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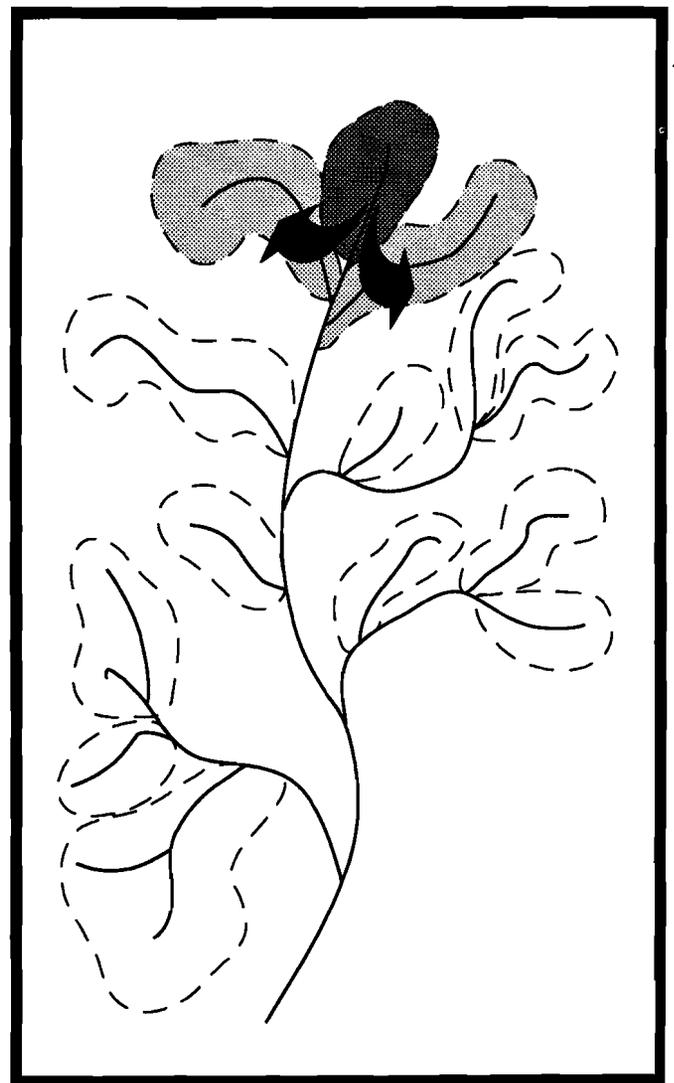
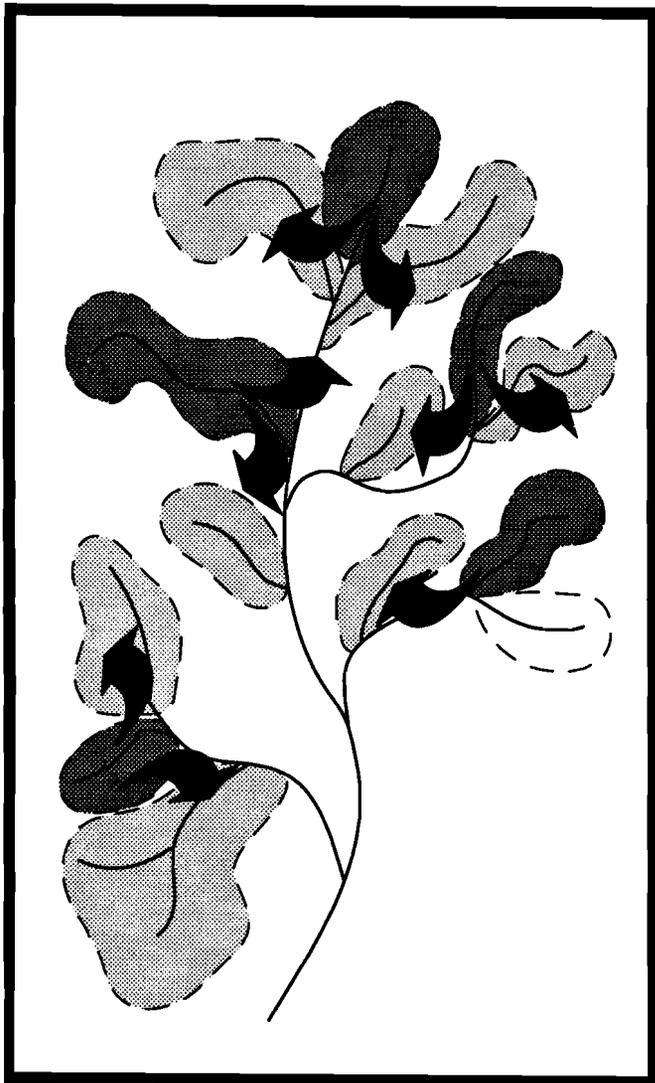
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Demographic and Habitat Requirements for Conservation of Bull Trout

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INTRODUCTION

The future of declining populations of bull trout (*Salvelinus confluentus*) has become a concern. Modern land-use practices alter the environments where salmonid fishes live, often in unpredictable ways. The expansion of exotic species and the harvesting of fish also can be harmful. Such changes appear to have influenced the decline or disappearance of a number of bull trout populations in recent years; the distribution of the species is clearly fragmented (Howell and Buchanan 1992; Thomas 1992). Many biologists believe that bull trout are particularly sensitive to environmental change. They are recognized as a "species of special concern" by State management agencies and the American Fisheries Society (Williams and others 1989) and as an "indicator species" by the Forest Service, U.S. Department of Agriculture. Concern for the persistence of the species has culminated in recent petitions for review or listing under the Endangered Species Act. One petition, submitted in October 1992 by the Alliance for the Wild Rockies, the Friends of the Swan, and the Swan View Coalition, asks the U.S. Fish and Wildlife Service for an emergency endangered listing in Montana, Idaho, Washington, Oregon, and Nevada. The other, submitted in January 1993 by the Oregon Chapter of the American Fisheries Society, asks the U.S. Fish and Wildlife Service for a status review for the purposes of listing bull trout in the Upper Klamath River basin in Oregon.

Bull trout are still widely distributed throughout the Northwestern United States and Western Canada. Important genetic and biological diversity exists across watershed, drainage basin, forest, State, and international boundaries. Conservation of the species and its inherent diversity requires a broad-based, interregional approach (Leary and others 1992). In June 1992, the Forest Service recognized that need by beginning an interregional conservation assessment. This report provides the technical background in bull trout biology, habitat use, and demographic characteristics necessary for the conservation assessment.

We identify elements in bull trout biology, habitat, and biotic interactions relevant to the persistence of populations in managed or otherwise changing environments. We did not try to summarize all available work on bull trout, but identified the important elements relevant to management. A reader seeking a more detailed review or specific information can reference a number of important summary documents (Brown 1992; Goetz 1989; Howell and Buchanan 1992; MacDonald 1985; Shepard and others 1984b; Thomas 1992).

We also consider the implications of habitat disturbance and land-use management. There is a substantial amount of literature with examples of habitat disruption and its effects on salmonid fishes. Most fisheries biologists are acquainted with that information, so we have not emphasized specific land-use effects or management activities designed to mitigate instream habitat disruption. Most biologists are not well acquainted with the emerging principles of conservation biology and metapopulation dynamics. Newer work introduces important concepts about the scale, distribution, and connection of habitats and populations, and the associated risks of extinction. We review the processes leading to extinction of populations of any species and then use existing information to consider the general extinction risks for bull trout. We use our results to outline a conservation strategy that will minimize the risks of extinction; we also identify critical uncertainties that require special attention by managers and additional research.

ECOLOGY

The general life history of bull trout is characteristic of chars. Bull trout are often found in habitats similar to those used by Dolly Varden (*S. malma*) and introduced brook trout (*S. fontinalis*). Taxonomically and behaviorally, bull trout have been related to members of the "Alpinus complex" (Arctic char [*S. alpinus*] and Dolly Varden), but the phylogeny is still unresolved (Phillips and others 1992). Only in recent years have bull trout been recognized as a

species separate from *S. malma* (Cavender 1978; Haas and McPhail 1991).

Biology and Life History

Bull trout spawn from August through November (Armstrong and Morrow 1980; Brown 1992; McPhail and Murray 1979; Shepard and others 1984b). Shepard and others (1984b) associated spawning with falling temperatures between 5 and 9 °C. Embryos incubate over winter. Hatching occurs in late winter or early spring (Weaver and White 1985); the alevins may stay within the gravel for an extended period after they absorb the yolk, feeding and growing there (McPhail and Murray 1979). Shepard and others (1984b) speculate the extended stay within the gravel may be a strategy that allows the young bull trout to be larger and more likely to survive when they emerge. Emergence has been observed over a relatively short time after a peak in stream discharge (Weaver and White 1985) from early April through May (Needham and Vaughan 1952; Pratt 1992; Ratliff 1992; Shepard and others 1984b).

Like other char, bull trout have multiple life-history forms or morphs, and complex age structures, behavior, and maturation schedules. Two distinct forms, resident and migratory, exist throughout the range. Resident populations are often found in small headwater streams where they spend their entire lives (Goetz 1989; Mullan and others 1992; Thurow 1987). Migratory forms live in tributary streams for several years (Bjornn 1957; Shepard and others 1984b) before migrating downstream into a larger river (fluvial form) or lake (adfluvial or lacustrine form). Migratory bull trout spend several years in larger rivers or lakes before returning to tributaries to spawn (Bjornn 1957; Shepard and others 1984b). Anadromy has not been demonstrated in bull trout, but may have been important in the past (Bond 1992).

Availability of forage in the various environments used by the different forms of bull trout has an important influence. Growth varies dramatically, depending on the form. Resident adults range from 150 to 300 millimeters in length (Goetz 1989; Mullan and others 1992), while migratory fish commonly exceed 600 millimeters (Goetz 1989; Pratt 1985; Shepard and others 1984b). Growth differs little between forms during their first years of life in headwater streams, but diverges as migratory fish move into larger and more productive waters (fig. 1).

Resident and migratory forms live together (Jakober 1992), but we do not know if they represent a single population or separate populations. Multiple life-history forms of other char live together and can give rise to one another (Balon 1984; Maekawa 1984; Nordeng 1983; Reist 1989; Schmitz 1992). Similar examples exist for other salmonids (Bjornn and

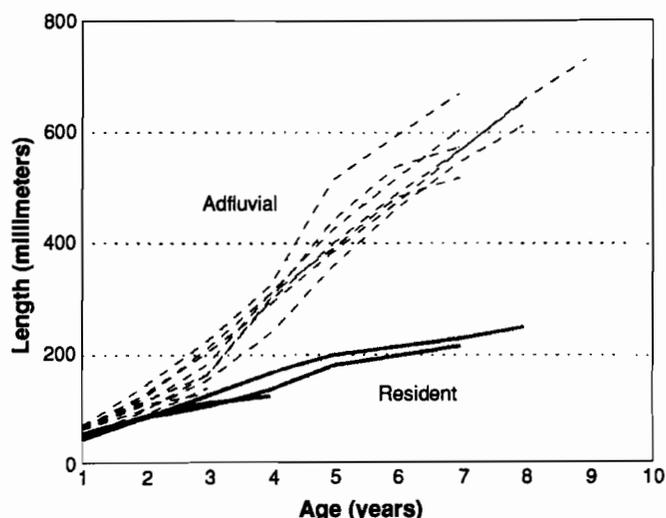


Figure 1—Estimated length at given ages for migratory and resident bull trout. Data summarized from Goetz (1989) and Mullan and others (1992).

others 1968; Kaeriyama and others 1992; Mullan and others 1992; Nelson 1968; Northcote 1992; Ricker 1940, 1959, 1972; Rounsefell 1958). Resident groups of other salmonids have also retained migratory phenotypes (Berg 1985; Foote and others 1992; Schmitz 1992; Staurnes and others 1992), even though the resident and migratory forms may become reproductively isolated (Birt and others 1991; Foote and Larkin 1988; Foote and others 1989; Wood and Foote 1990).

Diverse life-history strategies are important to the stability and persistence of populations of any species. Such diversity is thought to stabilize populations in highly variable environments or to refound segments of populations that have disappeared (Balon 1984; Gross 1991; Mullan and others 1992; Poff and Ward 1990; Titus and Mosegaard 1992; Warren and Chesson 1985). A particular life-history strategy may dominate under stable conditions, but another life-history strategy may be favored with a changing environment (Gross 1991; Northcote 1992; Sibly 1991). For example, because fecundity depends on size, the migratory strategy of salmon could confer an adaptive benefit through increased reproductive potential (Gross 1991). In a stable environment, migratory forms could easily dominate resident forms, but when migrant survival varies or is low, the balance may shift. The Flathead River system, for example, supports bull trout that grow to large size in Flathead Lake (Shepard and others 1984b). Resident fish are rare throughout much of the basin (Thomas 1992). In the Bitterroot basin, however, migratory bull trout have been virtually eliminated by water diversions or habitat disruption, and only resident bull trout exist in many of the

tributary systems (Clancy 1992; Jakober 1992; Thomas 1992). Scudder (1989) argues that populations can represent an important source of the genetic variation that is critical to the long-term persistence of populations. Northcote (1993) made a similar argument for resident and migratory populations.

Variation in the timing of outmigration and in the timing and frequency of spawning also represents diversity in life history. Most information indicates bull trout mature when they are between 5 and 7 years of age (Brown 1992; Fraley and Shepard 1989; Goetz 1989; Leathe and Enk 1985; McPhail and Murray 1979; Mullan and others 1992). Bull trout may spawn each year or in alternate years (Block 1955; Fraley and Shepard 1989; Pratt 1985; Ratliff 1992). Armstrong and Morrow (1980) believed that resident populations of *S. malma* spawned every year, while adfluvial fish spawned less frequently. Shepard and others (1984b) reported age 1, 2, and 3 bull trout emigrated from Flathead River tributaries. It is possible that four or more year classes could compose any spawning population, with each year class including up to three outmigration strategies (four, if resident fish spawn with migratory fish). Although one or two year classes may dominate the outmigration and the population of spawners (Shepard and others 1984b), as many as 12 to 16 combinations could occur in any spawning year.

