseline simulations (Fig. 9a), which was not evident in Fig. 7.

Discussion

Model predictions suggest that the status of white sturgeon metapopulations without upstream passage is higher in river configurations that have high interspersion of source and sink segments and a source segment far upstream. This implies that the configuration of dams can influence restoration efforts and that the siting of dams could be done in a way that better protects white sturgeon and similar species.

Simulation results for upstream passage differed from my initial expectations. Simulated efforts to reconnect populations by providing upstream passage alone did not augment the status of fragmented river metapopulation. To succeed with upstream reconnection, it was also necessary to simulate narrower screening or downstream passage at the dam with upstream passage.

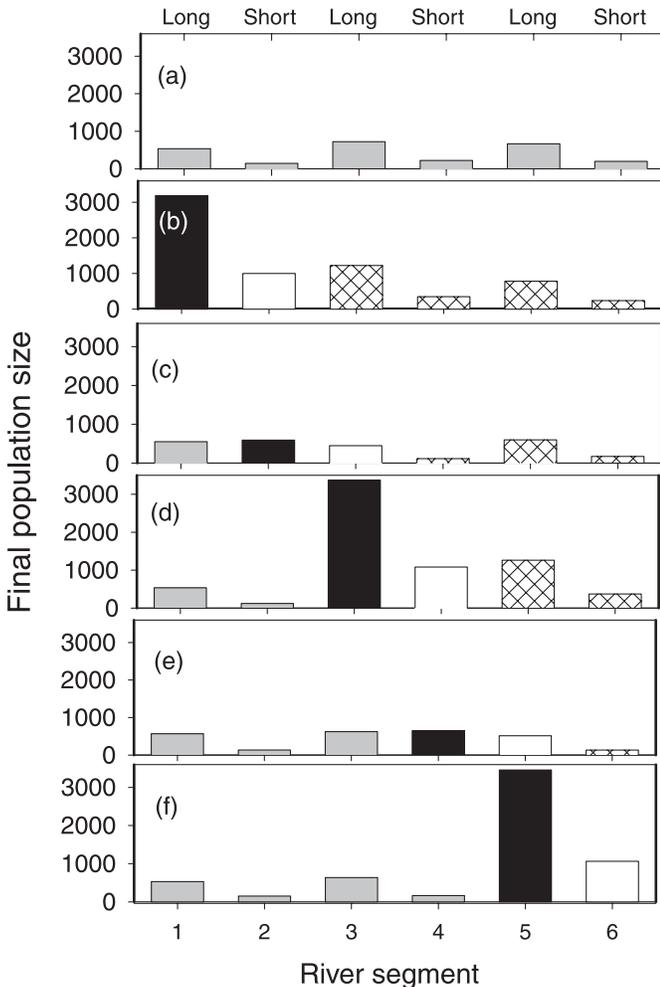
Two scenarios that gave the best demographic results excelled under different circumstances. Both benefited simulated river metapopulations by providing positive effects downstream. Upstream passage combined with narrow screening increased metapopulation status in most cases. Narrow screening alone also benefited metapopulations, especially at dams between long upstream segments and short downstream segments.

Downstream passage was effective when combined with upstream passage. This scenario differs from that of a single river segment without a dam present only by the proportion of reservoir habitat. Passage in both directions was particularly beneficial for short upstream segments and long downstream segments.

The two scenarios (narrow screening alone and downstream with upstream passage) provided similar benefits for the remaining situations (both segments short or long). Both scenarios were more successful than upstream passage alone because they bolstered the combined populations, which in turn subsidized downstream segments.

This simulation study offers two take-home lessons. First, this study suggests that it is a good idea to monitor populations below the dam with passage to ensure that downstream demographic costs do not outweigh upstream benefits. Second, risks during downstream migration should be sufficiently low before providing upstream passage.

Fig. 9. Example of upstream passage combined with downstream passage for river configuration 15. The top graph (a) shows baseline results, where the x axis indicates the river segment (left is upstream) and the y axis indicates final population size in the segment. Panels b – f show the results of upstream passage at the dam below segment 1 (b), segment 2 (c), segment 3 (d), segment 4 (e), and segment 5 (f). In each graph, the solid bar is the upstream segment, the open bar is the segment immediately downstream, and other downstream segments are crosshatched. Shaded bars denote river segments not affected by passage.



