Theoretical Study of Fitness Reduction in Stream-dwelling Fish by the Fixation of Slightly Harmful Mutations under Habitat Fragmentation

By

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Summary : Fragmentation of habitat can result in serious consequences for organisms. In particular for stream-dwelling fish, habitat fragmentation by dams or other artificial barriers limits their migration to only one way from upper to lower stream. This asymmetry in migration is unique to aquatic organisms and may result in problems that do not exist in terrestrial organisms. Among them, we analyze the fitness reduction by the fixation of harmful mutations using a numerical simulation model. In two population model, the fitness reduction depends almost entirely on the size of upper population, and is almost the same as one population model of a similar sized population. We show that artificial transport from lower to upper stream could greatly reduce the likelihood of the fixation of harmful mutation even if the amount or frequency of transport is small, and that the reduction of fitness becomes smaller than that without transporting. We also consider the influence of sex ratio of fish that are transported and find that it is not so large, but in the case of similar sex ratio between swimming down and transporting up, the fitness reduction becomes smaller. In conclusion, we recommend artificial transportations to upper stream over artificial dams or barriers.

Key words : fitness reduction, genetic fixation, harmful mutation, habitat fragmentation, theoretical model

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Introduction

Dams or other barriers in a river physically divide populations of aquatic organisms into fragments. The size of each fragment becomes much smaller than the original population size, and this event can impact on organisms in various ways such as the loss of Allee effect, edge effect, inbreeding depression, decrease of genetic diversity and fixation of harmful mutants.[1,2] In white-spotted char *Salvelinus leucomaensis,* a stream dwelling salmonid, Morita and Yamamoto (2000) showed that deformed individuals occurred in a small isolated population. They considered inbreeding in small population as a potential cause of body deformations. Further, Sato (2006) found reduced fitness and deformed fish in a small isolated population in Kirikuchi charr *Salvelinus leucomaenis japonicus.*

In addition to the impact caused by the small size of fragments, several studies have suggested that the establishment of dams can reduce species diversity[5], change the life history of white-spotted charr[6] and bull trout *Salvelinus confluentus*[7], cause the extinction of white-spotted charr upper stream[8], and result in genetic differentiation among fragmented populations.[9,10]

Mutations can occur in any population, but they are more easily fixed in smaller ones because the probability that only individuals with the mutant gene will by chance reproduce increases.[11] Fixation of slightly harmful mutations can cause a reduction in the mean fitness of the population[12], especially in a small population. If a barrier is constructed in a stream, an isolated subpopulation is established above the barrier, and the organisms that live in it may be able to be swept to the lower stream but cannot swim back up. Once a harm-

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ful mutation becomes fixed in this upper stream sub-population and individuals in the upper stream sub-population are continuously swept lower stream, frequency of the harmful mutation in the lower stream will increase. So even if population size is large in the lower stream, a small population size in the upper stream may be able to have a negative effect on the entire population in the stream. This type of genetic risk is systematically different from the risk of fitness reduction by inbreeding because this risk will occur by not only the biological reason ; population size but also structure of stream should be analyzed separately.

Similar situations can be produced by human activities other than making dams. In many mountain streams, fish cannot pass natural falls, and upper streams than the falls are empty areas for fish distribution. In such mountain streams, anglers sometime carry the fish from down steam of the fall to the upstream once and establish sub-populations there without further management.[13]   As a result, the distributions of fish may be expanded in range. However, the resulting upper streamers are smaller than the lower streamer, and the genetic changes in upper streamer can propagate in the lower streamer by biased migration. In other words, the establishments of small streamer sub-populations above the falls have the same effect as habitat fragmentation by dams. We can evaluate this releasing effect by the same model as that of damming.

It is possible to reduce the negative effects of barriers by either transporting individuals from lower to upper streamers, or making fish passages from lower to upper streamer. It is important in designing conservation measures to know the number of individuals and the frequency of transport to reduce the negative effects. These are especially important when the cost of the conservation operation is high. For fish passage, we need to check whether the transport is sufficient before and after construction.

