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Status and Risk of Extinction for Westslope Cutthroat Trout in the Upper Missouri River Basin, Montana

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Abstract.—Westslope cutthroat trout *Oncorhynchus clarki lewisi* now occupy less than 5% of the subspecies' historical range within the upper Missouri River drainage in Montana. We assessed the risk of extinction for 144 known populations inhabiting streams within federally managed lands in the upper Missouri River basin using a Bayesian viability assessment procedure that estimates probability of persistence based on subjective evaluation of population survival and reproductive rates as influenced by environmental conditions. We first customized this model using estimates of demographic parameters from the literature and field data. Each population was classified into one of three risk groups based on their Bayesian probability of persistence over 100 years (p_{100}). Most (71%) of the 144 populations had a very high predicted risk of extinction ($p_{100} \leq 50\%$), 19% exhibited a high risk ($50\% < p_{100} \leq 80\%$), and 10% had a moderate risk ($80 < p_{100} \leq 95\%$). Higher average predictions of p_{100} were consistently associated with populations inhabiting watersheds with lower levels of management activities. Analysis of variance and a matrix of information divergence measures indicated that livestock grazing, mineral development, angling, and the presence of nonnative fish had the greatest association with both estimated population parameters and persistence probabilities. Of 26 major subbasins within the upper Missouri River drainage, 16 support at least one known westslope cutthroat trout population on federal lands, and 14 of these 16 support at least one population with an estimated p_{100} value of 0.5 or greater. Results of our analysis have led to action by citizens of Montana, prompting state and federal managers to develop a conservation and restoration program for this subspecies in the upper Missouri River basin.

The abundance and distribution of westslope cutthroat trout *Oncorhynchus clarki lewisi* have declined dramatically throughout the subspecies' historical range, which included the upper Columbia, Missouri, and South Saskatchewan river basins, as well as disjunct, isolated populations in the John Day drainage of Oregon and in the Lake Chelan, Methow, Entiat, Yakima, and Wenatchee drainages of Washington (Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995). Behnke (1992) stated that the original distribution of westslope cutthroat trout within the upper Missouri River basin is not known with certainty and suggested that their native range included "the upper Missouri basin (main river and all tributaries) downstream to about Fort Benton, Montana, about 60 km below Great Falls, as well as headwaters of the Judith, Milk, and Marias rivers, which join the Missouri downstream from Fort Benton" (Figure 1). Hanzel (1959) suggested that their original range extended down to the Musselshell River.

Factors identified as leading to declines of

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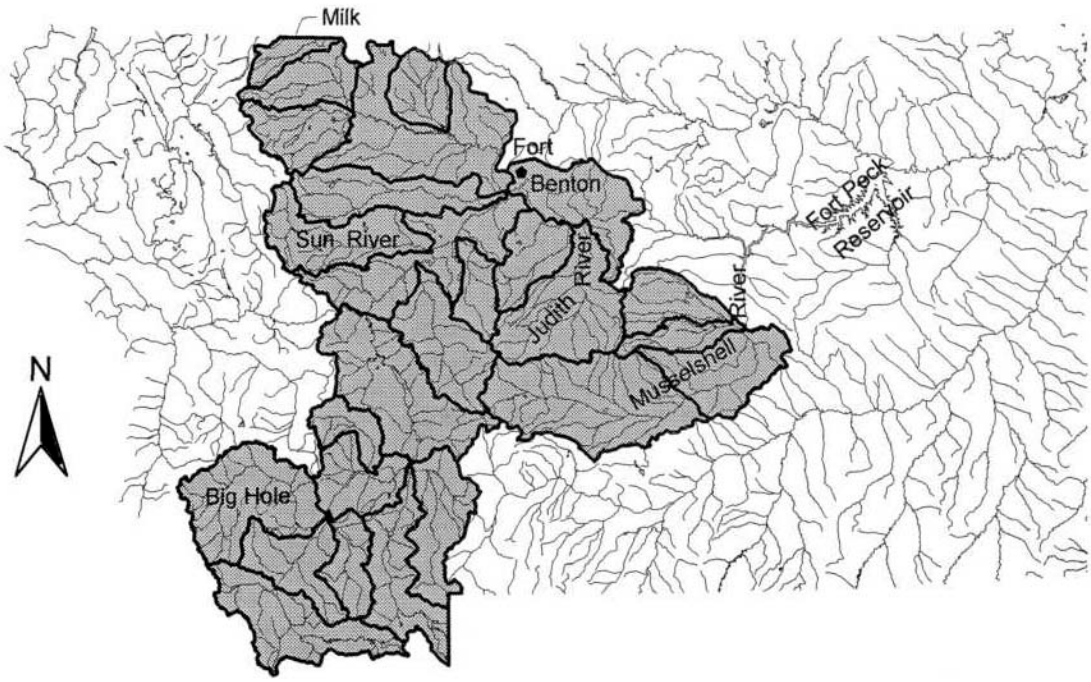

FIGURE 1.—Map of Montana showing the subbasins (shaded) believed to have been occupied historically by westslope cutthroat trout within the upper Missouri River basin at the time of European expansion into the basin.

westslope cutthroat trout include introductions of nonnative fishes, habitat alterations caused by land and water use practices, and overharvest (Hanzel 1959; Liknes and Graham 1988; McIntyre and Rieman 1995). Allendorf and Leary (1988) suggested that genetic introgression is the most important factor responsible for the loss of native cutthroat trout populations. Montana's Department of Fish, Wildlife and Parks (FWP) recently (1996) changed angling regulations for westslope cutthroat trout in streams and rivers in the upper Missouri basin to catch and release to lessen potential population losses caused by angling.

Remaining populations within the upper Missouri basin are now restricted to isolated headwater habitats. Many of these habitats have been affected by land and water management activities, invaded by nonnative salmonids, or both. These factors could lead to an increase in the deterministic risk of extinction, as well as increasing the risk from stochastic (random catastrophic) environmental effects (Shaffer 1987, 1991; Rieman and McIntyre 1993). Fish survey data collected by the Montana FWP, the U.S. Forest Service (FS), and the U.S. Bureau of Land Management (BLM) revealed that: (1) at least three populations have been extirpated within the past 10 years; (2) many existing populations have been invaded by nonnative salmonids and have declined; and (3) most remaining populations occupy isolated habitat fragments less than 10 km long.

