WILEY

Society for Conservation Biology

Effects of Habitat Fragmentation by Damming on the Persistence of Stream-Dwelling Charr Populations
Author(s): Kentaro Morita and Shoichiro Yamamoto
Source: *Conservation Biology*, Vol. 16, No. 5 (Oct., 2002), pp. 1318-1323
Published by: Wiley for Society for Conservation Biology
Stable URL: http://www.jstor.org/stable/3095327
Accessed: 17-12-2017 18:14 UTC

REFERENCES
Linked references are available on JSTOR for this article:
http://www.jstor.org/stable/3095327?seq=1&cid=pdf-reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://about.jstor.org/terms

JSTOR

Society for Conservation Biology, *Wiley* are collaborating with JSTOR to digitize, preserve and extend access to *Conservation Biology*

This content downloaded from 128.193.164.203 on Sun, 17 Dec 2017 18:14:04 UTC
All use subject to http://about.jstor.org/terms

Effects of Habitat Fragmentation by Damming on the Persistence of Stream-Dwelling Charr Populations

KENTARO MORITA* AND SHOICHIRO YAMAMOTO†

*Ocean Research Institute, University of Tokyo, 1-15-1 Minamidai, Nakano-ku, Tokyo 164-8639, Japan,
email morita@ori.u-tokyo.ac.jp
†National Research Institute of Fisheries Science, Ueda, Nagano 386-0031, Japan

---

Abstract: *Dam construction has serious consequences for aquatic ecosystems, and one of the most serious is the "barrier effect," the prevention of organism migration throughout a system. We assessed the effect of habitat fragmentation by damming on the population persistence of a stream-dwelling fish, the white-spotted charr (*Salvelinus leucomaenis*), in streams of southwestern Hokkaido, Japan. We sampled for charr at 52 dammed-off sites by electrofishing or snorkeling and measured five habitat characteristics: isolation period, watershed area, gradient, elevation, distance from sea. Of the 52 study sites above dams, white-spotted charr were absent at 17 sites and were present at 35 sites. Because the charr occupied all undammed upstream reaches, the damming would cause the absence of charr upstream. Among five habitat characteristics examined, stepwise logistic-regression analysis showed that disappearance was promoted with increasing isolation period, with decreasing watershed area (i.e., habitat size), and with decreasing gradient. The resulting logistic model explained 82.7% of the present white-spotted charr occurrence and forecasted that 12 of 35 extant populations will disappear after 50 years. Our findings imply that extirpation of small, dammed-off populations is inevitable unless efficient fish ladders are installed or dams are removed.*

Efectos de la Fragmentación del Hábitat Debido a la Construcción de Presas sobre la Persistencia de Poblaciones de la Trucha de Montaña que Habita Arroyos

Resumen: *La construcción de presas tiene serias consecuencias sobre los ecosistemas acuáticos y uno de los mas serios es el "efecto de barrera" (la prevención de que un organismo migre a través del sistema). Evaluamos los efectos de la fragmentación del hábitat ocasionados por la construcción de presas en la persistencia de un pez morador de arroyos, la trucha de montaña de manchas blancas (*Salvelinus leucomaenis*), en arroyos del suroeste de Hokkaido, Japón. Muestreamos en 52 sitios con represas empleando electropesca o buceo con esnórquel y medimos cinco características del hábitat (periodo de aislamiento, área de la cuenca, gradiente, elevación y distancia al mar). De los 52 sitios de estudio ubicados arriba de las represas las truchas de montaña estuvieron ausentes en 17 sitios y presentes en 35 sitios. Debido a que las truchas de montaña ocupaban todos los rangos sin represas arroyo arriba, la creación de represas pudo causar la ausencia de truchas de montaña arroyo arriba. Dentro de las cinco características del hábitat examinadas, el análisis de regresión logística mostró que la desaparición era promovida por un incremento en el periodo de aislamiento, con una disminución en el área de la cuenca (i.e. tamaño del hábitat) y con una disminución del gradiente. El modelo logístico resultante explicó 82.7% de la presencia de truchas de montaña y pronosticó que 12 de la 35 poblaciones actuales desaparecerían después de 50 años. Nuestros resultados implican que la extirpación es pequeña y que la exclusión por construcción de represas es inevitable a menos que se instalen desvíos para peces o que se remuevan las presas.*

Paper submitted October 1, 2001; revised manuscript accepted November 21, 2001.

