

Chutes and ladders and other games we play with rivers. II. Simulated effects of translocation on white sturgeon

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Abstract: Restoring connectivity is viewed as an important recovery option for fish species adversely affected by river fragmentation. This simulation study quantified the genetic and demographic effects of translocation on metapopulations of white sturgeon (*Acipenser transmontanus*) inhabiting a series of long (source) and short (sink) river segments. Genetic effects were predictable; upstream translocations increased introgression and downstream translocations had no effect. Demographic results suggest that indiscriminant efforts to reconnect populations may do more harm than good. Simulated river systems with high interspersion of long and short segments and a long segment far upstream tended to benefit most from translocation, but only when narrow screening or downstream passage was also provided below the river segment receiving fish. When combined with narrow screening, upstream translocation to a long segment subsidizing several downstream short segments produced the best results. Downstream passage outperformed narrow screening only when the translocation recipient was a short segment in a river system with low interspersion and no long, upstream river segment. This model-based evaluation of reconnection options has helped to refine ideas about restoring populations in fragmented rivers by predicting which options benefit riverine metapopulations as a whole.

Résumé : Le rétablissement de la connectivité est considérée comme une solution potentielle importante pour la récupération d'espèces de poissons affectées négativement par la fragmentation des rivières. La présente étude de simulation permet de quantifier les effets génétiques et démographiques des transferts de poissons sur les métapopulations d'esturgeon blanc (*Acipenser transmontanus*) qui habitent des segments longs (sources) et courts (pertes) de rivière. Les effets génétiques sont prévisibles: les transferts vers l'amont augmentent l'introgression et les transferts vers l'aval restent sans effet. Les données démographiques indiquent que des efforts sans discernement pour relier les populations peuvent causer plus de tort que de bien. Les systèmes de rivière simulés, avec une forte alternance de segments longs et courts et avec un long segment dans la partie amont tout à fait supérieure, ont tendance à recevoir le plus d'avantages des transferts, mais seulement lorsqu'il se fait un tri serré ou lorsqu'il y a aussi un passage vers le bas de la rivière en aval du segment qui reçoit les poissons. Combiné à un tri serré, un transfert vers l'amont à un segment long de rivière, qui alimente plusieurs segments courts en aval, produit les meilleurs résultats. La présence d'un passage vers l'aval donne de meilleurs résultats que le tri serré seulement lorsque le segment de rivière qui reçoit les transferts est court, qu'il fait partie d'un système hydrographique avec peu d'alternances et qu'il n'y a pas le long segment en amont. Cette évaluation des choix de rétablissement des connexions à l'aide des modèles contribue à préciser les théories sur la restauration des populations dans les rivières fragmentées, en prédisant quels choix sont avantageux aux métapopulations des rivières dans leur ensemble.

[Traduit par la Rédaction]

Introduction

Dams have transfigured the landscape of large rivers in the United States and elsewhere. Fragmentation by dams has caused localized extinctions of fish species and reduced diversity of native, river-adapted fishes upstream of high dams (Peter 1998; Pringle et al. 2000; Gehrke et al. 2002). Migratory fishes experience a particularly high risk of local extirpation after losing access to upstream habitat needed to

complete their life cycle (Waidbacher and Haidvogel 1998). These negative consequences are blamed, in part, on the fact that dams isolate populations by preventing upstream movement and restricting downstream movement of fishes.

It is widely believed that river connectivity enhances the viability of fish populations (e.g., Fausch et al. 2002). Connected fish populations share access to more diverse habitat, thereby fulfilling seasonal and life-stage-specific habitat needs (Schlosser 1991). In the shifting, dynamic landscape of rivers, access to refuge habitat, though rarely needed, is likely to be important (Schlosser 1991). This is especially true for long-lived species like sturgeons, which, for example, occasionally require free-flowing habitat as refuge from summer episodes of low dissolved oxygen in some reservoirs (Jager et al. 2001). Connected metapopulations of fishes are more likely to be recolonized by neighboring river seg-

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ments after local extirpation, an event that is more likely in short river segments fragmented by dams. The paradigm described above suggests that reconnection of river segments currently separated by dams should benefit riverine fish populations.

Reconnection can be accomplished by building structures that allow voluntary movement or by assisted fish movement by translocation. Trapping and transporting fish around a dam is less expensive in the short term than constructing passage facilities (Cada and Sale 1993). Translocation has several drawbacks. Maintaining connection via translocation requires a long-term commitment to intervention. Because movement is not voluntary, translocation requires understanding the spatial life history and habitat requirements of the species. For example, it might be counterproductive to move juveniles upstream in a species that, left to its own devices, would choose to move upstream only to spawn. Finally, genetic homogenization becomes a concern when fish are moved between distant populations. For species adapted to local conditions, introgression could potentially reduce fitness.

Fish translocations are typically used to reintroduce a rare species to previously occupied habitat, not to reconnect populations. Fish reintroductions have succeeded in some cases and failed in others. Minkley (1995) estimated that only 30% of reintroductions in the arid southwest succeeded. Translocations that released individuals into good habitat have been more successful. For example, translocations of cutthroat trout (*Oncorhynchus clarkii clarkii*) succeeded only in sufficiently large watersheds having deep pools, but not in higher elevation headwater reaches (Harig and Fausch 2002).

