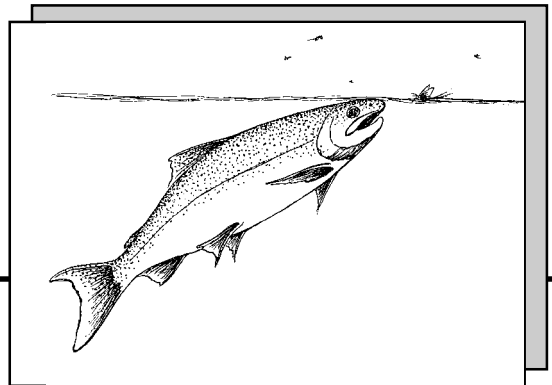


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Currents...

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Consideration of Extinction Risks for Salmonids

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Abstract

Under the National Forest Management Act of 1979, the USDA Forest Service is charged with maintaining viable populations of all existing native vertebrate species on lands they administer. Accomplishment of this responsibility requires complete assessment of all federally authorized, funded, or implemented projects that may jeopardize the continued existence of a species. An understanding of the processes of extinction and the characteristics of populations that make them more or less likely to persist is fundamental to such assessments. We review processes contributing to extinction and characterize them as deterministic, stochastic, and genetic. Factors that strongly influence risks of local and regional extinction include replication, dispersal and connection among populations representing a regional metapopulation. Project planning and assessments must address habitat disruption and population responses at both the local and regional scale. Maintaining strong populations in the best possible habitats throughout the landscape and preserving the ecological processes characteristic of metapopulations are the best hedges against extinction.



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The USDA Forest Service Fish Habitat Relationships Program was established to further the development of fisheries technology and transfer this technology to field biologists. With ever increasing demands for natural resources, protection and management of aquatic communities require biologists to be knowledgeable of current research findings and state-of-the-art techniques. The purpose of *FHR Currents* is to provide a vehicle to quickly disseminate information important to field-level biologists in the USDA Forest Service.

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Introduction

Assessing the viability of individual fish populations is a major problem for many fisheries biologists. Unfortunately, there is little quantitative support or guidance for such assessments. Extinction risks for salmonids are influenced by complex and interacting factors that are often difficult, if not impossible, to identify and measure. Despite this difficulty, understanding the nature of the extinction process can lead to management prescriptions that minimize risks to local populations. Theoretical insights from the developing field of conservation biology can provide guidance to population managers. In this report, we review factors influencing the persistence of populations and suggest means for managing resident trout and char populations to mitigate extinction risks.

The Basics of Extinction

The first step in discussing population extinction is to define population. For this discussion, a population is a group of animals that has a high probability of mating among its members relative to mating with members of other populations of the same species. For example, a trout population might consist of a group of fish that spawn and rear in a specific tributary but not in the mainstem. By virtue of homing or stream residency, they are isolated to various degrees from fish in other tributaries. A collection of such populations that interact through the exchange of individuals is termed a metapopulation. Metapopulations are associated with large watersheds, lakes, or river basins -- depending on the level of connection among streams and the straying or dispersal rates and distances typical of each species. When habitat is lost or streams are blocked, metapopulations may become fragmented into isolated local populations.

Commonly, extinction refers to the loss of a species. Extinctions also occur at the level of a local population and at regional levels represented by metapopulations. Because Forest Service policy directs the maintenance of a species throughout its range, local and regional extinctions are important

to fisheries biologists. We focus our discussion on extinction processes relevant to local populations and then consider metapopulation dynamics that are important to both local and regional persistence.

Extinction occurs when population losses (defined as the per capita death or emigration per unit time) exceed population gains (defined as the per capita reproduction or immigration per unit time) long enough to extinguish the population. The population growth rate (R) is defined as the natural log of the birth rate minus the death rate. When R is negative, the population declines; if R is positive, the population increases. The mechanisms leading to extinction can be characterized in three general categories: deterministic, stochastic, and genetic (Leigh 1981; Gilpin and Soulé 1986; Gilpin 1987; Shaffer 1987; Shaffer 1991) which can operate in complex combinations. In the following, we will discuss each of these in turn.