This content downloaded from 128.193.164.203 on Sun, 17 Dec 2017 18:14:04 UTC
All use subject to http://about.jstor.org/terms

Introduction

Dam construction has serious consequences for aquatic ecosystems (Pringle et al. 2000). Besides environmental changes, one of the most serious impacts is the "barrier effect," which is the prevention of migration throughout each system. Dams prevent aquatic animals from reaching upstream habitats; so upstream populations become isolated. The high incidence of damming in the twentieth century has cut connections to many upstream aquatic habitats (Dynesius & Nilsson 1994). Habitat fragmentation has a harmful influence on population persistence (Wilcox & Murphy 1985). Various studies have shown that some freshwater fishes (e.g., Winston et al. 1991; Reyes-Gavilán et al. 1996; Morita & Suzuki 1999), shellfishes (Watters 1996; Kelner & Sietman 2000), and crustaceans (Miya & Hamano 1988; Holmquist et al. 1998) were extirpated and that species richness decreased in dammed-off habitats, but few studies have clarified the factors responsible for population persistence. Conservation biologists have long believed that small populations face a higher risk of extinction through demographic, environmental, and genetic stochasticity (Shaffer 1981; Lande 1988). We postulated that dammed-off populations in small habitats tend to be extirpated more quickly than those in large habitats.

The white-spotted charr (*Salvelinus leucomaenis*), a salmonid fish, is commonly distributed in mountain streams of Hokkaido, the northern island of Japan (Fausch et al. 1994). The life cycle of this species is highly variable. Some fish descend to the sea and return to their natal stream to reproduce as a large "migrant form," whereas other fish remain in their natal stream and reproduce as a small "resident form" (Yamamoto et al. 1999). In undammed reaches, reproduction occurs by both resident and migrant forms, and different forms belong to the same gene pool (Morita et al. 2000). Currently, many white-spotted charr populations are fragmented by dams installed to control erosion, and extant populations above dams are sustained by the resident form only (Morita et al. 2000). The Japanese Ministry of Construction (1999) has reported that 53,028 dams were built on Japanese streams to control erosion (the total number of dams exceeds this value because many dams were built by other institutions). Most erosion-control dams were constructed after 1970 (e.g., Nakamura 2001). Unlike dams that store water, Japanese erosion-control dams are small and have no impoundment area. Even small (2–10 m high) erosion-control dams prevent fish from moving upstream (Morita et al. 2000). We examined dammed-off systems to assess the status of white-spotted charr populations and to determine habitat characteristics, such as habitat size, physical features, and isolation period, related to population persistence.

Methods

Field Observations

We conducted field observations on the Oshima Peninsula in southwestern Hokkaido Island, Japan. On the Oshima Peninsula, the white-spotted charr is abundant and inhabits rivers from the source to mouth (elevation range, 0–600 m; gradient range, 0–35%; Fausch et al. 1994). We have surveyed the white-spotted charr on the Oshima Peninsula from 1996 to 2001 (Morita & Takashima 1998; Morita & Suzuki 1999; Morita et al. 2000; Morita & Yamamoto 2001), but we could not find unoccupied upstream reaches except for above barriers and in apparently poor habitats, such as sulfur springs and channels paved with concrete. All undammed upstream reaches were occupied ($n = 32$), and we used those as controls. Because all unoccupied sites above the dams were restricted to first- or second-order streams, controls were chosen from first- or second-order streams.

We established the presence or absence of white-spotted charr in 52 habitats upstream of dams from June through October 1999 by snorkeling or using an electrofishing unit (Smith-Root, Inc., Vancouver, Washington). These dams were installed on first- to fourth-order streams. The white-spotted charr inhabited all 52 streams below the dams. We always used an electrofishing unit to determine the absence of charr above the dam (capture probability of stream-dwelling salmonid by electrofishing generally ranges from 0.4 to 0.9; Riley & Fausch 1992; Kruse et al. 1998). Electrofishing progressed upstream from the dam to a point 500 m upstream or until the stream clearly was too small to support fish or a natural dispersal barrier was encountered (e.g., waterfall). If one assumes a capture probability of 0.4 and only 10 fish in the surveyed section, the probability of a false absence becomes small ($0.6^{10} = 0.006$). Whereas false absence was possible in an absolute sense, false absence due to a very small population would nevertheless indicate a high risk of extinction.

