A theoretical study of river fragmentation by dams and its effects on white sturgeon populations

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Synopsis

Most of the world's large rivers are fragmented by dams. Fragmentation of the river ecosystem alters migration patterns among fish populations and converts free-flowing river to reservoir habitat. In this study, we used an individual-based genetic metapopulation model to study the effects of fragmentation on the population viability and genetic diversity of a large-river fish, the white sturgeon, *Acipenser transmontanus*. In the first of two simulation experiments, we fragmented a 200 km river reach by building 1 to 20 virtual dams. Increased fragmentation produced an exponential decline in the likelihood of persistence, but no extinction threshold to suggest a minimum viable length of river. Compounding isolation with the loss of free-flowing habitat did not further reduce viability until free-flowing habitat was nearly eliminated, at which point extinction was certain. Genetic diversity within (among) populations decreased (increased) as we 'built' the first several dams. Adding more dams caused the number of persisting populations to decline and eroded genetic diversity within and among populations. Our second simulation experiment evaluated the effects of different levels of upstream and downstream migration between river segments. The results of these migration experiments highlighted the importance of balanced migration rates. We found that extinction risk was high for populations linked by high downstream, and low upstream, migration rates, as is often the case in impounded rivers. Our results support the view that migration patterns will play a significant role in determining the viability of riverine fishes, such as the white sturgeon, in river ecosystems fragmented by dams.

Introduction

A landscape perspective can provide new insights into the dynamic spatial organization of lotic ecosystems (Grossman et al. 1995). Lotic fishes form metapopulations, which may be defined simply as a set of local populations that undergo exchange of individuals. The spatial dynamics of such metapopulations are often hierarchical, with patchy-population dynamics among nearby patches and core-satellite dynamics among distant patches (Schlosser & Angermeier 1995). Although the classic metapopulation structure as defined by Hanski et al. (1995) may be rare among

river fishes (Schlosser & Angermeier 1995), migration remains an important process that should not be neglected when evaluating the viability of populations.

Riverine fish metapopulations, like metapopulations in general, may be changeable, hierarchical entities that conform to one or another ideal structure briefly and at one spatial scale (Rieman & Dunham 2000). Among river fishes, salmonids are the most likely to brush shoulders with the ideal of a classic metapopulation. This is because salmonid metapopulations have a distinct stock structure created by homing behavior, and their persistence is enhanced by the few individuals that stray into neighboring rivers (Quinn & Dittman 1990,

Waples 1995, Policansky & Magnuson 1998). At times, a core population may play a central role in supporting salmonid metapopulations (Li et al. 1995, Rieman & McIntyre 1995, Dunham & Rieman 1999, Rieman & Dunham 2000). Most riverine fishes have weaker stock structures than salmonids, although new genetic tools are beginning to reveal patterns of spatial and temporal fidelity among other fishes (e.g., Gross & Kapuscinski 1997). The challenge is to understand the effect of fragmentation by man-made barriers that artificially isolate populations and the role of migration among populations for the full spectrum of spatial life histories.

Because metapopulation dynamics have rarely been studied in rivers, it is unclear whether demographic and genetic consequences of fragmentation predicted by landscape models of other ecosystems apply. The idea of a critical minimum habitat size required for persistence is one example (Soule 1980, Gilpin & Soule 1986). This idea has stimulated both enthusiasm and controversy: enthusiasm over the important management implications and controversy over whether such sharp threshold sizes actually occur in nature (e.g., Quinn et al. 1989, Kareiva 1990). In rivers, this concept translates into a minimum segment length required for population persistence. Another example is the prediction that habitat fragmentation has adverse genetic effects on populations that elevate the risk of extinction (McCauley 1993). Spatial genetic models predict that genetic diversity declines when alleles are lost from each remnant population due to random genetic drift. However, the dire predictions made at the scale of a single population contrast with those at the scale of the metapopulation. At a metapopulation scale, genetic models predict that genetic diversity among populations increases with fragmentation because the particular alleles lost through genetic drift (and gained by mutation) differ from one population to the next (Wright 1978). These predictions have not been examined in river ecosystems.

The unique spatial features of rivers suggest that the process of habitat fragmentation and its effects differ from those of other ecosystems. In 2-dimensional landscapes, isolation of patches is often treated as a chance by-product of many disturbances that are independent random events. In rivers, fragmentation is not random. Fragmentation is a purposeful goal that must be achieved to realize the economic and social benefits of hydropower and flood control. Because large rivers played, and continue to play, such an important role in the development of human societies, they are among the most intensively fragmented ecosystems that exist. By the early 1900s, most large rivers in temperate regions had already been modified, and nearly all large rivers in the world are now fragmented by dams (Welcomme 1995). In rivers, fragmentation is easy to accomplish. A single damming event can isolate adjacent river segments and obstruct avenues of fish dispersal (Schlosser & Angermeier 1995).

The directional nature of river flow causes fragmentation to have different effects on populations in rivers than it does in other ecosystems. Colonization and extinction probabilities in unfragmented rivers follow a longitudinal gradient with lower colonization and higher extinction probabilities in upstream populations than in downstream populations of fishes (Gotelli & Taylor 1999). This violates the assumption of constant colonization and extinction probabilities required by Levins-style models of metapopulations used in other ecosystems. Fragmentation of rivers by dams further biases colonization rates by blocking upstream, more than downstream, movement.

In this study, we use a metapopulation[1] model to understand the effects of habitat fragmentation on fish populations. Specifically, we focus on land-locked populations of white sturgeon, historically a wide-ranging anadromous species adapted to the large-river environment. The model represents a series of white sturgeon populations that reside in adjacent river segments. We track the demographic attributes (e.g., age at maturity) and the genome of each individual in the metapopulation. This hypothetical genome is assigned to individuals present at the start of the simulation, but is inherited by later generations, which enables us to simulate changes in genetic diversity. In this study, the main predictions are the likelihood of persistence (viability) and the change in genetic diversity within and among simulated white sturgeon populations.