The success of translocation programs designed specifically to establish upstream reconnection has not been assessed. To succeed, these translocation programs must meet not only the requirements of translocation in general, but also new requirements specific to adjacent segments separated by dams. Thus, ensuring that suitable habitat is available in the target reach is a first step, after which the effect of the dam on the peculiar, biased metapopulation dynamics of adjacent river segments must be considered. Translocated individuals do not always fare well; 3 of 17 westslope cutthroat trout moved above a dam in Montana, USA, in the hope of providing them access to upstream spawning tributaries ended up below the dam again before spawning season (Schmetterling 2003). Clearly, attention must be paid to downstream as well as upstream movement.

Although upstream movement is most severely curtailed by dams, downstream movement past dams carries its own risks. Without special provisions, fish have but two options: to become entrained into the hydroelectric project or spill over the dam during high flows. Larger fish that are entrained risk being struck by the turbines or the hydraulic forces that they generate. Safer passage around dams can be facilitated by constructing bypass facilities or trapping fish in a downstream segment and transporting them by barge or truck. Screens and trash racks are used to prevent entrainment of fishes. Screening not only reduces entrainment, it also curtails downstream migration and shifts the size structure of emigrants.

This study uses a model of linked white sturgeon (*Acipenser transmontanus*) populations in rivers to understand when translocation is beneficial as a strategy for reconnecting populations. The companion to this paper examines upstream passage (Jager 2006). The costs and benefits of translocation are evaluated with and without mitigation efforts to restrict downstream migration or make it safer. I evaluate translocation in rivers with different combinations of long (source) and short (sink) river segments to better understand how the success of translocation depends on river configuration and the attributes of the segments involved. In summary, the overarching question addressed by this paper is, "Under what circumstances does translocation benefit white sturgeon metapopulations?" The circumstances considered include (i) river configuration, (ii) attributes of the river segments involved, and (iii) assumptions about downstream migration. Answers to this question will provide guidance to those considering translocation programs to help ensure that reconnection efforts have the intended effect of restoring populations of sturgeons and similar fish species in rivers.

Model description

This study uses a population viability analysis (PVA) model to evaluate the benefits of translocation on white sturgeon metapopulations. The PVA model was designed to simulate the population dynamics and future viability of nine isolated white sturgeon populations in the Middle Snake River, Idaho, USA (hereafter referred to as Snake River). Isolation of populations between dams contributes to the fact that only two of the nine Snake River segments now support healthy populations (Cochner 1983; Cochner et al. 1985). Consequently, methods for establishing upstream connection are of interest.

The goal of this study is to extend results from the Snake River and to seek a more general understanding that can provide guidance for those working to restore fish populations in other rivers. The source-sink dynamics of white sturgeon metapopulations simulated here are driven by segment length. Compared with longer river segments, short segments provide less spawning habitat for white sturgeon and they are more likely to export larvae downstream. Consequently, short segments are considered demographic sinks for this species. I use a PVA model to examine the influence of translocation within the context of this simplified conceptual framework.

Many aspects of the model have been described previously (Jager et al. 2002, 2003; Jager 2006). Here, I describe aspects of the model specifically related to simulating translocation. Because fish can be moved farther using translocation than upstream passage, genetic influences are a concern. Therefore, introgression is also simulated and reported, as described below.

Simulation of translocation

Translocation programs relocate fish from a donor population in one river segment to a recipient population in another segment. The model simulates the capture of white sturgeon in a donor segment, calculates the probability of survival, and

simulates release of captured white sturgeon into a recipient river segment. The chance of catching an individual white sturgeon, $P_{\text{cap},i}$, is simulated as a function of its size, the size-selectivity of gear, population density, and the annual effort expended in donor river segment j ($E_j = 0.1$ angler-days·km⁻¹) (eq. 1).

$$(1) \quad P_{\text{cap}} = E_j F_1(D_j) F_2(L_i)$$

The two vulnerability factors in eq. 1 increase from zero to one. Fishing pressure typically increases with fish population density, D_j , in segment j . The density factor, $F_1(D_j)$, follows a Holling type 3 functional response to population density, where the density at which the inflection point occurs is D_h and the limit on daily catch·person⁻¹ is $F_{\text{max}} = 4$ (eq. 2).

$$(2) \quad F_1(D_j) = \frac{F_{\text{max}} D_j^2}{D_h^2 + D_j^2}$$

Larger individuals are more vulnerable to capture by anglers and by gear used for translocation (setlines and 2–23 cm mesh, sinking gillnets). With these gears, capture efficiency of encountered white sturgeon increases from zero to one as sturgeon size, L_i , increases from $L_{\text{min}} = 43$ cm to $L_{\text{max}} = 90$ cm fork length (Lepla and Chandler 1995) (eq. 3).

$$(3) \quad F_2(L_i) = \frac{L_i - L_{\text{min}}}{L_{\text{max}} - L_{\text{min}}}$$

Indicator function, $I_{i \in \text{move}}$ indicates whether a given individual has been captured and survived hooking mortality, $S_{\text{hook}} = 0.98$ (eq. 4). For a donor population with $N_j(t)$ individuals age 1 and older, eq. 5 counts those that survive and are relocated to the specified recipient river segment in year t .

$$(4) \quad I_{i \in \text{move}} = \begin{cases} 1, & u_i \leq P_{\text{cap},i} \cdot S_{\text{hook}}, u_i \in U[0,1] \\ 0, & \text{otherwise} \end{cases}$$

$$(5) \quad \text{Number translocated from } j = \sum_{i=1}^{N_j(t)} I_{i \in \text{move}}$$

Simulation of population genetics

The PVA model used in these simulations keeps track of each individual's genome. Genetic aspects of the model are further described elsewhere (e.g., Jager 2001; Jager et al. 2003). Genetic effects of reconnection scenarios are quantified by comparing final population-level measures of genetic introgression. For a species with homing ability and a strong stock structure, local adaptation is likely, and the goal would be to avoid reconnection options that reduce population subdivision and increase introgression. Otherwise, these effects are less of a concern.