There is a genetic rule of thumb called one-migrant-per-generation rule (OMPG) that one migrant individual per local population per generation is sufficient to obscure any disruptive effects of genetic drift.[14]   OMPG is sometimes used as a guiding principle for the conservation of genetic diversity, but the real situations often violate the assumptions of OMPG and more than one migrant per generation are required for the achievement of the genetic goal.[15]

In the case of fragmentation of riverine habitat, it is difficult to control the number of fish swimming to lower streamer and in some cases that number could be too substantial to count. It is important to evaluate whether it is sufficient to transport to the upper stream only one individual per each generation when more than one individual is moving from the upper to the lower streamer under mitigation. It is also important to know whether the mitigating effect is affected by both total number of transported fish and the transport interval. If transport intervals do not have effects, we can, for example, transport ten fish in five-year intervals instead of two fish every year and achieve the same mitigation effect.

Sex biased dispersals are observed in some stream dwelling fishes such as brook trout, *Salvelinus fontinalis*[16] and differential downstream migration from upstream of the barrier is expected and such a biased sex ratio of the transports may have an effect of genetic risk intensity.

In this paper we examine the extent of mutant gene fixation in a spatially structural population using simulation modeling. In particular we assess the effect of fixation of a deleterious mutant gene, enhanced by fragmentation of a river, in the mean fitness of the population and investigate the effectiveness of conservation efforts to mitigate potential loss in fitness. In the analyses we pay special attention to the implications of deviations from the OMPG, in particular the number and the sex ratio of lower migrants and upper transports, and the interval between upper transport events.

Materials and Methods

We consider a population separated into two subpopulations as upper and lower streamers in this paper. The individuals can move from the upper to lower streamers but they cannot move from the lower to upper streamers without human transportation. A simulation model is used to calculate the probability of mutant gene fixation in such a population.

The simulation settings used are described as follows. We assumed discrete generations. The numbers of mature individuals in the upper and lower streamers are denoted by N_u and N_d, respectively. We assume that these are constant. We further assume, mainly for simplicity, that the sex ratio of reproducing individuals in each sub-population is 1 : 1, which means we neglect demographic fluctuations in sex ratio. We also assume random mating and that the sex ratio of births is 1 : 1 in each sub-population.

A constant percentage of the juveniles in the upper streamers swim down to the lower streamers. This ratio is defined as $e_{u,f}$ and $e_{u,m}$ for female and male, respectively. Subscripts "*f*" and "*m*", respectively, denote female and male throughout this paper. For example, if $e_{u,f}=0.1$, 10% of female juveniles in the upper stream

swim down to the lower stream.

We consider a situation in which a constant percentage of juveniles in a lower streamer is transported to the upper streamer in every T generation, and we define the ratio as $e_{d,f}$ and $e_{d,m}$, respectively. For example, if $T=10$, $e_{d,m}=0.2$ and $e_{d,m}=0.1$, 20% of female juveniles and 10% of male juveniles in a lower streamer are transported to the upper streamer once in every 10 generations. We assume that both upper transport and lower migration occur at the same time. After that, natural selection works on the juvenile population, and the ratios of the juvenile's genotypes change deterministically, without genetic drift. After the operation of natural selection, N_u and N_d individuals among the juveniles survive and mature at random in the upper and lower streamer, respectively. In this process, the genetic drift occurs in each sub-population.

We consider one locus fixed by a wild type gene, 'A'. We calculate the fixation probability of a mutant, 'a', on this locus. We assume that this mutant gene reduces the fitness of its homozygote, 'aa', to $1-s$ compared to that of the wild type homozygote, 'AA', i.e. s means the instance of harmfulness in mutant. The fitness of the heterozygote, 'Aa', is assumed to be $1-hs$. Here, h is set as 0.36 as LYNCH et al. (1995) suggested based on the experimental data of Drosophila.

As a consequence of this fitness difference, the frequency of genotype in the juvenile population changes. For example, if the frequencies of each genotype at birth is $AA : Aa : aa = 1 : p_{Aa} : p_{aa}$, after the selection, the frequency of genotype AA becomes

$$\frac{1}{1+(1-hs)p_{Aa}+(1-s)p_{aa}}$$ and then, the adult individuals

are picked up randomly from juvenile population with this genotype frequency. We neglect genetic drift in juveniles assuming that the population size of juveniles is large.

The fixation probability of a mutation that appears in upper streamers is denoted by F_u, and that of the mutant which appears in the lower streamer is by F_d. Both F_u and F_d are function of N_u, N_d, $e_{u,f}$, $e_{u,m}$, $e_{d,f}$, $e_{d,m}$, T and s.