Characterization of Risks

Deterministic Processes

Deterministic extinctions occur with the cumulative loss or otherwise permanent change of a critical component in the species' environment (Gilpin and Soulé 1986). Such changes result in progressive increases in the population death rate, decreases in the population birth rate, or both. If the environment changes sufficiently, natural compensatory mechanisms, which tend to increase the birth rate as the death rate increases, can be overwhelmed. This leads to a negative expectation of R . Despite occasional increases in the population due to stochastic factors (see below), the population will move inexorably towards extinction.

For salmonids, a variety of factors might contribute to deterministic extinction. Bull trout populations might decline, for example, with the elimination of pools or woody debris that are necessary as overwinter habitat; or with an increase in fine sediments that degrade spawning

habitats and lead to increased mortality of incubating embryos. Salmon populations have declined with increasing mortality at dams in the migratory corridor. Alternatively, competition or predation might increase with the introduction of exotics. Changes that might be tolerated separately may lead to extinction in combination. Displacement of bull trout by brook trout, for example, may occur more commonly in degraded habitat. Relatively subtle changes in habitat quality may favor one species over another (Everest et al. 1987). Mortality from some causes can increase as populations become smaller, even with no further change in the environment. Such compensatory effects may be particularly relevant for salmonids (Peterman 1977; Peterman and Gatto 1978; Rieman and Apperson 1989; Rieman and Myers 1991).

A population's response to environmental change depends on somatic growth, mortality, fecundity, longevity, and age-at-maturity. In combination, these factors determine the reproductive potential of the population, and thus its ability to compensate for increased levels of mortality. Given similar age structures, sex ratios, mortality, and maturation rates, for example, populations with higher reproductive potentials should be more resistant to disturbance. A fluvial population of cutthroat trout that matures at age four and 400 mm will likely have a higher reproductive potential than a resident population of cutthroat trout that mature at age four and 200 mm.

Additional or cumulative stress will progressively decrease the compensatory capacity of a population. Simply put, habitat disruption that results in lower survival or growth at one stage means that less mortality can be sustained at another stage if the population is to maintain its current numbers. Most populations can absorb some increased mortality, hence the ability to withstand harvest. Cumulative mortality related to habitat loss reduces that reserve. Clearly, all populations are not equal in their ability to absorb additional stress -- but we cannot accurately estimate the differences. Any habitat change that irreversibly reduces survival or growth at any life stage increases the risk of deterministic extinction.

Much, if not most, of the loss of salmonid populations probably results from habitat change and other actions (e.g., fishing regulations, species introductions, pollution) that induce deterministic responses. These problems are well known among fisheries biologists. Restrictive angling regulations and habitat management efforts are often used to increase survival and mitigate such risks in individual populations. The long term declining trends in many populations suggest that such efforts are not always successful.

Stochastic Processes

Less familiar to fisheries biologists are risks associated with stochastic processes, or chance events. Such processes result in unpredictable fluctuations in population numbers. At times, such fluctuations can portend disaster for populations, especially if the populations are very small. Stochastic processes generally are grouped into two categories, demographic and environmental, depending on their origin. For example, Nisbet and Gurney (1982) distinguish the two as:

- (a) Demographic stochasticity, which is the name given to fluctuations that arise because populations contain a discrete number of members, with population changes being caused by a succession of individually unpredictable births and deaths;
- (b) Environmental stochasticity, which is the name properly applied to a periodic environmental variation and often applied loosely to the resulting population fluctuations.

Demographic stochasticity arises from small magnitude differences among individuals that might ordinarily be viewed as similar. In population models, demographic stochasticity is introduced through a discrete sampling process. For example, survival of a group of N fish in a given year might be modeled as X successes in N trials where X is the number surviving. If P is the probability of success in each trial (i.e., probability of survival), the expected number surviving would

be ($N \cdot P$). The difference between X and ($N \cdot P$) is demographic stochasticity, often referred to as the sampling error. The ratio of the expected sampling error to the expected outcome (the coefficient of variation) decreases as the sample size increases. Thus, this type of variation is most important at low population abundances. Demographic stochasticity is considered inconsequential unless population sizes are very small (i.e., 20 adults) (Leigh 1981; Shaffer and Samson 1985; Quinn and Hastings 1987; Shaffer 1987).

Environmental stochasticity includes chronic and catastrophic fluctuations of higher amplitude (Shaffer 1987; Shaffer 1991). Such variations in survival and birth rates can be attributed to normal variability in such characteristics as temperature and stream flow, or low frequency, extreme events such as flood, drought, fire storms and debris torrents.