As with any modeling study, these results depend on several model assumptions. First, this study applies to riverine fishes that require longer river segments and free-flowing habitat to reproduce. In rivers of the Pacific northwest, long river segments tend to support larger inland white sturgeon populations, but there are exceptions; a few large populations in the Lower Columbia River exist in short reservoirs that also provide access to the estuary. Results probably apply to other large-bodied fishes with life histories similar to that of the white sturgeon. For fish species that thrive in reservoir habitat, qualities other than segment length might distinguish source and sink habitat.

Second, sensitivity results suggest that the benefits of upstream passage decrease as density dependence becomes stronger. Because these simulations included a density-dependent spawning interval, the benefits of upstream pas-

sage could be higher if density dependence is weak. Third, decisions by fish to avail themselves of upstream passage in real-life situations might not match model assumptions about the number and sizes of fish that move upstream. One encouraging note is that simulated translocation experiments that moved fish upstream one segment produced similar results (Jager 2006), although the total number of white sturgeon moving upstream was higher for simulated upstream passage than for simulated translocation. As in this study, translocations to a recipient segment directly upstream of the donor were not usually beneficial, except for translocation combined with downstream passage (Jager 2006). Thus, model results were qualitatively similar in the two cases despite differences in the numbers of fish moved upstream. Other sensitivity results for this model are presented in Jager (2006).

If we wish to predict the effectiveness of mitigation measures at different dams, it is necessary to conduct regional-scale studies that include a sample of representative projects. Because we consider relicensing decisions in the USA on a case-by-case basis, monitoring requirements differ from one hydroelectric project to another. Monitoring to determine whether fish benefit from passage at the population level has been recommended (Cada and Sale 1993), but such studies have not been conducted. Ideally, regional-scale field research would be designed to obtain and provide consistent scientific guidance on the effectiveness of upstream passage in different situations. The results of this theoretical study provide testable hypotheses for future field studies to test and refine.

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Appendix A

The processes of reproduction, recruitment, and juvenile and adult survival are described below (see also Jager et al.

2001, 2002, 2003). Simulation of juvenile and adult movement was described earlier in the Model description section, along with other aspects of the model specifically relevant to simulating passage.

Initialization

Simulations were initialized with a density of 25 individuals $>43 \text{ cm}\cdot\text{km}^{-1}$. The initial size structure was 73% $<95 \text{ cm}$, 22% between 95 and 171 cm, and 5% $>171 \text{ cm}$.

Reproduction

The population viability analysis (PVA) model evaluates reproduction annually for each subpopulation. Each year, the model identifies the pool of adults eligible to spawn. Whether a particular individual belongs to this pool depends on its having reached maturity, its last spawning date, and its assigned rematuration interval. The onset of reproductive maturity is later for females than for males and is quite variable among individuals. The PVA model assigns each individual, i , a threshold length at maturity, L_{C_i} , at birth from a normal distribution with mean \bar{L} and standard deviation L_{SD} , which are based on the length distribution observed among Snake River adults (Table 1). The indicator function in eq. A1 determines whether a white sturgeon has reached a mature size based on its current length, L_i .

$$(A1) \quad I_{i \in \text{mature}} = \begin{cases} 1, & L_i(t) \geq L_{C_i} \\ 0, & \text{otherwise} \end{cases}$$

The number of years between successive spawning events is also variable. An extended resting period between spawning events is a likely response to density-dependent limitation. Let $t_{\text{last},i}$ denote the last year that individual i spawned. In the model, the interval between spawning events increases when the density of adults is high enough to deplete food resources. Because white sturgeon do not show territorial social behavior and are often seen foraging with others, density-dependent effects are applied equally to all individuals. The spawning interval for females in river segment j increases with the density of adults $D_j(t)$, which is defined as the number with fork lengths longer than 170 cm divided by the length of free-flowing habitat in segment j plus a small length of reservoir habitat assumed to be suitable for spawning, H_{res} (Table 1). Female spawning interval rises from a minimum value, SI_{min} , at low densities to a maximum of SI_{max} at high densities, with a midpoint at optimal density D_{opt} (eq. A2).

$$(A2) \quad SI_j(t) = SI_{\text{min}} + SI_{\text{max}} \left(\frac{D_j^2}{D_{\text{opt}}^2 + D_j^2} \right)$$

Spawning aggregations in segment j include all individuals i eligible to spawn, where indicator function $I_{i \in \text{ripe}}$ denotes the collection of individuals that are ready to spawn in year t , and t_{last} is the year this individual last spawned or first reached maturity (eq. A3).