Case study—white sturgeon in the Snake River

This study focuses on the white sturgeon in the Snake River, Idaho. Concerns about the white sturgeon

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[1] The term 'metapopulation', as used here, refers broadly to a collection of local populations potentially connected by migration. This definition allows us to avoid changing terminology in describing simulations with different levels of migration (including none).
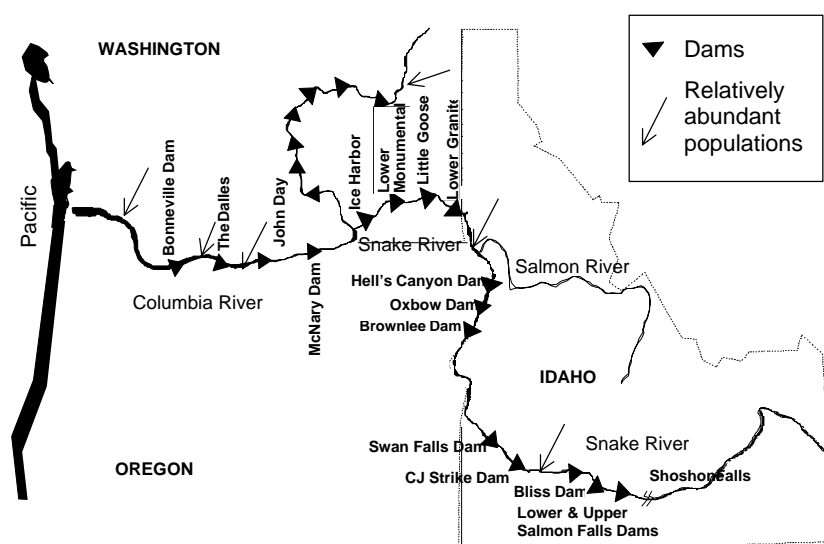
Figure 1. Fragmentation of the Columbia and Snake River system by dams. Six river segments with the healthiest populations are indicated by arrows.

stem, in part, from the declines observed in other species of sturgeon and paddlefishes (Rochard et al. 1990, Birstein et al. 1997). When rivers are impounded, migratory species, such as sturgeon, are the first to disappear (Poddubny & Galat 1995, Welcomme 1995). More than half of the land-locked white sturgeon populations in North America have declined (Cochnauer et al. 1985, Beamesderfer & Farr 1997). Six sizable populations remain in the Columbia River system (Figure 1). The population below Bonneville Dam is the healthiest (DeVore et al. 1995). In addition, white sturgeon populations in five other segments are abundant, but below historical levels. One population in the Kootenai River has been listed by the U.S. government under the Endangered Species Act.

White sturgeon populations in the Columbia River basin historically migrated from the Columbia River estuary up into the Columbia River and farther inland into the Snake River to spawn (Brown et al. 1992b, Schaffter 1997). Access to the estuary was blocked by the construction of the first dam on the Columbia River in 1933. Since that time, construction of additional dams has sequentially divided the river habitat into smaller segments, many of which lack free flowing river habitat. Population fragmentation has probably contributed to the decline of some white sturgeon populations in the Snake and Columbia rivers.

Model description

The metapopulation model is individual-based, tracking the demographic and genetic attributes of each individual fish. This allows us to represent the variation in life history traits observed in this species. For example, the age at maturity differs substantially among individuals (Jager 2000). It also gives us the ability to simulate changes in genetic diversity of populations over time by tracking the inheritance by individuals.

The model simulates both demographic and genetic currencies to describe population response to fragmentation and altered migration patterns in rivers. The likelihood of persistence simulated over 1000 years is our main demographic currency for population viability. We track two genetic currencies: (1) average heterozygosity within populations and (2) genetic diversity among populations.

Simulated river habitat

Our white sturgeon model represents serially linked river segments separated by dams. Each segment is divided into a reservoir portion downstream and a free-flowing portion upstream. The model tracks a number of attributes of individual white sturgeon. These include age, size, sex, genetic composition, age at
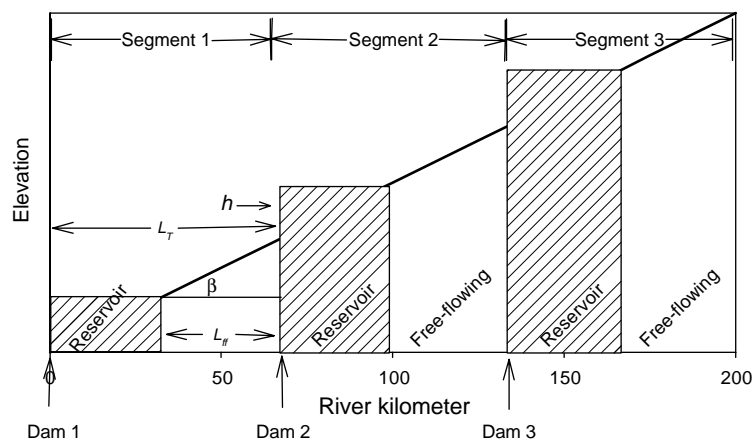
Figure 2. Diagram of a typical 200 km segment of river fragmented by three dams. We estimated the length of free-flowing habitat (L_{ff}) from total segment length (L_T), dam height (h), and river slope (β).

maturity, spawning interval, and location in one of the river segments. To initialize the model, we specify the number of dams and divide the river's length evenly into the specified number of segments. We use a simple geometric argument to estimate reservoir length as one leg of the triangle defined by dam height, converted to km (h), and river slope (β, in km per km) (Figure 2). The length of river that remains free flowing (L_{ff}, in km) in each segment is the difference between the total length of the segment (L_T, in km) and reservoir length (Eqn. 1).

$$L_{ff} = L_T - \frac{h}{\beta}\sqrt{1 - \beta^2}. \tag{1}$$

This simple approach to estimating the length of river converted to reservoir habitat does not account for increased channel width in reservoirs or other site-specific factors, but it serves as a reasonable first-order approximation.