The variance in the population growth rate resulting from the combination of demographic and environmental stochasticity interacts with population size to determine the probability of extinction over a given time period (Dennis et al. 1991; Leigh 1981; Boyce 1992). The expected time to extinction decreases as population size decreases and as the variation in the population growth rate increases. Small populations tend to vary relatively more than large populations (Gilpin and Soulé 1986). They are likely to experience high temporal variation, lower genetic and phenotypic diversity, and have few refuges available (Gilpin and Soulé 1986; Shaffer 1987; Saunders et al. 1990).

Population viability analyses, based in both simulation and analytic models, provide estimates of stochastic risks for a variety of taxa (see for example, Shaffer and Samson 1985; Dennis et al. 1991; Stacey and Taper 1992). Such efforts require data that often are not available for many populations of salmonids. Results for a variety of species, however, suggest that populations isolated from other populations face higher risks through stochastic effects. For example, our analysis (Rieman and McIntyre 1993) of local bull trout populations indicates that few have a high

probability of persisting for 100 years in isolation from other populations. Such analyses also suggest that extinction risks for local, isolated populations increase sharply as population sizes drop below roughly 1,000 to 2,000 total individuals (Figure 1).

Historically, stochastic processes may have posed little threat to most local and regional salmonid populations. However, with the loss of habitat, many populations have declined dramatically in size and have been restricted to marginal or highly variable habitats, thus increasing the risk from stochastic factors. Habitat change can influence not only the amount of environmental variation, but also the sensitivity of a population to that variation. Populations in complex habitats should be more stable than populations in simple or restricted habitats because they have more refuges from extreme events and greater capacity to buffer the effects of environmental change (Schlosser 1982; Saunders et al. 1990; Sedell et al. 1990; Schlosser 1991; Pearson et al. 1992). Even without any further habitat loss, we anticipate further loss of already restricted populations.

Genetic Risks

Conservation of a species depends on protection of its genetic diversity. The consequence of losing diversity is loss of genetic combinations, some of which may be crucial to survival in highly variable environments. Although adaptations to local conditions are difficult to identify, their presence is generally supported by data (for example, Hynes et al. 1981; MacLean and Evans 1981). At present, available data does not provide a basis for specifying the minimum amount of genetic diversity that must be maintained to ensure persistence of salmonid populations.

The literature is replete with arguments that one cannot define general guidelines for the minimum number of organisms needed in a population to mitigate the effects of genetic loss. Soulé (1987) argues, however, that the public deserves guidance from the scientific community so that conservation programs can proceed. He proposes the "50/500" rule: in a completely closed population, an effective population size of 50 is