Population Structure

The multiple life-history strategies found in bull trout populations represent important diversity within populations. The distribution of bull trout populations among river basins and watersheds, and even within streams, represents additional spatial and genetic diversity. Leary and others (1991) found the variation in gene frequencies was greater among groups from different streams than within groups from a single stream. The genetic similarity of groups is a result of migratory fish homing to natal streams where they spawn, or other mechanisms that tend to isolate reproductive groups (Reisenbichler and others 1992). Because environments tend to be heterogeneous, a consequence of this behavior is that natural selection will tend to produce adaptations to local environments and diversity within the larger population. Under normal environmental variation, such behavior will also result in local populations that do not respond to environmental change in synchrony with others.

The concept of subpopulations or local populations within larger or regional populations has been termed a metapopulation (Hanski and Gilpin 1991). Such a structure provides a species with a mechanism of spreading risk. Because the local populations occur in a range of environments, the loss of all populations at any one time becomes less likely. In addition, the

dispersal of fish among the local populations provides a mechanism for supporting weaker populations or refounding those that do become extinct. The study of metapopulation dynamics suggests that such mechanisms may strongly influence the probability of persistence for a species (Fahrig 1990; Gilpin 1987; Stacy and Taper 1992). When we searched the literature, we did not find any consideration of bull trout metapopulations, but the distribution and hypothetical structuring of most bull trout populations are consistent with the concept.

Biotic Interactions

Bull trout eat terrestrial and aquatic insects (Shepard and others 1984b), macrozooplankton, mysids, and fish (Rieman and Lukens 1979). Fish are common in the diet of individuals 110 millimeters long or longer (Shepard and others 1984b). Large bull trout may feed almost exclusively on fish (Fraley and Shepard 1989; Rieman and Lukens 1979; Shepard and others 1984b). Bull trout begin growing rapidly once they move to waters with abundant forage that includes fish (Carl 1985; Shepard and others 1984b; Thurow 1987). The distribution of bull trout in rivers may parallel the distribution of potential prey such as whitefish or sculpins (Carl 1985; Shepard and others 1984b). Vigorous populations may require abundant fish forage. For example, in several river basins where bull trout evolved with large populations of juvenile salmon, bull trout abundance declined when salmon declined (Ratliff and Howell 1992).

Bull trout evolved with and continue to coexist with cutthroat trout (*Oncorhynchus clarki*), rainbow trout (*O. mykiss*), chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*), mountain whitefish (*Prosopium williamsoni*), and several species of sculpins (*Cottus* spp.) and minnows (Cyprinidae) (Mullan and others 1992; Platts 1974; Pratt 1984; Shepard and others 1984b). Interactions between bull trout and native species have not been widely studied. Available research indicates that bull trout and other native species use different resources, reducing direct competition (McPhail and Murray 1979; Nakano and others 1992; Platts 1974; Pratt 1984). Dolly Varden and cutthroat trout also use habitats differently and forage differently in ways that appear related to physical and physiological differences between the species (Henderson and Northcote 1985, 1988; Hume and Northcote 1985).

Interactions with introduced nonnative fishes may decrease the likelihood that some bull trout populations will persist. Introduced brown trout (*Salmo trutta*) and rainbow trout have been associated with the decline of bull trout populations (Bond 1992; Moyle 1976; Mullan and others 1992; Nelson 1965). Bull trout often appear restricted to cold

waters upstream from those used by introduced rainbow trout and brown trout (Mullan and others 1992; Pratt 1985). The expansion of lake trout (*S. namaycush*) may have severely depressed migratory bull trout in Priest Lake, ID (Bowles and others 1991; Rieman and Lukens 1979) and in Flathead Lake, MT (Weaver 1991). Lake trout may prey on juvenile bull trout. In addition, a dramatic increase in fishing pressure for lake trout in Priest Lake increased harvest of bull trout (Rieman and Lukens 1979). Competitive displacement also seems likely where lake trout have been introduced (Donald and Alger 1992).

Hybridization appears to be a common problem where isolated or remnant bull trout populations overlap with brook trout (Cavender 1978; Leary and others 1983, 1991; Markle 1992). Both species are likely to spawn at about the same time and in some of the same places (Balon 1984; Scott and Crossman 1973) and have similar optimum temperatures for incubation (Hokanson and others 1973; McPhail and Murray 1979). Spawning locations for both species are often associated with springs (Graham and others 1981; Shepard and others 1984b; Webster and Eiriksdottir 1976). Hybrids are likely to be sterile and experience developmental problems (Leary and others 1983, 1991). Brook trout likely have a reproductive advantage over resident bull trout because they mature earlier (Leary and others 1991; Mullan and others 1992); hybridization could eliminate a bull trout population. Leary and others (1983, 1991) documented a progressive shift from a community dominated by bull trout to one dominated by brook trout after brook trout appeared in Lolo Creek, MT.

Several factors probably influence the interaction of bull trout and brook trout. Hybridization should be most important in remnant or isolated resident bull trout populations. Migratory bull trout probably have a reproductive advantage over resident brook trout because adult bull trout are larger (400 to 700 millimeters compared to 150 to 250 millimeters for brook trout) and have higher fecundity. Size may also isolate the species through assortative mating (large fish mate with large fish) as it does in other species (Foote and Larkin 1988). Brook trout have been widely introduced (Scott and Crossman 1973) and now live in most basins occupied by bull trout (fig. 2). In many streams or reaches occupied by bull trout, brook trout are not important or even present, even though brook trout may live in adjacent streams and presumably have access to the same streams or reaches. Within the Middle Fork and South Fork of the Salmon River, reaches that supported large numbers of brook trout contained few, if any, bull trout (Thurrow 1985, 1987). Similar results have been observed in other basins (Buckman and others 1992; Clancy 1992; Dambacher and others 1992;

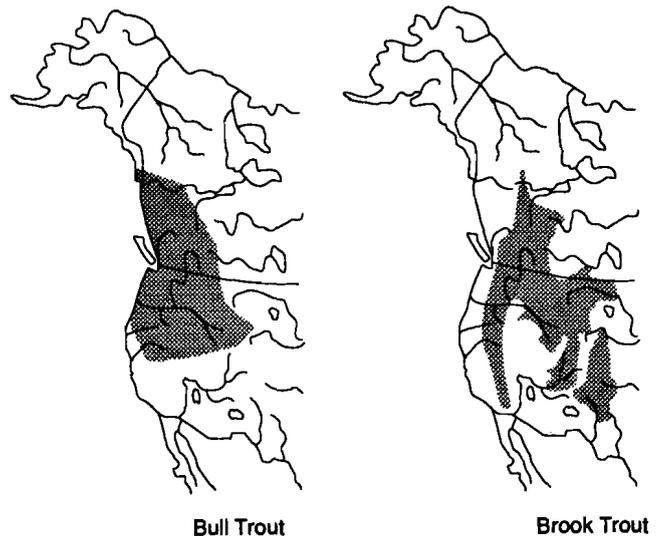


Figure 2—Distributions of brook trout and bull trout in Western North America. All populations of brook trout are introduced. Adapted from Meehan and Bjornn (1991).

Leathe and Enk 1985; Pratt 1985; Ziller 1992). Habitat characteristics must also influence each species' distribution, the interactions between the species, and consequently the degree of hybridization (Campton 1987; Hobbs and Huenneke 1992; Markle 1992; Mullan and others 1992); see Fausch (1988, 1989) for discussion of habitat-related interactions between cutthroat trout and brook trout.

Habitat Relationships

Bull trout appear to have more specific habitat requirements than other salmonids. Although bull trout may be present throughout large river basins, spawning and rearing fish are often found only in a portion of available stream reaches (table 1, fig. 3) (Fraley and Shepard 1989; Graham and others 1981; Mullan and others 1992; Pratt 1985; Shepard and others 1984b; Thurrow 1985, 1987; Weaver and Fraley 1991). Migratory forms may use much of the river basin through their life cycle (Bjornn and Mallet 1964), but rearing and resident fish often live only in smaller watersheds or their tributaries (second- to fourth-order streams) (fig. 3) (Armstrong and Morrow 1980; Fraley and Graham 1981; Mullan and others 1992; Oliver 1979; Platts 1974; Platts and Partridge 1983; Thurrow 1985, 1987; Ziller 1992). Mullan and others (1992) observed that bull trout often were not found in the smallest headwater streams. Shepard and others (1984b) found bull trout occurred most frequently in third- and fourth-order streams.

Table 1—Distribution of bull trout and cutthroat trout in available habitat

Basin	Bull trout		Cutthroat	Source
	Rearing	Spawning		
	----- Percent -----			
Flathead	50	—	100	Shepard and others 1984a
Flathead	—	28	—	Fraley and Shepard 1989
Clark Fork	30	—	93	Kramer 1993
Methow	1.4	—	Widely distributed	Mullan and others 1992
Pend Oreille	42	23	84	Pratt 1985

Bull trout were more widely distributed historically than at present (Howell and Buchanan 1992; Mullan and others 1992; Thomas 1992). It is not clear, however, to what degree the current fragmented distribution reflects the historic patterns typical of a species with specific habitat requirements or of a species that has had its distribution restricted by habitat change, overfishing, and competition with introduced fishes. In any case, species with specific requirements are likely more sensitive to habitat change and less able to persist in the face of change (Rothschild and DiNardo 1987).

Channel and hydrologic stability, substrate, cover, temperature, and the presence of migration corridors consistently appear to influence bull trout distribution or abundance (Allan 1980; Fraley and Graham 1981; Leathe and Enk 1985; Oliver 1979; Thurow 1987; Ziller 1992). Although observed relationships do not demonstrate habitat requirements, they do suggest

habitat characteristics that may be particularly important to maintaining strong populations.

Channel Stability—Young bull trout are closely associated with stream channel substrates. Incubation occurs over a prolonged period through the winter. Juvenile fish are found in close association with the bottom of the channel, often using substrate for cover (Fraley and Shepard 1989; Oliver 1979; Pratt 1984; Shepard and others 1984b). The association with substrate appears more important for bull trout than for other species (Nakano and others 1992; Pratt 1984).

The extended tie to substrate and the presence of embryos and alevins in substrate during winter and spring suggests that highly variable stream flows, bed load movements, and channel instability will influence the survival of young bull trout (Goetz 1989; Weaver 1985). The embryos and young of fish that

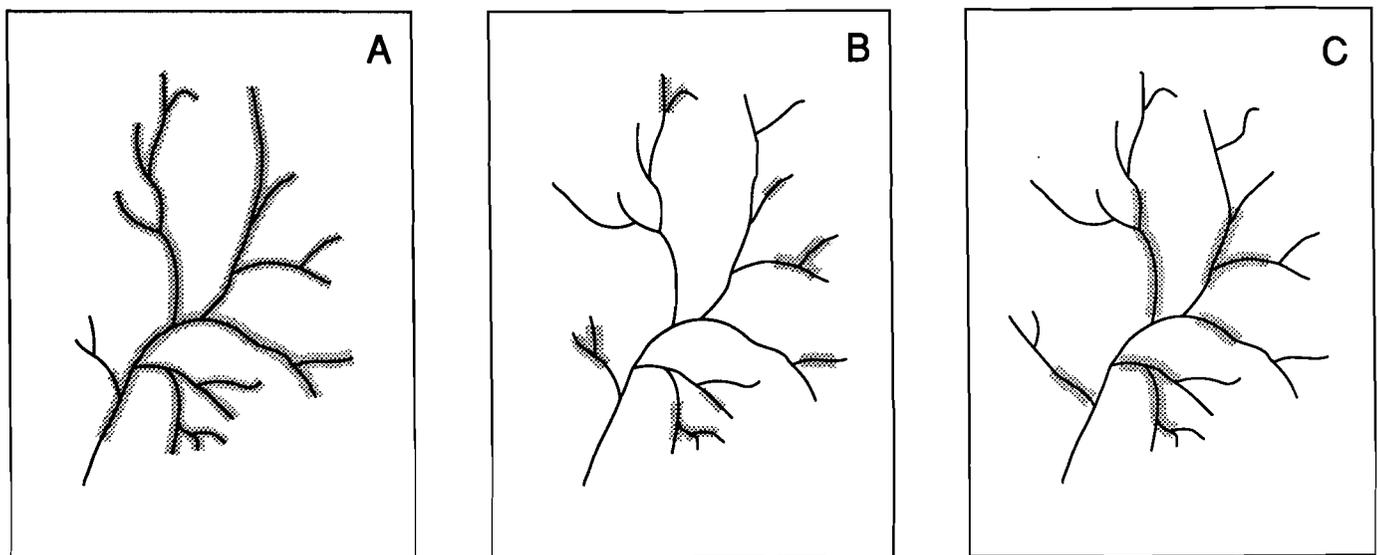


Figure 3—Distributions of resident and juvenile migratory bull trout and cutthroat trout in a hypothetical drainage. (A) The distribution of resident and juvenile migratory cutthroat trout. (B) The distribution of resident bull trout in the absence of a migratory population. (C) represents the distribution of juvenile migratory bull trout. The distributions were generalized by the authors based on descriptions of habitat use in the available literature.

spawn in the fall are particularly vulnerable to flooding and scouring during winter and early spring (Elwood and Waters 1969; Seegrist and Gard 1972; Wickett 1958) and to low winter flows or freezing within the substrate. Murphy and others (1986) found population densities of *S. malma* in winter were directly related to channel stability. In the Belt geologies that typify much of the area where bull trout are distributed in northern Idaho and western Montana, stream channels in managed watersheds often exhibit high bed load movement, scour, aggradation, and relatively low diversity in substrates (Kappesser 1992). Rain-on-snow events that lead to flooding may present particular problems in some basins. We anticipate that low habitat complexity, the frequency of bed load scour, and the frequency of low flows will be aggravated by watershed disruption and problems of channel instability in many bull trout streams.

We expect stable channels and relatively stable stream flows to favor the persistence of bull trout populations. Frequent disruption in unstable streams will increase the variations in survival and increase the risk of extinction for local populations (Horowitz 1978; Poff and Ward 1989, 1990; Schlosser 1982). We found unusually high variation in bull trout redd numbers in some streams in Idaho's Pend Oreille basin that have low channel stability and frequent winter floods (see following section on stochastic risks). High bed load movement and low channel stability are also associated with low numbers of bull trout in the Coeur d'Alene River drainage and some tributaries to the St. Joe River (Cross 1992).

