An Assessment of Headwater Isolation as a Conservation Strategy for Cutthroat Trout in the Absaroka Mountains of Wyoming

Abstract
Isolation of native cutthroat trout (Oncorhynchus clarki) populations in headwater tributaries (by means of human-made barriers that prevent upstream movement of exotic Salmonidae) has been used as an approach to preserve extant populations from hybridization and competition. We evaluated this conservation strategy for Yellowstone cutthroat trout (O. c. bouvieri) in the Absaroka Mountains of northwestern Wyoming. We surveyed four existing populations to assess the potential for isolating Yellowstone cutthroat trout populations in 23 individual headwater tributary streams. It appeared that 21 of the populations would be large enough to minimize demographic risks of extinction, but only seven populations may be large enough (effective population size > 500) to lower the risk of extinction due to genetic limitations. Additionally, there is high potential for unpredictable environmental events to cause severe reductions in population size or local extinctions of Yellowstone cutthroat trout populations above barriers due to the unstable flow and habitat conditions. Isolation of Yellowstone cutthroat trout populations in headwater tributaries upstream from barriers appears to have a low probability of preserving sustainable populations of Yellowstone cutthroat trout in the Absaroka Mountains in the long term.

Introduction
As a result of anthropogenic influences, native salmonids in the Rocky Mountains have experienced dramatic declines in distribution and abundance over the past half-century (Gresswell 1988; Rieman and McIntyre 1993; Young 1995). Cutthroat trout (Oncorhynchus clarki), the only trout native to the majority of the interior Rocky Mountains (bull trout Salvelinus confluentus overlap with cutthroat trout on the western slope in Montana and Idaho), have been severely impacted by water development projects (e.g., agriculture, hydropower), intentional introductions and invasions of introduced trout, and habitat alterations associated with mineral extraction and other development, especially on non-public lands (Young 1995; Thurow et al. 1997; Shepard et al. 1997; Dunham et al. 1999). All seven of the major interior (non-coastal) subspecies of cutthroat trout (Behnke 1992) have experienced some decline in occupied habitat, and several have experienced losses exceeding ninety percent (Gresswell 1988; Liknes and Graham 1988; Dunham et al. 1997; Kruse et al. 2000). The Lahontan (O. c. henshawi) and greenback (O. c. stomias) cutthroat trout are categorized as threatened and the Yellowstone (O. c. bouvieri), westslope (O. c. lewisi), Colorado River (O. c. pleuriticus), Rio Grande (O. c. virginalis), and Bonneville (O. c. utah) subspecies have recently been petitioned for listing under the Endangered Species Act. Although the ecological importance of the decline and potential loss of these native trout is unknown, the premature loss (i.e., human induced) of native species is generally considered detrimental for overall ecosystem health (Frissell 1993). Because of their evolutionary history, cutthroat trout are considered to be well, if not uniquely, adapted to the variable habitat and flow conditions associated with high-elevation climes (Fausch 1989; Behnke 1992). Their decline has required biologists to consider the consequences of their demise and to implement conservation strategies.

Large populations of cutthroat trout that once encompassed several watersheds are now mostly restricted to isolated headwater tributaries (Young 1995; Dunham et al. 1997; Sheppard et al. 1997; Kruse et al. 2000). Expanding populations of introduced salmonids continue to impose a threat to native cutthroat trout persistence (Young 1995; Thurow et al. 1997; Dunham et al. 1999), and a
substantial body of literature has focused on both the interactions among native and introduced salmonids and the uncertainty associated with the persistence of small, isolated populations of native salmonids (Allendorf and Leary 1988; Rieman and McIntyre 1993; Wang and White 1994; Fausch and Young 1995; Dunham et al. 1997; Hanski and Gilpin 1997; Shepard et al. 1997). The probability of a single population persisting is generally considered to decrease as the population becomes smaller and more separated from others, increasing the genetic (e.g., reduced heterozygosity and adaptability) and stochastic (e.g., environmental events) risks of extinction.

One management option with potential to minimize the threat posed by introduced trout in moderate to high gradient stream systems is intentional isolation of allopatric cutthroat trout populations (Behnke and Zam 1976; Young 1995; Young et al. 1996). Isolation is generally achieved by constructing barriers near the downstream terminus of a native salmonid population or population segment (e.g., individual stream) to prevent upstream movement of rainbow trout (O. mykiss) and brook trout (S. fontinalis), thus minimizing the hybridization and competition risks associated with these introduced species. Management by isolation can also involve reintroduction of genetically pure native fish above natural geologic barriers to fish migration (waterfalls) or in reclaimed stream systems where naturalized populations of introduced trout have been removed with piscicides or electrofishing above a natural or man-made barrier (Gresswell 1991; Thompson and Rahel 1996, 1998). However, it is difficult to totally remove naturalized populations of introduced salmonids or intergrades of cutthroat trout and rainbow trout from streams. Consequently, isolation of allopatric populations of cutthroat trout in headwater streams prior to invasion by exotics salmonids has been considered the preferred and proactive approach.