Founder population

The model generates a historical founder population with ages drawn from an exponential distribution with the mean age as its parameter. The gender of each individual is drawn from a binomial distribution with a mean sex ratio of 0.5. Individuals entering the population draw two life history attributes from normal distributions with parameter values listed in Table 1: age at first maturity and the interval between subsequent spawning events.

We initialize the populations with 8 of 32 possible alleles at each of 10 loci. The genotype of each individual in the founder population is generated from a uniform distribution of initial allele frequencies for each locus under the assumption that loci are independent. The remaining 24 alleles may enter the population later in the simulation through the process of mutation. The genetic component of the model is described in more detail in Jager (2000).

Other than age, each individual retains these assigned demographic and genetic attributes throughout its life. Other attributes (e.g., fecundity and mortality risk) vary among individuals as a function of age or size.

Individual-based simulation

The individual-based population model operates on an annual time step. During each time step, model sturgeon may experience three events: reproduction, migration, and death. We describe the simulation of these events in the next three sections. Table 1 gives definitions and values for all model parameters described below.

Reproduction

Simulated reproduction has four components. First, each year we identify a pool of eligible spawners. Second, we simulate formation of spawning aggregations. Third, we simulate the fecundity of each female that successfully spawns. Finally, we simulate the inheritance of genetic material by offspring.

Table 1. Model parameters. Two sensitivity indices, the standardized regression coefficient (SRC) and the relative partial sum of squares (RPSS), are listed for parameters included in the sensitivity analysis for each of two response variables: likelihood of population persistence (P_{1000}) and among-population genetic diversity (G_{ST}).

Name	Parameter description	Reference and/or equation number	Baseline value	Persistence		Genetic diversity	
				SRC	RPSS	SRC	RPSS
N_0	Initial density of age 1 and older fish (# km^{-1})		1.0				
A_0	Initial population average age (y)		8	+0.0394	0.0001	+0.0427	0.0012
h	Average dam height (m)	Eqn. 1	30				
β	Average slope of riverbed	Eqn. 1	0.001				
S_y	First year survival rate (y^{-1})		0.0005	+0.0134	0.0001	+0.0739	0.0036
S_j	Survival rate of juveniles (y^{-1})	(Cochnauer 1983)	0.70	+0.3567	0.0848	+0.2091	0.0291
S_a	Survival rate of adults (y^{-1})	(Cochnauer 1983)	0.70	+0.1496	0.0149	+0.1568	0.0164
K	Carrying capacity of refuge from anoxic conditions (# km^{-1})	Eqn.4	210	−0.0154 −0.2289	0.0002 0.0357	−0.0058 −0.0448	0.0000 0.0014
Agemat_avg	Average age at first maturity for females, males (y)	(Cochnauer 1983)	18, 14	+0.0003 −0.0565,	0.0000 0.0021,	−0.0094 +0.0602,	0.0001 0.0024,
Agemat_SD	Std. dev. of age at maturity for females, males (y)	(Cochnauer 1983)	1.5, 1.5	−0.0210	0.0003	+0.0380	0.0009
SI_avg	Average spawning interval for females, males (y)		5, 2	−0.0659, −0.0078	0.0028, 0.0001	+0.0668, +0.0214	0.0029, 0.0004
SI_SD	Std. dev. of spawning interval for females, males (y)		0.8, 0.3	−0.0482, −0.0624	0.0015, 0.0025	+0.0320, +0.1060	0.0007, 0.0073
feca	Fecundity (#eggs) vs. fork length (cm) intercept	(DeVore et al. 1995), Eqn.3	0.072	+0.0252	0.0004	+0.0553	0.0020
fecb	Fecundity (#eggs) vs. fork length (cm) exponent	(DeVore et al. 1995), Eqn.3	2.94	+0.7694	0.4127	+0.3008	0.0631
lek_size	Maximum number of female spawners per km		0.5	+0.0148	0.0001	+0.0283	0.0005
sex_ratio	Maximum number of males per female spawner		5	−0.0295	0.0009	+0.0445	0.0019
Kvb	Rate of change in fork length (cm) with age (y)	Eqn.2, unpublished data[1]	−0.045	−0.1223	0.0096	−0.0289	0.0005
T_0	Initial age (y)	Eqn.2, unpublished data[1]	−0.795	−0.0245	0.0004	+0.0694	0.0031
L_∞	Maximum size of adults (cm)	Unpublished data[1]	275	+0.0240	0.0006	+0.0188	0.0003

[1]Lepla, K.B. & J.A. Chandler. 1995. A survey of white sturgeon in the Bliss reach of the middle Snake River, Idaho. Technical Report Appendix E.3.1-E, Idaho Power Company, Boise.

The pool of eligible spawners includes all mature adults that reach reproductive readiness in a given year. Whether an individual white sturgeon is eligible is determined by its age at first maturity and the interval between its spawning events. In the model, we assign these two reproductive parameters to individual fish from specified normal distributions (Table 1).

White sturgeon form spawning aggregations during spring. In the model, we simulate one aggregation in each river segment. We impose density-dependent limits on the density of female spawners allowed to join the spawning aggregation. We calculate the maximum number of spawning females as the product of the maximum density per 1 km of river (lek_size) multiplied by the length of spawning habitat. When the ratio of males to females is high it is unlikely that excess males will fertilize eggs. Therefore, we limit the sex ratio of spawning aggregations (sex_ratio) by randomly excluding excess adult males.

The fecundity of adult females increases with size (Cochnauer 1983, Chapman et al. 1996, Van Eenennaam et al. 1996). The model estimates the fecundity of each female in two steps. We predict fecundity, #eggs, from female length, L, which we obtain from a Von Bertalanffy relationship with age, A.

$$L = L_\infty(1 - e^{Kvb(A+T_0)}), \quad (2)$$

$$\#eggs = feca \, L^{fecb}. \quad (3)$$

After simulating egg production by females in the spawning aggregation, we simulate the inheritance of alleles by offspring. We assume that all males in the spawning aggregation are equally likely to fertilize a given egg. At each locus, we draw one allele from each parent at random. We assume that the white sturgeon genome is functionally diploid (Van Eenennaam et al. 1998), meaning that all but two alleles per locus have been silenced. After offspring inherit alleles from each parent, mutation from the inherited allele to an adjacent one occurs randomly and infrequently (Kimura & Ohta 1978).