Substrate Composition—Increased sediments reduce pool depth, alter substrate composition, reduce interstitial space, and cause channels to braid (Beschta and Platts 1986; Clifton 1989; Everest and others 1987; Lisle 1982; Megahan and others 1980). Initial work on the influence of fine sediments (Shepard and others 1984a; Weaver and White 1985) suggested that incubating bull trout embryos tolerated fine sediments (less than 6.35 millimeters) better than cutthroat trout, steelhead trout, and brook trout. Their tolerance appeared similar to that of chinook salmon (Hausle and Coble 1976; Irving and Bjornn 1984; Tappel and Bjornn 1983). More recent work (Weaver and Fraley 1991), however, indicated that any increase in fine sediments reduces survival. Others have found that when the percent of fine sediments in the substrate was higher, rearing bull trout were also less abundant (Leathe and Enk 1985; McPhail and Murray 1979; Shepard and others 1984a; Weaver and Fraley 1991). Success of embryo survival, fry emergence, and overwinter survival are considered important mechanisms in the observed relationships (Pratt 1984; Weaver and Fraley 1991).

Spawners may also "select" sites where the substrate is not highly compacted (Graham and others 1981; McPhail and Murray 1979).

It is difficult to predict how much a particular change in substrate composition will affect survival for any salmonid (Chapman 1988; Everest and others 1987; Weaver and Fraley 1991). Some substrates are more likely to accumulate fines than others, and some populations probably are more sensitive than others. In the absence of detailed local information on population habitat dynamics, any increase in the proportion of fines in substrates should be considered a risk to productivity of an environment and to the persistence of associated bull trout populations.

Cover—Bull trout usually associate with complex forms of cover and with pools. Juveniles live close to in-channel wood, substrate, or undercut banks (Goetz 1991; Pratt 1984, 1992). Young-of-the-year bull trout use side channels, stream margins, and other areas of low velocity. Older fish use pools (Hoelscher and Bjornn 1989; Pratt 1984) and areas with large or complex woody debris and undercut banks (Graham and others 1981; Oliver 1979; Pratt 1985; Shepard and others 1984b). Woody debris correlated significantly with densities of bull trout sampled in streams in the Bitterroot National Forest (Clancy 1992). Densities of salmonids including bull trout in Flathead River tributaries were best predicted by models that incorporated cover as an independent variable (Fraley and Graham 1981). Population density of *S. malma* declined with the loss of woody debris after clearcutting (Bryant 1983; Cardinal 1980; Heifetz and others 1986; Murphy and others 1986) or with removal of logging debris (Dolloff 1986; Elliott 1986). Cover is important in winter and is thought to limit many fish populations (Chapman 1966; Cunjak and Power 1986). Cover clearly influences population density and overwinter survival of brook trout (Boussu 1954; Hunt 1976; Saunders and Smith 1962).

Although in-stream wood correlates with the distribution and abundance of bull trout, habitat complexity in any form can be important (Mullan and others 1992). Gold Creek, a tributary to Lake Pend Oreille, supports some of the highest numbers of spawning and rearing bull trout in the basin. Gold Creek has little woody debris, but has a lot of cover in pocket pools formed by boulders and large rubble (authors' observation).

We believe that strong bull trout populations will require high stream channel complexity. Channel complexity provides cover and contributes to the growth, survival, and stability of other salmonid populations as well. We cannot, however, quantify the amount of cover needed to maintain a strong bull trout population. Although estimates of cover were useful in a model of trout density in the Flathead

River basin (Fraley and Graham 1981), such models rarely work well when applied outside the range of the original data (Fausch and others 1988). Models with sufficient generality to predict bull trout production or abundance in relation to habitat condition are not available. Attempts to quantify habitat preference, availability, and limiting characteristics could improve understanding of habitat productivity (for example, Moore and Gregory 1988a,b); but it will remain difficult to predict the influence of habitat on population stability and resilience.

Temperature—Temperatures in excess of about 15 °C are thought to limit bull trout distribution (Allan 1980; Brown 1992; Fraley and Shepard 1989; Goetz 1991; Oliver 1979; Pratt 1985; Ratliff 1992; Shepard and others 1984b). Goetz (1989) believed that optimum temperatures for rearing were about 7 to 8 °C. Others suggested that bull trout grew more quickly in cold waters than in warm waters (McPhail and Murray 1979; Pratt 1984; Shepard and others 1984b). Mullan and others (1992), however, found that bull trout growth declined with increasing elevation and, presumably, declining temperature. Spawning areas often are near springs (Allan 1980; Ratliff 1992; Shepard and others 1984) and often are in the coldest streams in the basin. Optimum temperatures for incubation are between 2 and 4 °C (McPhail and Murray 1979).

Researchers recognized temperature more consistently than any other factor influencing bull trout distribution. The evidence is mostly correlative, however, leaving critical thresholds poorly defined. We do not know, for example, whether the influence of temperature is consistent throughout life or whether a particular stage is especially sensitive. Useful experimental work would define the energetic efficiencies and performance of bull trout in relation to other species. Efforts that describe broad-scale distributions of bull trout in relation to normal variation in water temperature will improve predictions of temperature limits or of the responses of bull trout to temperature changes in altered environments. Even though we do not have such information, we must conclude that temperature represents a critical habitat characteristic. Increased temperature can limit the distribution of other char (Meisner 1990a,b) and likely will exacerbate fragmentation of bull trout populations. Temperature changes also increase the risks of invasion by other species that may displace bull trout (Mullan and others 1992).

Migratory Corridors—Migratory corridors tie safe wintering areas to summering or foraging areas. Movement is also undoubtedly important to the persistence and interaction of local populations within the metapopulation. Gene flow, refounding of locally extinct populations, and support of locally weak

populations require open corridors among populations. Migratory populations of fish are likely to stray more between streams than resident populations, increasing the potential for such dispersal. Disruption of migratory corridors will increase stress, reduce growth and survival, and possibly lead to the loss of the migratory life-history types. Resident stocks live upstream from natural barriers and an increasing number of barriers caused by human activities. Because these stocks are sometimes isolated in marginal or extreme habitats, they will be at increased risk of extinction (Horowitz 1978).

Summary

Bull trout have complex life histories. Because diversity represents an important mechanism leading to the persistence of a species in a variable environment, maintaining diversity is important to bull trout conservation. The distribution and abundance of bull trout correlate with a variety of habitat characteristics. The patchy distribution of bull trout in relation to other species suggests that bull trout have relatively specific habitat requirements; populations are likely prone to habitat disruption and fragmentation. Five habitat characteristics are particularly important for bull trout: channel stability, substrate composition, cover, temperature, and migratory corridors. We could not define clear limits or thresholds in habitat condition that directly control the distribution and abundance of the species. New work defining the spatial and temporal variation in the most important habitat characteristics for bull trout will help identify such requirements. More rigorous attempts are needed to describe the range of variability in available habitat conditions tolerated by persistent populations. In the absence of new information, managers must consider any disruption in important habitat characteristics a threat to the persistence of a bull trout population.

IMPLICATIONS OF HABITAT DISTURBANCE

Human activities can strongly influence habitats for salmonids. Timber harvest and associated activities affect the amount, form, and function of woody debris, the composition of substrate, and the stability and form of channels (Bisson and others 1987; Hicks and others 1991; Sullivan and others 1987). Clearcutting and watershed disruption are linked to increased water yields, bed load movement, more frequent flooding or scour events (Chamberlain and others 1991; King 1989; Sullivan and others 1987), and to channel instability (Kapesser 1992).

The distribution and abundance of bull trout have been associated with patterns of habitat condition

that suggest habitat disruption has directly influenced many populations. Swanson (1992) summarized the presence and absence of bull trout populations in the Bitterroot River basin and found that most remaining populations were in the least-disrupted watersheds. Watershed monitoring in the Idaho Panhandle National Forests has demonstrated a difference in hydrologic response among watersheds depending on the intensity of timber harvest (fig. 4). An estimated 80 to 100 percent of the bed materials may be transported under bank-full flows on heavily harvested watersheds in the Panhandle Forests. Such bed load movement may explain the virtual absence of bull trout in the Coeur d'Alene drainage (Cross 1992).

Edwards and Burns (1986) linked levels of fine sediments in streams to road densities. Weaver and Fraley (1991) and Shepard and others (1984a) linked levels of fine sediment to other management activities disrupting watersheds. Substrate composition and management activities have been repeatedly correlated with estimates of bull trout survival, distribution, and abundance (Leathe and Enk 1985; Shepard and others 1984a; Thurow 1987; Weaver and Fraley 1991). Although there is no direct evidence that alteration of temperature patterns has influenced the persistence or distribution of bull trout, the strong influence of temperature on distribution makes such a response highly likely. Stream temperatures have been altered with changes in the forest canopy and riparian shading, in water yield, and

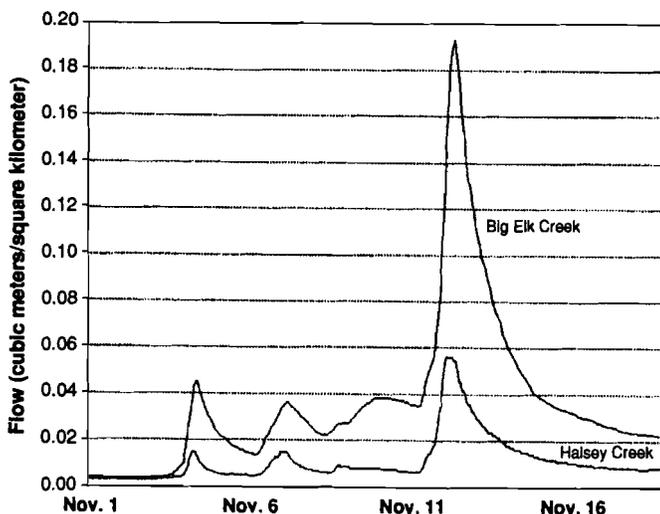


Figure 4—Comparison of relative discharge (cubic meters per square kilometer) following rain-on-snow events in two adjacent drainages in the upper Coeur d'Alene River basin. Halsey Creek had not been entered for at least 50 years. Big Elk Creek had been heavily clearcut in recent years (Kappesser 1992).

in hydrologic patterns (Anderson 1973; Barton and others 1985; Beschta and others 1987; McGurk 1989; Rishel and others 1982). Dams and irrigation diversions that dewater or block streams are common in many interior basins. Migratory bull trout often live above cascades or aggraded channels that block fish at low flows (B. Rieman's personal observations). Channel aggradation and high bed-load movement dewater channels in many streams in northern Idaho. In some streams in the Flathead River basin, dry channels blocked spawning bull trout, leading to year-class failures (Weaver 1991).

Climate change also threatens bull trout populations. Neitzel and others (1991) summarized several models of climate change, concluding that mean air temperatures in the Pacific Northwest may increase by 2 to 3 °C in the next 50 to 100 years. They predicted catastrophic effects for many salmon stocks. Meisner (1990a,b) predicted global warming would restrict the current range of brook trout substantially. Kelehar and Rahel (1992), using a similar approach, predicted that the current range of brook trout in Wyoming would decline by 57 percent if the average summer air temperature warmed 3 °C. They predicted that cutthroat trout distribution would decrease by 65 percent. Given that bull trout require similar or even lower temperatures than brook trout and cutthroat trout, we expect global warming would restrict the range of bull trout similarly or even more severely.

Responses of salmonid populations to habitat alteration have been difficult to quantify (Hicks and others 1991). Most efforts with bull trout have focused on linkages between habitat condition and survival at a specific life stage (Weaver and Fraley 1991; Weaver and White 1985) or on relationships between habitat characteristics and the relative number of individuals (Leathe and Enk 1985). Work with other salmonids has been along similar lines (Hicks and others 1991). Fewer studies have demonstrated population-level responses for any species (Hicks and others 1991). Although we are certain that intensive forest management will degrade bull trout habitats, we cannot predict with any certainty how a specific activity, or the accumulation of activities, will influence the abundance, resilience, or long-term persistence of a population. Managers have used thresholds of acceptable change for stream channel or watershed characteristics (such as percent fine sediments or water yield) to minimize the risk to individual populations. Such thresholds must be used cautiously, however, because some watersheds and populations may be far more sensitive to disruption than others (Hicks and others 1991). In any case, assuring that bull trout populations persist requires more than just maintaining fish in individual streams. The processes of extinction are linked to

the resilience of local populations as well as to the condition, structure, and interaction of populations and habitats at larger scales.

Extinction Risks

Extinctions may occur through a wide variety of causes and through complex interactions of biotic and abiotic processes. Extinctions occur naturally, but the disruption of habitats has likely influenced the frequency and extent of population losses. To consider the risks associated with the effects of management, we characterize the processes of extinction in three general areas: deterministic, stochastic, and genetic (see Gilpin 1987; Gilpin and Soulé 1986; Leigh 1981; Shaffer 1987, 1991).

Deterministic Risks—Deterministic extinction can occur with the permanent or long-term loss or change of a critical component of habitat (Gilpin and Soulé 1986). It occurs through factors that cause birth or survival rates to decline to the point that increases in one of the rates cannot compensate for declines in the other. When population growth is negative, the population simply declines to extinction. Bull trout populations might decline, for example, if pools or woody debris necessary for overwinter habitat are eliminated, or if an increase in fine sediments degrades spawning habitats, increasing mortality of incubating embryos.

The importance of mortality related to fishing, predation, or competition with introduced species may increase sharply when populations decline from other causes. Bull trout may not be displaced by brook trout, for example, unless habitat has been degraded. Peterman and Gatto (1978) and Peterman (1977) consider compensatory effects (mortality increases as numbers decrease) that can be important for many species. Habitat changes as well as management actions (such as fishing regulations or species introductions) may well influence deterministic risks.

The resilience of fish populations depends on differences in growth, mortality, longevity, age at maturity, and reproductive potential (Francis 1986; Rieman and Beamesderfer 1990). Given similar age structures, sex ratios, mortality, and maturation rates, for example, populations with fast individual growth should be more resilient to increased mortality or other stresses related to habitat change than populations with slower growth.

To illustrate, we used simple population simulations with four combinations of growth, longevity, and maturity to describe differences that might exist among populations. In each simulation we varied the survival from egg to age 1 to determine the level of mortality each population could sustain without collapsing. Details of the simulations are in appendix A.