As predictors of the occurrence of white-spotted charr in 52 dammed habitats, we measured the following five independent variables: (1) isolation period, (2) watershed area above the dam, (3) gradient at the dam, (4) elevation at the dam, and (5) distance of the dam from sea. The isolation period was determined by subtracting the year of the dam construction from 2000. The watershed area, elevation, gradient, and distance from the sea were determined from 1:25,000- or 1:50,000-scale topographic maps. We also measured watershed area, gradient, elevation, and distance from the sea for 32 control (undammed) habitats at the stream mouth or juncture. Natural logarithmic transformations were made on independent variables before the analyses.

This content downloaded from 128.193.164.203 on Sun, 17 Dec 2017 18:14:04 UTC
All use subject to http://about.jstor.org/terms

Analyses

Because the data of the dependent variable was binary (presence or absence), we used logistic-regression analysis (Christensen 1997). The logistic function form is

$$p = \frac{e^{a + b_1X_1 + b_2X_2 + \ldots + b_nX_n}}{1 + e^{a + b_1X_1 + b_2X_2 + \ldots + b_nX_n}}, \qquad (1)$$

where p is the probability of occurrence, a and b_n are regression constant and coefficients, respectively, and X_n are independent variables. The parameter values were obtained by the maximization of the likelihood function L described by

$$L = \prod_{i=1}^{52} p_i^{q_i}(1-p_i)^{1-q_i}, \qquad (2)$$

where p_i is the estimated probability of occurrence for the ith dammed-off site calculated in Eq. 1 and q_i is the observed occurrence of the ith dammed-off site: $q_i = 1$ for presence, $q_i = 0$ for absence.

To identify subsets of independent variables that were significant predictors of white-spotted charr occurrence, we used backward, stepwise elimination, which starts with all of the variables in the model. At each step, variables are evaluated for entry and removal through a likelihood-ratio test ($p \leq 0.05$ to add and $p \geq 0.10$ to remove). The statistic of the likelihood-ratio test G^2 is described by

$$G^2 = -2(\ln L_R - \ln L), \qquad (3)$$

where $\ln L$ is the log-likelihood for the model and $\ln L_R$ is the log-likelihood for the model if the variable is removed. G^2 is compared with a chi-square distribution; if the test statistic G^2 is significantly greater, the null hypothesis of equality is rejected and the variable is significant and included in the model. To calculate the predictability of the model and forecast white-spotted charr occurrence, an estimated probability of occurrence (p_i) of 0.5 or greater was classified as presence.

Results

Among the 52 dammed-off sites surveyed, white-spotted charr were present in 35 and absent in 17; charr occurred in all undammed sites (Table 1). All absent sites were restricted to first- or second-order streams. The distribution of each habitat measure overlapped broadly between dammed-off absence and undammed presence. The null hypothesis that dammed-off absence sites have the same habitat measures as undammed presence sites was not rejected (multivariate analysis of variance, $F_{4,44} = 1.327, p = 0.275$), suggesting that dammed-off absent sites were suitable habitats before fragmentation.

Among the five explanatory variables examined, stepwise logistic regression identified three variables—watershed area above the dam, isolation period, and gradient—as the best predictors of white-spotted charr occurrence in dammed-off sites (Table 2), although the effect of gradient was marginally significant. The resulting logistic model predicted 82.7% of white-spotted charr occurrence in dammed-off sites. Regression coefficients were negative for isolation period and positive for watershed area and gradient. The occurrence of white-spotted charr increased with increasing watershed area, with decreasing isolation period, and with increasing gradient (Fig. 1). Although a strong negative correlation occurred between watershed area and gradient ($r = -0.67, p < 0.001$), both explanatory variables apparently influenced the occurrence of white-spotted charr (Fig. 1b).