Concern for the status of westslope cutthroat trout led the FWP to form an interagency (members are scientists from the FWP, FS, BLM, and universities) Upper Missouri Westslope Cutthroat Trout Technical Committee in early 1995 to make recommendations for conserving and restoring westslope cutthroat trout in the upper Missouri basin. To justify and prioritize conservation and restoration efforts, federal land and state fish managers needed to know the overall status of the subspecies within the upper Missouri basin and the relative extinction risk to each remaining population. Effective conservation of native fishes, such as the westslope cutthroat trout, requires understanding their current distribution and status, and threats to their existence. To support the efforts of the technical committee, we described the current status and distribution of westslope cutthroat trout in the upper Missouri basin and provided a comprehensive evaluation of the relative risks of extinction for 144 populations inhabiting streams

within federally administered lands. We used a Bayesian viability assessment module (BayVAM) developed at the FS Rocky Mountain Research Station (Lee and Rieman, 1997 this issue).

The BayVAM procedure was designed to provide a rigorous method of incorporating subjective judgments about habitat quality in a quantitative risk assessment that explicitly acknowledges uncertainty in parameter estimates and uncertainty due to random environmental fluctuations. The BayVAM procedure has three main components: (1) an assessment survey in which users judge the relative condition of the habitat and estimate survival and reproductive rates for the population in question; (2) a stochastic simulation model that provides a mathematical representation of important demographic and environmental processes; and (3) a probabilistic network that uses the results of the survey to define likely parameter ranges, mimics the stochastic behavior of the simulation model, and produces probability histograms for average population size, minimum population size, and time to extinction. The structure of the probabilistic network allows partitioning of uncertainty due to ignorance of population parameters from that due to unavoidable environmental variation. Although based on frequency distributions of a formal stochastic model, the probability histograms also can be interpreted as Bayesian probabilities (i.e., the degree of belief about a future event). By using the estimates of demographic parameters for stream-resident westslope cutthroat trout from Downs et al. (1997), the parameters used in the BayVAM model component were customized for this analysis.

Methods

Distribution and Status

To assess the present status and distribution of westslope cutthroat trout in the upper Missouri basin we examined evidence from the historical record to estimate the length of streams and rivers once occupied by westslope cutthroat trout. Anecdotal evidence suggests that the upper Sun River drainage (above a natural barrier, now occupied by an irrigation diversion dam, about 155 km above its mouth) was barren of fish (B. Hill, FWP, personal communication). Two tributaries in the lower Musselshell River drainage (one in the Box Elder drainage and one in the Flatwillow drainage) contain populations of genetically pure westslope cutthroat trout (R. Leary, University of Montana, personal communication), which may support inclusion of the Musselshell River drainage in the historical distribution. Numerous releases of "fine spotted, native trout," a description used for both westslope cutthroat and Yellowstone cutthroat trout *O. clarki bouvieri* from the Yellowstone River drainage in Wyoming, were made by residents of Lewistown, Montana in unnamed local waters during the early 1900s (Montana Game and Fish Commission 1914). A report in the Lewistown *Castle News* (April 26, 1888) suggested that trout were absent from the Musselshell and its branches. This evidence makes it impossible to discern whether westslope cutthroat trout populations in the Musselshell River drainage originated from releases of hatchery stocks. Headwater capture of streams from the Judith River drainage by the Musselshell River drainage might have allowed the interbasin transfer of westslope cutthroat trout. For this analysis, we assumed that westslope cutthroat trout originally occupied the entire Missouri River drainage down to, and including, the Musselshell River and the upper Milk River basin, but not the upper Sun River basin.

Present status and distribution of westslope cutthroat trout in the upper Missouri basin was estimated with the Montana River Information System (MRIS) and a 1:100,000 geographic information systems hydrography layer. We estimated total kilometers of historically occupied habitats and currently occupied habitats by genetic status. The MRIS is a relational database linked to the hydrography layer by stream reach. Reaches have been segregated by physical attributes (gradient, valley shape, flow volume, and landform) and land ownership. The MRIS contains fish information for each reach of stream that has been surveyed. This information includes relative abundance and genetic status determined by allozyme electrophoresis (Leary et al. 1987). We summed the length and number of reaches (by major subbasins) that supported both westslope cutthroat trout electrophoretically determined to be at least 90% genetically pure and fish classified as westslope cutthroat trout in the field but not genetically tested. Westslope cutthroat trout electrophoretically determined to be less than 90% pure were classified as hybrids and not tallied. We recognize the problem of relying on field examination to determine levels of introgression, as reported by Leary et al. (1984; 1996), and acknowledge that an unknown number of reaches listed in the database as supporting untested westslope cutthroat trout may contain hybrid fish.

Extinction Risk Assessment

Populations of westslope cutthroat trout were relatively easy to define because each discrete population was isolated either physically, by a barrier to upstream movement of fish, or biologically, by the presence of a nonnative salmonid population. Each population occupied relatively small habitat patches (<35 km of continuous stream length). We assessed extinction risk for 144 westslope cutthroat trout populations inhabiting federally administered lands of the upper Missouri basin. Nine of these populations were believed to be genetically pure based on field morphometric examinations, and 135 populations had been genetically tested (by allozyme electrophoresis on a sample of individuals from the population) as being at least 90% pure.

For each population, a two-part assessment questionnaire was completed. The first part was completed by local fisheries biologists familiar with the individual fish populations, usually via field surveys or reviews of survey data. The second part was completed by the same biologists along with a team of resource specialists familiar with the watersheds containing each population. Watersheds were delineated according to sixth-level hydrologic boundaries, consistent with the methods of Maxwell et al. (1995), and ranged from about 8,000 to 16,000 ha. These watersheds were used to assess possible effects of present land management activities on the predicted persistence of westslope cutthroat trout populations. The sixth-level watershed was the smallest scale for which federal land use information existed throughout the upper Missouri basin. Eight fisheries biologists and six teams of resource specialists completed assessment questionnaires for 144 populations in 117 watersheds.

Part 1: population survey.—Local biologists completed questionnaires for each population; the questionnaire called for estimates of population demographic parameters and stream habitat capability. Responses to questionnaires were based on biologists' field surveys of fish populations and stream habitats, which are integral parts of the BayVAM approach (Lee and Rieman 1997). For each population, biologists were asked to assign likelihood values by using preestablished range criteria for each of 11 life history (demographic) and population parameters (Table 1). The ranges were set to correspond with reasonable values that might be expected for westslope cutthroat trout within the upper Missouri basin based on field research (Downs et al. 1997). Guidelines were prepared to provide a common set of assumptions (standards) for assigning likelihood values (Appendix). The guidelines directed the biologists to evaluate instream conditions directly, not to infer conditions based on land-use activities within the watershed. Biologists also estimated the length of stream habitat occupied by each population, although length of occupied habitat was not explicitly used in the BayVAM model.