The minimum survival (egg to age 1) to sustain our hypothetical populations ranged from 1 percent under high individual growth to 10 percent under slow growth and late maturity. We assumed a range of survival from emergent fry to age 1 so that our simulations would represent necessary survival from egg to emergent fry. If fry survive to age 1 at rates from 0.2 to 0.4, the minimum egg-to-fry survival to maintain the range of hypothetical populations ranges from 0.03 to 0.05 under fast growth to 0.25 to 0.50 for slow growth (table 2). Results of intergravel survival estimates and habitat surveys indicate that egg-to-fry survival rates of 0.25 to 0.50 may approach the highest values possible in many streams (Weaver 1992; Weaver and Fraley 1991). We would expect survival rates of 0.03 to 0.05 only in severely degraded streams. The results show that life-history patterns can make a big difference in the relative significance of habitat change. A slow-growing resident population may not persist in the face of even modest habitat change, while a migratory or fast-growing stock might remain viable in similar or even worse conditions.

Populations subjected to additional, or cumulative, stresses will be less resilient than those that are not.

Table 2—Simulation results for hypothetical bull trout populations under varied growth and maturation rates. See appendix A for details

Population	Survival necessary to sustain the population		Eggs/spawning female
	Egg to age 1	Egg to fry	
Slow growth late maturity	0.10	0.25 – 0.49	355
Slow growth early maturity	.07	.18 – .36	150
Fast growth late maturity	.01	.03 – .05	3,368
Fast growth early maturity	.01	.03 – .05	1,022

Simply put, habitat disruption that results in lower survival or growth at one stage means less mortality can be sustained at another stage. Because most populations have some compensatory reserve, they can absorb additional mortality, from fishing or predation, for instance. Cumulative mortality related to habitat loss reduces that reserve. Clearly, all populations are not equal in their ability to absorb additional stress, and we are not capable of accurately estimating the differences. Any habitat disruption is likely to represent an important deterministic risk for some component of a bull trout population.

Deterministic processes have probably been the dominant influence in the loss of bull trout populations throughout the range. Declines have occurred over extended periods and have been regional in scope. The associations of distribution and abundance with habitat condition suggest that cumulative effects in habitat disruption have led to an extended loss of suitable habitat. Even if habitat disruption were halted, however, populations would remain fragmented and restricted to small areas. Under those circumstances, processes other than deterministic effects may lead to continued extinctions.

Stochastic Risks—Recent works consider stochastic (random) processes and their relation to extinction. Stochastic processes have been classified as demographic and environmental (Ginzburg and others 1990; Leigh 1981; Shaffer 1987, 1991). Demographic stochasticity includes random variation in birth and death rates, sex ratios, or other demographic characteristics, even though the underlying rates may be stable from one year to the next. Demographic stochasticity may be thought of as the influence of a binomial sampling process with small samples. For example, if underlying mortality is 0.50 but only nine individuals are subjected to that mortality in any year, the number dying will not be 4.5 and might range from 0 to 9. If a population is small enough, random variation among individuals can lead to negative growth in the population long enough for the population to go extinct. Demographic stochasticity has been considered unimportant unless population sizes are very small (for instance, 20 adults) (Leigh 1981; Quinn and Hasting 1987; Shaffer 1987; Shaffer and Samson 1985). Environmental stochasticity includes both chronic and catastrophic effects (Shaffer 1987, 1991). These represent the variation in survival, birth rate, or population size that can be attributed to normal environmental variability (such variables include temperature and stream discharge patterns) and to the frequency of extreme events such as wildfires, floods, or debris torrents. Theoretically, population size and the frequency and magnitude of disturbance (its temporal variation) will determine the probability of extinction for a population in some given period

of time (Dennis and others 1991; Leigh 1981). As a population is restricted in abundance, or as the variation in its birth rate or survival increases, the predicted mean time to extinction will decrease.

Habitat change may influence the amount of environmental variation and a population's sensitivity to that variation. Small populations are expected to vary relatively more than large populations (Gilpin and Soulé 1986). They are likely to experience higher temporal variation, have lower genetic and phenotypic diversity, and have fewer refuges available (Gilpin and Soulé 1986; Saunders and others 1990; Shaffer 1987). Populations in complex habitat are expected to be more stable than populations in simple habitat because they have more refuges from extreme events and greater capacity to buffer the effects of environmental change (Saunders and others 1990; Schlosser 1982, 1991; Sedell and others 1990). There is little empirical evidence that stochastic extinctions play an important role in the current distribution of bull trout. Such processes are well supported in the theoretical literature, however, and are strongly documented in other species. Some of the quantitative approaches to viability analysis may provide clues to the relative importance of such risks to bull trout. We consider the application of one approach in the section on viability.

Genetic Risks—Because nature is unpredictable, conservation of a species depends on protecting its genetic diversity. If diversity is lost, genetic combinations that permit survival in highly variable environments may be lost. Although adaptations to local conditions are difficult to identify, their presence generally is confirmed as data become available (see Hynes and others 1981 and MacLean and Evans 1981). At present, available data do not provide a basis for specifying the minimum amount of genetic diversity that must be maintained to ensure the persistence of bull trout.

The literature is replete with arguments that one cannot define general guidelines for the minimum number of organisms needed to mitigate the effects of genetic stochasticity in a population. Soulé (1987) argued, however, that the scientific community should provide guidance for the public so conservation programs can proceed. He proposed the "50/500" rule in 1980. That is, in a completely closed population, an effective population size of 50 is needed to prevent excessive rates of inbreeding, and 500 are needed to maintain genetic variation. 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 be three-quarters or less of the actual number of individuals (Falconer 1960). Salwasser and Marcot (1986) concluded that effective size is 50 percent of actual size; Nelson and Soulé (1987) concluded that the ratio should be 10 percent

for fish populations, meaning the ratio would be 500/5,000. Lehmkuhl (1984) provides examples of the application of these concepts.

Although the number of organisms that must be maintained to prevent excessive rates of inbreeding in a closed population can be estimated (Franklin 1980; Shaffer 1991), predictions based on data for bull trout (see below) and other species (Shaffer 1987; Stacey and Taper 1992) show that isolated populations are more likely to disappear as a result of environmental and demographic stochasticity than as a result of genetic effects. Because many small populations seem to persist, and because it is difficult to find evidence of the effects of inbreeding in natural populations, immigration (as little as one individual per year) must keep these small populations alive (Stacey and Taper 1992). Several authors (Lande 1988; Shaffer 1987; Stacey and Taper 1992) support the general statement that small, closed populations are jeopardized by environmental or demographic stochasticity before inbreeding or the loss of genetic variation becomes a problem. It seems likely that management prescriptions established to minimize the effects of environmental or demographic stochasticity (for example, multiple populations with open migratory corridors) will at the same time minimize genetic risks.

The processes of extinction do not operate independently. Loss of genetic diversity, for example, may reduce fitness and increase sensitivity to environmental variation. Habitat changes that eliminate or isolate segments of populations may increase the population's susceptibility to stochastic processes because the number of individuals will be smaller and the population will be less diverse in structure or distribution. Those same habitat changes might increase mortality or isolate the population in less productive habitat, leading to increased deterministic risk as well.

Viability

Fragmentation and isolation of bull trout populations or subpopulations has occurred through habitat changes caused by human activities. Overfishing and competition by introduced species of fish have restricted the distribution of bull trout to a small portion of the original range. Habitats have been degraded and lost. The original populations have been restricted in the number of individuals they contain, their resilience, and in their proximity to or connection with other populations. As a result, some populations are extinct and the risk of extinction for many of the remaining populations has increased.

Population viability analyses attempt to quantify the risks of extinction through stochastic and deterministic processes (Shaffer 1991). Two general approaches, one based in population simulation

(Ferson and Akcakaya 1988) and the other based in analytical projections of population trends (Dennis and others 1991), have been used. The first requires extensive information or assumptions on demographics unavailable for most bull trout populations. The second requires data on time series (a sequence of years) of abundance.

Data from long-term monitoring of bull trout spawning escapements or redd numbers are useful in the second approach. Annual bull trout redd counts are available for tributaries to Flathead and Swan Lakes in Montana (Weaver 1992) and Lake Pend Oreille in Idaho (Nelson and others 1992). Counts of adult fluvial bull trout are also available from a salmon collection weir on Rapid River, tributary to the Little Salmon River in Idaho (Schill 1992). We used these data to estimate the instantaneous rates of change, variances in those rates, and the expected probabilities of persistence for individual populations as described by Dennis and others (1991). Details of the analyses are in appendix B. Annual bull trout redd counts are in appendix C.

We found a wide range in the estimated variances for rates of change among populations. Streams with fewer redds on average varied the most (fig. 5, table 3). The data support the general observation that small populations vary more than large populations.

Habitat condition may also influence stability. We found exceptionally high variances for some streams from the Pend Oreille basin (table 3, fig. 5). Those

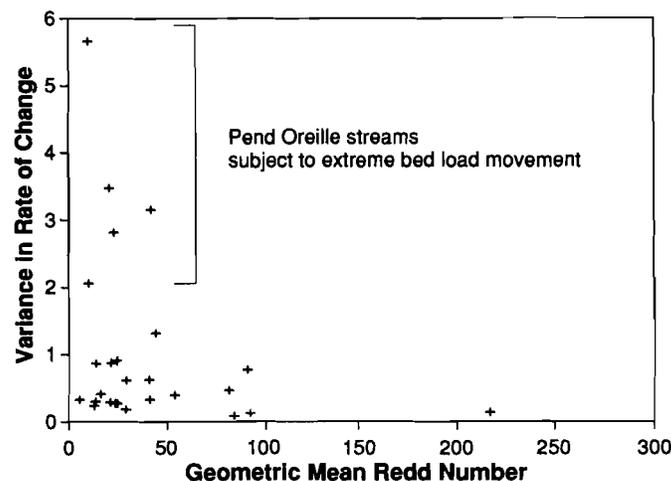


Figure 5—Relation of estimated variance in the infinitesimal rate of change and geometric mean number of redds for bull trout populations monitored in the Flathead, Swan, Metolius, and Pend Oreille River basins and in the Rapid River. All streams with fewer than 5 years of monitoring were excluded. Estimated variances are for annual redd numbers. Influential observations were not removed for this analysis.

Table 3—Estimated mean (μ), variance ($\hat{\sigma}^2$), and their 95 percent confidence intervals (CI) for instantaneous rates of change in redd numbers monitored in Idaho and Montana. See appendix B for methods

River basin Stream	Years obs.	Annual redd count					Two-year moving sum						
		Mean number redds	$\hat{\sigma}^2$	CI $\hat{\sigma}^2$	μ	CI μ \pm	Mean number redds	$\hat{\sigma}^2$	CI $\hat{\sigma}^2$	μ	CI μ \pm		
North Fork													
Flathead (MT)													
Big	14	18	0.25	0.14	- 0.55	0.04	0.27	37	0.12	0.07	- 0.26	0.02	0.03
Coal	14	34	.57	.33	- 1.26	-.13	.41	77	.12	.07	- .25	-.04	.03
Whale	14	88	.43	.25	- .94	-.08	.36	206	.21	.11	- .42	-.01	.04
Trail	14	47	.29	.16	- .63	-.02	.29	99	.16	.08	- .32	-.02	.03
Middle Fork													
Flathead (MT)													
Morrison	14	46	.58	.33	- 1.27	-.03	.42	104	.05	.03	- .11	-.04	.02
Granite	14	25	.25	.14	- .54	.01	.27	54	.04	.02	- .09	-.02	.02
Lodgepole	14	20	.36	.20	- .79	¹ -.07	.33	42	.15	.08	- .30	-.06	.03
Ole	13	28	.24	.13	- .54	-.01	.28	60	.12	.06	- .25	<.01	.03
Swan River (MT)													
Elk ²	11	98	.25	.15	- .69	.09	.06	210	.28	.14	- .65	.07	.06
Goat	11	34	.14	.07	- .35	¹ -.07	.23	71	.03	.01	- .06	-.05	.02
Squeezer	11	50	1.25	.68	- 3.18	.10	.71	110	.13	.06	- .29	.09	.04
Lion ²	11	59	.18	.09	- .41	.36	.05	120	.07	.03	- .16	.06	.03
Pend Oreille (ID)													
East Fork	9	47	3.08	1.53	- 9.95	-.19	1.33	108	.52	.26	- 1.71	-.22	.10
Johnson	10	18	.81	.43	- 2.19	.02	.60	40	.37	.17	- .89	-.01	.08
Trestle	10	225	.12	.06	- .32	¹ -.08	.23	460	.02	.01	- .06	-.05	.02
Grouse ²	10	28	.87	.41	- 2.09	.24	.12	83	.17	.08	- .42	-.10	.05
North Gold ²	10	29	.35	.17	- .85	.10	.10	65	.09	.04	- .22	.05	.04
Gold ²	10	99	.04	.02	- .10	¹ -.04	.03	199	.04	.02	- .10	.03	.03
Salmon (ID)													
Rapid River ³	19	97	.27	.18	- .61	.05	.03	201	.14	.09	- .10	.02	.02

¹Significant ($P \leq 0.10$) declining trends in redd count detected by significant negative rank correlation with year.

²A single transition was eliminated as an influential observation for analyses based on annual redd counts.

³Rapid River data represent counts of fish across a weir. We assumed a 1:1 sex ratio and one redd per female to approximate the mean number of redds in the spawning escapement.

streams are among the most unstable in the Pend Oreille system, with very high bed load movement and frequent floods (Cross 1992).

Estimated probabilities of persistence for individual populations varied with the mean size of the population (redd number), our method for estimating variance in rates of change, and the threshold of extinction (table 4). In general, the variance strongly influenced estimated probabilities at all levels (fig. 6). Increases in redd abundance, however, had a progressively smaller influence on persistence. The estimated probability that any of the monitored bull trout populations will persist for 100 years ranged from less than 0.10 to more than 0.95 among the sampled populations (table 4). In any case, few exceeded 0.95.

We found less information for estimating persistence probabilities for resident bull trout populations. Only three sets of annual population estimates could be used to approximate the variance in the instantaneous rates of change (table 5). We

found no estimates of total population size for resident populations. We used density estimates from tributaries to the Bitterroot River to approximate a likely range of numbers for individual streams (Clancy 1992). We estimated that total populations (excluding age 0 fish) probably range from a few hundred to about 8,000 individuals. These results also show that isolated resident populations cannot be expected to persist indefinitely (fig. 7).