Migration

To simulate migration, each individual in river segment k is assigned an annual probability, $M(k, j)$, of moving from its current segment k to each alternative segment j in the river. Thus, the number of sturgeon emigrating increases in proportion to population size.

Mortality

We assign a much higher natural mortality risk to age-0 individuals (S_y) than to juveniles (S_j) and adults (S_a) (Table 1). In addition to natural mortality, one of the two habitat-loss scenarios that we consider represents mortality associated with poor water quality in reservoir habitat. We assume that individuals able to remain in the refuge (free-flowing habitat) are not exposed to mortality risks associated with anoxic conditions during these episodes. S_x, calculated in Eqn. 4, is the average fraction of individuals killed due to exposure to anoxic reservoir conditions. N is the number of individuals in the population, K is the carrying capacity, and L_{ff} is the length of free-flowing river habitat.

$$S_x = \min\left(1, \frac{KL_{ff}}{N}\right). \tag{4}$$

Demographic and genetic measures of population viability

In all simulation experiments, we report one demographic and two genetic measures of viability. Values for these three model response variables represent averages from 25 replicate populations that are each simulated over a period of 1000 years with the parameter values listed in Table 1. Our demographic response is the likelihood of persistence to year 1000, P_{1000}. In these simulations, persistence reflects the ability of white sturgeon populations to recover from a catastrophe.

We simulate a catastrophe by starting with a population density low enough that demographic stochasticity may prevent recovery. Demographic stochasticity in these simulations can result from variation in the age structure and reproductive life history parameters of individuals in the initial populations and from random deaths.

As our genetic response variables, we report two indices describing change in the genetic diversity of neutral markers within and among populations. As our first index, we focus on average heterozygosity, a commonly measured index of genetic diversity within populations. An individual's heterozygosity measures the fraction of gene loci that have two distinguishable alleles. For each population, H is heterozygosity averaged over the loci of all individuals. H_I, the average H over populations, is the probability of heterozygosity of any one gene drawn from the metapopulation. Because our simulated populations are random mating, $H_I \approx H_S$, the probability of heterozygosity of a gene drawn from an equivalent random mating population (Hartl & Clark 1989).

Our second index, G_{ST}, quantifies the effects of population subdivision on inbreeding and reflects genetic differentiation among populations (Nei 1973). This is an extension of the hierarchical F-statistics to the case of multiple alleles,

$$G_{ST} = \frac{H_T - H_S}{H_T}, \tag{5}$$

where H_T is the probability of heterozygosity of a gene drawn from an equivalent random-mating total population. Because mating is random in these simulations, population subdivision is the only factor contributing to inbreeding. In our simulations, both genetic drift (chance loss of alleles) and mutation (chance gain of alleles) can increase diversity among populations. We report the percent change in the two indices above (H and G_{ST}) between the start and finish of the simulation, with a standard error to describe variation among replicates.

Sensitivity analysis

Because there is uncertainty associated with the parameter values used in our simulations, we conducted a sensitivity analysis to evaluate the sensitivity of a model's predictions to its parameters. The analysis was conducted with the basic model (i.e., not the version set

up specifically for these simulation experiments), and included the main demographic parameters. This analysis allowed us to rank model parameters by their impact on final population size.

We used PRISM software for sensitivity analysis (Jager et al. 1997, Van Winkle et al. 1998). The white sturgeon model was run with 1000 different parameter combinations drawn as a Latin-hypercube sample from a truncated multivariate Gaussian distribution with specified mean (baseline) values (Table 1) and a coefficient of variation of 1%. This variation is used to estimate the influence of varying the parameters near one point in parameter space.

We report sensitivities for the two response variables predicted by the model: the average likelihood of population persistence to year 1000 (P_{1000}) and among-population genetic diversity (G_{ST}). We also calculated three response variables that are not reported in the results, but that show nearly identical patterns of parameter sensitivity to other model responses. The sensitivities of metapopulation persistence (the likelihood that all populations persist) and average final population size mirrored those of population persistence, P_{1000}. Average heterozygosity, H, showed similar patterns of parameter sensitivity to G_{ST}.

Two sensitivity indices reported in Table 1 are the standardized regression coefficient (SRC) and the relative partial sum of squares (RPSS). SRC is estimated from a least-squares regression analysis in which the model parameters are independent variables and the response variable is the dependent variable. This index gives the change in the model prediction in standard deviations corresponding to one standard deviation change in the model parameter, given that all other parameters are constant. The sign of the index indicates the direction of the response. The second index, RPSS, indicates the additional percentage of variance explained by each parameter, given that all other parameters are in the model. RPSS values range from zero to one.

The results show that both P_{1000} and G_{ST} predictions are most sensitive to the exponential rate of increase in fecundity, fecb, with fish size (Table 1). Fortunately, we have a good estimate of this parameter from Columbia River populations (DeVore et al. 1995). P_{1000} predictions have a secondary tier of sensitive parameters that includes juvenile survival, S_j, the average female age at maturity, agemat_avg, and adult survival, S_a. Among these, survival parameters are the most uncertain. As expected, increased fecundity or survival had a positive influence on P_{1000}, while increased female age at maturity had a negative influence. Although genetic parameters were not included in the sensitivity analysis, we did some comparisons with different numbers of alleles and loci. These comparisons indicated that changing the assumed values for numbers of alleles and loci would not alter the results in a qualitative fashion (i.e., the simulated final value of G_{ST} might change, but not the response of G_{ST} to simulated fragmentation).

Simulation experiments

We conducted three simulation experiments. The first considers the effect of fragmentation alone; the second considers the effect of fragmentation combined with habitat loss; and the third considers the effects of migration patterns. Methods, results and discussion of each set of simulations are presented in the following three sections.