Part 2: land-use assessment.—Management ac-

TABLE 1.—Criteria ranges for eight life history and three population parameters used within the BayVAM model to assess the relative risk of extinction for each of 144 westslope cutthroat trout populations in the upper Missouri River basin of Montana.

Parameter	Range or category
Life history parameters	
Spawning habitat availability	60–80%
	85–95%
	100%
Fecundity (eggs/female)	200–500
	500–800
	800–1,100
	1,100–1,500
Incubation success	5–20%
	20–35%
	35–50%
Maximum fry survival	10–20%
	20–30%
	30–40%
Fry capacity	1,000–4,000
	4,000–7,000
	7,000–20,000
Juvenile survival	14–26%
	26–38%
	38–50%
Adult survival	10–30%
	30–50%
	50–70%
Age at first maturity (% of population)	age = 3 (30%)
	age = 4 (40%)
	age = 5 (20%)
	age = 6 (10%)
Population parameters	
Initial population (adults)	<450
	450–850
	>850
CV of fry survival[a]	<40%
	40–65%
	>65%
Risk of catastrophe (year interval)	120–170
	70–120
	20–70

[a] Coefficient of variation: CV = 100·SD/mean.

tivities within each watershed occupied by a westslope cutthroat trout population were assessed by rating the effects of each activity on the portion of stream channel occupied by westslope cutthroat trout. These ratings were completed by local FS, BLM, and FWP resource scientists. Four FS and two BLM resource area interdisciplinary (ID) teams ranked nine land, water, or angling impacts: (1) roads, (2) livestock grazing, (3) mineral or oil and gas development, (4) timber harvest, (5) water withdrawals and impoundments, (6) angling pressure, (7) distribution and abundance of nonnative fishes, (8) catastrophic risk associated with wildfire, and (9) land use designations that might affect stream habitats within the land management plans for each watershed (e.g., the area of the watershed allocated to commercial resource extraction by a local forest plan). Each management risk factor was subjectively ranked on an ordinal scale as no, low, moderate, or high effect based on a combination of empirical data and professional judgment.

General guidelines were provided to ID teams to promote consistency. These guidelines specified that land management risk factors (factors 1–5, 8 and 9) be ranked according to the proportion of the stream network within the watershed that potentially could be affected by each factor. Angling (factor 6) was rated from none to high based on existing fishing regulations and access. Effects of introduced species (factor 7) were ranked by the presence and relative abundance of introduced fishes within each watershed. A tenth category (cumulative effect) was intended to capture the ID teams' views on the cumulative effect of all watershed activities on aquatic resources. The original watershed assessment was directed at the entire watershed and stream system, not just that portion supporting westslope cutthroat populations; however, ID teams were asked to rank impacts specifically to occupied habitats for the final analysis.

Part 3: data analysis.—Survey responses for each population parameter were summarized for each population and across all populations. Data were summarized by tabulating the frequency of likelihood scores that biologists assigned to each life history and population parameter range class used in the BayVAM model. For each population, the associated set of likelihood values for the population parameters was used in the probabilistic network provided within the BayVAM procedure to calculate probabilities associated with minimum population size, average population size, and time to extinction (if applicable) based on a 100-year simulation period. We then ran the BayVAM model for each population and compared the probabilities of persisting for 100 years (p_{100}) to provide a perspective on the perceived condition of the populations.

We used p_{100} values as a standard for comparisons among populations. Populations were classified into three risk groups based on their estimated probabilities of persistence: very high risk ($p_{100} \leq 50\%$), high risk ($50\% < p_{100} \leq 80\%$), or moderate risk ($80\% < p_{100} \leq 95\%$). None of the assessed populations had a p_{100} value greater than 95%, a criterion proposed by Shaffer and Sampson (1985) for low risk. Populations also were classified genetically: one class contained populations at least 90% pure as measured by allozyme electrophoresis; another class contained populations suspected of being pure but untested by genetic techniques.

The BayVAM procedure uses a 100-year simulation period, which is roughly 20 times the generation time of westslope cutthroat trout (Downs et al. 1997). Although longer time frames may be appropriate for some species (Marcot and Murphy 1996), 100 years is sufficient to characterize the dynamics of model populations and provide useful indices of risk. We recognize that changes in environmental conditions and management are certain to occur within the next 100 years. The 100-year time frame was used as a standard of reference for the assessment based solely on conditions assessed at the time of analysis.

We had two concerns about observer bias. We relied on opinions from local experts on the status of populations in their management areas. Thus, each expert was responsible for assessing several populations in roughly adjacent areas that might share similar land management histories. We were unable to assign populations randomly to observers (because we used local expert opinion) or to replicate population assessments (i.e., have more than one biologist assess each population). We explored potential observer bias by testing for differences in predicted probabilities of persistence among observers using the Kruskal–Wallis test (Daniel 1978). We attempted to minimize the effect of observer bias on our assessment of land use effects by the use of ID teams, which should mitigate some of the bias associated with individuals.

We examined the relationship between management risk factors identified by the ID teams and populations in two ways. First, we looked for dif-

ferences in likelihood assignments for each population parameter that could be associated with different management risk factors. We calculated an information divergence measure (Kullback and Leibler 1951) that compares a conditional probability distribution (the likelihood function for a population parameter conditional on a given ranking of a risk factor) to the marginal probability function (the likelihood function for a population parameter generated by summing over all rankings) for each parameter–risk factor combination. This information divergence measure can be interpreted as an average measure of the information difference between two sets of probabilities (Whittaker 1990). It provides a convenient means of illustrating which risk factors might have a causal association with the habitat conditions that led to the likelihood values assigned to a given population parameter.

Second, we compared risk factors with the probability of persistence using a multifactor analysis of variance (ANOVA) in a general linear models approach (SAS Institute 1988). We used ANOVA as an exploratory tool to identify coarse patterns in the data, not to test specific hypotheses rigorously. We conducted two analyses. The first included roads, livestock grazing, mining (including oil and gas development), timber harvest, water diversion, angling, and presence of nonnative fishes, because ratings of these activities were provided for all 144 populations. We excluded cumulative effect because this variable incorporated effects from the individual activity classes above. The second analysis included cumulative effect, forest plan allocation, and risk of a catastrophic event for the 134 populations so rated. Ratings of all the above effects, except cumulative effect, were classed as none, low, moderate, or high. The none rating was not used for cumulative effect.