The PVA model quantifies potential for introgression by simulating private alleles, defined as alleles initially present in one population but not in others. In the simulations described here, I simulated a single locus with four private alleles and four shared alleles initially present in each population.

These alleles are passed to future generations by simulating inheritance. After simulating egg production by females in the spawning aggregation (see Reproduction section in

Appendix A of Jager 2006), the model simulates the inheritance of alleles by offspring. All males in the spawning aggregation are equally likely to fertilize a given egg. Once the male parent is determined, one of two alleles is drawn from each parent at random at each locus. Normally, mutation would be simulated after inheritance, but the mutation rate was set to zero, so that the only source of new alleles in these simulations is immigration.

Introgression is measured by the number of alien alleles present in each population at the end of the simulation, where an allele is considered alien to a population if it was not present at the start of the simulation. Note that downstream migration results in gene flow from upstream to downstream populations, so that the results do not solely reflect the influx of alleles from translocated individuals. Genetic effects are summarized at the metapopulation level by an index of introgression, the average number of alien alleles, N_{all} , in the final metapopulation.

Simulation experiments

Each scenario was simulated for 20 river configurations representing all possible combinations of three short and three long river segments (see River configurations section in Jager 2006). Simulating a variety of different river configurations provides information on the effects of segment length and upstream–downstream position on the benefits of translocation because these two influences are not confounded. Because individual-based population models are stochastic, results are averages from 30 replicate simulations. Each replicate simulation of a metapopulation of white sturgeon in a river configuration is run for 300 years, which corresponds to approximately 16 generations for this species. (Parameters for these simulations are listed in tables 1 and 2 in Jager 2006).

Fish moved upstream as part of a translocation program might later migrate downstream, risking a fatal encounter with turbines. This suggests that reducing mortality during downstream migration could increase the efficacy of translocation. Turbine mortality can be reduced by providing a bypass route downstream that avoids entrainment into the turbines or by screening fish to prevent entrainment. These two options both reduce turbine mortality, but they differ in where the survivors end up. Screening prevents downstream movement for larger size classes of fish, thereby reducing the downstream migration rate and keeping survivors upstream, whereas downstream passage moves survivors downstream.

Six scenarios simulated are as follows: (i) baseline: wide screening alone, (ii) narrow screening alone, (iii) downstream passage alone, (iv) translocation with wide screening, (v) translocation with narrow screening, and (vi) translocation with downstream passage. Below, the three options without translocation are described in one section and the three corresponding options with translocation are described in the following section.

No translocation with three options for downstream movement

The baseline scenario with no translocation and wide screening corresponded roughly to the current situation in

the Snake River. For each river configuration, I simulated the response of the metapopulation with (i) wide screening, (ii) narrow screening, and (iii) downstream passage. These simulations included no translocation and were applied to each dam, one at a time. Results of these simulations were used to separate the effects of translocation from those of the downstream mitigation option.

Translocation with three options for downstream movement

All translocation scenarios were simulated with the nominal downstream option (wide screening). Narrow screening (e.g., closer spacing of trash bars) below the dam of the recipient segment reduces the number and size of fish entrained. Simulated screening causes intermediate-sized white sturgeon to be retained upstream, except during high-flow events that cause water to spill over the dam. Narrow screening was simulated only below the segment receiving transplants (screening at the other dams was wide).

Translocation simulations were repeated for a third scenario that simulated downstream passage at the dam below the recipient segment. To simulate downstream passage, all sizes of white sturgeon were permitted to migrate downstream (i.e., no screening), and they experienced no risk of mortality.

Metapopulation responses

One demographic and one genetic response variable are reported here. The demographic index of metapopulation status, NT_{500} , is the sum of final population sizes, where the maximum counted in any population is 500. Truncating at 500 individuals prevents the index from being dominated by increases in already large populations and makes the index more sensitive to increases in small populations. The threshold of 500 individuals is a somewhat arbitrary minimum viable population size first proposed by Franklin (1980).

The ratio of NT_{500} for a given translocation scenario to NT_{500} for the corresponding baseline scenario measures the demographic benefit of translocation. Values greater than one indicate that translocation was successful. Genetic introgression among populations in the metapopulation is measured by the total number of alien alleles, N_{all} , at the end of the simulations, averaged over river segments. The ratio between N_{all} under translocation and that in the baseline scenario is also presented.

Statistical analysis

Patterns that one might expect are as follows. (i) Upstream translocations will be more successful than downstream translocations because the recipient population becomes an upstream source supporting downstream segments. (ii) Benefits of upstream translocations will be higher when short, sink segments are positioned below the recipient segment. (iii) Benefits of upstream translocations will also be higher if there is no long, source population upstream of the recipient segment. (iv) Using a source population as a donor will be more successful because it would be better able to withstand removals. (v) Translocation will be more beneficial if the recipient segment has the habitat needed to support a growing population (i.e., is a demographic source rather than a sink). However, on this last point, one could

also argue that fish moved into a source population are wasted because density-dependent factors would diminish returns.