Fragmentation experiment without habitat loss

In large, impounded rivers such as the Columbia and Snake rivers, breeding populations of sturgeon are isolated to a considerable extent from those in other river segments by dams. Sturgeon tend to stay near the bottom of deep pools and are too large to use fish ladders as effectively as salmon do, although some ladder designs appear to work[2]. There is no evidence that white sturgeon in the Snake River move upstream between river segments (Cochnauer 1983), but downstream movements by juvenile sturgeon have been documented.

Once populations are isolated, loss of genetic variation and inbreeding may contribute to population declines. Genetic studies of white sturgeon indicate that land- or dam-locked populations have lower genetic diversity than populations with ocean access (Brown et al. 1992b, Bartley et al. 1995).

Methods

We designed the first simulation experiment to address the effects of population isolation on demographic and genetic attributes of white sturgeon populations. We simulated fragmentation of a 200 km river habitat into segments of equal length created by building

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[2] Warren, J.J. & L.G. Beckman. 1993. Fishway use by white sturgeon on the Columbia River. WSG-AS 93-02, Washington Sea Grant Program, Seattle.
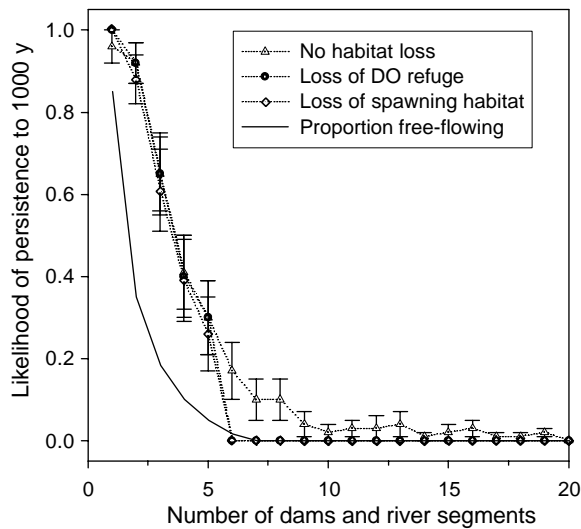
Figure 3. Simulated effect of increased fragmentation on the average likelihood of persistence, P_{1000} for isolated white sturgeon populations. Results are shown for simulations with no loss of habitat and for two habitat-loss scenarios. Circles indicate the average of P_{1000} over populations and error bars show the standard error in P_{1000} among replicate simulations, averaged over populations.

1 to 20 virtual dams. The length of the river segments, L_T, ranged from 200 to 5 km as we added dams.

Results

In simulations with no migration or habitat loss, the average likelihood of population persistence to 1000 y decreased from near one to near zero with progressive fragmentation of the river (open circles in Figure 3). The exponential pattern of decline did not suggest a particular minimum length of river habitat as a threshold. A small fraction of replicate populations persisted even in very short segments of river.

Average heterozygosity, H, within isolated, fragmented populations decreased with fragmentation as expected (open circles in Figure 4a). The genetic diversity among populations (G_{ST}), however, increased initially as expected (open circles in Figure 4b), but then decreased.

Discussion

These simulation results suggest that a single population in one large river segment has a better chance of long-term persistence than several populations divided among many small segments summing to the river
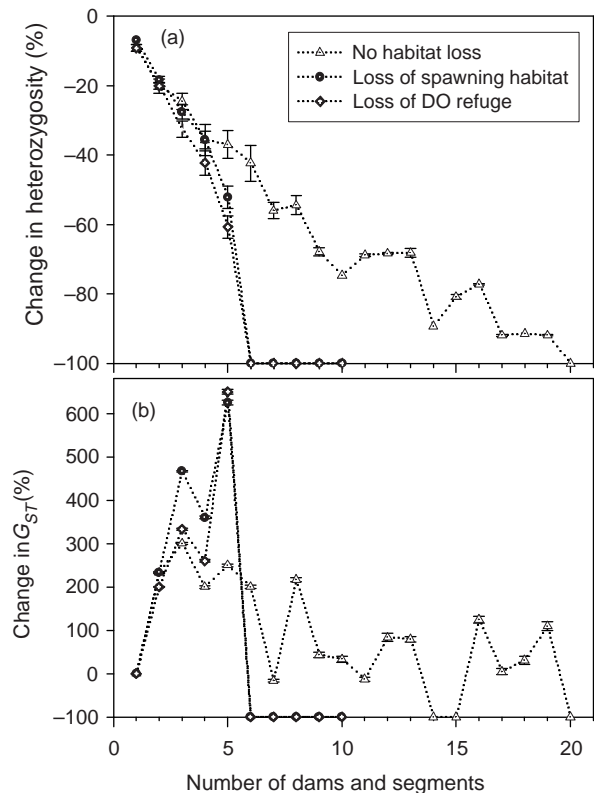

Figure 4. Simulated effects of river fragmentation on genetic diversity: a – change in average heterozygosity (H) within populations from an initial value of 0.87, and b – change in genetic diversity among populations (G_{ST}). Results are shown for the first simulation experiment (no habitat loss) and the second simulation experiment with two habitat-loss scenarios: one that involved loss of spawning habitat and one that involved loss of DO refuge. Error bars show one standard error calculated from 25 replicate simulations.

length. This result is similar to those reported for 2-dimensional landscape models (e.g., Burkey 1988).

We did not find a threshold minimum length of river needed to ensure long-term viability. Rather, an acceptable extinction risk must be specified before estimating a minimum length from our results. Perhaps this is fortunate because threshold values identified by models have not provided a sound basis for policy in the past (Ludwig et al. 1993).

Because of the directional flow environment, recommendations for a minimum river length should consider the spatial life history of the fish species. For example, Plantania & Altenback (1998) studied the early life history of broadcast-spawning cyprinids with semi-buoyant eggs that disperse with flow. They determined

that several species in this reproductive guild were extirpated from the Rio Grande River because the distances traveled by eggs and embryos under modified flow regimes in the fragmented river exceeded reach boundaries. Auer (1996a) focused on adult movements. She defined minimum river length as the minimum historical migration distance prior to dam construction, which was 715 km in the Fraser River (Lane 1991) for white sturgeon. However, there is also a population upstream of a natural barrier in the Fraser River, suggesting that this distance is not a strict requirement for population persistence.