Results

Distribution and Status

Based on 1:100,000-scale digital hydrography, we estimated that approximately 93,000 km of streams were historically occupied by westslope cutthroat trout in the upper Missouri at the time of European expansion into the basin. Westslope cutthroat trout at least 90% genetically pure (based on allozyme electrophoresis) presently inhabit less than 3% of the subspecies' historical range within the upper Missouri basin. An additional 3% of the historical range contains westslope cutthroat trout suspected of being pure based on field morphometric examinations. If only reaches that had been surveyed are assessed, about 5% of the basin contains westslope cutthroat trout of confirmed purity and another 8% contains apparently pure fish. Altogether, 199 reaches were occupied by westslope cutthroat trout that were at least 90% pure.

Extinction Risk Assessment

Biologists did not enter values for all population parameters in all cases; therefore, sample sizes varied by parameter. All biologists used the default values for age at maturity and fecundity parameters that were based on field observations of Downs et al. (1997). Biologists had relatively high confidence that spawning habitat availability was high for a majority of populations and that initial population sizes were low. They were fairly confident that most of the populations did not fall into the high category for fry capacity and juvenile survival, but they were less certain whether ratings should be low or moderate. For all other parameters, biologists were less confident in their assessments or believed parameters fell into the moderate range for a majority of populations.

The BayVAM model predicted that most (103 or 71%) of the populations had less than a 50% probability of persisting for 100 years (Figure 2). The cumulative distribution plot showed a relatively clear change in slope above 50% probability of persistence (Figure 2). Thus, 71% of the 144 populations had a very high risk of extinction ($p_{100} \leq 50\%$), 27 populations (19%) exhibited a high risk of extinction ($50\% < p_{100} \leq 80\%$), and 14 (10%) of the populations had a moderate risk of extinction ($80\% < p_{100} \leq 95\%$). Slightly more than half of the populations in all extinction risk categories had been genetically tested as 100% pure.

Average predicted probabilities of persistence differed significantly ($p < 0.001$) among observers (Figure 3). It is unclear whether these differences were due to observer bias or to regional effects. Observer 7 gave higher-than-average probability values, but the populations he assessed—the subjects of his ongoing research—were mostly healthy. Observer 2 gave lower-than-average probabilities, but most populations this observer assessed inhabited streams affected by livestock grazing. Although observer bias cannot be dismissed, the assessments seemed to be fairly consistent across observers.

The matrix of information divergence measures indicated that grazing, mineral development, angling, and the presence of nonnative fish had the

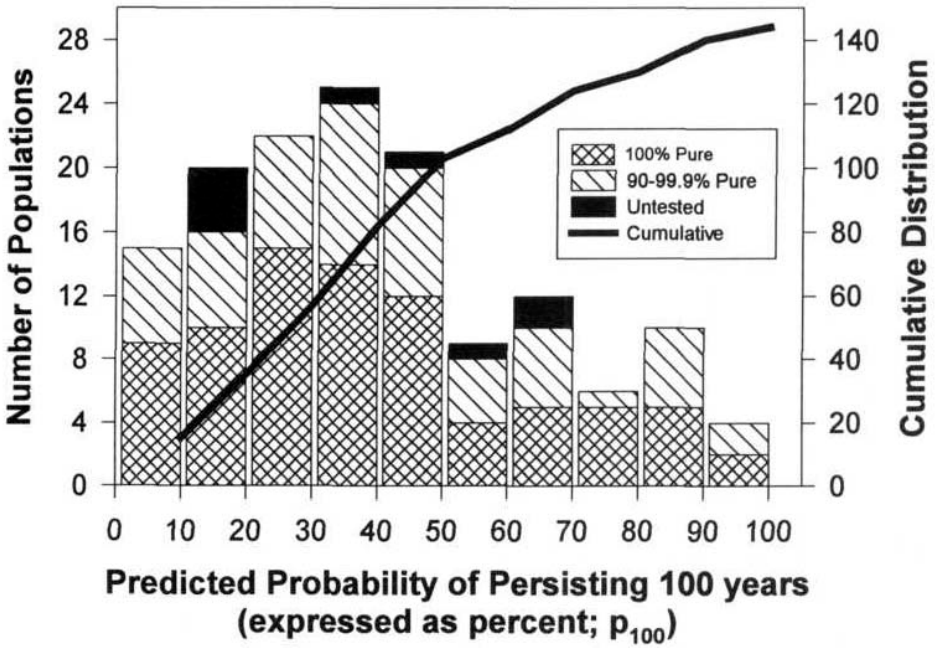

FIGURE 2.—Number of westslope cutthroat populations within each 10% class of persistence probability (bars) and cumulative numbers over 144 populations (line) in tributaries within the upper Missouri River basin. Bars are stratified by genetic status.

greatest association with assigned likelihood values across all parameters. These are the activities that produced the 13 highest observed values in the information matrix (Table 2). We did not attempt to estimate the significance of these values; to do so would require a more intensive analysis based on the sampling properties of the information divergence measure. Rather, we defined noteworthy high values as those greater than 0.668, which is the overall mean of the observed values plus one standard deviation. Fourteen (14%) of the elements within the information matrix exceeded this threshold. Noteworthy values occur for all population parameters except spawning habitat availability, fecundity, initial population, and age at maturity. (Because age at maturity was constant for all populations, its information divergence was zero and it was omitted from Table 2.)

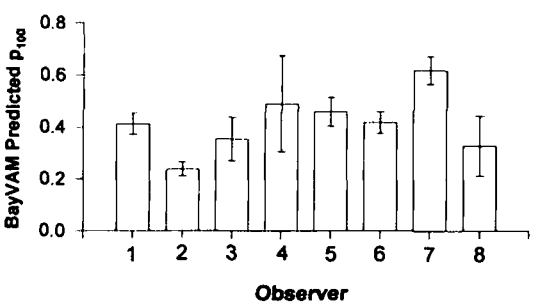

FIGURE 3.—Means (bars) and SEs (vertical lines) of predicted probabilities of persistence by observer for westslope cutthroat trout populations inhabiting federal lands in the upper Missouri River basin.