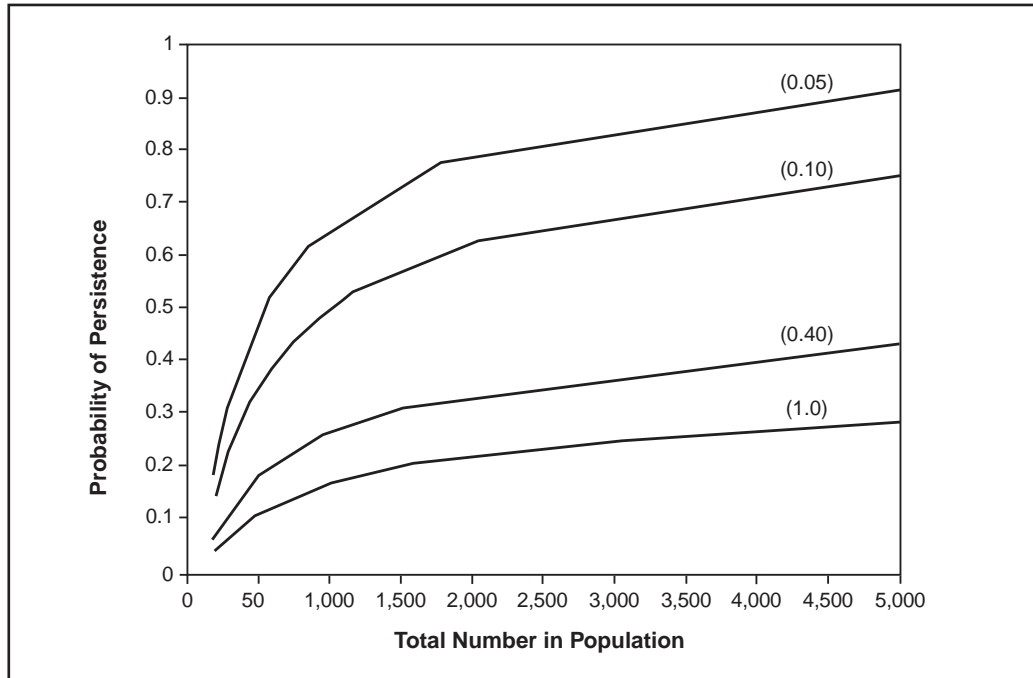


Figure 1. Estimated probability that a hypothetical population will persist above a minimum threshold of 20 adults for 100 years given an initial population size and the variance (σ^2) in the annual population growth rate. Populations were assumed to be fluctuating around some equilibrium. Estimates of variances are not available for most salmonid populations but existing data suggest that many may range from 0.05 to 0.50 or higher. These results indicate that risks of dropping below the threshold increase sharply with initial population sizes less than 1,000 to 2,000 total individuals. Thresholds do not represent true extinction but a point where risks through demographic stochasticity, lost genetic variation and inbreeding, or depensatory mortality may make recovery unlikely without support from other populations. The estimates follow the method of Dennis et al. (1991) as outlined in Rieman and McIntyre (1993).

needed to prevent excessive rates of inbreeding, but 500 is needed to maintain the genetic variation necessary for long term adaptation. Effective population size refers to the level of genetic variability represented in the breeding individuals and not to the total population size; the effective number may equal three-quarters or less of the actual number (Salwasser and Marcot 1986; Falconer 1989). Nelson and Soulé (1987) suggested that genetic variation can be lost with fewer than 5,000 total individuals.

Historically, much of the thinking in species conservation focused on genetic issues associated with small population size and isolation (Franklin 1980; Shaffer 1991). More recent work suggests that many populations are at higher risks from environmental stochasticity or catastrophic events than through inbreeding or the loss of genetic variation (Lande 1988; Shaffer 1991; Stacey and

Taper 1992). It seems likely that management prescriptions taken to minimize stochastic and deterministic effects will at the same time minimize genetic risks.

Although we have classified the risks of extinction in three general areas, it is important to recognize that the processes of extinction do not operate independently. Genetic restriction, for example, may reduce fitness and increase sensitivity to environmental variation. Cumulative habitat changes that eliminate or isolate segments of populations may increase both demographic and environmental stochasticity because of lower numbers and lower diversity in population structure or distribution. Those same habitat changes might increase mortality directly by restricting the population to less productive habitat, also leading to increased deterministic risk.

Metapopulation Dynamics

If the odds seem stacked against the local population, how then does one explain the apparent persistence in nature of large numbers of relatively small populations in highly variable environments? One possible mechanism contributing to population persistence involves organization of populations at a higher level. An expanding literature in conservation and population biology suggests that large scale spatial structure and dispersal mechanisms are critical to the persistence of populations of many taxa (Gilpin 1987; Shaffer 1987; Hanski 1991; Hanski and Gilpin 1991; Sjogren 1991; Boyce 1992). Many species exist in spatially heterogeneous environments with local groups of animals associated with patches of suitable habitat. These local groups are more likely to interact and interbreed among themselves than with other groups, but exchange of individuals occurs through a range of dispersal mechanisms. Populations within populations in this context are again defined as metapopulations in the emerging jargon of conservation biology (Shaffer 1987; Hanski and Gilpin 1991).

Theoretically, the diversity of local populations in variable environments conveys stability to the larger metapopulation. Local extinctions are a natural if not common part of the regional population dynamics for many species (Hanski 1991; Hanski and Gilpin 1991; Sjogren 1991). Multiple component populations in complex habitats spread the risk of synchronous extinctions (Morrison and Barbosa 1987; Quinn and Hastings 1987). Stronger populations provide sources for recolonization (Brown and Kodric-Brown 1977; Sjogren 1991), or support of other weaker populations through dispersal of surplus animals (Hanski 1985; Pulliam 1988) (Figure 2).

Metapopulation dynamics may be particularly important to the persistence and recovery of populations following catastrophic events (Yount and Niemi 1990), but probably play a role in normally variable environments as well. The probabilities of persistence and relative stability of the metapopulation are strongly influenced by the

sizes, spatial distribution, temporal variation and synchrony, and dispersal among the component populations (Fahrig 1990; Hanski 1991; Sjogren 1991; Doak et al. 1992).