I conducted a multiple linear regression analysis to determine what circumstances, if any, would lead translocation to increase NT_{500} . The response variable was the ratio of NT_{500} in the translocation scenario to NT_{500} in the baseline scenario. Each observation in the analyses represented one translocation scenario (i.e., one of 30 donor and recipient combinations).

The full model included as explanatory variables attributes of the river configuration and of the spatial relationship between donor and recipient segments in a given translocation scenario. The first two predictors are attributes of a river configuration. LongPosition measures the position (1, 2, 3, etc.) of the long segment farthest upstream. Interspersion describes the number of transitions from a short to a long segment or vice versa. The remaining predictors are attributes that describe the translocation and the segments involved. Distance measures the number of segments between the donor and recipient segment, where a negative number indicates upstream relocation. SubsidizedShorts measures the number of short segments below the recipient segment. LongDonor indicates if the donor segment is long, and LongRecipient indicates whether the recipient segment is long. In the special case when a segment is above the first upstream long segment, these variables are set to the largest possible value plus one (= 7). The largest pairwise correlation between predictors is 0.314.

Sensitivity analysis

Because this is a modeling study, there is a legitimate concern that its results depend on model assumptions. For one river configuration, I therefore evaluated sensitivity of translocation results to several factors, including assumptions about how individuals are captured for translocation and the assumed rate of downstream migration. First, I compared the effect of using effort-based versus quota-based capture of fish for translocation. In both cases, a range of values was examined. Next, I simulated one river configuration (15) with a lower (0.02 year^{-1}) and a higher rate (0.07 year^{-1}) than that in the simulations reported (0.05 year^{-1}). In addition, sensitivity results varying density dependence are reported.

Results

Translocation effects within a river configuration

This section evaluates how translocation influences the river segments involved in a particular river configuration. Translocation showed a general pattern within configurations of decreasing the final size of donor populations and increasing the final size of recipient populations. In 76% of cases (20 configurations \times 30 translocation scenarios), the size of the recipient population increased. Whether or not the recipient population increased did not depend on whether it was a long or a short segment. In 73% of cases, the size of the donor population decreased. Decreases were more common among long donor segments.

In addition to main effects on the donor and recipient, two kinds of trickle-down effects were evident. First, the average final population size of the segment directly downstream of

Table 1. Standardized coefficients for models to predict the demographic index of metapopulation status (NT_{500}) using six predictor variables (rows) that describe the river configuration and the river segments involved in translocation.

Predictor variable	T+W	T+N	T+D	(T+D) – (T+N)	T+W:baseline	T+N:N alone	T+D:D alone
LongPosition	-0.254*	-0.369*	-0.451*	0.091*	0.005	-0.254*	-0.139*
Interspersion	0.592*	0.304*	0.267*	-0.178*	-0.126*	0.188*	0.301*
Distance	-0.007	-0.093*	-0.017	0.118*	-0.019	-0.116*	-0.148*
SubsidizedShorts	0.085*	0.435*	0.275*	-0.358*	0.140*	0.271*	0.123*
LongRecipient	-0.095*	0.324*	0.062*	-0.405*	-0.186*	0.230*	0.104*
LongDonor	0.001	0.006	0.123*	0.112*	0.008	0.006	0.132*
RMSE	76.11	132.6	119	122.8	0.024	0.092	0.061
Adjusted R^2	0.513	0.696	0.466	0.461	0.056	0.313	0.196

Note: Translocation scenarios (T+) are shown with the downstream movement option (W, wide screening; N, narrow screening; D, downstream passage). All models are statistically significant ($p \leq 0.0001$) for 593 degrees of freedom. Asterisks indicate coefficients significant at $\alpha = 0.05$. RMSE, root mean squared error.

the recipient segment exceeded that of the same segment in the scenario without translocation in 61% of cases. Second, the population directly downstream of the donor segment was smaller in translocation scenarios than it was in the baseline scenario in 63% of cases.

Translocation effects among river configurations

This section addresses the question, “Under what conditions does reconnecting white sturgeon populations by translocation benefit the metapopulation?” I discuss the influence of mitigating entrainment mortality during downstream movement and patterns associated with attributes of the segments involved in the translocation.

Wide screening

Translocation with wide screening at each dam, including the dam below the recipient segment, did not benefit the metapopulation. The average NT_{500} among baseline simulations without translocation (mean = 2256, standard error (SE) = 25) was almost identical to the average among translocation scenarios (mean = 2253, SE = 25).

Most variation in NT_{500} was explained by differences among river configurations and not by translocation-related attributes. Translocations in river configurations with high interspersion and a long segment far upstream tended to have high NT_{500} values (scenario T+W, where T denotes translocation, and W denotes wide screening; Table 1). This pattern is driven by differences in metapopulation status among river configurations without translocation (as illustrated in fig. 5 of Jager 2006).

In contrast, there were no patterns in NT_{500} when focusing specifically on variation associated with translocation. The regression model fitted to variation in the ratio between NT_{500} for each translocation scenario and NT_{500} for the corresponding baseline scenario had almost no explanatory power (Table 1).