Higher average estimates of the probability of persistence were consistently associated with populations inhabiting watersheds with lower management risk factors (Table 3). The association of each risk factor with probability of persistence was examined both in terms of the sequential sum of squares when each factor was entered into the ANOVA model first, and in terms of the partial sum of squares when each factor was entered into the ANOVA model last. These ANOVAs suggested interaction effects or confounding among the management activities, evidenced by substantively different significance values for partial and sequential sums of squares for many parameters (Table 3). However, sample sizes were insufficient to test comprehensively for interaction effects. The presence of interaction effects, combined with the heavily unbalanced design and potential confounding, made the significance levels highly suspect

TABLE 2.—Information divergence (Kulback and Leibler 1951) calculated for each combination of population parameter (node) and land use activity for westslope cutthroat trout. This divergence can be interpreted as an average measure of the information difference between the marginal proportion distribution for each node and a nodal proportion distribution conditioned on the level of each activity. Bold values are "noteworthy," exceeding 0.668 (see text).

	Land use activity									
Population parameter	Roads	Grazing	Mineral development	Timber harvest	Water withdrawal	Angling	Nonnative fishes	Forest plan allocation	Major risk	Cumulative effect
Spawning habitat availability	0.21	0.26	0.36	0.36	0.43	0.08	0.09	0.42	0.16	0.17
Incubation success	0.57	**0.70**	0.46	0.18	0.11	0.60	0.11	0.12	0.17	0.22
Maximum fry survival	0.06	0.34	0.52	0.09	0.17	**0.83**	**1.22**	0.05	0.23	0.40
Fry capacity	0.19	0.24	**0.84**	0.43	0.36	0.43	0.57	0.18	0.15	0.06
Juvenile survival	0.19	0.32	**0.97**	0.43	0.27	**0.78**	**1.19**	0.07	0.19	0.44
Adult survival	0.45	0.19	**1.05**	0.38	0.17	**1.92**	**0.77**	0.22	0.22	0.42
Fecundity	0.09	0.16	0.22	0.10	0.23	0.18	0.19	0.06	0.31	0.12
Initial population	0.33	0.20	0.34	0.20	0.36	0.38	0.23	0.07	0.17	0.26
CV fry survival	0.15	**0.69**	0.48	**0.67**	0.22	0.50	0.17	0.05	0.17	0.17
Risk of catastrophe	0.30	**0.75**	**0.76**	0.31	0.32	0.34	0.57	0.06	0.66	0.10

for hypothesis testing. Nevertheless, the significance values were useful guides to potentially important main effects.

All risk factors except mineral development and timber harvest showed meaningful effects (i.e., low P values) when entered first in the ANOVA model, suggesting they would be important if examined in isolation. Only livestock grazing and nonnative fish explained significant variation in p_{100} when entered last in the model containing all individual risk factors. This result suggests that these factors remain important after all other factors are accounted for. Catastrophic risk and cumulative effect were consistently important in the more reduced analysis of integrated risk factors.

The historical range of westslope cutthroat trout within the upper Missouri basin embraces 26 subbasins, aggregations of watersheds classified as fourth-code hydrologic units by the U.S. Geological Survey. Sixteen of these subbasins still support at least one westslope cutthroat trout population on federal land. Of these 16 subbasins, 14 contain populations with a moderate or high estimated risk of extinction. These subbasins are

TABLE 3.—Means (with sample size in parentheses) of probabilities of persistence for 144 westslope cutthroat trout populations within the upper Missouri River basin from the BayVAM model by rating categories assigned by biologists for effects of management-related disturbances on those populations, along with results from ANOVA tests. "Major event" = catastrophic risk from major event; "forest plan" = forest plan allocation; NA = no data.

	Individual management class[a]									
Rated impact or statistic	Grazing	Nonnative fish	Roads	Mineral development	Timber	Water withdrawal	Angling	Major event[b]	Cumulative effect[b]	Forest plan[b]
None	0.701	0.592	0.481	0.402	0.407	0.454	0.378	0.255	NA	0.414
	(7)	(27)	(18)	(84)	(68)	(61)	(21)	(12)		(2)
Low	0.456	0.357	0.407	0.412	0.393	0.366	0.420	0.339	0.573	0.491
	(42)	(14)	(73)	(39)	(55)	(47)	(104)	(86)	(26)	(49)
Moderate	0.412	0.400	0.374	0.328	0.345	0.314	0.343	0.519	0.405	0.321
	(40)	(30)	(32)	(12)	(13)	(15)	(11)	(32)	(58)	(30)
High	0.297	0.328	0.313	0.341	0.390	0.348	0.192	0.481	0.309	0.308
	(55)	(73)	(21)	(9)	(8)	(21)	(8)	(6)	(60)	(53)
Sequential (type I) sum of squares for each treatment when entered first in the model										
F	11.53	11.83	2.55	0.83	0.37	3.40	3.64	8.65	16.89	8.27
P	0.0001	0.0001	0.0591	0.4795	0.7738	0.0199	0.0147	0.0001	0.0001	0.0001
Partial (type III) sum of squares for each treatment when entered last in the model										
F	9.63	12.30	1.61	0.03	1.17	1.36	0.98	7.15	11.85	1.09
P	0.0001	0.0001	0.1913	0.9927	0.3225	0.2598	0.4047	0.0002	0.0001	0.3545

[a] ANOVA test results for individual management classes (N = 144): model F value = 4.33; $P < 0.001$.

[b] ANOVA test results for forest plan, cumulative effect, and catastrophic (major) events (N = 134): model F value = 8.09; $P < 0.001$.