For a parameter s, we used following values in the simulation: 0, 1×10^{-4}, 2×10^{-4}, 3×10^{-4}, 5×10^{-4}, 7.5×10^{-4}, 1×10^{-3}, 2×10^{-3}, 3×10^{-3}, 5×10^{-3}, 7.5×10^{-3}, 1×10^{-2}, 2×10^{-2}, 3×10^{-2}, 5×10^{-2}, 7.5×10^{-2}, 1×10^{-1}, 2×10^{-1}, 3×10^{-1}, 5×10^{-1}, 7.5×10^{-1} (21 values in total and these values were determined arbitrarily). Ten thousand simulations were run from the occurrence of mutation to its fixation or disappearance using each value of s. We then estimated the relationship between the fixation probability and the value of s.

The total mutation rate, or the average number of mutations that occur in one individual in one generation, is assumed to be 1.5, as LYNCH et al. (1995) suggested based on the experimental data of Drosophila. We assume that the probability of mutation in an individual whose homozygote has fitness of $1-s$, is $\mu(s)$, whose distribution is assumed exponential with the expected value of s is 0.01.[12] In other words, we set $\mu(s) = \beta\exp(-\alpha s)$, where

$$\int_0^1 \mu(s)\,ds = 1.5$$

and

$$\frac{\int_0^1 s\mu(s)\,ds}{\int_0^1 \mu(s)\,ds} = \bar{s} = 0.01.$$

We can obtain α and β by solving these equations simultaneously as

$$\mu(s) = 150\exp(-100s).$$

In this case, the average fitness of the population is reduced by the fixation of a slightly harmful mutation. Eventually, the geometric average rate of the reduction in mean fitness of a population approaches a constant value. The geometric average of the population mean fitness ($\hat{m}_t$) is computed as:

$$\hat{m}_t = \exp(-tN_u\int_0^1 sF_u\mu(s)\,ds - tN_d\int_0^1 sF_d\mu(s)\,ds).$$

Here, $N_u\mu(s)$ is the probability of a mutant whose homozygote has fitness of $1-s$ occurring in the upper population. So $sF_uN_u\mu(s)$ is the expected reduction of fitness in one generation caused by the fixation of such one mutant. Integrating over s, $N_u\int_0^1 sF_u\mu(s)\,ds$, computes the expected rate of fitness reduction in one generation by all mutants occurring in a upper population. Similarly, due to mutation in the lower stream population, have their fitness reduced by $N_d\int_0^1 sF_d\mu(s)\,ds$. Thus we obtain

$$\frac{d\hat{m}_t}{dt} = -(N_u\int_0^1 sF_u\mu\,ds + N_d\int_0^1 sF_d\mu\,ds)\hat{m}_t.$$

and

$$\hat{m}_0 = 1.$$

By substitution in $\hat{m}_t$, we can solve for this formula. We used $\hat{m}_{100}$ under various conditions of population size, migration rate and/or migration interval, as the measure of the deleterious effect of mutation fixation. naminowa1

We focused to analyze the effect by changing the size of sub-populations (N_u, N_d), the fraction and the sex ratio of individuals swimming from upper to lower streamer reaches ($e_{u,f}$, $e_{u,m}$), the fraction and the sex

ratio of individuals carried up from lower to upper streamer reaches ($e_{d,f}$, $e_{d,m}$,) and the time interval between the "transport event" (T).

Parameter values used in the simulations are shown in Table 1. We made five main scenarios of simulation. The 1st scenarios "A" are no separation. The 2nd scenarios "B" are the simplest case with separation. The 3rd scenarios "C" are the simplest case with the transport of fish from the lower to upper stream. The 4th scenarios "D" have a time interval between transporting events. The 5th scenarios "E" are set to evaluate the effect of the sex ratio of fish swimming down and