Using the logistic model identified from stepwise procedure (Table 2), we predicted the relationships between the probability of occurrence and watershed area for different periods of isolation (Fig. 2). The effect of watershed area on the occurrence of charr was most pronounced in small habitats, and the probability of occurrence decreased dramatically with increasing isolation period, especially in watersheds of <1 km^2. According to this model, a watershed area of 2.3 km^2 is necessary to maintain a population for 50 years. Although we found 35 extant populations above dams,

Table 1. Habitat features for undammed and dammed-off sites with (presence) and without (absence) of white-spotted charr (mean ± SD).[a]

	Undammed site		*Dammed-off site*	
	presence (n = *32*)	*absence* (n = *0*)	*presence* (n = *35*)	*absence* (n = *17*)
Isolation period (year)	—	—	23.7 ± 12.1 (1-47)	30.1 ± 9.7 (7-39)
Watershed area (km^2)	1.5 ± 1.5 (0.1-5.8)	—	5.5 ± 6.8 (0.1-33.6)	1.1 ± 1.5 (0.1-5.9)
Gradient (%)	6.6 ± 4.7 (1.8-26.7)	—	5.8 ± 5.9 (1.1-33.3)	6.9 ± 5.4 (1.5-20.0)
Elevation (m)	81.9 ± 60.2 (0-220)	—	109.1 ± 76.1 (10-315)	122.9 ± 84.0 (20-305)
Distance (km)	7.8 ± 8.8 (0-34.4)	—	10.7 ± 10.4 (0.5-37.1)	13.4 ± 12.4 (0.6-37.4)
Stream order[b]	first or second order	—	first to fourth order	first or second order

[a] *Ranges are given in parentheses.*

[b] *Stream order as defined by Strahler (1957).*

This content downloaded from 128.193.164.203 on Sun, 17 Dec 2017 18:14:04 UTC
All use subject to http://about.jstor.org/terms

Table 2. Results of stepwise multiple logistic regression of occurrence of white-spotted charr and five independent variables in dammed-off sites.*

Step	*Variable*	*ln*L	*ln*L_R	G^2	*df*	*Coefficient*	p
1	elevation	−17.55	−17.60	0.09	1	0.361	0.763
	distance from sea		−17.79	0.46	1	−0.524	0.497
	gradient		−18.94	2.76	1	1.254	0.096
	isolation period		−22.70	10.28	1	−2.436	0.001
	watershed area		−29.43	23.74	1	2.099	>0.001
	constant					5.424	
2	distance from sea	−17.60	−18.00	0.81	1	−0.318	0.369
	gradient		−19.21	3.22	1	1.305	0.073
	isolation period		−22.70	10.20	1	−2.376	0.001
	watershed area		−29.47	23.73	1	2.083	>0.001
	constant					6.363	
3	gradient	−18.00	−19.87	3.73	1	1.404	0.054
	isolation period		−22.90	9.79	1	−2.389	0.002
	watershed area		−29.78	23.55	1	2.071	>0.001
	constant					5.668	

**Abbreviations: ln*L*, log-likelihood for the full model at each step; ln*L_R*, log-likelihood for the model if the variable is removed;* G^2*, statistic of the likelihood-ratio test as in Eq. 3.*

our model forecasted that 12 of these extant populations would disappear within 50 years.

Discussion

White-spotted charr often did not occur in dammed-off habitats, even though the charr occupied all undammed upstream reaches. Because habitat measures did not differ between dammed-off absence and undammed presence, white-spotted charr should be able to establish populations in all the dammed-off sites. Nevertheless, our results revealed that probability of occurrence decreased with decreasing watershed area (a surrogate for habitat size), with increasing isolation period, and with decreasing gradient. These empirical data are a good example of extinction events in natural populations that are a function of both temporal and spatial factors. Our study confirmed the importance of habitat connectivity for the persistence of populations, particularly for small populations. Also, we provided an incidence function based on dammed-off habitat characteristics, which may be useful for managing white-spotted charr populations.

Demographic and environmental stochasticity, natural catastrophes, and genetic stochasticity could cause extinction in small, isolated populations (Shaffer 1981). Theoretical studies show that the mean time to extinction increases with carrying capacity under either demographic, environmental, or genetic stochasticity (reviewed by Lande 1998). Although we cannot identify the relative importance of each kind of stochasticity, our empirical findings were consistent with these theoretical expectations: populations in small habitats tended to disappear more quickly than those in large habitats. Some researchers argue that genetic stochasticity has little influence on population persistence because it acts more slowly than other factors (Caro & Laurenson 1994; Caughley 1994). We have evidence, however, indicating