$$(A3) \quad I_{i \in \text{ripe}} = \begin{cases} 1, & t - t_{\text{last},i} \geq SI_j(t) \\ 0, & \text{otherwise} \end{cases}$$

Each spawning female releases eggs, where the fecundity of female white sturgeon increases with female size (Cochnauer 1983). The model currently estimates fecundity of each female in two steps. Equation A4 estimates fork length, L_i , in centimetres from age in years, A_i , with Von Bertalanffy parameters (estimated by Lepla and Chandler (1995); Table 1). Fecundity, E_i , increases with fork length for females as shown in eq. A5 (DeVore et al. 1995).

$$(A4) \quad L_i = L_\infty \{1 - \exp[-K_{vb}(A_i + T_0)]\}$$

$$(A5) \quad E_i = \begin{cases} A_{\text{egg}} L_i^{B_{\text{egg}}}, & \text{female} \\ 0, & \text{male} \end{cases}$$

The total pool of eggs spawned in a population of size N_j in segment j and year t is given by

$$(A6) \quad \text{Total eggs}(t) = \sum_{i=1}^{N_j(t)} I_{i \in \text{mature}} \cdot I_{i \in \text{ripe}} \cdot E_i$$

If at least one male is ready to spawn, these eggs are fertilized and a male parent is assigned to eggs at random from the pool of spawning males.

Recruitment

The PVA model determines recruitment to age 1, $R(t+1)$, as the number of eggs that independently survive four sequential mortality risks during the first year of life: (i) natural mortality, S_y , (ii) density-dependent mortality, S_d , (iii) temperature-related mortality during incubation, S_{temp} , and (iv) larval export, S_{larva} :

$$(A7) \quad R(t+1) = S_y \cdot S_d \cdot S_{\text{temp}} \cdot S_{\text{larva}} \cdot \text{Total eggs}(t)$$

S_d increases from zero at zero egg density to one at an optimal egg density, D_{egg} . Values of S_{temp} listed in Table 2 are calculated for dry, normal, and wet hydrologic years.

Larval export can lead to substantial losses in shorter segments. The PVA model simulates larval export as follows. First, spawning is assumed to be in the free-flowing section, if there is one. The proportion of larvae that migrate is the product of the probability that a larva will reach the reservoir, $P\{\text{reservoir}\}$, and the probability that a larva that has reached the reservoir will be swept downstream, $P\{\text{swept}|\text{reservoir}\}$. The simulated probability that a larva enters the reservoir decreases exponentially as the length of free-flowing river, L_{ff} , increases. The probability of a larva being swept downstream once it is in the reservoir decreases as reservoir retention time, t_R , increases and as the duration of the demersal stage, t_{larva} , increases. The retention time of each reservoir differs for the three hydrologic year types (Fig. 2a). Equation A8 estimates the proportion of larvae moving downstream. Survival of larval export, S_{larva} , equals the fraction of total larvae not swept downstream.

$$S_{\text{larva}} = 1 - P\{\text{swept}|\text{reservoir}\}P\{\text{reservoir}\}$$

$$(A8) \quad P\{\text{reservoir}\} = \begin{cases} 0, & L_{\text{ff}} \geq L_0 \\ \frac{(L_{\text{ff}} - L_0)}{(L_1 - L_0)}, & L_1 \leq L_{\text{ff}} \leq L_0 \\ P_{\text{sweep}}, & L_{\text{ff}} \leq L_1 \end{cases}$$

$$P\{\text{swept}|\text{reservoir}\} = \begin{cases} \frac{t_{\text{larva}}}{t_R}, & t_{\text{larva}} \leq t_R \\ 1, & \text{otherwise} \end{cases}$$

If spawning aggregations are equally likely to occur anywhere in the free-flowing stretch, then the average upstream distance of spawning sites increases with the length of the free-flowing habitat. As the upstream distance increases, both the distance that must be traveled to reach the reservoir and the opportunities for settling out of the water column also increase. Two parameters, L_0 and L_1 , are the free-flowing river lengths associated with a minimum (0) and maximum (P_{sweep}) probability of reaching the reservoir, respectively (Table 1).

Juvenile and adult survival

The PVA model simulates several potential sources of mortality for juveniles and adults, only two of which apply in these simulations. First, white sturgeon ages 1 and older are exposed to a baseline mortality of S_j for juveniles and S_a for adults (Table 1). Second, individuals that migrate downstream are exposed to entrainment mortality (see Model description in main text).

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