Table 1 Parameter setting and result in each scenarios

Scenarios		N_u	N_d	$e_{u,f}$	$e_{u,m}$	$e_{d,f}$	$e_{d,m}$	T	$\hat{m}_{100}$	Remarks
A	A-1	100	0	0	0	0	0	-	0.784	Small population
	A-2	1000	0	0	0	0	0	-	0.997	Large population
B	B-1	100	1000	0.4	0.4	0	0	-	0.810	Simplest case with separation. Baseline scenario.
	B-2	50	1000	0.4	0.4	0	0	-	0.693	Smaller upper population than B-1
	B-3	1000	1000	0.4	0.4	0	0	-	0.994	Larger upper population than B-1
	B-4	100	2000	0.4	0.4	0	0	-	0.820	Larger lower population than B-1
	B-5	100	1000	0.01	0.01	0	0	-	0.795	The average number of individuals which swept down and were reproducing in the lower stream is about 1
C	C-1	100	1000	0.4	0.4	0.01	0.01	1	0.986	Simplest case with transport of fish from the lower to upper stream every generation.
	C-2	100	1000	0.4	0.4	0.001	0.001	1	0.936	The number of transport is one-tenth of that in C-1
	C-3	100	2000	0.4	0.4	0.0005	0.0005	1	0.981	Larger lower population and half transport ration than C-2
	C-4	100	1000	0.4	0.4	0.04	0.04	1	0.993	The same number of individuals as swim lower are carried up.
	C-5	100	1000	0.01	0.01	0.001	0.001	1	0.989	The average number of exchanging individuals between upper and lower stream population is about 1.
D	D-1	100	1000	0.4	0.4	0.01	0.01	10	0.923	10 years interval between transporting events. Other parameters are same with C-1. Annual average of transported number is same with C-2
	D-2	100	1000	0.4	0.4	0.001	0.001	10	0.852	10 years interval between transporting events. Other parameters are same with C-2. Annual average of transported number is one tenth of C-2.
	D-3	100	1000	0.4	0.4	0.1	0.1	100	0.887	100 years interval between transporting events. Annual average of transported number is same with C-2.
E	E-1	100	1000	0.8	0	0	0	-	0.798	Only female swim down without transporting up.
	E-2	100	1000	0.8	0	0.001	0.001	1	0.974	Only female swim down with transport of both sexes.
	E-3	100	1000	0.8	0	0.002	0	1	0.980	Only female swim down with transport of only female.
	E-4	100	1000	0.8	0	0	0.002	1	0.936	Only female swim down with transport of only male.

Denotes: N_u and N_d : The numbers of mature individuals in the upper and lower streamers. $e_{u,f}$ and $e_{u,m}$: The ratios of the juveniles in the upper streamers swim down to the lower streamers. $e_{d,f}$ and $e_{d,m}$: The ratios of juveniles in a lower streamer is transported to the upper streamer. T : The interval of transportation.

being transported up. Each main scenario has sub-scenarios. The details of sub-scenarios are noted in Table 1.

Results

The total simulation $\hat{m}_{100}$ has very small variation and is robust number even if we re-run the simulations, so we concluded that the actual number of $\hat{m}_{100}$ can be comparable among scenarios.

For the control scenarios "A", $\hat{m}_{100}$ is larger in larger population size (A-2, $N_u = 1000$) compared to smaller population size (A-1, $N_u = 100$). No fragmentation implies that the deleterious effect of mutation fixation is determined by population size and a large population size is able to maintain a high level of fitness.

In scenarios with no transport and difference only in the upper streamer size (B-1, B-2 and B-3), B-2 has the smallest upper streamer size ($N_u = 50$) and $\hat{m}_{100}$ in B-2 is the smallest among these three scenarios ($\hat{m}_{100} = 0.693$). In contrast, B-3 has the largest upper streamer size ($N_u = 1000$) and $\hat{m}_{100}$ is the largest ($\hat{m}_{100} = 0.994$) among these three scenarios. The comparison of $\hat{m}_{100}$ in B-1, which has a small lower streamer size ($N_d = 1000$), with that in B-4, which has a large lower streamer size ($N_d = 2000$), reveals that $\hat{m}_{100}$ in both scenarios are similar.

The comparisons of scenarios with same upper streamer size, i.e. A-1 and B-1 ($N_u = 100$), and A-2 and B-3 ($N_u = 1000$), show that $\hat{m}_{100}$ in fragmented population is similar as that in an isolated population of the same size as upper streamer. In B-1 more individuals are swept down to the lower stream ($e_{u,f} = e_{u,m} = 0.4$) than in B-5 ($e_{u,f} = e_{u,m} = 0.01$), but $\hat{m}_{100}$s in both scenarios are almost identical, therefore the ration of swimming down also has little effect on $\hat{m}_{100}$.

The results derived for the "B" scenarios show that if there is no artificial transport, the upper streamer size determines the rate of the deleterious effect of mutation fixation and that the lower streamer size and the number of individuals which are swept down do not influence the rate, i.e. fitness.