Populations of salmonids have features characteristic of metapopulations. Spawning and early rearing often occur in streams tributary to larger river or lake systems. Homing and fidelity to nursery areas creates some isolation among populations within streams and represent the basis of the stock concept (Ricker 1972). Local adaptations provide further evidence of isolation in a heterogeneous environment. Dispersal among groups may be maintained through the straying of migrating adults (Simon 1972; Labell 1992; Reisenbichler et al. 1992), density-dependent displacement of individuals (McMahon and Tash 1988; Northcote 1992), or maintenance of pioneering or colonizing phenotypes (Northcote 1992).

Implications for Fisheries Management

Metapopulation dynamics are important considerations in conservation planning and species maintenance and recovery efforts (Murphy and Noon 1992; Noon and McKelvey 1992). There has been some application of these ideas to aquatic environments and fish populations (for example, Sheldon 1988; Moyle and Sato 1991; Reeves and Sedell 1992). There is a general consensus that preserving phenotypic and genetic diversity requires maintaining populations through a wide geographic range in a variety of habitats (Allendorf and Leary 1988; Leary et al. 1991; Moyle and Sato 1991; Reeves and Sedell 1992). Diversity in life-history characteristics may be critical to the persistence of and dispersal of populations in changing or variable environments (Gross et al. 1991; Northcote 1992; Titus and Mosegaard 1992).

For the most part, however, management and research of interior salmonid populations have continued to focus on the intra-population processes of recruitment, mortality and growth, and production or yield. Management and

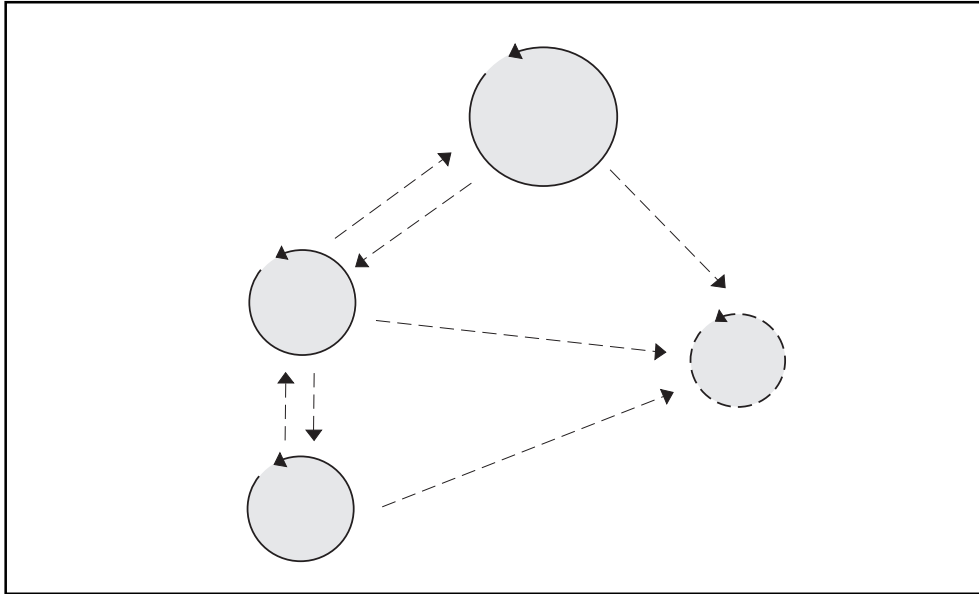


Figure 2. Schematic representation of a metapopulation. Size of the circle represents the relative size of a population and the potential for emigration of individuals. Arrows represent the pathways of exchange among populations. The broken circle represents a population that has a high probability of local extinction, and is likely to persist only through support from other populations.

research have typically focused on characteristics of individual habitat units or stream reaches, and the links between distribution, abundance, and survival of fish at that scale (see Fausch 1988). Growing attention has been placed on consideration of fish habitat relations from a larger scale (Frissell 1993; Frissell et al. 1993); but little is known about the links between spatial diversity in habitat characteristics among streams and the corresponding spatial diversity in the characteristics and dynamics of populations. Similarly, little is known about how populations interact via migration and dispersal. Concern for, and the relative importance of, individual populations is likely to be based more on the relative size or potential yield of a population than on its contribution to stability or diversity of the whole (though the two may be related). For example, marginal environments and discrete life history forms are often overlooked in management decisions focused on the dominant or most productive stocks (Northcote 1992; Wright 1993).