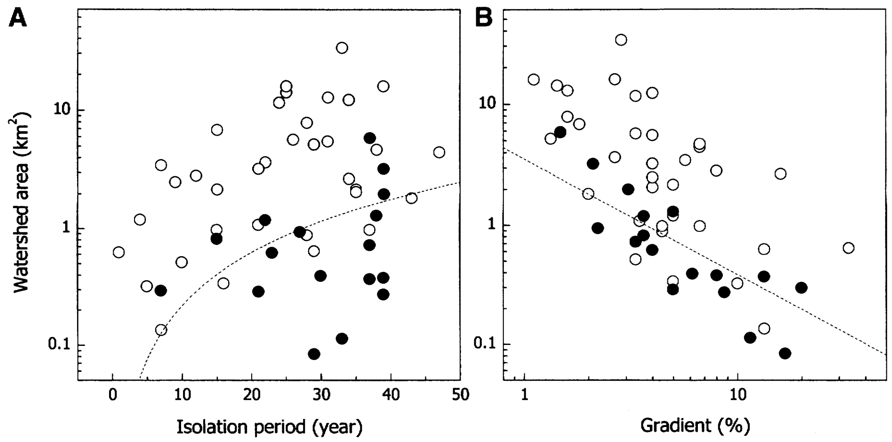


Figure 1. Presence (open circles) and absence (solid circles) of white-spotted charr in 52 dammed-off sites in relation to (a) isolation period and watershed area and (b) gradient and watershed area. Dashed lines represent 50% probability of extinction obtained from logistic-regression analyses.

This content downloaded from 128.193.164.203 on Sun, 17 Dec 2017 18:14:04 UTC
All use subject to http://about.jstor.org/terms

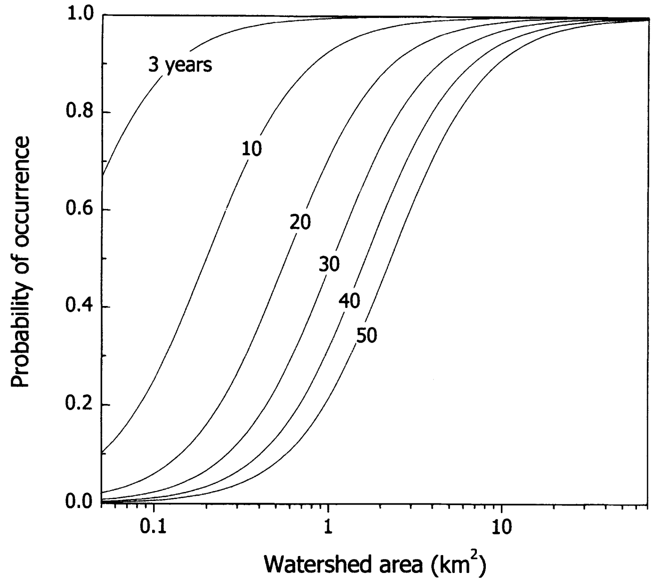


Figure 2. Relationships between watershed area and probability of white-spotted charr occurrence in dammed-off sites with different isolation periods (3, 10, 20, 30, 40, and 50 years). These curves were predicted from the logistic-regression model shown in Table 2. In this illustration, we used the average gradient for a given watershed area (i.e., ln(gradient) = 1.70-0.35 ln(watershed area), r = *−0.67,* n *= 52).*

that genetic deterioration occurred in extant dammed-off populations. Extant above-dam fish have lower genetic diversity, higher morphological asymmetry (S. Yamamoto, K. Morita, I. Koizumi, & K. Maekawa, unpublished data), and a genetically based lower growth rate compared with below-dam fish (Morita et al. 2000). A dammed-off population in which all individuals have deformities has also been reported (Morita & Yamamoto 2000). Hence we believe that genetic deterioration may have an important effect on these isolated populations.

In addition to stochasticity, there are two possible deterministic reasons that white-spotted charr disappeared in dammed-off habitats. First, population growth rates in dammed-off areas would decrease because of the loss of migrant forms. Migrant forms attain large body sizes and are twice as fecund as resident forms (Morita & Takashima 1998). Only resident forms can populate dammed-off habitats, so spawning biomass is decreased in dammed-off populations (Morita et al. 2000).