This lack of pattern is evident when examining differences among river configurations and translocation scenarios visually. Average NT_{500} was not higher among upstream translocations (Fig. 1a) and did not increase with the distance moved upstream (Fig. 2a). The number of short segments downstream of the recipient segment also had little effect on NT_{500} (Fig. 3).

Translocation-related effects on introgression showed clearer patterns among translocation scenarios with wide down-

stream screening than NT_{500} did. Simulated translocation from a downstream donor to an upstream recipient increased introgression, but no genetic effects were detected in downstream translocations. Introgression increased as the distance upstream between the donor and recipient segments increased (compare with horizontal lines showing results with no translocation in Fig. 4b).

Narrow screening

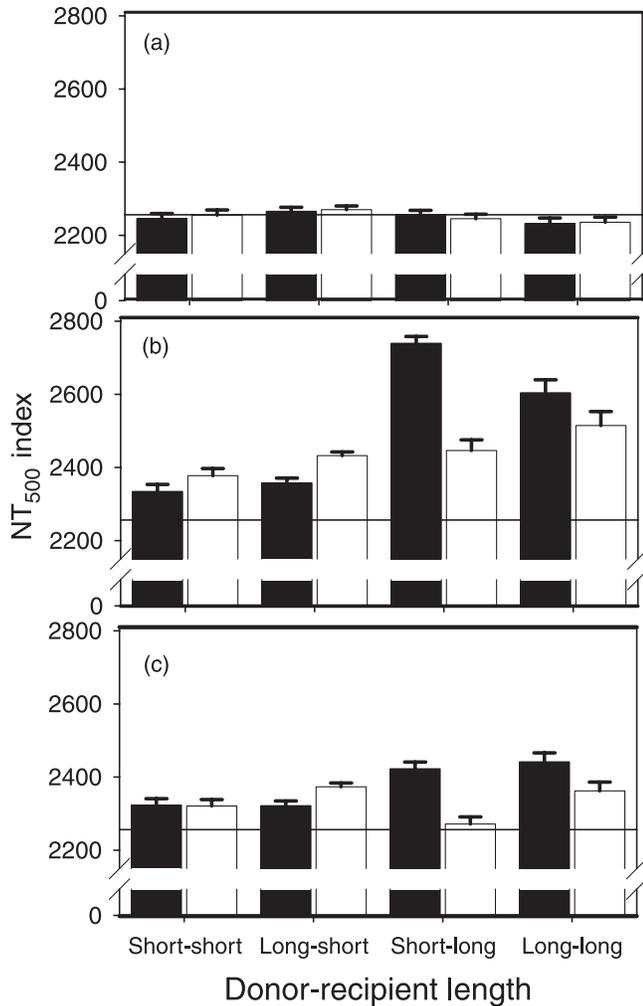
Narrow screening at the dam directly below the translocation recipient population usually increased average NT_{500} and N_{all} compared with the same translocation scenarios with wide screening at all dams. NT_{500} increased in 88% of cases (river configurations and translocation scenarios), with an average increase of 227 (SE = 8.6). Introgression increased in nearly all cases, by an average of 1.15 alleles (SE = 0.03). Translocation usually improved metapopulation status relative to that in the no-translocation baseline scenario when narrow screening was simulated below the recipient segment.

In the case of narrow screening, multiple regression analysis identified more patterns leading to an increase in NT_{500} than it did with wide screening, collectively explaining nearly 70% of variation in NT_{500} . Higher values of NT_{500} occurred in river configurations with high interspersion and a long segment far upstream and also in those with translocations to a long recipient segment supporting multiple downstream short segments (Table 1).

These patterns are visually apparent. NT_{500} for translocation scenarios with narrow screening was higher for upstream than for downstream translocations (Fig. 1b), particularly when sturgeon were moved to a long recipient segment (Fig. 2b). The effectiveness of upstream translocations from a long donor to a long recipient segment increased strongly with distance upstream (Fig. 2b). This might be because translocations farther upstream result in a larger number of intervening short segments subsidized by the upstream recipient population (Fig. 3).

Partitioning the demographic effect between narrow screening and translocation revealed that translocation augmented the demographic benefits of narrow screening in 36% of river configuration – translocation scenario combinations. In the remaining cases, narrow screening was more (or equally) effective alone. A multiple linear regression model showed that translocation provided added benefits in situa-

Fig. 1. Comparison of average metapopulation status ($NT_{500} + 1$ standard error) across river configurations between downstream (open bars) and upstream (solid bars) translocations for each of four combinations of donor and recipient segment lengths (e.g., category short-short on the x axis represents the average for translocations from short donor segments to short recipient segments). Three downstream mitigation scenarios shown are translocations with (a) wide screening, (b) narrow screening, and (c) downstream passage. The horizontal reference line shows the average for baseline simulations with wide screening and no translocation.