The simulated change in genetic diversity among populations, G_{ST}, did not continuously increase with fragmentation as expected. G_{ST} was influenced by the number of populations remaining at the end of the simulations, which initially increased with fragmentation, but decreased as more populations reached extinction. This result highlights a potentially important interaction between genetics and demography that is neglected by purely genetic and by purely demographic models (see Whitlock 1992).

Fragmentation experiment with habitat loss

Construction of dams on the Snake River has converted 37% of free-flowing habitat to reservoir habitat (Cochnauer 1983). Reservoir habitat may provide some benefits to white sturgeon. For example, the relative weight of individuals caught in reservoirs with good water quality tended to be higher than that of individuals caught in free-flowing sections of the Snake River. However, two commonly cited drawbacks of reservoir habitat for sturgeon are (1) poor water quality and (2) lack of turbulent flow conditions for spawning. Fragmentation may reduce the viability of white sturgeon populations indirectly by removing free-flowing river habitat.

Conversion of free flowing river to reservoir habitat can have adverse effects on survival during episodes of poor water quality. Seasonal deterioration of water quality can be severe enough to kill fish in deep storage reservoirs that receive high nutrient loadings from the surrounding watershed (Cochnauer 1983). This is a particular concern for sturgeon because they reside on river bottoms in deep pools or reservoirs. Episodes of anoxic conditions occur during periods of high summer temperatures, when high water temperatures limit access to shallower, but better-oxygenated, habitat. When this occurs, the reservoir habitat becomes intolerable during summer for white sturgeon and other species adapted to free-flowing environments.

Conversion of free flowing to reservoir habitat can have adverse effects on reproduction. Like most sturgeon species, the white sturgeon depends on free-flowing rivers and seasonal floods for spawning (Parsley et al. 1993, Beamesderfer & Farr 1997). Typically, spawning takes place during high spring runoff, and positive correlations between spring river flows and sturgeon recruitment have been reported in the literature (Tsyplakov 1978, Votinov & Kas'yanov 1978, Kohlhorst et al. 1989, Auer 1996b). Adults form spawning aggregations in fast, turbulent waters with backwaters used for staging nearby. Specific flow-related habitat requirements for spawning may serve as a mechanism that allows spawners to find each other. Reservoirs have less fast, turbulent habitat than free-flowing sections of river do, potentially reducing reproductive success.

Several hypotheses about the adaptive role of fast, turbulent waters during spawning remain untested. High river flows may clear spawning areas (Votinov & Kas'yanov 1978). Broadcasting demersal, adhesive eggs in fast, turbulent water may enhance egg viability by dispersing eggs and preventing clumping. Clumping may (1) reduce the proportion of eggs fertilized; (2) reduce aeration and removal of wastes; (3) increase the incidence of fungal infection; and (4) attract the attention of egg predators. Turbulence associated with high water velocity may exclude visual egg predators. Finally, dispersal by flow may reduce competition among embryos and larvae and provide access to a wider array of feeding areas (McCabe & Tracy 1994).

Methods

We designed a simulation experiment to evaluate the effects of habitat loss associated with impoundment on population viability and genetic diversity. We evaluated two scenarios. The first scenario evaluated the effect of reduced spawning habitat, and the second scenario evaluated the effect of reduced water quality. These two scenarios contrasted habitat losses that influence demography through reproductive parameters with those that act through survival parameters.

The methods for the two habitat loss scenarios repeated those of the previous simulations that varied the number of dams in a fixed length of river. In these simulations, we distinguished between free-flowing and reservoir habitat. We addressed two scenarios. In

the first, we restricted spawning habitat to free flowing river (L_{ff}, rather than L_T, in Figure 2). In the second, we simulated the mortality due to anoxic reservoir conditions with free-flowing habitat serving as a refuge (Eqn. 4).

Results

The two habitat-loss scenarios gave similar predictions. Both reached certain extinction when six or more dams were simulated (Figure 3). This level of fragmentation nearly eliminated free flowing river between dams. In simulations with fewer than six dams, neither habitat-loss scenario showed significantly different behavior from the fragmentation scenario without habitat loss.

We can only compare the two genetic response variables for simulations with six or fewer dams because the populations reached extinction at this point in both habitat-loss scenarios. Habitat loss amplified the genetic effects of population subdivision. Within populations, both habitat-loss scenarios caused heterozygosity (H) to decline faster than in the no habitat-loss scenario as fragmentation increased (Figure 4a). Among populations, genetic diversity (G_{ST}) increased faster with fragmentation in the two habitat-loss scenarios than it did in the scenario with no habitat loss (Figure 4b).

Discussion

In our simulations, the fate of each isolated white sturgeon populations was determined by the presence of limiting habitat, as well as by the length of the river segments. Simulation of the fragmentation process in rivers showed that the effects of habitat loss outweighed isolation effects only when free-flowing habitat became scarce. In contrast, the effects of isolation outweighed those of habitat loss until a large proportion of habitat was lost in simulated 2-dimensional landscapes (Bascompte & Sole 1996). Our simulations suggest that the presence of a small amount of critical habitat serving as a refuge, or a site for spawning, was sufficient to prevent habitat loss from aggravating the effects of fragmentation alone. This result may be species-specific, reflecting the high fecundity and potential for population increase of white sturgeon when environmental conditions are good.

We found that habitat loss amplified the effects of habitat fragmentation on simulated genetic diversity. For a specified number of segments (up to 6), simulated genetic diversity within (among) populations showed a larger decrease (increase) in simulations with habitat

loss than in simulations without habitat loss. This is the expected shift of genetic diversity from within to among populations predicted by Wright's (1978 and earlier) shifting balance theory.

Migration experiment

The migration simulations addressed questions about isolation effects on demographic and genetic population attributes.