Second, the loss of habitat connectivity among populations could promote extinction. Recent evidence suggests that the population structure of some salmonids may fit the characteristics of a metapopulation (that is, a group of populations inhabiting discrete habitats connected by the migration of individuals) (Dunham & Rieman 1999; Rieman & Dunham 2000). Before damming, most dammed-off habitats are assumed to have been interconnected via the sea. A mark-recapture study reported that migrant fish can move up to 185 km in the sea (Aoyama 1997). According to a source-sink metapopulation model (Pulliam 1988), sink populations that have a negative growth rate would deterministically become extinct after being dammed off. Source populations with good-quality habitat would provide a continual source of immigrants to sink populations that might otherwise become extinct (cf. Cooper & Mangel 1998).

We found a significant relationship between gradient and white-spotted charr occurrence in our study. Gradient influences the availability of habitat type and the abundance of stream-dwelling salmonids, but the relationships between gradient and abundance may be either positive or negative (Kozel & Hubert 1989; Bozek & Hubert 1992). Unfortunately, no previous relationships between gradient and white-spotted charr abundance have been reported.

Recommendations

Our findings suggest that the disappearance of small, dammed-off fish populations is inevitable. Installations of efficient fish ladders or removal of dams is necessary to restore dammed-off populations. However, artificial barriers sometimes protect populations of native fishes from encroaching on non-native fishes (Thompson & Rahel 1998; Nakamura 2001). On Hokkaido Island, exotic rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) are increasing considerably (Aoyama et al. 1999*a*, 1999*b*; Takami & Aoyama 1999), and their negative effect on white-spotted charr is certain (Taniguchi et al. 2000; Takami et al. 2002). Exotic fishes approach just below the dams, turning dammed-off habitats into refuges for native fishes in some rivers (e.g., Takami et al. 2002). Therefore, managers should consider this potential benefit of dams before fish ladders are installed.

Acknowledgments

We thank Y. Kanno, K. Nishimura, T. Matsuishi, and S. H. Morita for their invaluable advice and encouragement and the Hokkaido Government and Hakodate and Hiyama Regional Forestry Offices for providing information on erosion-control dams. This paper benefited from critical reviews by J. R. Bower, M. Willson, K. Fausch, and several anonymous reviewers. The electrofishing surveys were made possible by sampling permits issued by the Governor of Hokkaido. This work was supported by a grant-in-aid for a Research Fellow of the Japan Society for the Promotion of Science (no. 07054) to K. M. from the Japanese Ministry of Education, Culture, Sports, Science and Technology.

This content downloaded from 128.193.164.203 on Sun, 17 Dec 2017 18:14:04 UTC
All use subject to http://about.jstor.org/terms

Literature Cited

Aoyama, T. 1997. Long distance movements of anadromous white-spotted charr (*Salvelinus leucomaenis*) in southern Hokkaido, Japan. Scientific Report of Hokkaido Fish Hatchery **51**:63–65.

Aoyama, T., K. Naito, and T. Takami. 1999*a*. Occurrence of sea-run migrant brown trout (*Salmo trutta*) in Hokkaido, Japan. Scientific Report of Hokkaido Fish Hatchery **53**:81–83.

Aoyama, T., T. Takami, M. Fujiwara, and H. Kawamura. 1999*b*. Natural reproduction of rainbow trout, *Oncorhynchus mykiss*, in the Shiribetsu River in Hokkaido, Japan. Scientific Report of Hokkaido Fish Hatchery **53**:29–38.

Bozek, M. A., and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Canadian Journal of Zoology **70**:886–890.

Caro, T. M., and M. K. Laurenson. 1994. Ecological and genetic factors on conservation: a cautionary tale. Science **263**:485–486.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63**:215–244.

Christensen, R. 1997. Log-linear models and logistic regression. Springer, New York.

Cooper, A. B., and M. Mangel. 1998. The dangers of ignoring metapopulation structure for conservation of salmonids. Fishery Bulletin **97**:213–226.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications **9**:642–655.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science **266**: 753–762.

Fausch, K. D., S. Nakano, and K. Ishigaki. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia **100**:1–12.

Holmquist, J. G., J. M. Schmidt-Gengenbach, and B. B. Yoshioka. 1998. High dams and marine-freshwater linkages: effects on native and introduced fauna in the Caribbean. Conservation Biology **12**:621–630.

Japanese Ministry of Construction. 1999. A handbook of erosion control. Japan Sabo Association, Tokyo.

Kelner, D. E., and B. E. Sietman. 2000. Relic populations of the ebony shell, *Fusconaia ebena* (Bivalvia: Unionidae), in the upper Mississippi River drainage. Journal of Freshwater Ecology **15**:371–377.