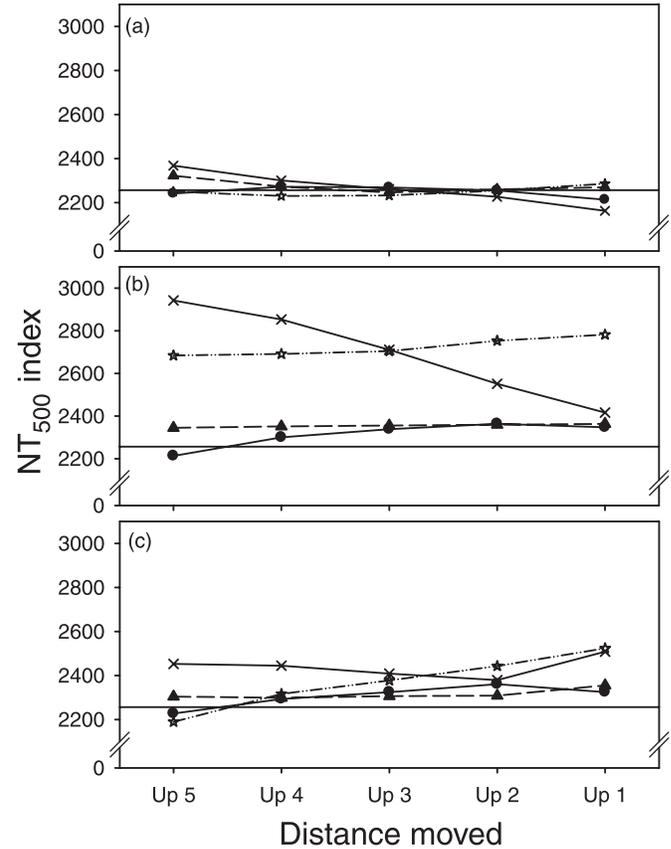


tions when the recipient supported multiple short segments downstream, when a long segment occurred far upstream, when the recipient was a long segment, and when interspersions of long and short river segments was high (ratio T+N:N alone (T, translocation; N, narrow screening) in Table 1). This suggests that one would have to know something about the river and the proposed recipient segment to predict whether the metapopulation would benefit more from the combination than from narrow screening alone.

Downstream passage

For translocation scenarios with downstream passage at the dam directly below the recipient, NT_{500} ranged between 2276 and 2470. Simulations with both downstream passage

Fig. 2. Longitudinal patterns in average metapopulation status (NT_{500}) for four combinations of donor and recipient segment lengths (circle, short-short; triangle, long-short; star, short-long; \times , long-long). Distance upstream on the x axis is measured by the number of segments. Three downstream mitigation scenarios shown are translocations with (a) wide screening, (b) narrow screening, and (c) downstream passage. The horizontal reference line shows the average for baseline simulations with wide spacing and no translocation.

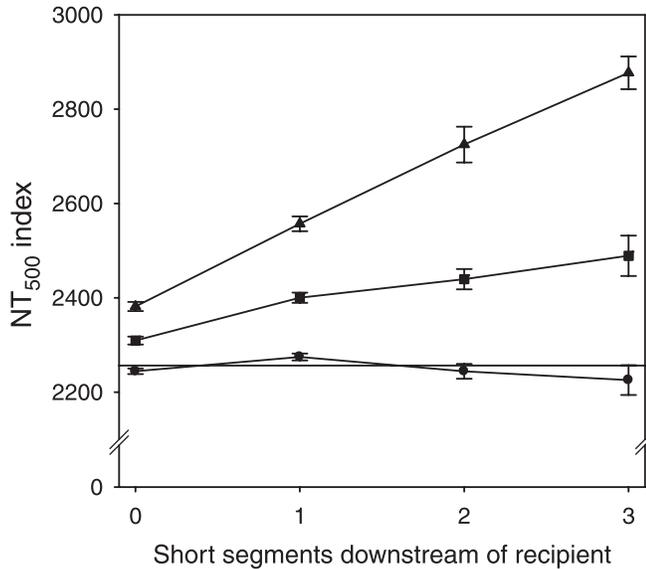


and translocation generally produced a higher average NT_{500} than the no-translocation baseline scenario (73% of configuration and translocation scenarios) and scenarios with downstream passage alone (59% of cases). NT_{500} was usually higher when compared with the same translocation scenario with wide screening below the dam (87% of cases). Note that connecting two adjacent segments increased NT_{500} compared with the baseline even if they were both short (Fig. 1c).

Simulated translocations produced a higher average NT_{500} when the recipient segment was long and upstream (solid bars in Fig. 1c). NT_{500} was highest when a long recipient was just upstream of the donor segment. Translocation with downstream passage provided the greatest benefit when sturgeon were moved up from the segment just below the recipient segment (i.e., from below to above the dam with downstream passage), but only if the recipient was long (UP 1 in Fig. 2c). This scenario most closely approximated reconnection of adjacent river segments.

A multiple regression model explained 19% of variation in the NT_{500} ratio with both translocation and downstream passage in the numerator and downstream passage alone in the denominator (Table 1, T+D:D alone). Translocation ben-

Fig. 3. Patterns in the average metapopulation index (NT_{500}), with bars indicating one standard error, for translocations with zero, one, two, and three short segments downstream of the recipient segments for wide or current screening (circles), narrow screening (triangles), and downstream passage (squares). The horizontal reference line shows the average for simulations without translocation or other mitigation.



efits, over and above those of downstream passage, were greatest in river configurations with high interspersion of long and short segments, in river configurations with a long segment far upstream, and for upstream translocations from a long donor segment.