Viability analyses for other salmonids are limited, but supportive. Nagel (1991) inferred from simulations that small, isolated populations of brook trout in Appalachian streams had less than a 50 percent chance of persisting for 30 years. Elliott (1986) found a substantial increase in annual variation of Dolly Varden numbers when debris that served as cover was removed from an Alaskan stream. We used Elliott's data to calculate variances in instantaneous rates of change of 0.09 before and 0.98 after debris removal. We calculated that probabilities of persistence for the Dolly Varden populations represented

Table 4—Estimated probabilities of persistence for bull trout populations monitored in Idaho and Montana. We alternately assumed μ = the estimate or 0, an extinction threshold of 1 or 10 redds, and a variance based on annual counts or 2-year sums. See appendix B for methods

River basin Stream	Annual redd count				Two-year moving sum			
	$\mu = 0$		$\mu = \text{estimate}$		$\mu = 0$		$\mu = \text{estimate}$	
	Threshold		Threshold		Threshold		Threshold	
	10	1	10	1	10	1	10	1
North Fork								
Flathead (MT)								
Big	0.094	0.437	0.197	0.683	0.291	0.698	0.449	0.845
Coal	.129	.360	.010	.033	.444	.793	.128	.395
Whale	.260	.505	.052	.145	.491	.757	.432	.703
Trail	.226	.526	.151	.399	.434	.751	.278	.585
Middle Fork								
Flathead (MT)								
Morrison	.159	.385	.100	.268	.706	>.950	.132	.520
Granite	.137	.480	.167	.547	.601	>.950	.261	.767
Lodgepole	.092	.382	.016	.099	.289	.666	.033	.161
Ole	.166	.504	.133	.435	.395	.765	.413	.780
Swan River (MT)								
Elk	.352	.641	.812	.950	.435	.689	.803	.947
Goat	.256	.655	.014	.093	.744	>.950	.037	.370
Squeezer	.114	.274	.253	.515	.494	.811	>.950	>.950
Lion	.324	.664	.655	.923	.653	>.950	>.950	>.950
Pend Oreille (ID)								
East Fork	.069	.174	.014	.039	.259	.484	.001	.002
Johnson	.259	.252	.067	.307	.180	.456	.151	.402
Trestle	.632	.891	.037	.154	>.950	>.950	.196	.795
Grouse	.088	.279	.434	.841	.392	.717	.009	.050
North Gold	.143	.431	.461	.861	.467	.841	.883	>.950
Gold	.750	.950	.116	.532	.872	>.950	.376	.829
Salmon (ID)								
Rapid River	.338	.622	.617	>.950	.578	.849	.742	.933

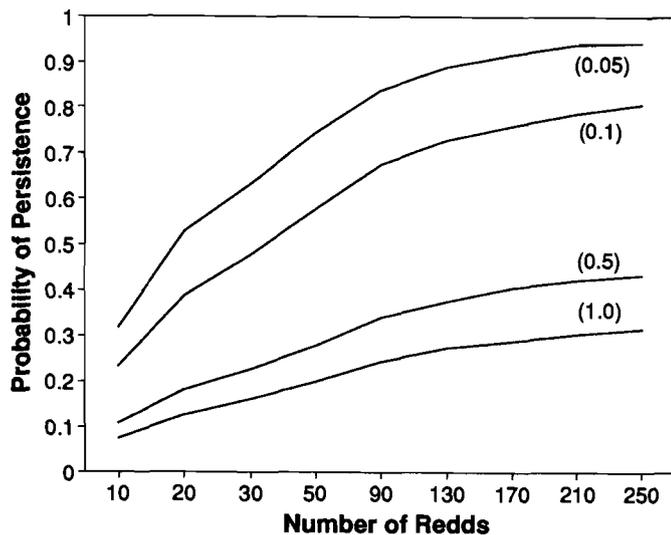


Figure 6—Relation of estimated probabilities of persistence for 100 years for migratory bull trout populations with a range of initial redd numbers and constant variances in infinitesimal rates of change. We calculated probabilities after Dennis and others (1991). We assumed all populations to vary around an equilibrium ($\mu = 0$), and arbitrarily set the threshold for persistence at four redds (see appendix B). Variances are shown in parentheses.

in Elliott's (1986) data declined from about 0.70-0.80 to 0.25-0.30 with the increased variability.

Our results indicate that stochastic extinction risks can be important for bull trout and other salmonids, and that habitat condition influences those risks. If habitat loss results in smaller population size, the probability of extinction will increase, particularly if there are substantially less than 100 redds or 2,000 total individuals (figs. 6, 7). Habitat changes that increase temporal variation will have a similar effect.

Our results also demonstrate the potential significance of deterministic risks. Our general calculations of persistence (figs. 6, 7) assumed populations varied around some equilibrium (the populations

were not declining over the long term). In other words, we assumed that stochastic rather than deterministic processes influenced the likelihood of extinction for individual populations. That almost certainly is not true, particularly where some habitat disruption has occurred. Several estimates of growth rates (μ) from the redd count data were negative (table 4). The data indicate declining trends in some populations, but the limited precision of the estimates makes it difficult to conclude that the declines are real. If population trends are negative, local extinction will occur unless the trend is reversed. We calculated probabilities of persistence for 100 years for each monitored population, using both the estimated mean growth rate and an assumed rate of 0 (the rate for a stable population) (table 4). Probability of persistence was always much lower when the estimated mean growth rates were negative. Although it is important to minimize variability and maximize population size to ensure persistence, such efforts are irrelevant if the population is in a long-term and irreversible decline. The first step in any attempt to conserve populations must be to minimize the risks of deterministic extinction.

There are no established criteria for determining the viability of an isolated population (Shaffer 1991). Probabilities of persistence represent relative levels of risk, and acceptable probabilities will differ among interested parties. A 95 percent probability of persisting for 100 years has been suggested as a goal consistent with management and planning activities, but more conservative goals (99 percent for 150 years or 95 percent for 1,000 years) have been proposed. Whether declining or not, few, if any, of the monitored bull trout populations would meet even the less restrictive criteria in isolation from other populations.

Our analyses are only first approximations. The theory and methods for estimating extinction risks are new and continually evolving. The results of analytic estimates differ from more complex simulations that attempt to incorporate density dependence, complex life-history strategies, and dispersal among populations (Ginzburg and others 1990; Shaffer 1991; Stacey and Taper 1992). Any approach

Table 5—Estimated mean (μ) and variance ($\hat{\sigma}^2$) of infinitesimal rates of change for bull trout populations monitored through total population estimates in Idaho and Montana. We calculated estimates after Dennis and others (1991)

Stream	Years in sample	μ	$\hat{\sigma}^2$	Source
South Fork Salmon (ID)	11	-0.01	0.64	Platts and Nelson 1988
Bear Valley (ID)	5	.22	2.15	Platts and Nelson 1988
Bitterroot River (MT) ¹	8	—	.52	Clancy 1992

¹Transitions from population estimates in several streams were pooled as independent observations from a single system.

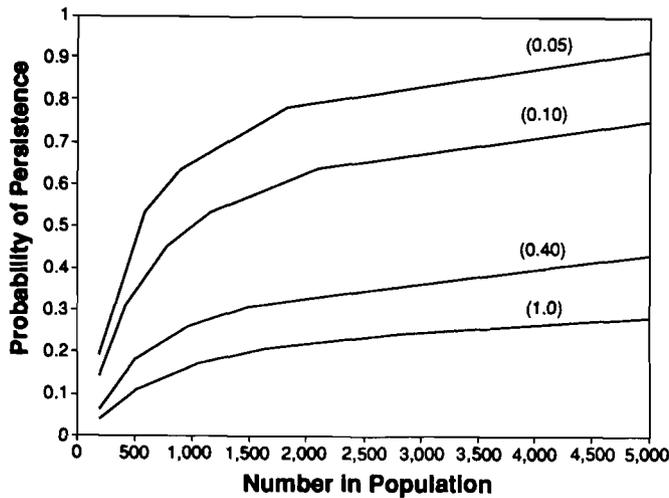


Figure 7—Relation of estimated probabilities of persistence for 100 years for resident bull trout populations with varied number of individuals (age 1 and older) and constant variances in the infinitesimal rates of change. We calculated probabilities after Dennis and others (1991). We assumed all populations to be stable ($\mu = 0$), and set the threshold for persistence at 120 individuals (see appendix B). Variances are shown in parentheses.

is limited by the quality and the amount of data available to fit or parameterize the models. Confidence intervals associated with the model parameters were generally large (table 3). The estimates are also based on theoretical models with little empirical support. Clearly, some populations of bull trout above geologic barriers (Thurow 1987) have persisted for long periods. Are these populations more resistant to extinction than suggested by the models or are the patterns of the presence and absence of bull trout over the historic range consistent with the hypotheses of local extinction and refounding? Our estimates of risk may underestimate the probability of persistence because the approach does not account for density dependence, refounding by adjacent populations or by overlapping generations, or because variances are overestimated due to sampling errors (Brown 1992). Alternatively, our estimates may be optimistic because variances are underestimated over the relatively short time period of observations (Pimm and Redfearn 1988). We also cannot estimate long-term risks associated with deterministic threats or catastrophic events. Better estimates of risk will require more detailed information on population dynamics, on the temporal and spatial variation in disturbance, on linkages between disturbance and population responses, and on mechanisms and rates of dispersal among populations. Empirical estimates of extinction rates and better descriptions of population distributions in

highly variable or disrupted environments will also be necessary to test model predictions.

Despite the obvious limitations, our results are useful for considering the nature of extinction risks for isolated populations of bull trout. The limited precision in parameter estimates is mitigated, for example, by the replication of observations across populations. Although the risks associated with any isolated population are poorly defined, the estimated variances for most populations probably will not fall far outside the range of our observations. The available data indicate that many isolated populations face serious risks of extinction, even with no further loss of habitat.

Role of the Metapopulation

The characteristics of bull trout populations are consistent with the metapopulation concept. Local populations are found in individual streams and are at least partially isolated there. For most species, the risk of extinction through any process increases with the loss of diversity represented by the loss or isolation of local populations (Gilpin 1987; Shaffer 1987). The presence of several subpopulations increases the probability that at least one will survive periods of disturbance. Metapopulations will protect the genetic variation available for adaptation to change. In metapopulations, some local populations are more stable or robust than others. Local extinctions may be common. Some subpopulations may act as "sources" and others as "sinks," switching roles at different times (Pulliam 1988; Stacey and Taper 1992). All can contribute, however, to the diversity (Poff and Ward 1990), stability, and persistence of the whole. If the temporal variation in the size of individual populations is high, long-term persistence of the metapopulation requires dispersal among local populations (Fahrig 1990; Stacy and Taper 1992). An isolated population has little chance of being refounded after a local extinction compared to a subpopulation close to other subpopulations. As populations become isolated, local extinctions become permanent; the entire metapopulation moves incrementally toward extinction.

Akcakaya and Ferson (1992) demonstrate metapopulation dynamics (correlation and dispersal) with a generalized simulation model. Their examples compare the extinction risk for a hypothetical population with a carrying capacity of 100 individuals to five populations, each with a carrying capacity of 20 individuals (table 6). Other examples demonstrate the influence of habitat degradation and migration of individuals between populations. The risk of losing a population increased nearly twofold when the total carrying capacity of the population was degraded just 3 percent a year for 30 years.

Table 6—Risk of extinction for a series of hypothetical populations¹ during 30 years (time steps) as predicted from simulation modeling (Akçakaya and Ferson 1992)

	Mixing	Environmental differences	Extinction risk ²
			Percent
Single population (100 individuals)	—	—	18
Single population (100 individuals) Reduce carrying capacity by 3 percent per time step	—	—	30
Five populations (20 individuals each)	none	correlated	36
	none	independent	24
	moderate	correlated	22
	moderate	independent	5
	full (density dependent)	independent	1

¹Population growth rate was 1.2 with standard deviation = 0.5 in all examples. Demographic stochasticity was assumed with survival = 0.5.

²Risk is represented as the percent of simulated populations going extinct within the 30-year period.

There was a small chance that a group of five populations residing in independent environments and exchanging individuals would go extinct in the 30 years. The chance increased fivefold when migrants were restricted to low numbers between any two populations, and increased 24-fold if there were no immigration. The examples also showed that even with moderate amounts of immigration, the risk of extinction was less than one-fourth as high in independent (uncorrelated) environments as in correlated environments. These examples support the notion that “spreading the risk” among the components of a metapopulation is a cornerstone of conservation management.

Our viability analyses further support the conclusion that regional persistence of bull trout depends on the maintenance of multiple local populations. For example, if populations are completely independent (uncorrelated variation through time and no re-founding), the probability of at least one population persisting can be calculated directly from the number of subpopulations and their probabilities of persistence (fig. 8). If the individual subpopulations are similar to those considered above (fewer than 50 redds and variances less than 0.20) five to 10 subpopulations are necessary to ensure persistence for 100 years. The number needed increases rapidly, however, with fewer redds in each population and with increasing variance.

Except for some populations upstream from migration barriers, it is unlikely that most local populations are actually independent of others as we have assumed. If climatic events drive temporal variation, populations close to each other are likely to vary

together. Nearby populations also are likely to exchange individuals and therefore support or refound each other. Theory indicates that the tradeoffs between the drawbacks associated with correlation and dispersal among subpopulations strongly

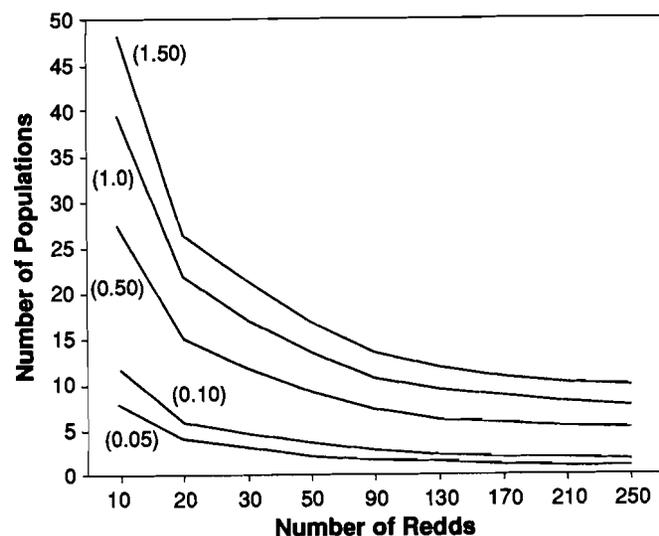


Figure 8—Estimated number of populations necessary to ensure a 0.95 probability of persistence for 100 years for at least one population with a varied number of redds in each population and constant variances in the infinitesimal rates of change. We assumed all populations to have equal initial size and variance and to be completely independent (see appendix B). Variances are shown in parentheses.

influence the dynamics and persistence of metapopulations (Doak and others 1992; Fahrig 1990; Gilpin 1987; Hanski 1991; Harrison and Quinn 1989). Populations that are too close together are likely to decline together in response to the same environmental change, while those too far apart will fail to refound or support each other. The influence of management on the spatial distribution of populations, therefore, is an important concern. Loss of habitats increases the distance among populations. Populations in small or altered habitats are also likely to be more sensitive to environmental changes (Saunders and others 1990), so bull trout populations in managed watersheds might be more highly correlated. We know little about temporal and spatial patterns in bull trout populations or about rates of dispersal. Research in these areas is necessary to understand the optimum distribution of habitats and populations.