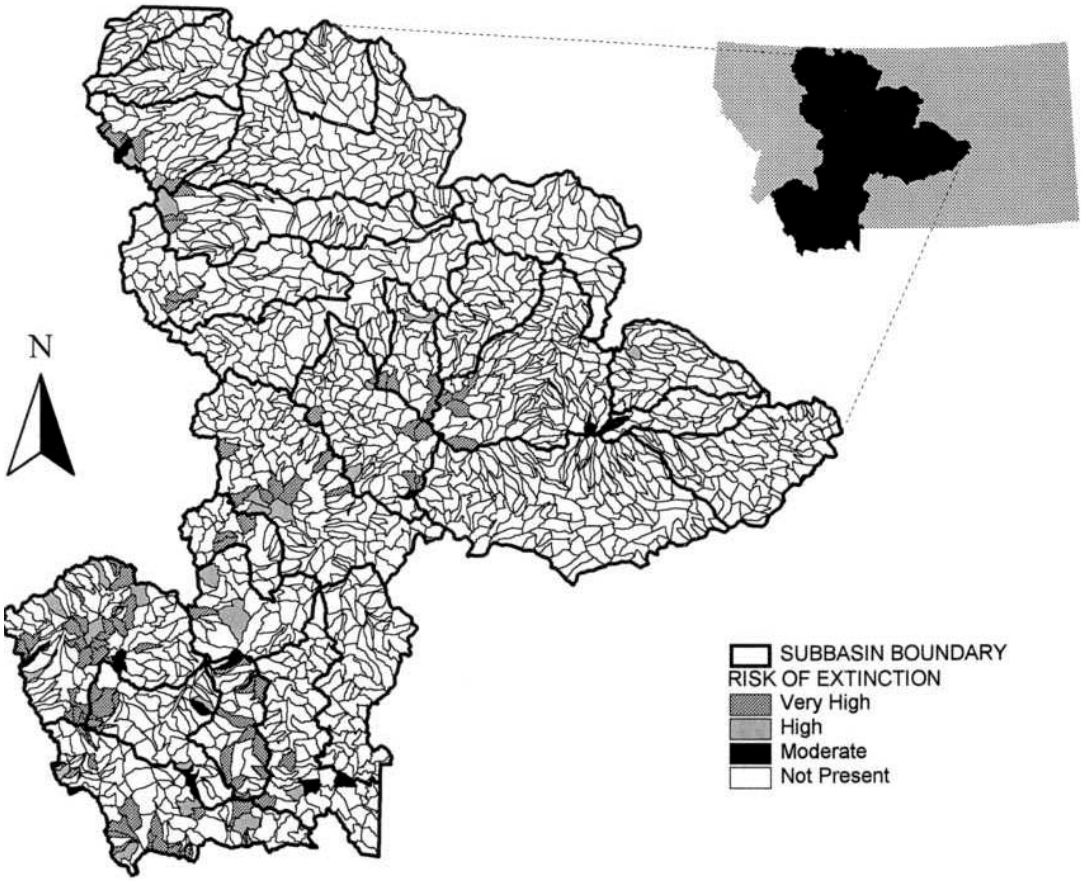

FIGURE 4.—Watersheds within subbasins of the upper Missouri River basin. Extinction risk classes for populations of westslope cutthroat trout are shown by watershed within subbasins of the upper Missouri River basin.

spread throughout the upper Missouri basin (Figure 4); however, almost all of the remaining populations occupy high-elevation, mountainous stream fragments.

Discussion

Liknes (1984) and Liknes and Graham (1988) conservatively estimated that westslope cutthroat trout historically occupied about 25,500 km of stream habitat in Montana, 11,400 km of which were in the upper Missouri basin. We estimated that westslope cutthroat trout historically occupied about 93,000 km of stream habitat in the upper Missouri basin. Liknes (1984) and Liknes and Graham (1988) worked with 1:250,000 scale maps; our estimates are based on 1:100,000 scale maps. An analysis of Liknes's (1984) data indicated that about 1,300 km (11%) of the historical 11,400 km remain occupied by westslope cutthroat trout; however, genetic data were very limited. We estimate that about 4,300 km (5%) of 93,000 km historically occupied streams now retain the subspecies, including both genetically tested and untested populations.

We believe we have analyzed extinction risk for most known westslope cutthroat trout populations (≥ 90% genetically pure) in the upper Missouri basin because (1) only 199 reaches in the basin were known to support 90% (or more) pure westslope cutthroat trout, (2) several populations analyzed in this risk assessment inhabited more than one reach, and (3) the only populations not assessed were restricted to streams totally within private ownership. Our analysis indicates that westslope cutthroat trout populations inhabiting federal lands within the upper Missouri basin are at serious risk of extinction under existing conditions. This conclusion is based on trends over time that show a major reduction in geographic range of genetically pure populations and the low estimated prob-

abilities of persistence for nearly all populations examined.

The low persistence probabilities arise from two factors. First, there are unmistakable impacts of land use activities, though the full nature of these impacts is not clear. Among the management risk factors, grazing and the presence of nonnative fishes have the most obvious and consistent impacts on population parameters and, subsequently, on probability of persistence. Mineral development and angling have noticeable associations with population parameters, but these associations do not translate clearly into measurably different probabilities of persistence. Perhaps this can be explained by confounding or interactions with more dominant factors, but we do not know. The impacts of roads, timber harvesting, and water withdrawal within the present context are even more obscure.

The second principal reason for low estimated persistence is poor information on demographic parameters for each population. This ignorance complicates our understanding of causal relationships and confuses relationships between risks and management effects. It also increases the Bayesian probability of extinction, because high uncertainty in demographic parameters, as expressed in the survey responses, connotes high uncertainty regarding the future status of the populations. Uncertainty, whether originating from a model, data used in the model, or random events, connotes higher risk. We contend that by incorporating the uncertainty arising from lack of knowledge into our assessment, we will estimate extinction risks better but not overestimate them. In reality, a population will persist or not (i.e., in a classical sense its probability of persistence is either one or zero), but we do not know the future outcome. We can only estimate of the chances of persistence given what we know. In outlining the BayVAM approach, Lee and Rieman (1997) take the position that ignorance of population parameters and processes is a genuine component of risk that must be addressed in viability assessments designed to aid management. We share this view.

The collective evidence suggests that even if estimates of risk could be reduced by reducing uncertainty about population parameters, it would not significantly change the overall picture that westslope cutthroat trout are in trouble in the upper Missouri basin. The p_{100} values estimated for most of these populations are so low that it would require both major reductions in uncertainty regarding population parameters and substantive shifts in the modal values of many known parameters to reduce the risks of extinction to moderate or low for most populations. The small habitat fragments these populations now occupy (Figure 5) and the lack of connectivity among these populations further contributes to their tenuous status (Rieman and McIntyre 1993). However, because 14 of the 16 subbasins within the upper Missouri basin that still contain westslope cutthroat trout have at least one population with a p_{100} value of greater than 50% and because these subbasins are distributed throughout the upper basin, some optimism over the conservation of this subspecies in the basin may be warranted.