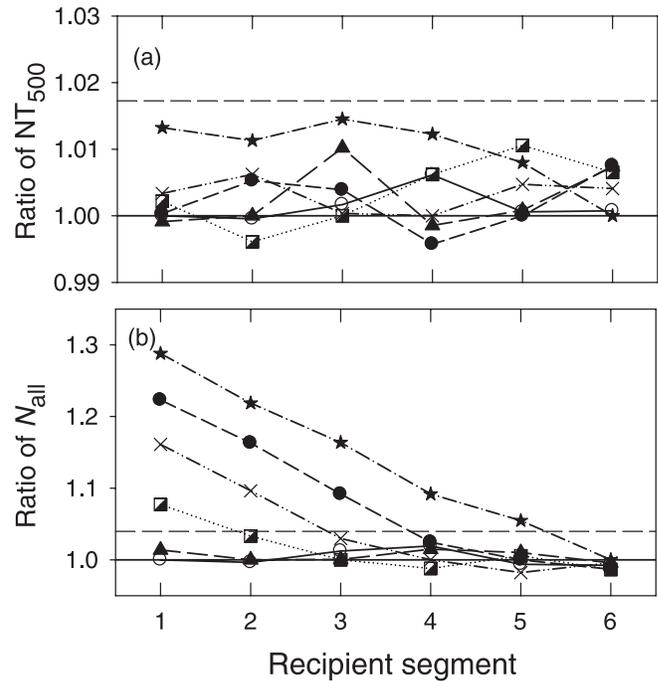
Comparing downstream passage and narrow spacing for each translocation scenario indicated that downstream passage performed better in 21% of cases. A multiple regression analysis of the difference between NT_{500} for the two mitigation options revealed that downstream passage was advantageous in rivers with low interspersion and with short segments upstream (middle column of Table 1). Downstream passage was favored over narrow spacing in translocations from a long segment to a short segment not supporting downstream short segments. Conversely, narrow spacing was favored in translocations of fish far upstream to long segments supporting short downstream segments.

Sensitivity analysis

The simulation experiment to compare effort-based with quota-based translocation shows that effort-based translocation (Fig. 5b) is less likely to result in extinction of the donor population (Fig. 5a). The decline in average final size of the donor population is steeper under quota-based removal (Fig. 5a). The cumulative number of white sturgeon translocated increases linearly under quota-based removal. The cumulative number of fish translocated by effort-based removal reaches an asymptote because it becomes harder to capture sturgeon (i.e., requires more effort) as their numbers decline.

The optimal benefit to the recipient population is reached at an intermediate removal of just under 1500 individuals,

Fig. 4. Metapopulation responses to translocation are measured by ratios of translocation to baseline values for two indices: (a) NT_{500} , the index of demographic status and (b) N_{all} , the index of introgression. A ratio of one shows no effect on translocation. Different donor segments are shown as different lines and symbols (segment 1, open circle; segment 2, triangle; segment 3, square; segment 4, x; segment 5, solid circle; segment 6, star). Numbers of segments increase downstream. The broken horizontal line shows one standard error, estimated by $1 + (1 \text{ baseline standard error}/\text{baseline average index})$.



regardless of the removal method (Figs. 5a and 5b). The final size of the recipient population decreases at high effort levels and quotas because of density-dependent factors that are simulated.

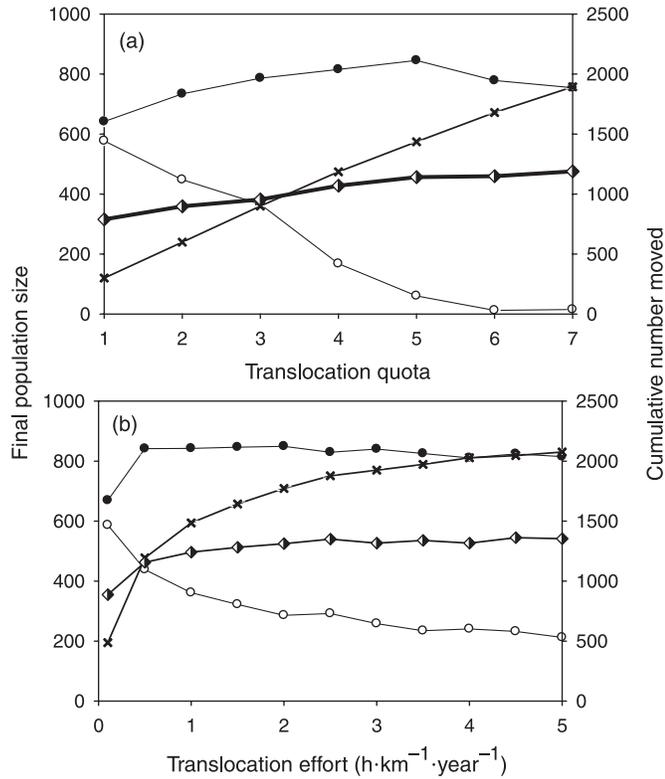
Simulations of translocations in configuration 15 with higher and lower downstream migration rates showed the same pattern observed with the nominal value; upstream translocations tended to be more successful than downstream translocations.

In an unpublished case study of the Snake River, I examined the role of density dependence on translocation benefits. The benefits of reconnection generally decreased as density dependence increased in the recipient segment. Simulations reported here imposed density-dependent mortality during the first year, but none thereafter. However, the spawning interval did increase with density. Simulation of density-independent downstream movement, rather than density-dependent movement, had little effect on results.