Land-use management and development influence metapopulation processes. Migration, dispersal, and the connection among populations are

influenced by changes in hydrologic and temperature patterns, water diversions and dams, channel conditions or barriers, and the distance among remaining populations and suitable habitats. In heavily disturbed environments, populations are isolated or clustered in undisturbed headwater areas (for example, Mullan et al. 1992) (Figure 3). Invasion by exotics may be hastened by habitat disruption (Hobbs and Huenneke 1992; Markle 1992; Mullan et al. 1992) and may produce further isolation or local extinction through competitive displacement (Leary et al. 1991; Mullan et al. 1992).

Conventional forest management can compromise the metapopulation structure by changing the natural mosaic of conditions in which it evolved. Under conventional management, habitat disruption is often spread widely throughout a basin to minimize impacts in any single stream. The use of habitat thresholds or levels of acceptable disturbance is likely to create more homogeneous conditions among streams that cluster about or below the threshold than a more natural range of habitat conditions. Under the former condition, the diversity, resilience, and

resistance to disturbance of all populations may be compromised, while the synchrony in response to disturbance is increased. When habitat disruption is spread among all populations, all populations are more likely to decline during unfavorable periods in the regional environment (for example, drought). Severe or prolonged conditions increase the potential for regional extinction.

Since forest management influences salmonid population persistence at both local and regional scales, planning and project assessments must address both. Tables 1 and 2 outline the relative risks of extinction associated with characteristics of both local and regional populations. A low risk of extinction means that a population has a high probability (for example, > 95%) of persisting through the period relevant to forest management (100 to 200 years), given existing or improving conditions. We judge a population at high risk of extinction as one with less than a 50% chance of persisting through the same period.

Our attempt to represent the risks for any population characteristic assumes that all other characteristics would represent a low risk. Though there is no exact way to combine the risks presented here, the additive model provides a suitable first approximation. For example, a population at moderate risk through several processes is likely to be at high risk overall.

We believe maintaining strong populations in the best possible habitats throughout the landscape and preserving metapopulation structure and function are the best hedges against extinction. Conservation goals that include maintaining spatially dispersed, high quality habitats will be more effective than goals based solely on estimates of minimum viable population sizes (see Boyce 1992), or goals that allow disruption of all streams. While more work is necessary to describe the appropriate scale for sustaining different species and in different environments, the creation or maintenance of a more natural mosaic of habitat conditions should commence wherever possible.