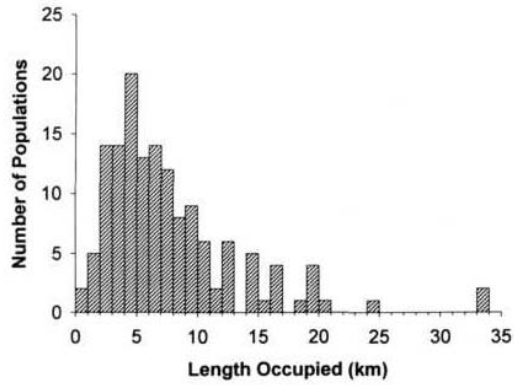

FIGURE 5.—Frequencies of estimated stream length (km) occupied by each of 144 westslope cutthroat trout populations in the upper Missouri River basin of Montana.

Management Implications

How should resource managers respond to a risk assessment showing that a combination of ignorance and random environmental processes leads to a poor outlook for survival of an important subspecies? They have three options: (1) ignore the assessment and proceed with business as usual, (2) postpone action until further information can be gathered that might change the tone of the assessment, or (3) act quickly to protect the subspecies while continuing to gather information which could promote effective management. Selection of option 1 is generally accompanied by an attack on the study methods and claims of a fatal flaw in the assessment. Option 2 has merit if the risks of not acting quickly are low, new information can be obtained efficiently, and new information likely will change the conclusions of the assessment. Option 3 is the logical choice when actions taken in the short term are not excessively costly and do

not preclude future actions that might seem more appropriate in light of new information.

The response of the State of Montana, the FS, and the BLM to our assessment has been in line with option 3. In September 1996, the Governor of Montana convened a Westslope Cutthroat Trout Conservation Workshop to initiate a statewide conservation effort. This conservation and restoration effort is being led by the FWP and already has begun in the upper Missouri basin. A steering group, which consists of agency and private representatives, has been formed to recommend conservation and restoration efforts to the FWP. The technical committee, which was formed in 1995, interacts with both the steering committee and the FWP to recommend technically sound conservation and restoration strategies. Local citizen watershed groups have been formed in some of the watersheds of the upper Missouri basin to implement conservation and restoration efforts. An ambitious restoration program recently was started in the upper Madison River drainage. All of these conservation and restoration efforts were stimulated, in part, by our extinction risk assessment of westslope cutthroat trout in the upper Missouri basin.

The FS and the BLM also asked the technical committee to make interim recommendations, based on preliminary results from this analysis, for conserving westslope cutthroat trout inhabiting federal lands within the upper basin until the FWP's conservation and restoration plan was adopted. The technical committee made the following two recommendations.

(1) Aquatic habitats in all streams that now support populations at least 90% genetically pure (144 populations at present) should be protected from existing and future land management impacts. The level of protection should be specified further and related to genetic purity of individual populations. It was recognized that the 144 streams presently supporting populations likely will change; some populations may become extinct and additional populations may be found. However, the BLM and the FS have defined all 144 streams as suitable habitats that will be protected regardless of future extinctions. The intent of this recommendation is that any habitats now supporting populations of westslope cutthroat trout (>90% pure) should be protected or restored to allow for recovery of this subspecies in known suitable habitats.

(2) Until the basinwide conservation strategy being developed by the FWP is adopted, management emphasis must be placed on westslope cutthroat trout in tributaries that support genetically pure populations with a moderate or high probability of extinction. Populations that are 100% pure should be secured first, followed by populations less than 100% pure. Twenty-one known genetically pure populations meet the moderate or high risk criteria. Again, it was recognized that these numbers are probably dynamic. Local opportunities and information for securing these populations also will be considered in setting priorities.

The rationale for recommending that healthier populations be secured first is that, generally, the level of effort needed to secure a relatively healthy population will be less than that needed to secure populations more at risk. We believe that this extinction risk assessment provides a valuable tool for illustrating the relative risk of extinction among populations and puts the regional basinwide extinction risks into perspective for land and fisheries managers.

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Appendix: Instructions for Surveys of Population Parameters

Guidelines were given to the biologists who participated in the BayVAM assessments. Using these guidelines, biologists completed a questionnaire survey in which they estimated life history and population parameters for each self-sustaining, reproductively isolated population of westslope cutthroat trout. In most cases, identification of local populations was based on isolation or fragmentation of suitable habitats. Narratives were used to identify data and other rationale used to support the survey responses. Elements of the guidelines follow.

Quantity and Distribution of Spawning Habitat

Three classes of spawning success, based on availability and quality of spawning habitat (gravel), are low (60–80%), moderate (85–95%), and high (100%). If high-quality spawning gravels are readily available throughout the watershed, spawning success is rated high. Unless there is clear evidence that spawning habitat limits the population, the high rating should be used. Where the quantity or distribution of spawning gravel severely limits the potential for egg deposition, re-

sulting in underseeding of rearing habitat, spawning success rate is rated low. The intermediate class applies to spawning habitats limited in either quantity or distribution, but not severely, allowing spawning success rates of 85–95%. In westslope cutthroat trout populations where females mature at relatively small sizes (lengths of 150–200 mm), suitable spawning habitat may consist of small isolated patches (0.2 m^2) of pea-sized gravel behind water velocity breaks.

Fecundity

Fecundity in the BayVAM procedure is rated low (200–500 eggs per female), moderate (500–800 eggs), high (800–1,100 eggs), or very high (1,100–1,500 eggs) for inland trout. Low fecundity is expected for most resident westslope cutthroat trout populations in which mean body size of mature females is less than 200 mm. Moderate fecundity is likely when mature females consistently exceed 200 mm. High fecundity, though rare, may occur in migratory populations in which mature fish exceed 300 mm. It is not expected that any westslope cutthroat trout within the upper Missouri system have fecundities over 1,100 eggs per female, so very high fecundity should not be used in the upper Missouri River basin analysis.

Incubation Success

The success of egg and alevin incubation to emergence is rated low (5–20%), moderate (20–35%), or high (35–50%). In the absence of natural or anthropogenic habitat disruption, survival to emergence should be similar to values documented in the field for the best cutthroat trout spawning habitats (35–50%). For this high rating to be selected, fine sediments or sediment loading should not differ from natural conditions, sediment distributions in the channel should reflect equilibrium with prevailing discharges, and high water quality and favorable stream flows should occur throughout the incubation period.