We know little about metapopulation structure in bull trout, but the importance of such processes to regional persistence is well supported by theory and by observations in other species. The connections and interactions among local populations, important

to both regional and local persistence, are likely to be disrupted or otherwise influenced by management (fig. 9). The risks of local extinction, through both deterministic and stochastic effects, may be partially addressed through management actions at the stream or small watershed scale. Long-term persistence of bull trout, however, will require conservation planning and management at the large watershed or river basin scale.

Summary

Fragmentation and disruption of bull trout habitats will increasingly isolate populations and isolate or eliminate life-history forms. Fragmentation and disruption of habitats will reduce survival, growth, and resilience of individual populations and increase variation in their sizes. Those effects will increase the risk of extinction. Bull trout conservation is a problem of maintaining an appropriate number, size, and distribution of self-sustaining populations. The level of acceptable habitat disruption depends on the characteristics of the populations and their habitats. The necessary number and size of populations

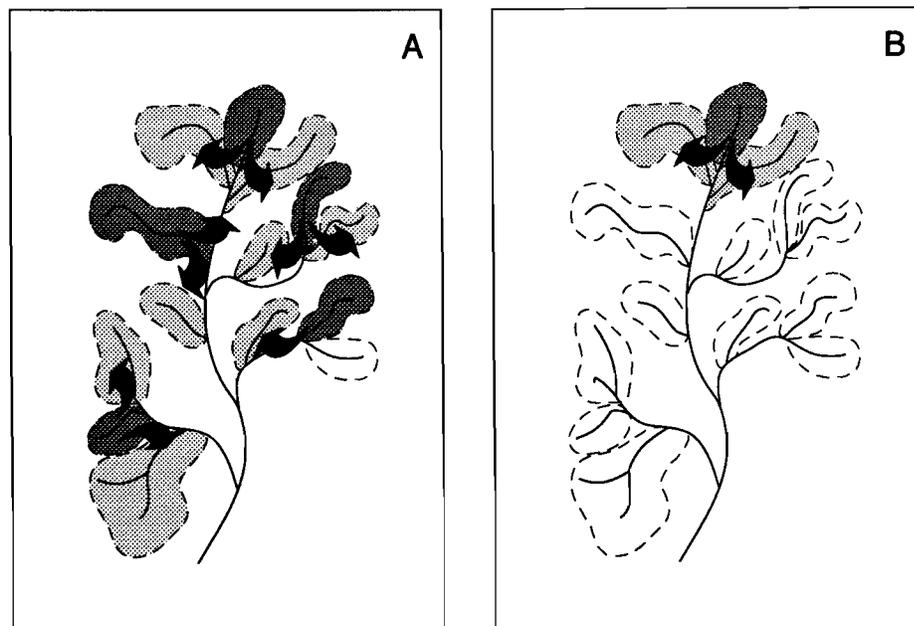


Figure 9—Schematic of a metapopulation with subpopulations associated with individual watersheds. The dark shading represents higher quality habitat and stronger populations that provide surplus production and dispersing individual bull trout. The light shading represents lower quality habitat that still supports populations, but with little dispersal to other populations. The unshaded areas represent still lower quality habitat where populations have not persisted. (A) represents a system where high-quality habitats have been maintained throughout the basin. (B) represents a system where most high-quality habitats have been lost in a fashion that may be typical with forest management.

depends on the stability or variation in each of the populations. The appropriate distribution depends on the level of correlation among populations and on the rates of dispersal from one population to another.

The present analysis provides first approximations of the risks associated with disruption of bull trout populations. The results are necessarily generalized. Better estimates for individual populations should be possible with more detailed and specific information on life-history and demographic characteristics, and on dispersal rates, but realistically, such information will be unavailable for most populations. In the absence of better information, we do not expect many populations to persist in isolation. If any population declines, the probability of extinction will increase. Risks may increase greatly where migratory populations include fewer than 50 to 100 redds, or where resident populations include fewer than 1,000 to 2,000 bull trout that are yearlings or older. Without better information on dispersal rates and the distances over which refounding and gene flow can be expected in biologically important time scales (one generation, for instance), managers should act conservatively. We must assume that subpopulations will tend to be more strongly correlated with habitat disruption as the distance between populations declines or the magnitude of disturbance increases. We must assume that dispersal among populations occurs slowly and declines as distances between populations increase. To ensure conservation of bull trout populations, it will be necessary to maintain multiple subpopulations of relatively large size and low temporal variation. It is also critical to minimize risks of long-term declines and deterministic extinction caused by cumulative reductions in survival or growth.

CONCLUSIONS

Stream channel stability, habitat complexity, substrate composition, temperature, and migratory corridors can influence the stability, growth, and survival of bull trout populations. Other factors may limit or influence populations, but these five appear most prominently in the available information. However, no thresholds in these or any other habitat characteristics can be set as clear "tolerance" limits for the maintenance of populations. Effects of fine sediments are often negative, for example, but it is not possible to precisely define tolerance thresholds. The habitat requirements for any single population may vary with the productivity of the basin, climate, geology, geomorphology, dominant life-history form, competition, predation, or fishing, the effects of which can rarely be predicted. It probably is impossible to identify a minimum habitat condition that will maintain a population. Maintenance, in any case, is an inappropriate goal. Populations will persist in

habitat conditions that are less than pristine. A loss or reduction in quality of critical habitat, however, will compromise the resilience of any population. Such populations will be more vulnerable to new or cumulative stressors and at greater risk in changing environments.

Habitat disruption and fragmentation threaten the diversity, stability, and persistence of bull trout populations. Critical mechanisms that may lead to decline or extinction of populations include elimination or isolation of the different life-history forms, predation, competition, or hybridization with exotic species, and increased temporal or spatial variation within populations and subpopulations. Conservation strategies should consider maintenance or restoration of migratory corridors wherever possible. If populations are declining, deterministic extinction is virtually guaranteed unless factors responsible for the decline are changed.

Conservation of bull trout populations requires maintenance of multiple local populations. Unless research shows otherwise, we must assume that those populations disperse slowly. Complex, high-quality habitats are necessary to minimize the variation in individual populations, to minimize correlation among populations, and to maximize the size of individual populations. Subpopulations should be distributed as evenly and widely as possible to maximize genetic diversity and minimize correlation among subpopulations. Maintaining high-quality habitats throughout the range of bull trout will not guarantee the persistence of healthy populations, but extinctions are certainly more likely otherwise.

A CONSERVATION APPROACH

Stable bull trout populations require high-quality habitat. Large rivers or lakes supporting migratory populations have the highest potential for supporting large, flourishing populations. Systems composed of a few small tributary streams provide less food and fewer areas for rearing and overwintering than do larger, more complex systems. Not only must all habitat requirements be available for bull trout to persist in a system, the population must be sufficiently large, or must be composed of enough subpopulations, to survive catastrophic events, normal environmental variation, and the effects of human activities. Even before human activities became important, the habitat suitability in any system no doubt varied, reflecting successional changes in each stream. The bull trout populations that persisted had the numerical and phenotypic diversity they needed to survive periods when suitable habitat was severely limited and to recolonize areas that recovered or otherwise became available.

The activities of humans have probably increased the homogeneity among landscapes. Management

programs that set thresholds for disturbance of habitats or goals for their restoration may create a collection of habitats and watersheds that cluster around the threshold rather than a complex of habitats that range from extremely productive to unproductive. The strong populations that ensure persistence despite deterministic and stochastic threats may be lost if management programs based on thresholds create a collection of populations of similar, but intermediate, quality that may collectively fail in the face of cumulative stress or catastrophic events.

We believe that successful conservation of bull trout depends on identifying core areas that contain bull trout populations with the demographic characteristics needed to ensure their persistence and with the habitat needed to sustain those characteristics. Bull trout in these core areas are the primary sources for recolonization if other areas fail, so their habitat productivity, life-history diversity, and genetic diversity need to be protected from excessive fishing, abusive land-use practices, and competition with introduced exotic species.

The likelihood that populations and habitats will persist in core areas must be as high as possible. Although risk is difficult to quantify, the characteristics of populations and habitats can be used to consider the relative risk among a collection of populations (table 7). Such assessment should be useful both in identifying the most important populations to incorporate in a conservation area and the relative influence of management actions within that area. In some locations, an area may be identified and actions taken that will ensure a high probability of persistence. In others, areas may have to be incorporated into core areas, even though the likelihood of persistence for local populations living there is less than desired. These units may require more intensive management and monitoring to ensure that their desirable characteristics are protected, enhanced, or restored.

Identifying core areas and developing mechanisms to protect the fish populations and the habitat they rely on is the basic requirement to ensure persistence of bull trout throughout their range. Most bull trout will still be distributed in areas surrounding the sanctuaries provided by the core areas. These populations have been and will be managed in altered habitat that reduces their likelihood of persistence; some populations will be lost. There is a continuing need for creative management that preserves as many of these populations as possible while land is developed for other uses.

As a first step to maintain existing diversity, management should identify and protect those habitats in the best condition with the strongest populations. The second step should be to develop a system of conservation (core) areas that are managed to

maintain or restore the ecological processes necessary for the long-term persistence of bull trout throughout the range. Realistically, biological, physical, and social considerations will constrain the number and distribution of core areas that can be established for bull trout conservation. The biological and physical constraints can be identified from this review and from conservation strategies developed for other populations and communities (Moyle and Sato 1991; Murphy and Noon 1992; Reeves and Sedell 1992; Saunders and others 1990) and the emerging principles of watershed restoration (Frissell 1993; Frissell and others, in preparation). We have identified five criteria that should guide the selection and development of core areas for bull trout conservation:

Core Areas Must Be Selected To Provide All Critical Habitat Elements—Ideally, core areas should meet the needs of migratory and resident forms, although strong migratory populations might limit resident populations. The highest priority areas should also incorporate forage species and other components of the aquatic community and critical elements of their habitats. Although it may be possible to restore populations that are depressed or populations that are absent from historic habitats, existing healthy populations are the best index for identifying potential core areas. Ideally, exotics that pose threats in the form of competition, hybridization, or predation should not dominate systems where managers seek to restore depressed or extirpated bull trout populations.

Core Areas Should Be Selected From the Best Available Habitat or From the Habitat With the Best Opportunity To Be Restored to High Quality—Long-term trends such as climate change should be considered when selecting core areas. Core areas must represent the best habitat to minimize the effects of climatic variation and also to minimize the cumulative effects of deterministic threats such as fishing, predation, competition, and hybridization.

It is not possible to quantify the effects of forest or watershed management on fish populations with certainty. Any habitat disruption represents a risk that may compromise resilience. This does not mean that core areas must be pristine. It does mean that management should not change the quality, complexity, or ecological and hydrologic processes in key watersheds in the core area.

As an example, the core area might consist of a collection of managed and pristine or carefully managed watersheds (see Reeves and Sedell 1992) that remain connected by normal migratory corridors. Even pristine watersheds vary in productivity and habitat condition. Natural variation may be critical

Table 7—Relative risk of extinction for local and regional bull trout populations with a variety of population characteristics

Characteristics of the population	Nature of risk primary (secondary)	Risk' 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 (up to 25-year) 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 throughout a major part of the watershed. Channel simplified, providing little hydraulic complexity in the form of pools or side channels. Population survival and recruitment responds sharply to normal 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 evenly represented in the population.	Adult population less than 500.	Adult population less than 50.	
Growth and 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 consistent with pristine habitat. Population has the resilience to support exploitation or to recover from catastrophic events or overfishing within one to two generations (5 to 10 years). Population is fluctuating around an equilibrium or is 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 the best habitats. The population is reduced in size, but the reduction does not represent a long-term trend.	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).	

Table 7 (Con.)

Characteristics of the population	Nature of risk primary (secondary)	Risk ¹ of local population extinction			
		Low	Moderate	High	Extreme
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 for the species. 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 2,000 fish.

Characteristics of the metapopulation	Nature of risk primary (secondary)	Risk ¹ of regional population extinction			
		Low	Moderate	High	Extreme
Replication	Stochastic (Genetic) (Deterministic)	Multiple (five or more) local populations with at least several thousand fish each. Each of the relevant local populations has a low risk of extinction.	Multiple population, but only one or two of those populations represent most of the fish production in the regional population.		Only a single population or several populations that are very small or that otherwise are at high risk remain.
Synchrony	Stochastic (Deterministic)	Environmental variation is low. Populations are found in high quality, complex habitats. Little evidence exists 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 are likely to respond to the same environmental variation. Frequent flood or drought produces highly variable and unpredictable flows throughout the region.	

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

in maintaining the phenotypic and genetic diversity that provides resilience in the face of extreme environmental variation (see Poff and Ward 1990). As our understanding of natural disturbance grows, it may be possible to manage core areas with some commodity extraction throughout, while still providing a diversity in successional stages that mimics natural processes (Grant and Swanson 1991).

A Core Area Must Provide for Replication of Strong Subpopulations Within Its Boundaries—Existing theory and our analysis suggest that a system of multiple, healthy subpopulations within a population is needed to minimize the risks of extinction. A collection of populations spreads the risk, improving the odds that at least one subpopulation will persist, and provides sources to refound subpopulations after local extinctions or to support less productive subpopulations. The number of subpopulations needed to provide a reasonable probability of persistence depends on circumstances that often are unknown. Important considerations include the amount of normal variation in number, the number of individuals in each subpopulation, the synchrony in variation among subpopulations, and the rate of dispersal among populations. Unless detailed information shows otherwise, a core area should incorporate no fewer than 5 to 10 subpopulations (fig. 10) and conservatively many more. If multiple subpopulations cannot be incorporated, a system should not be eliminated from consideration, but it will require more

careful management. Many resident populations are likely to include few subpopulations. The persistence of such isolated populations will present a challenge for managers.