Kozel, S. J., and W. A. Hubert. 1989. Habitat features and trout abundance relative to gradient in some Wyoming streams. Northwest Science **63**:175–182.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 1998. Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. North American Journal of Fisheries Management **18**:940–946.

Lande, R. 1988. Genetics and demography in biological conservation. Science **241**:1455–1460.

Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Research on Population Ecology **40**: 259–269.

Miya, Y., and T. Hamano. 1988. The influence of a dam having no fishway on the distribution of decapod crustaceans in the Yukinoura River, Nagasaki, Japan. Nippon Suisan Gakkaishi **54**:429–435.

Morita, K., and T. Suzuki. 1999. Shifts of food habit and jaw position of white-spotted charr after damming. Journal of Fish Biology **55**: 1156–1162.

Morita, K., and Y. Takashima. 1998. Effect of female size on fecundity and egg size in white-spotted charr: comparison between sea-run and resident forms. Journal of Fish Biology **53**:1140–1142.

Morita, K., and S. Yamamoto. 2000. Occurrence of a deformed white-spotted charr, *Salvelinus leucomaenis* (Pallas), population on the edge of its distribution. Fisheries Management and Ecology **7**:551–553.

Morita, K., and S. Yamamoto. 2001. Contrasts in movement behavior of juvenile white-spotted charr between stocks above and below a dam. Fisheries Science **67**:179–181.

Morita, K., S. Yamamoto, and N. Hoshino. 2000. Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. Canadian Journal of Fisheries and Aquatic Sciences **57**:1300–1306.

Nakamura, T. 2001. Estimation of the distribution of genetically pure populations of the Japanese charr by inquiring survey. Journal of the Japan Society of Erosion Control **53**:3–9.

Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. BioScience **50**:807–823.

Pulliam, H. R. 1988. Sources, sinks and population regulation. The American Naturalist **132**:652–661.

Reyes-Gavilán, F. G., R. Garrido, A. G. Nicieza, M. M. Toledo, and F. Braña. 1996. Fish community variation along physical gradients in short streams of northern Spain and the disruptive effect of dams. Hydrobiologia **321**:155–163.

Rieman, B. E., and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish **9**:51–64.

Riley, S. C., and K. D. Fausch. 1992. Underestimation of trout population sizes by maximum-likelihood removal estimates in small streams. North American Journal of Fisheries Management **12**:768–776.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience **31**:131–134.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union **38**:913–920.

Takami, T., and T. Aoyama. 1999. Distributions of rainbow trout and brown trout in Hokkaido, northern Japan. Wildlife Conservation Japan **4**:41–48.

Takami, T., T. Yoshihara, Y. Miyakoshi, and R. Kuwabara. 2002. Replacement of white-spotted charr *Salvelinus leucomaenis* by brown trout *Salmo trutta* in a branch of the Chitose River, Hokkaido. 2002. Nippon Suisan Gakkaishi **68**:24-28.

Taniguchi, Y., Y. Miyake, T. Saito, H. Urabe, and S. Nakano. 2000. Redd superimposition by introduced rainbow trout, *Oncorhynchus mykiss*, on native charrs in a Japanese stream. Ichthyological Research **47**:149–156.

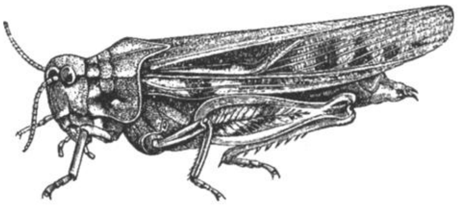
Thompson, P. D., and F. J. Rahel. 1998. Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of brook trout. North American Journal of Fisheries Management **18**:206–210.

Watters, G. T. 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoida) and their hosts. Biological Conservation **75**:79–85.

Wilcox, B. A., and D. Murphy. 1985. Conservation strategy: the effect of fragmentation on extinction. The American Naturalist **125**:879–887.

Winston, M. R., C. M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. Transactions of the American Fisheries Society **120**:98–105.

Yamamoto, S., K. Morita, and A. Goto. 1999. Geographic variations in life-history characteristics of white-spotted charr (*Salvelinus leucomaenis*). Canadian Journal of Zoology **77**:871–878.



This content downloaded from 128.193.164.203 on Sun, 17 Dec 2017 18:14:04 UTC
All use subject to http://about.jstor.org/terms