Discussion

Connecting populations has potential risks as well as benefits. This simulation study suggests that at the metapopulation level, indiscriminate efforts to reconnect populations via translocation might decrease rather than increase metapopulation status in a fragmented river. One con-

Fig. 5. Comparison of (a) quota-based and (b) effort-based translocation effects on a long donor (segment 5) and long recipient (segment 1) in river configuration 15. The left axis measures average final population sizes of the donor (open circles) and recipient (solid circles) segment. The right axis measures the total number of fish moved (×) and total emigration from the recipient reach (diamond symbols; to get emigration, multiply axis value by 10).



cern confirmed by this modeling study is that donor populations tend to decrease in size, along with their downstream neighbors. Parameter explorations show this result to be insensitive to the number of individuals moved.

A second concern is that reconnecting populations that are now isolated could have adverse genetic consequences. In this study, simulated translocation from a downstream donor to an upstream recipient increased genetic introgression. Although fitness effects were not simulated here, introgression caused by translocation from populations adapted to conditions in a different part of the river could pose a demographic threat by reducing the average fitness within a population that is already small (Riechert 1993). However, theory suggests that locally valuable alleles will be lost only if the fitness difference is smaller than the fraction of immigrants (Slatkin 1987). Questions remain about the extent to which white sturgeon populations are genetically distinct within, and even among, river systems (Anders et al. 2001). Concerns about local adaptation are warranted when a distant population is used as a donor for a population that has been isolated for a long time.

This study identified specific situations in which translocation was predicted to confer a demographic benefit on metapopulations. First, benefits were greater in certain river

configurations: those with high interspersion and a long source segment far upstream. However, translocation did not have clear benefits unless accompanied by either narrow screening (to slow emigration) or downstream passage (to allow safe emigration). Translocation provided the most benefit when the population receiving transplanted fish was in a long segment and positioned upstream, where it could provide support to populations in multiple, downstream, short segments.

Second, downstream passage increased the effectiveness of translocation, particularly when individuals were moved from one long segment to the one immediately upstream. Translocation to the next upstream segment combined with downstream passage most closely resembles a true reconnection of adjacent river segments, although the amount of free-flowing river is still reduced. Note that translocations farther upstream were probably less effective here because they required white sturgeon to pass downstream dams lacking passage facilities. Presumably, providing downstream passage at all intervening dams would improve results for translocations farther upstream.

Narrow screening had a strong positive effect on simulated metapopulation status with or without translocation. By slowing the rate of downstream migration by adults, screening builds populations in long upstream segments. Because small fish (larvae and juveniles) are able to pass downstream safely, the bolstered upstream source population is able to support shorter, sink populations downstream.

The benefits of narrow screening simulated here were probably higher than those that would be realized using other fractional reductions. First, according to the model, reducing screen size by half is near optimal for the downstream segment. If spacing is too narrow, no immigrants arrive from upstream, but if it is too wide, losses to the upstream population result in fewer immigrants (Jager 2006). Second, impingement, which was not simulated here, might reduce the benefits of screening. As the spacing on these devices becomes smaller and more effective at preventing entrainment, fish risk being trapped against the screen or trash rack, particularly in fast-flowing water. Impingement is more of a concern for smaller fish species than for sturgeons and other large fishes to which these results apply. Translocation was more likely to provide an added benefit over narrow screening if the river configuration had a long segment above shorter segments to serve as a recipient far upstream.

These results provide some practical guidance for choosing between preventing emigration from a segment targeted for translocation (narrow screening) or making it safe (downstream passage). If the recipient segment is short and segment(s) downstream are long, the model predicts that downstream passage is preferable. Note that translocation is often contemplated for shorter river segments with declining white sturgeon populations. If the recipient is a long segment upstream of short segments, then narrow screening is predicted to be the better option for the metapopulation.

If these results apply to other ecosystems, they would suggest that (i) translocations may not be beneficial if the matrix of habitat between patches is too dangerous, and (ii) translocations to a patch of potential source habitat lacking immigration would be most beneficial when the patch is

surrounded by sink habitats and when the emigration is restricted and safe.

Translocation benefits can be compared with those of upstream passage reported in the companion paper (Jager 2006). Translocation provided an average benefit across river configurations in some cases without mitigating risk during downstream movement, whereas upstream passage was never beneficial without mitigating risk. This result was robust to variations in translocation effort, suggesting that it did not depend on the number of fish that moved, which was higher in the passage simulations. Upstream passage is a special case in which the metapopulation benefits only if trickle-down benefits (more downstream migrants) offset reductions in the donor population below the dam.

Because density-dependent factors moderate demographic benefits of reconnection to the recipient segment and reduce the potential for trickle-down benefits, translocation may be less suitable for recipient segments with strong habitat limitation. This is demonstrated by noting that the benefits of translocations between long segments (source populations) increased with upstream distance between the segments for narrow and wide screening.

I am not aware of field studies against which these modeling results could be compared at present, although a translocation study is underway in the Columbia River. Whereas the success of translocation to reintroduce species to previously occupied habitat has been studied, the success of translocation as a means of reestablishing upstream connection has not. Translocation for the purpose of reintroduction has been less successful than expected, with less than even odds of success (Minkley 1995). This mediocre success has been attributed to failures of one-time reintroductions from distant populations for species with strong local adaptations. Success in selected cases has been attributed to careful attention to the habitat requirements of a species (e.g., Harig and Fausch 2002).

Although no recipe for success of translocation for the purpose of upstream reconnection has yet been discovered, this study suggests ingredients for successful reconnection programs designed for large, riverine fishes that can now be tested in the field.

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