Methods

In the migration experiment, we simulated different annual migration rates by varying the individual probabilities of downstream and upstream migration (5×10^{-2}, 4×10^{-2}, 3×10^{-2}, 2×10^{-2}, 10^{-2}, 10^{-3}, 10^{-4}, 10^{-5}, 10^{-6}, and 0 yr^{-1}). We simulated all combinations with upstream migration rate less than or equal to the downstream rate.

Results

Longitudinal position of a river segment influenced the effect of migration on populations, but only when upstream and downstream rates were unbalanced. When we compared migration scenarios for a series of three segments, scenarios with no migration or equal upstream and downstream rates did not show strong longitudinal trends (solid and open bars in Figures 5a,b). However, upstream populations simulated with higher downstream than upstream migration were less likely to persist and lost more genetic diversity than downstream populations (hatched bars in Figures 5a,b).

Asymmetry between up and downstream migration rates caused the lowest viability and the highest loss of heterozygosity in the middle population (bottom, right-hand corner and top, left corner of Figures 6a,b). Simulations with no upstream migration illustrate the effects of unopposed downstream migration on the population in the middle segment (open bars in Figure 7). We found that the likelihood of persistence decreased (Figure 7a) and more heterozygosity was lost (Figure 7b) as the rate of downstream migration increased. Under a high rate of downstream migration, viability of the middle population improved as the rate of upstream migration increased to match the downstream rate (striped bars in Figure 7a). Loss of heterozygosity also decreased as the rate of upstream migration increased (striped bars in Figure 7b).
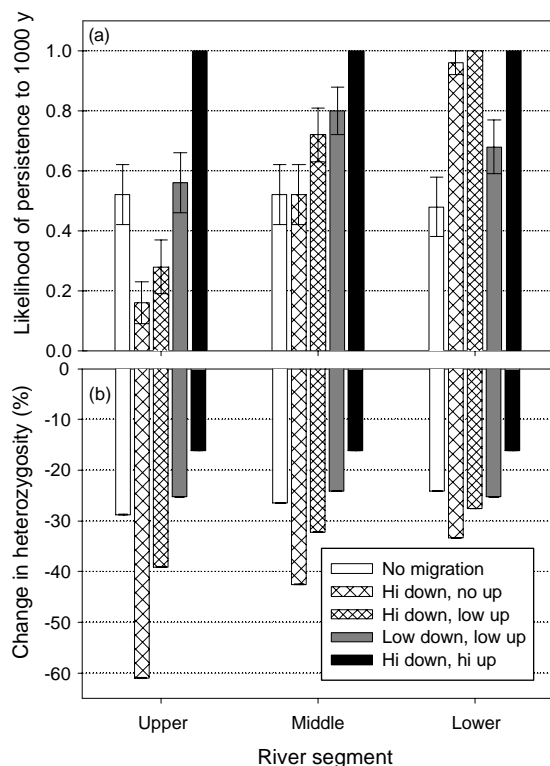
Figure 5. Populations in three connected river segments with various combinations of upstream and downstream migration rates are compared with respect to (a) the likelihood of persistence and (b) percent change in average heterozygosity. The low migration rate is 1×10^{-5} y^{-1} and the high rate is 0.03 y^{-1}. Error bars show one standard error calculated from 25 replicate simulations.

Figure 6. Contours of (a) the likelihood of persistence (P_{1000}) and (b) percent change in average heterozygosity (H) simulated for the middle population are shown for various annual downstream and upstream migration rates. In the absence of migration, $P_{1000} = 0.53 \pm 0.10$.

Viability of the middle population was highest when migration rates were nearly equal (the plateau along the diagonal in Figure 6a). Populations linked by high and equal migration rates retained the most heterozygosity (top, right corner of Figure 6b).

Discussion

Landscape models of 2-dimensional metapopulations suggest that low levels of migration can substantially increase persistence through rescue effects (Brown & Kodric-Brown 1977). As in 2-dimensional landscapes, we found that intermediate levels of balanced migration in our 1-dimensional model improved simulated viability. As in 2-dimensional genetic models (Gaggiotti & Smouse 1996), we found that increased migration reduced erosion of genetic diversity within populations.
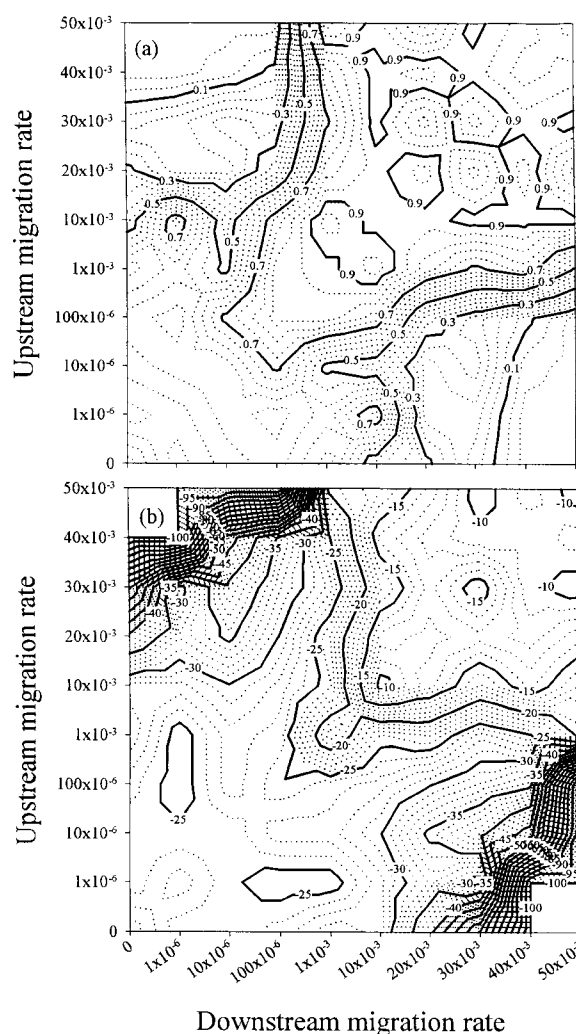
We identified one concern that is associated with fragmentation in rivers. The extinction risk associated with unbalanced migration may be great. Our simulations suggest that unbalanced migration outweighs isolation as an extinction risk in fragmented rivers. When simulated migration rates were relatively low in both directions, unbalanced migration was less of a concern. Practical ways of achieving balanced migration for sturgeon are not obvious because of the difficulties in providing upstream passage. Fish elevators

(Rochard et al. 1990) and assisted movements are two possible solutions.