Components, or local populations, can be characterized as the smallest group of animals that represent a clearly interacting reproductive unit. In the case of migratory stocks, a local population would be consistent with the units in typical redd surveys (Trestle Creek, a tributary to Lake Pend Oreille in Idaho, or Whale Creek, a tributary to the North Fork Flathead River in Montana). Such units are represented by watersheds with areas ranging from 25 to 100 square kilometers. If core areas consider only resident fish, clearly identifiable subpopulations can occur on a smaller scale. Individual streams and watersheds on the order of 5 to 25 square kilometers may support important populations.

Core Areas Should Be Large Enough To Incorporate Genetic and Phenotypic Diversity, but Small Enough To Ensure That the Component Populations Effectively Connect—Dispersal rates should determine the size of core areas. If subpopulations are too close to one another, their responses to environmental changes may be correlated, or they may become vulnerable to the same deterministic threat. If subpopulations are too far apart, they will not refound or support each other and may suffer the long-term consequences of genetic drift or inbreeding. There are few data with

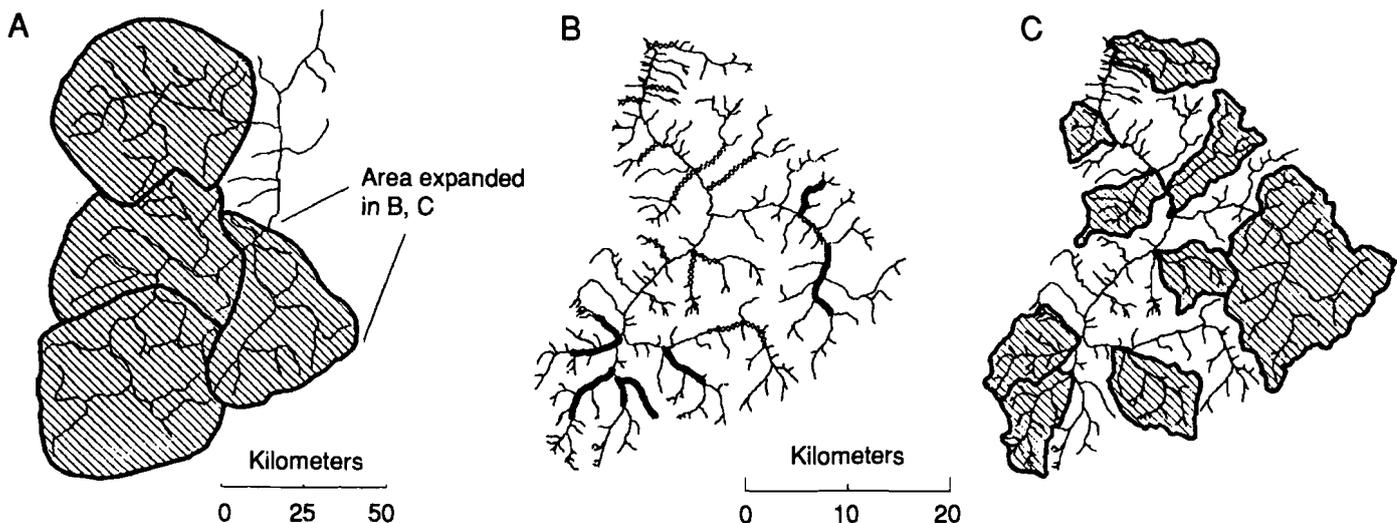


Figure 10—Example of hypothetical core area and watershed selection for conservation management of bull trout. (A) represents a large river basin with subbasins outlined to identify potential core areas for fluvial bull trout. (B) represents an expansion of one subbasin identified as a core area; the continuous lines represent reaches of stream that support relatively strong numbers of spawning and rearing bull trout; the broken dark lines represent reaches or streams with few or no fish that could support more fish if habitat improved or populations from other reaches expanded. (C) represents the watersheds selected for replication of subpopulations.

which the optimum distribution of subpopulations of bull trout can be judged. Thurow (1982) found that just 3.3 percent of the cutthroat trout in tributaries 1 kilometer apart strayed from one tributary to the other during a year. Other migratory salmonids may stray over relative large distances (more than 100 kilometers) (Reisenbichler and others 1992; Simon 1972), but the effective rates of dispersal or re-founding are poorly documented. Reist (1989) found evidence of significant dispersal in Arctic char over distances of 7 to 50 kilometers, but not from 50 to 300 kilometers. In Coeur d'Alene Lake, chinook salmon introduced at a single location effectively pioneered new spawning areas over a range of 30 to 50 kilometers within three generations (B. Rieman's observation). Kokanee have shown similar potential for dispersal when populations are large (B. Rieman's observation and unpublished data). In the absence of information on dispersal rates or local genetic structuring, core areas for migratory bull trout should be small enough that the distances among streams or watersheds supporting key component populations do not exceed 30 to 50 kilometers. The disturbance of local populations within a core area should also be more even than clumped to promote diversity and reduce environmental correlation among subpopulations (fig. 10). For migratory bull trout, core areas should be represented by drainages or basins ranging from about 250 to 2,500 square kilometers. Examples of such core areas should be the Swan River basin or the Lake Pend Oreille basin (excluding the Clark Fork River above Cabinet Gorge Dam). For strictly resident populations, core areas will be much smaller and might consist of adjacent streams.

Core Areas Must Be Distributed Throughout the Historic Range of the Species—Leary and others (1991) demonstrated that most of the genetic variation for bull trout is contained among different populations rather than within any single population. Conservation of genetic diversity, then, implies conservation of populations throughout the historic range. Replication of core areas is also important to further reduce extinction risks. Regional bull trout populations found in areas consistent with our definition of a core area have declined in recent years. Bull trout declined throughout the Priest Lake basin over a relatively short period, for example (Mauser and others 1988), and bull trout populations in both the North Fork Flathead and Middle Fork Flathead Rivers have shown simultaneous declines in the last 3 years (Weaver 1992). Even collections of populations in areas consistent with our definition of a core area are not buffered from deterministic threats that may exist when component populations share common waters during their life history. Catastrophic events such as floods and major fires can also

influence areas that would incorporate significant portions, if not all, of a core area.

Whenever possible, we propose that managers replicate core areas so that any seriously degraded or lost population throughout the distribution of bull trout could be recolonized from other core areas over a biologically meaningful period of time. (That is, multiple core areas should exist within larger river basins that allow some natural connection whenever possible.)

MANAGEMENT CONSIDERATIONS

A realistic conservation strategy for bull trout cannot proceed in isolation from other conservation efforts. Management that attempts to maintain a target species rather than the integrity and function of ecosystems is destined to omit important components and processes that we have yet to understand (Hunter 1991).

Metacommunities and Ecosystems

Conservation requirements for other sensitive species such as cutthroat trout, amphibians, salmon, spotted owls, grizzly bears, woodland caribou, and bull trout have many common elements. The distribution of conservation areas will overlap and the general need for ensuring natural diversity, a more natural disturbance regime, and connectedness among important habitats will be central to most efforts. Management that maintains ecosystem processes will be good for all. Design of a comprehensive management system that satisfies the spatial needs for all components will be complex and difficult. Murphy and Noon (1992) developed an iterative approach to optimize the selection of conservation reserves for spotted owls that was based on the critical needs of the species and the availability of suitable and manageable habitats. Land ownership was a key concern. A similar approach is needed here.

Monitoring

Once a system of conservation units is developed and instituted as a basis for management, its success must be monitored. Monitoring programs should provide sufficient data to show that bull trout persist in all waters of the unit and that they successfully reproduce. New or expanded programs should provide such data on a continuing basis, enabling managers to make "on demand" reports to show that the bull trout in each unit are maintaining their distribution and viability (are reproducing). More intensive monitoring is needed to identify and assess trends in habitat productivity and in bull trout abundance.

The elements of any monitoring plan will be determined, in part, by the elements and goals of the management or conservation plan. If habitat restoration is critical to maintaining a particular core area, for example, it will be important to monitor habitat conditions. The distribution and abundance of bull trout are likely elements of any monitoring program tied to species conservation. From the preceding review we suggest that the stability of metapopulations is related to the number, size, and relative distribution of component populations. Conserving or restoring spatial diversity in populations is an important goal. Declining populations must be recognized and stabilized, or extinction is inevitable.

Available resources and the commitment of managers also determine the elements and intensity of any monitoring program. We suggest ranking monitoring needs based on their utility, urgency, and cost:

1. The first need of any management or monitoring program is knowledge of bull trout distribution. At present, we lack even basic inventory, knowledge of whether bull trout are present or absent, throughout much of the species' range. Without inventory, even designation of appropriate conservation areas is a difficult, if not impossible, task. If the complete distribution is unknown, sites near the periphery of the unit are most likely to be in question, so sampling should be directed to these locations. Once the boundaries of the distribution are known, watersheds altered either by natural disturbances (such as fire or landslides) or disturbances caused by human activities (such as livestock grazing, logging, road construction, urbanization, and irrigation) become most important for monitoring.

Generally, the historic distribution of life-history types and the frequency with which they are lost naturally are unknown. Therefore, streams where bull trout have not been found, but reasonably might be expected to occur, should be included in the initial inventory to enable bull trout dispersal and recolonization to be detected through future monitoring.

2. The next logical monitoring priority is to estimate the relative abundance of bull trout rather than just to provide information about their presence or absence. The spatial diversity in the distribution of populations will influence their persistence. A conservation plan should maintain a large number of evenly distributed populations. Walters and Cahoon (1985) provide a simple measure of spatial diversity for salmon stocks based on the rank order of relative population size. We used their method to contrast the spatial diversity of bull trout populations inventoried throughout the Flathead River basin and throughout the Lake Pend Oreille basin (fig. 11). The shape of the curve reflects the relative spatial diversity. As curves rise more sharply, a larger

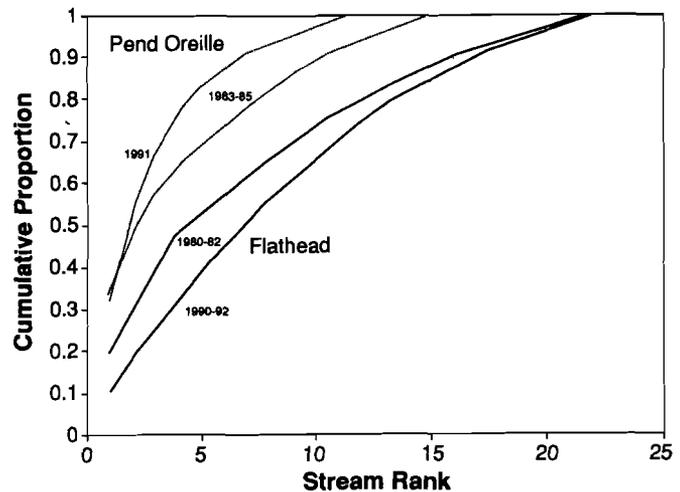


Figure 11—Cumulative bull trout redd distribution in rank order (streams with the most redds are ranked as 1) for streams in the Pend Oreille basin from 1983 to 1985 and in 1991 (Nelson and others 1992) and in the Flathead River basin from 1980 to 1982 and from 1990 to 1991 (Weaver 1992). Data are only for years of basinwide surveys. Distributions were calculated after Walters and Cahoon (1985).

proportion of the bull trout in each system is concentrated in fewer component populations. Steeper curves represent lower spatial diversity and, presumably, lower biological diversity and stability. Flatter curves should represent systems with greater health. Comparable estimates or indices of total abundance among all (or all significant) component populations within a management or core area are needed to describe spatial diversity. Basin-wide inventories of spawning escapement, such as those conducted periodically in the Flathead (Weaver 1992) and Pend Oreille (Pratt 1985) river systems, are ideal. Inventory of densities of rearing or resident fish could be used, but they would have to be extrapolated so the total numbers in a population were represented, or estimates would have to be standardized in some other way.

3. True monitoring must be repeated over a period of years. Once the general distribution and spatial diversity of bull trout are understood, all or some portion of the sampling must be repeated so trends can be detected. Trends in spatial diversity can be detected by changes in the slope for a rank order curve described above. Trends in abundance can be detected by following individual populations. Both inherent variation in population size and sampling error may determine whether important trends can be detected. It is more difficult to detect trends in unstable populations (those with inherent variation)

than in stable populations. Sampling error depends on sampling intensity and on the nature of the sample variable. Estimates of total spawning escapement based on trapping adults at a weir or on counting redds are likely to be more precise than estimates of population size based on instream sampling of resident fish.

In summary, when monitoring resources are limited, sampling should be focused in areas with the greatest stress. The first areas to be monitored for bull trout distribution and viability might be those that are most intensively managed or otherwise considered to be at the highest risk. Later, a sample of the available streams might be monitored in both impacted and unimpacted areas where there are no previous records. A selection of "representative" streams maintained through time could be used as an index of spatial diversity. If resources were available, monitoring could include all areas in the basin to detect changes both in abundance and true spatial diversity.

Regardless of the type or intensity of monitoring, care should be taken in designing the monitoring program. Monitoring or inventory variables should be consistent with the goals of the conservation plan. Managers should use existing data wherever possible to consider the sampling design, its statistical power, and the criteria on which management decisions will be based.

PRIORITIES FOR RESEARCH

Habitat Requirements—Bull trout are associated with specific habitat types, but the range of conditions tolerated by stable populations is unknown. Temperature is likely to be an important and inflexible habitat requirement, but its role has not been defined.

Interaction Between Bull Trout and Brook Trout—Brook trout appear to be an important threat to the persistence of many bull trout populations. Hybridization has been identified as a mechanism of displacement, but other factors that may influence displacement are unknown. We speculate that habitat condition and temperature may play a role and that some stocks will be more vulnerable than others. It is not clear, however, whether displacement by brook trout is inevitable in many habitats or whether habitat disruption hastens the process. Intentional isolation of bull trout populations by constructing barriers to migration has been proposed to limit the expansion of brook trout. The relative risks of isolating a bull trout population compared to the risk of its possible displacement by brook trout are unknown.

Metapopulation Structure and Dispersal—Dispersal and interaction of subpopulations may strongly influence the dynamics and persistence of bull trout populations. Dispersal mechanisms and dispersal rates are unknown, making it difficult to establish meaningful guidelines for conservation areas. New work on fine-scale genetic structuring, existing spatial distribution and correlation among populations, and simulation of metapopulation dynamics could provide useful insights.

Environmental Variation—Temporal variation in populations influences the risk of extinction through stochastic processes. We speculate that winter flood or low-flow events during migration, spawning, incubation, and rearing, and during the winter are important factors. Those relationships have not been described. Identification of the driving factors in extinction through stochastic processes and of the frequency, spatial scale, and magnitude of important disturbances in different geologic and climatic regions could support any assessment of management risks.