Maximum Fry Survival (Density-Independent, Early-Rearing, and Overwinter Survival)

Fry survival ranges, inferred from habitat conditions, are low (10–20%), moderate (20–30%), and high (30–40%). Superior habitat conditions are needed to produce high survival rates (> 30%), including extensive off-channel and stream margin habitats, high levels of instream cover, and widely available, unembedded, cobble substrates for age-0 cutthroat trout to use during winter. Nonnative fish species should be absent or have limited potential for reaching a stream through natural dispersal. Where early rearing habitats are not widely distributed, woody debris or other cover is very low, and off-channel habitats are either lacking because of channel geomorphology or seriously degraded because of channel instability, maximum fry survival should be rated low (<20%). Low survival also is indicated where substrates are moderately to highly embedded and alternative cover is lacking. In addition, low survival would be expected where one or more species of nonnative competitors occur within the watershed and either are, or could be, widely distributed throughout it.

Fry Capacity

Fry capacity classes were low (1,000–4,000 fry), moderate (4,000–7,000 fry); and high (7,000–20,000 fry). These are numbers of fry—up to age 1—in the delineated population area. Occurrence of more than 7,000 age-1 westslope cutthroat trout indicates that fry rearing habitat is widely distributed throughout the watershed, particularly in relation to spawning sites. For high fry capacity to be selected, no nonnative trout species should occupy, or have easy access to, habitat used by cutthroat trout fry up to age 1, and the length of stream occupied by cutthroat trout should be at least 4 km. Low fry habitat capacity (≤ 4,000 fry or age-1 fish) indicates that rearing habitat is in short supply and poorly distributed in relation to spawning sites. The presence of nonnative fish species, particularly brook trout *Salvelinus fontinalis*, should indicate a low fry capacity.

Juvenile Survival

The ranges for juvenile survival are low (14–26%), moderate (26–38%), and high (38–50%). Survival from age 1 to adult may vary substantially between resident and migratory life history forms and may be strongly influenced by environmental conditions. Interactions with nonnative salmonids, especially brook trout, may influence juvenile survival. Competition for space and food or direct mortality from predation may reduce survival. High juvenile survival rates (38–50%) generally are expected for resident populations that do not migrate out of the local watershed if the watershed contains abundant high-quality pools, complex cover, or other habitats important for rearing and overwintering and if nonnative competitors are absent. Moderate juvenile survival rates (26–38%) may occur in allopatric populations occupying degraded habitats or those occupying

high-quality habitats but exposed to competition or predation from nonnative fishes. Low juvenile survival (<26%) is expected for populations in degraded habitats with limited rearing and overwintering habitats and with nonnative species. Low juvenile survival also would be expected for migratory populations that must use migratory corridors and associated rearing environments (larger rivers, lakes, ocean) where anthropogenic or natural changes (dams and diversions, introduced and or enhanced predator populations, water quality) have significantly reduced survival.

Adult Survival

Adult survival (annual survival during and after the year of first maturity) is classed as low (10–30%), moderate (30–50%), or high (50–70%). Of the several factors that can influence adult survival, exploitation is particularly common for westslope cutthroat trout. When growth rates are moderate or slow in unproductive waters, unrestricted fishing effort of 100–200 angler-hours/km of stream can result in serious overexploitation of mature fish (Rieman and Apperson 1989).

Age at First Maturity

Distributions of age at first maturity vary among salmonid species and subspecies, Downs et al. (1997) found the following maturity proportions for westslope cutthroat trout in the upper Missouri basin: 30% at age 3, 40% at age 4, 20% at age 5, and 10% at age 6. Unless specific data exist for the population being evaluated, these proportions should be used for this subspecies.

Initial Adult Population Size

Initial adult population size is considered low (<450 fish), moderate (450–850 fish), or high (>850 fish). Large watersheds are likely to support more adults in a population than small ones, but the relationship has large variance and population size is best inferred from some basic information on fish density and distribution. If local data that can be extrapolated to larger areas are available, they should be used. Adults counted should include all mature fish alive in a given year, not just those spawning. It should be noted that initial population size has relatively little effect on model outputs other than the setting of initial conditions.

Coefficient of Variability (CV) of Fry Survival

Variability in fry survival to age 1, measured as the coefficient of variation of survival (CV = 100·SD/mean), is classed as low (<40%), moderate (40–65%), or high (>65%). Estimates of the CV are best made from time series of population size or density, especially if the series covers 10 or more years. Alternative but weaker estimates can be made from habitat and age structure data. Low fry survival variability could be inferred from low variability in channel dynamics such as flows and from other environmental conditions that likely influence rearing conditions, particularly if systems have diverse, widely distributed, and complex habitats that buffer environmental fluctuations. The availability of refuges and distribution of the population over a broader area makes the overall fry population less vulnerable to localized disturbance. Such complexity is characteristic of large watersheds where all resident life stages or necessary habitats (spawning, early rearing) are widely distributed. There should be no evidence or expectation of year-class failure and all age-classes should be fully represented in population samples. High temporal variability (CV of fry survival between 65 and 90%) is expected in systems where survival and recruitment clearly respond to frequent extreme disturbances (e.g., extreme high or low flows) that occur once or more per generation. Year-class failures would be common and population samples often would show uneven distribution of age-classes in such cases. High variability might be anticipated in simplified or spatially restricted habitats critical for early life stages and in watersheds with only a single tributary stream available for any life stage, especially where extreme flows are common.

Risk of Catastrophe

Catastrophic risk is classed by estimated recurrence time; it may be low (120–170-year interval), moderate (70–120 years), or high (20–70 years). Catastrophic events substantially affect all members of a population, and habitats may recover from them only after several years. Populations affected by a catastrophe are likely to be less resilient and thus at greater risk to some future disturbance. Massive debris flow and scour, droughts, volcanic eruptions, earthquakes, glaciers, fire storms, toxic spills, and dam failures are all examples of catastrophic events for salmonid populations. The potential for a catastrophic event is influenced by physiographic characteristics of the watershed, and its effect is influenced by the distribution of fish, critical habitats, and refuges. In some cases, human disturbance or development of a watershed may cause an "extreme" event within a natural range to become a catastrophe. For ex-

ample, a watershed that has been heavily logged and roaded is more vulnerable to debris or sediment torrents than a fully forested watershed (Meehan 1991). A high catastrophic risk assignment is appropriate where 50% or more of the population could be lost in a single event expected within 20–70 years. Watersheds with high risk also are prone to major channel disturbances such as debris torrents, massive bedload scour, and extensive channel dewatering, some of which can result from major fires. Moderate catastrophic risk is appropriate for most watersheds exposed to some human disturbance. Low catastrophic potential can be applied to large watersheds that are subject to low human disturbance or development, that are stable geologically and hydrologically, and that (because of altitudinal and stream diversity) support populations with all life stages.