We observed a pattern of decreasing genetic diversity upstream when simulated rates of downstream migration exceeded upstream rates. These results suggest that any observed pattern of decreasing genetic diversity upstream may indicate an imbalance between upstream and downstream migration. Such a longitudinal pattern has, in fact, been reported for white sturgeon. Heterozygosities determined from protein allozyme electrophoresis in three upstream populations were lower than those of downstream populations of white sturgeon [H = 1.4% above vs. 5.9% below Libbey Dam in the Kootenai River (Bartley et al. 1995); H = 0.30% above vs. 0.49% below Bonneville Dam, Columbia River; H = 0.22% above vs. 0.70% below Hell's Gate Rapids, Fraser River (Brown et al. 1992b)]. If such a pattern exists, it may also be explained by other factors, such as (1) cumulative genetic contributions from headwater populations (Hernandez-Martich & Smith 1996), (2)
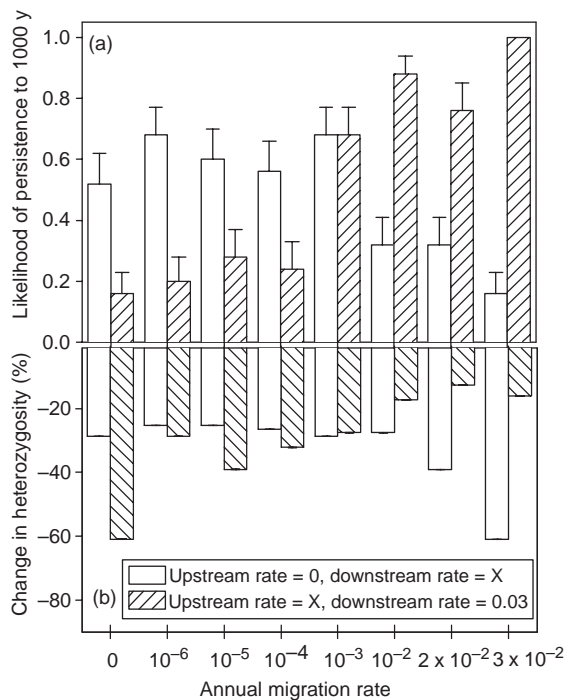
selective pressures associated with impoundment in upstream reaches (Brown et al. 1992a,b), or (3) straying among anadromous populations of diverse origins in downstream reaches.

Management implications

How do model results compare with field observations of population viability in shorter vs. longer reaches? We are interested in the potential role of fragmentation in explaining observed densities of white sturgeon populations among segments of the Snake River. The number of river segments is too small to support a rigorous quantitative analysis, but we can compare observed population estimates and free-flowing habitat among segments. The amount of free-flowing habitat appears to influence the ability of these river segments to support remnant white sturgeon populations in that no very short segments support measurable populations (open circles in Figure 8). However, two river segments support smaller populations than expected from the amount of free-flowing habitat, perhaps because other factors limit population size. Evidence from the Snake River supports the idea that viability is improved by providing longer reaches.
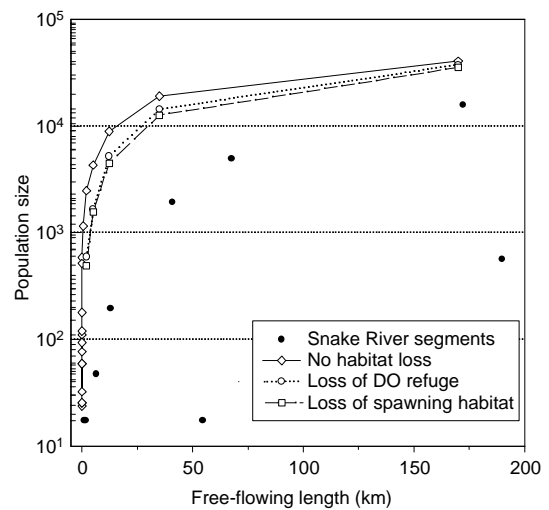

Figure 7. We fixed the upstream (solid) and downstream (striped) annual migration rates to show the effect of the other rate on (a) the likelihood of persistence and (b) percent change in average heterozygosity of the population inhabiting the middle of three linked river segments. Error bars show one standard error calculated from 25 replicate simulations.

Figure 8. Relationship between estimated sizes of white sturgeon populations in each of eight Snake River segments and the length of free-flowing habitat. To include segments with populations so small that no reliable estimates are possible, we assigned an arbitrary value of two fish. Three curves describe the relationship between final population size and free-flowing segment length simulated in fragmentation scenarios with and without loss of habitat.

Is free-flowing habitat necessary? Two reservoirs on the Columbia River are counter-examples that suggest impounded populations can persist in reservoirs if conditions are right. The Bonneville and Dalles reservoirs have populations of white sturgeon that are abundant, but smaller than historical abundances and those of the unimpounded population below Bonneville Dam (Beamesderfer et al. 1995). The tailwaters in these two segments are more riverine in character, suggesting that more detail is required than the reservoir vs. free-flowing distinction used in this paper.

This study has implications for fish population management of large rivers. If a fish species is managed as a metapopulation, then costs involve facilitating movement among river segments. If the species is managed as a series of distinct populations, then costs involve providing adequate habitat for all life intervals in each segment and under a broad range of environmental conditions. These alternatives present different ecological and economic costs and benefits. Understanding how river habitat (size, quality, and diversity) and movement between impounded reaches influence riverine fish fauna at the scale of the metapopulation is an important part of this equation. In this paper, we quantified the costs and benefits of migration to white sturgeon populations in terms of demographic and genetic risk. In the future, we will examine alternative management options in a metapopulation context.

Acknowledgements

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