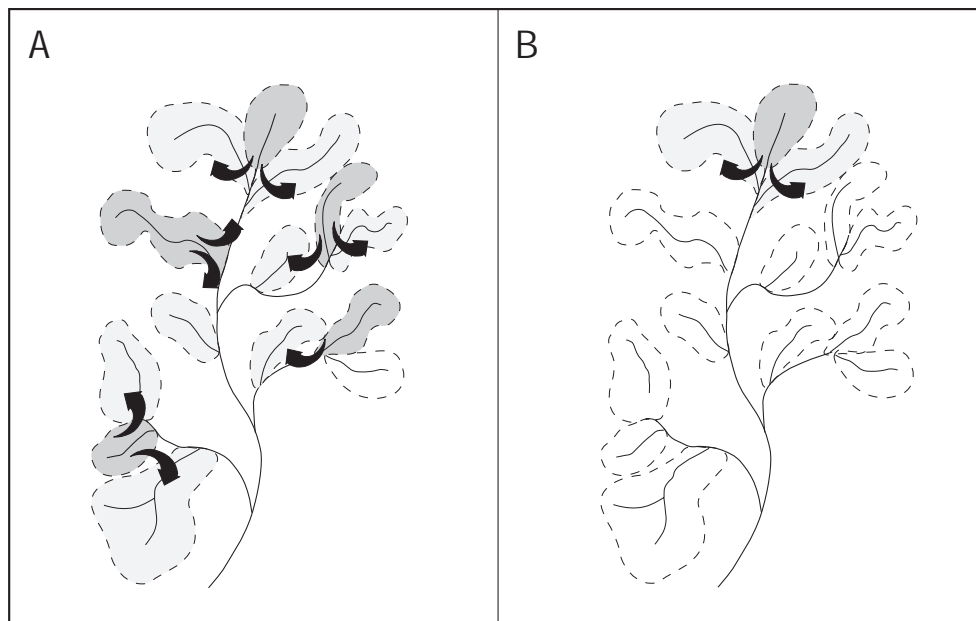


Figure 3. Hypothetical representation of the distribution of salmonid populations within undisturbed (A) and disturbed (B) basins. The darkest shading represents the best habitats supporting the strongest populations with potential for dispersal to and support of other surrounding populations. The lighter shading represents intermediate or disrupted habitats that support fish either because of support from other populations or because habitat is still suitable over the short term. The unshaded areas represent disrupted habitats that support no fish. The arrows represent dispersal among populations. Metapopulation theory suggests that persistence throughout the region may be strongly influenced by the distribution of strong populations.

Table 1. Relative risk of extinction for local populations of salmonids with a variety of populations

Characteristics of the Population	Nature of Risk Primary (Secondary)	Risk ¹ of Local Population Extinction			
		Low	Moderate	High	Extreme
Temporal Variability in recruitment or survival	Stochastic (Genetic)	Environmental disturbance short lived, predictable hydrograph, high habitat and watershed complexity providing refuge and rearing space for all life stages or multiple life history forms. Environmental and hydrologic events (frequency of >1 per 25 years) are unlikely to markedly influence the entire population.		Frequent flood or drought producing highly variable and unpredictable flows, scour events, debris torrents, or high probability of catastrophic fire through a major part of the watershed. Channel simplified providing little hydraulic complexity. Population survival and recruitment respond sharply to annual environmental events. Year class failures common.	
Population Size	Stochastic (Genetic)	Mean total population size or local habitat capacity more than several thousand individuals. All life stages represented in the population.	Adult population fewer than 500. Periodic year class failures.	Adult population fewer than 50. Year class failures common.	
Growth, Survival	Deterministic (Stochastic) (Genetic)	Habitat quality is high and disturbance has not altered channel equilibrium. Fine sediments and other habitat characteristics influencing survival or growth are within the range of pristine habitat. Population has the resilience to support exploitation or to recover from catastrophic events or over-fishing within one to two generations (5 to 10 years). Population is fluctuating around an equilibrium or growing.	Fine sediments, stream temperatures, or the availability of suitable habitats have been altered and will not recover to predisturbance conditions within one generation (5 years). Survival or growth rates have been reduced from those in undisturbed habitats. The population is reduced in size but no long-term trend in abundance exists.		Cumulative disruption of habitat has resulted in a clear declining trend in population size. Under current management habitat conditions will not improve within two generations (5 to 10 years).
Isolation	Stochastic (Genetic) (Deterministic)	Population exists in close proximity to other spawning and rearing groups. Migratory corridors and rearing habitat (lake or larger river) are in good to excellent condition. Neighboring populations are large with high likelihood of producing surplus individuals or straying adults that will mix with the local population.	Migratory form is present, but population is not close to other populations or habitat disruption has produced strong correlation among populations that do exist in proximity to each other.		Migratory form is absent and population is isolated to the local stream or a small watershed not likely to support more than 2000 fish.

Table 2. Relative risk of extinction for regional populations of salmonids with a variety of population characteristics.

Characteristics of the Population	Nature of Risk Primary (Secondary)	Risk ¹ of Local Population Extinction			
		Low	Moderate	High	Extreme
Replication	Stochastic (Genetic) (Deterministic)	Multiple (5 or more) local populations each of at least several thousand animals. Each of the relevant local populations has a low risk of extinction.	Multiple populations but a small number (1 or 2) represent most of the fish production in the regional population.		Only a single population, several very small populations, or populations otherwise at high risk remain.
Synchrony	Stochastic (Deterministic)	Environmental variation is low. Populations are found in high quality/complex habitats. Little evidence that populations fluctuate together. Frequency of large scale catastrophic events (flood, low flows, fire) is low throughout all populations. No evidence of regional decline in species.		Populations are clustered in close proximity and likely respond to the same environmental variations. Frequent flood or drought producing highly variable and unpredictable flows, throughout the region.	

¹ Risk levels are subjective and are based on the author's interpretations and summary of materials in the text. The risks associated with any set of characteristics are examples and are not to be exhaustive. Each classification assumes that the risk associated with other characteristics is low.

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