In the "C" scenarios, transport from the lower to upper streamer occurs every generation ($T = 1$). C-1 is same as B-1 but with the added effect of transport from the lower to the upper streamer ($e_{d,f} = e_{d,m} = 0.01$). Since $\hat{m}_{100}$ in C-1 is much larger than that in B-1. This suggests that we can keep $\hat{m}_{100}$ large by artificial transport from the lower to the upper streamer. Scenario C-2 is similar to C-1 but assumes a lower transport rate ($e_{d,f} = e_{d,m} = 0.001$). The estimate of $\hat{m}_{100}$ in C-2 is smaller than that in C-1, but the difference is small. The estimates of $\hat{m}_{100}$ in both scenarios C-1 and C-2 are much larger than that in B-2. Therefore, even if the transport ratio is

small, $\hat{m}_{100}$ becomes much larger than in the case without out any upper transport. The number of transported individuals in scenarios C-2 and C-3 is the same (both 1 individual in each time unit), but the lower streamer size in C-2 ($N_d = 1000$) is smaller than that in C-3 ($N_d = 2000$). The $\hat{m}_{100}$ value in C-2 is slightly smaller than that in C-3. This suggests that with upper transport, lower streamer size has an effect on $\hat{m}_{100}$. This is different from the case without upper transport, i.e. the results of the "B" scenarios.

In scenarios C-4 and C-5, the same numbers of individuals are transported to the upper from the lower streamer. In C-4, 40 adults on average, and in C-5, one adult on average, are exchanged between the upper and lower streamer. C-5 corresponds to the OMPG situation. In both cases, $\hat{m}_{100}$ is larger than scenarios without any transport.

In the "D" scenarios, the transport from the lower streamer occurs with varying time intervals (T generations). In all "D" scenarios, $\hat{m}_{100}$ is much greater than base scenario B-1. When T is increased from 1 to 10 (scenario C-1 versus D-1 and scenario C-2 versus D-2) $\hat{m}_{100}$ becomes smaller. D-1 and C-2 have the same annual average number of transported individuals and the corresponding $\hat{m}_{100}$ are similar. D-3 has the same annual average number of transported individuals with D-1 and C-2 but the interval is much larger, 100 years ($T = 100$), than D-1. The $\hat{m}_{100}$ in D-3 is slightly smaller D-1 and C-2. Thus, if the annual average number of individuals transported to the upper streamer are the same and the time interval of upper transport is relatively short ($T \leq 10$), the corresponding values of $\hat{m}_{100}$ are similar. In contrast if the interval (T) is very long, e.g. $T = 100$, the corresponding value of $\hat{m}_{100}$ is reduced.

The "E" scenarios set the number of individuals swimming to the lower streamer and the number transported upper streamer by their sex. For all the "E" scenarios, only females swim to the lower streamer ($e_{u,f} = 0.8$ and $e_{u,m} = 0$). E-2, E-3 and E-4 are the scenarios the same as E-1 but with upper transport. The corresponding values of $\hat{m}_{100}$ in E-2, E-3 and E-4 are larger than that observed in E-1. Among these three scenarios with upper transport, i.e. E-2, E-3 and E-4, E-3 has the largest $\hat{m}_{100}$, the next is E-2 and E-4 has smallest one.

Discussion

The simulation study demonstrates that fitness of population can be reduced under circumstances of asymmetric migration, caused by the construction of barriers (Table 1). This is caused by the fixation of slightly harmful mutations, which are enhanced by the small size of the upper stream sub-population. The fitness

reduction may not be great enough to cause extinction, but we cannot neglect it because the effect is not confined to the upper sub-population. It also occurs in the lower stream sub-population. In this study we consider only the situation with two separated sub-populations and if there is no upper transport, in the situation with more separated sub-populations the fitness reduction occurs over the total lower stream and can spread to the whole river. The intensity of the genetic effect in the entire population depends only on the population size in the upper stream (Table 1 B-1, B-2 and B-3). The intensity of the effect is not affected by the number of individuals that swim lower (Table 1 B-1 and B-5), and it is comparable to the case where there is only one population of the same size as the upper stream sub-population (Table 1 A-1 and B-1 or A-2 and B-3). In other words, the lower streamer would be better off if they could be completely separated from small sub-population in the upper stream.

The establishment of a small isolated sub-population in the upper stream occurs not only when a dam is constructed, but also when fish are introduced, intentionally or unintentionally, above the barrier where previously there were no fish. This study shows clearly that the establishment of a sub-population above the barrier can have negative genetic effects on the lower population. This kind of practice, which is sometimes promoted by anglers wishing to expand the distribution of the fish and to protect them from overexploitation and extinction is not always helpful to a fish population, and should be cautiously planned under the advice of scientists. It can be argued that small sub-populations artificially established above the barrier should be destroyed, so that no deleterious genetic exchange occurs. Although this may not be an acceptable option in fisheries management thus extreme caution is advised when artificially creating small sub-populations above an artificial barrier. If we cannot transport from lower to upper streamer, such a operation should become alternative.