The Role of Life-History Forms—We speculate that both resident and migratory forms play an important role in the persistence of populations. The interaction between resident and migratory forms and the potential of one to produce the other is unknown in bull trout. We know little about differences in their habitat use and requirements, or in their distribution.

Extinction Risks—Our analyses provide a first approximation of extinction risks for some populations. Our approach did not account for complexity in life history and the interaction among populations. New work should explore alternative simulation methods for estimating risks. Model predictions could be tested by observing the distribution and persistence of populations in isolated habitats.

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APPENDIX A: METHODS FOR SIMULATIONS OF BULL TROUT POPULATIONS WITH VARIED GROWTH AND MATURITY RATES

We used a generalized, age-structured population model, MOCPOP (Beamesderfer 1988) to simulate population structure and potential egg deposition for four hypothetical bull trout populations. We used the results to estimate the minimum survival necessary to avoid collapse (population decline to extinction) for each population. Our objective was to demonstrate the relative differences in resilience that might be expected for bull trout populations with different growth and life histories.

We selected parameters for the von Bertalanffy growth model to represent a migratory population with relatively fast growth and a resident population with relatively slow growth. The models for length (L) at age (A) for fast and slow growth were $L = 1,037 * (1 - \exp(-0.1006 * (A - 0.34)))$ and $L = 298 * (1 - \exp(-0.1971 * (A - 0.29)))$, respectively. For a migratory population with relatively fast growth, the model projected lengths to the fork in the tail of about 390 millimeters at age 5 and 650 millimeters at age 10, consistent with observed growth in adfluvial populations (see text, fig. 1). For a resident population with slow growth, the model projected lengths of 180 millimeters at age 5 and 250 millimeters at age 10.

Age- or size-specific maturation, longevity, fecundity, and survival rates have not been well defined for bull trout. Available information suggests that first maturity may occur from age 4 to 7. To encompass that range we selected two maturity schedules: (1) fish first matured at age 7 and lived through age 10 and (2) fish first matured at age 4 and lived through age 5. We assumed a 1:1 sex ratio and

alternate-year spawning (50 percent of the females spawn in any year) in all simulations.

Fraley and Shepard (1989) reported adult female average length and fecundity of 645 millimeters and 5,482 eggs, respectively. Carlander (1969) reported 2,000 to 7,000 eggs for Arctic char 460 to 660 millimeters long, and 50 to 160 eggs for brook trout 100 to 126 millimeters long. We selected a fecundity (F) by length (L) relationship ($F = 0.0003 * L^{2.57}$) that projected about 5,000 eggs for a 650-millimeter long female and about 120 eggs for a 150-millimeter female.

We found no estimates of age-specific survival for bull trout to guide our simulations. Annual survival rates for other subadult salmonids have often been estimated to range from about 0.30 to 0.70 (Rieman and Apperson 1989; Schill 1992). We assumed a constant survival after age 1 among ages and years of 0.60 in all simulations.

In each simulation we held recruitment to age 1 constant and used the model to generate a stable age distribution and potential egg deposition. Scully and others (1990) estimated egg to parr survival for chinook salmon to range from about 0.03 to 0.29, depending on the level of fine sediments in stream substrates; they also estimated survival of stocked fry to parr to be 0.14 to 0.33. Because the latter estimates were based on hatchery fry that might be poorly adapted to a natural environment, their estimates of survival could be low. We assumed survival from emergent fry to age 1 of either 0.20 or 0.40 and calculated the minimum survival from egg to emergent fry necessary to keep the population from declining.

APPENDIX B: METHODS FOR THE ESTIMATION OF INSTANTANEOUS MEAN RATES OF CHANGE, THEIR VARIANCE, AND THE PROBABILITIES OF PERSISTENCE FROM TIME SERIES INFORMATION ON BULL TROUT POPULATIONS

Dennis and others (1991) developed an analytical approach to estimate extinction parameters for age structure populations based on a stochastic model of exponential growth. Time series of population size are necessary to parameterize the model. We used time series information from bull trout redd surveys or population estimates to estimate the mean instantaneous rate of change (μ) and the variance in the rate of change (σ^2) for several systems as:

$$\hat{\mu} = \frac{q \sum_{i=1}^q X_i}{\sum_{i=1}^q T_i}$$

and

$$\hat{\sigma}^2 = \frac{q \sum_{i=1}^q (1/T_i) (X_i - \hat{\mu} T_i)^2}{q - 1}$$

where

$X_i = \log_e (n_i/n_{i-1})$
 $T_i = t_i - t_{i-1}$
 $n_i =$ number of redds or individuals at time i
 $t_i =$ time of observation in years (Dennis and others 1991).

We used these parameters, an assumed minimum threshold for persistence, and the geometric mean population size to estimate the probability of persistence for 100 years for each population. Calculations follow directly from Dennis and others (1991). We identified transitions that had an unusually large influence on parameter estimates in some data sets as suggested by Dennis and others (1991).

Selection of the threshold for persistence was arbitrary. True extinction occurs when the total population reaches 0 and may not necessarily coincide with the absence of adults in any single year. However, very low population sizes may increase extinction risks dramatically because processes other than environmental stochasticity become important. Depensation caused by predation (Peterman and Gatto 1978) or fishing, extinction vortices (Gilpin and Soulé 1986), and Allee effects (Ferson and Akcakaya 1988) are all discussed as processes that lead to increasing mortality or accelerated population decline at small population sizes. We have no evidence that such effects are important for bull

trout. Population models, however, suggest that demographic stochasticity might aggravate extinction risks for any species when breeding adults number about 20 or less (Quinn and Hastings 1987). Genetic risks resulting from inbreeding might increase risks in isolated populations when numbers drop below about 50 breeding adults (Lehmkuhl 1984; Soulé 1980). We chose two extinction thresholds for our analysis of migratory populations: 1 and 10 redds. One redd represents risks near that of true extinction; 10 redds represent a more conservative level where other risks might make recovery doubtful, but not impossible. We assumed the sex ratio to be 1:1 so that 10 redds represented 20 adults. For time series based on population estimates of resident fish (age 1 and older) we estimated the relative proportion of adults to the total population from our simulations described in appendix A. We estimated that a total population of 120 fish was equivalent to an adult population represented by 20 adults. Although the threshold does not represent absolute extinction, it does represent a point of serious concern for management of stocks where other risks could increase substantially. A conservative viability analysis or management plan for any specific population might consider using a higher threshold to minimize risks associated with very small population sizes. In any case, our estimates of extinction risk must be considered only first approximations, as discussed in the text. They are most useful as measures of the relative risk associated with characteristics of the populations considered here.

We estimated the mean and variance of the instantaneous rates of change and the geometric mean population size for migratory stocks from redd counts conducted annually on tributaries of the North Fork and Middle Fork of the Flathead River and of the Swan River in Montana (Weaver 1992) and tributaries to Lake Pend Oreille in Idaho (Nelson and others 1992). We also used counts of bull trout passing a salmon collection weir on Rapid River in Idaho (Schill 1992) and converted the total counts to an equivalent redd number by dividing by 2 (assuming a 1:1 sex ratio). We assumed that the redd count data represented a census of the adult female population associated with each stream and estimated the model parameters from the data in two ways. Bull trout may spawn over several years once mature, but both annual and every-other-year spawning have been reported (Block 1955; Fraley and

Shepard 1989; Pratt 1985). Because of the uncertainty in spawning frequency, we calculated the annual transitions in redd numbers from the annual counts (assuming annual spawning) and from the 2-year moving sum (assuming every-other-year spawning). Dennis and others (1991) used a 3-year moving sum in the same way for their analysis of the observed number of female Yellowstone grizzly bears with cubs, because the bears probably do not reproduce more than once every 3 years. We used only the annual estimates of population densities to estimate the annual transitions in resident populations. We estimated model parameters for resident populations from annual population estimates in the upper South Fork of the Salmon River and Bear Valley Creek (Platts and Nelson 1988), and from several tributaries to the Bitterroot River (Clancy 1992). The resident density estimates for tributaries to the Bitterroot River represent only limited time series (2 or 3 years). We therefore substituted replication in space for time. We assumed that all of the tributaries represented suitable replicates of a single population and pooled estimates of the annual transitions among streams to estimate a single variance in the instantaneous rate of growth.

We estimated probabilities of persistence for 100 years for migratory populations using both the estimated instantaneous growth rates and an assumed rate of 0. Because the time series are relatively short and the variances are sometimes high, the estimated growth rates are often imprecise. Both negative and positive growth rates can have a substantial

influence on the estimates of persistence (table 4). Because unchecked negative growth will ultimately lead to deterministic extinction and because permanent positive growth is unrealistic in any natural system, we considered the estimates based on a growth rate of 0 the best representations of purely stochastic risk.

To consider the risks associated with habitat restriction and fragmentation, we also estimated generalized probabilities of persistence for a range of population sizes and variances that bracketed the observations in both migratory and resident populations. For the example with migratory fish, we selected a threshold of persistence (four redds) that lay between the two thresholds used in the more extensive series of estimates. The parameter estimates for resident populations were only for selected stream reaches, so we could not estimate the total population size and the probability of persistence for any specific populations. To consider the relative extinction risks for resident populations, we approximated the range of likely population sizes from population density estimates extrapolated over the total available habitat.

To consider the relative reduction in risk associated with multiple subpopulations, we estimated probabilities of persistence for systems composed of multiple migratory populations as $1-(P_1 * P_2 * \dots * P_i)$ where P_i is the probability of declining below the threshold (1-probability of persistence) in each of i component populations. We assumed no temporal correlation and no refounding among populations.

APPENDIX C: ANNUAL BULL TROUT REDD COUNTS FOR STREAMS IN IDAHO AND MONTANA

Table 8—Annual bull trout redd counts for streams in Idaho (Nelson and others 1992; Schill 1992) and Montana (Weaver 1992)

River basin Stream	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
North Fork														
Flathead (MT)														
Big	10	20	18	41	22	9	9	12	22	19	24	25	24	16
Coal	38	34	23	60	71	53	40	13	48	52	50	29	34	7
Whale	35	45	98	211	141	133	94	90	143	136	199	109	61	12
Trail	34	31	78	94	56	32	25	69	64	62	51	65	27	26
Middle Fork														
Flathead (MT)														
Morrison	25	75	32	86	67	38	99	52	49	50	63	24	45	17
Granite	14	34	14	24	31	47	24	37	34	32	31	21	20	16
Lodgepole	32	14	18	23	23	23	20	42	21	19	43	12	9	13
Ole	—	19	19	51	35	26	30	36	45	59	21	20	23	16
Swan (MT)														
Elk	—	—	—	56	91	93	19	53	162	201	186	136	140	143
Goat	—	—	—	33	39	31	40	56	31	46	34	27	31	17
Squeezer	—	—	—	41	57	83	24	55	64	9	67	42	101	115
Lion	—	—	—	63	49	88	26	46	33	65	84	58	94	100
Pend Oreille (ID)														
Lightning	—	—	—	—	28	9	46	14	4	—	—	—	—	—
Eastfork	—	—	—	—	110	24	132	8	59	79	100	29	—	32
Savage	—	—	—	—	36	12	29	—	0	—	—	—	—	—
Char	—	—	—	—	18	9	11	0	2	—	—	—	—	—
Porcupine	—	—	—	—	37	52	32	1	9	—	—	—	—	—
Wellington	—	—	—	—	21	18	15	7	2	—	—	—	—	—
Rattle	—	—	—	—	51	32	21	10	35	—	—	—	—	—
Johnson	—	—	—	—	13	33	23	36	10	4	17	33	25	16
Trestle	—	—	—	—	298	272	298	147	230	244	217	218	243	145
Grouse	—	—	—	—	2	108	55	13	56	24	50	48	33	17
Granite	—	—	—	—	3	81	37	37	30	—	—	—	—	—
N. Gold	—	—	—	—	16	37	52	8	36	24	37	35	41	41
Gold	—	—	—	—	131	124	111	78	62	111	122	84	104	93
Salmon (ID)														
Rapid ¹	210	215	135	75	120	340	140	140	120	130	160	240	275	—

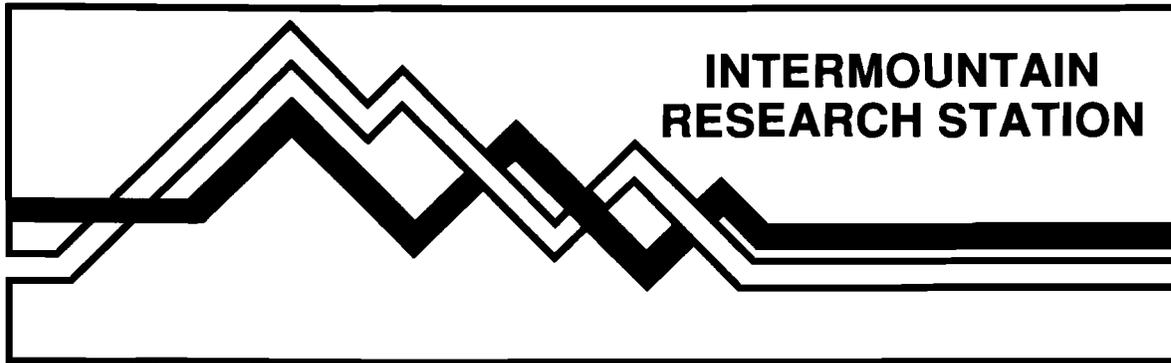
¹Counts taken on the Rapid River before 1979 are as follows: 1973—115; 1974—290; 1975—465; 1976—415; 1977—210; 1978—125.

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Elements in bull trout biology, population dynamics, habitat, and biotic interactions important to conservation of the species are identified. Bull trout appear to have more specific habitat requirements than other salmonids, but no critical thresholds of acceptable habitat condition were found. Size, temporal variation, and spatial distribution are likely to influence the stability of local and regional populations. Disruption of key habitat characteristics threatens the persistence of local populations, and isolated populations are not likely to persist indefinitely. Conservation of bull trout will require maintenance or restoration of multiple, high-quality, connected habitats distributed throughout conservation areas, which in turn should be distributed throughout the species' range.

KEYWORDS: Salmonidae, char, *Salvelinus confluentus*, population dynamics, persistence, sensitive species, metapopulation, conservation biology





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