We have shown that transport from the lower to upper streamer is an effective countermeasure against the reduction of fitness in a population caused by a barrier (Table 1, Scenarios "C"). We demonstrate the necessity for artificial upper transport of individuals or the construction of an appropriate fish passage through the barrier. Similarly, when a small sub-population is established above a barrier through introductions of the fish from below the barrier, the introduction should not be terminated after the sub-population is established unless we can destroy that upper streamer sub-population.

The required number of fish transported to the upper streamer depends on the number of fish swept lower streamer. If the average number swept lower to reproduce is one individual per generation, the negative genetic effect almost disappears with transporting one reproducing adult to the upper streamer. This result concurs with the OMPG rule. If the average number of individuals swept lower to reproduce is larger than one, the fitness becomes greater as the number of fish transported upper increases. Although even the upper transport of a small number of individuals is positive, it is necessary to transport upper a similar number as those swept lower to maintain the population fitness (C-2 and C-4 ; Table 1).

While upper transport has a positive effect, it is not necessary to do it in every generation. This fact may be important when considering the cost of a conservation measure involving upper transport. If yearly operations are too costly, transporting every ten generations could be substituted along with a corresponding 10 times increase in the number of individuals transported (C-2 and D-1 ; Table 1). Thus, if there is a severe restriction in the frequency of upper transports, we should increase the number of fish transported at one time. Making transport, even if it is not in every generation, is much better than no transport.

In our study, the effect of sex ratios of fish swept lower and transported upper was examined. We found small advantages associated with matching them (E-2, E-3 and E-4 ; Table 1). The result, however, may depend on the model's assumptions. In this study we assumed that the numbers of male and female individuals that reproduce do not depend on the number of juvenile fish of each sex after the events of swimming lower and transporting upper. If this assumption is removed, the correspondence of the sex ratio of swimming lower and upper transport may have a significant effect. But even in such a case, if there are sufficient numbers of individuals transported, these factors are not important (Kanaiwa and Harada, unpublished data).

We cannot determine a general rule for an acceptable level of genetic effect because it is based on two sources. The first is the historic population size and/or historic mutation rate. The second is the maximum level of genetic risks acceptable to managers. The results of this study suggest that the mean fitness of whole population with upper transport in some or all generations is greater than situations without any upper transport. Even if in situations with little artificial upper transport, there is positive benefit. This is exemplified in scenarios C-2, D-1 and D-2 where increasing the frequency of artificial transport controlled the reduction

of fitness better than increasing the number of individuals transported to the upper stream.

In actual streams, SWANBERG (1997) reported 8% of bull trout migrated lower stream over a dam and SCHMETTERLING and MCEVOY (2000) showed the lower stream fishes come to the dam and try to swim over it. SCHMETTERLING (2003) showed that if we make artificial transporter then the fish can spawn in the upper stream. These facts show our simulation setting is realistic and the probability that if we try such a conservation measure, it can work well.

TALLMON et al. (2004) reviewed the fitness benefit of immigration, and in many cases, observed benefits greater than predicted by theoretical models. Therefore, the benefit of artificial migration may actually be greater than our prediction.

In this paper, we only assessed the effect of fixations of harmful mutations enhanced by the construction of a barrier in a river. Small population sizes not only increase the probability of fixation of a harmful mutant gene but also cause the loss of genetic diversity, inbreeding depression and a host of other effects. However, there is evidence that demonstrates that even if effective population size in a river is small[22], the population can still be viable. Thus, a population size which is regarded as small may not always have a serious effect on the population of freshwater fishes. RIEMAN and ALLENDOLF (2001) suggest that managers should increase the number of adult bull trout spawners to 1000 per year since current levels are not sufficient for sustainability of bull trout population and LANDE (1995) suggests keeping an effective population size at about 5000 rather than 500 for wild animals. These are showing that a manager should decide the object of conservation level depending on each local characteristic.

We show how artificial transport can reduce the adverse effect of fixation of a harmful mutation. Transport may also mitigation other types of genetic effects which were not addressed in this study. Future research should be conducted to shed more light on these issues.

Acknowledgments

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