An isolation strategy has already been implemented to maintain small populations of genetically pure Colorado River cutthroat trout (Wyoming and Colorado, Young et al. 1996) and Bonneville cutthroat trout (Utah, Lentsch et al. 1997) and is being considered for westslope and Rio Grande cutthroat trout restoration projects in Montana and New Mexico, respectively (Turner Endangered Species Fund, Bozeman, Montana). Barriers have also been applied to conservation of native Gila trout (O. gilae) in the Gila River drainage of New Mexico and Arizona (Propst et al. 1992) and, ironically, to protect brook trout from invading rainbow trout in the Appalachian Mountains (Guffey et al. 1998).

Yellowstone cutthroat trout were once the most widely distributed of all the cutthroat trout subspecies and could be found throughout all but the most downstream (warmer) portions of northwestern Wyoming river drainages (Behnke 1992). As a result of past water development projects and non-native salmonid introductions, Yellowstone cutthroat have been extirpated from a large portion (70%) of their fluvial habitat in northwestern Wyoming and are generally restricted to spatially disjunct, headwater streams. Introduced rainbow trout and brook trout have become established in streams throughout this region and continue to invade and reduce the size of remaining populations of Yellowstone cutthroat trout (Kruse et al. 2000). Thus, constructing barriers to prevent upstream movement of introduced trout and isolating allopatric populations of Yellowstone cutthroat trout in headwater streams might be an attractive option for conservation. If this alternative is chosen, it is critical that the increased level of isolation and lack of genetic exchange do not compromise long-term survival of the resulting populations; this limitation can only be overcome, at least in theory, by ensuring adequate habitat and refugia above the barrier. However, faced with the knowledge that introduced salmonids are responsible for Yellowstone cutthroat trout declines in many areas, managers may be willing to accept the uncertain risks (i.e., population fragmentation and isolation) of using barriers as a management tool in an attempt to decrease the known and immediate risk of introgression or competition.

Kruse et al. (2000) previously defined the geographical distribution of the remaining native Yellowstone cutthroat trout in northwestern Wyoming. Because these populations encompass several connected tributaries, but are threatened by non-native trout, isolation could be considered as a conservation tool for a portion of these populations. Thus, our goal was to evaluate possible demographic and genetic consequences of purposefully fragmenting (with man-made barriers) Yellowstone cutthroat trout populations into individual headwater streams. We also consider this strategy relative to the potential for stochastic events
that could lead to extinctions of isolated populations and the life history needs of Yellowstone cutthroat trout in these stream systems.

**Study Area**

Viable populations of Yellowstone cutthroat trout remain in the Bighorn River drainage in portions of the Greybull, Wood, and South Fork of the Shoshone watersheds (Figure 1). These rivers originate in the southeastern portion of the Absaroka Mountains, which are a rugged, 250-km-long northwest-trending mountain range in northwestern Wyoming and southwestern Montana (Sundell 1993). The mountains are erosional remnants of a vast accumulation of volcanic material with elevations ranging from 1,830 to 4,006 m above mean sea level. The mountain range has been described as a plateau having abundant V-shaped valleys with narrow floodplains and sharp ridges with steep cliffs and abundant talus (Sundell 1993). An important feature of the Absaroka Mountains is the occurrence of ubiquitous mass-wasting events (Sundell 1993). Rock slides, rockfall, slumps, earthflows, mudflows, soil creep, and virtually all combinations of these phenomena are common. Large mass movements are most frequent in the southwestern portion of the Absaroka Mountains, the area of focus in this study. Partially as a result of the rugged and unstable features of these mountains, the mountain range encompasses the largest roadless area in the conterminous United States. Headwater streams are generally steep (> 5% channel slope) with erosive, unstable channels (Keef er 1972; Nelson et al. 1980; Kent 1984) and substrate dominated by coarse-grained, poorly sorted, fragmented rocks (Sundell 1993). Annual precipitation is predominately snow; causing torrential spring flows (Martner 1982).

The Greybull, Wood, and upper South Fork Shoshone river drainages are predominately on public lands, generally within designated wilderness areas, and are relatively pristine. The downstream portions of the South Fork Shoshone River and its tributaries in the lower portions of the watershed are affected by human perturbations associated with roads, agriculture, and irrigation withdrawals. Non-native salmonids were introduced in the study area as early as 1915, and stocking continued until the 1970’s, resulting in large, naturalized populations of rainbow trout, brook trout, and brown trout (*Salmo trutta*), as well as intergrades of cutthroat trout and rainbow trout resulting from interbreeding of these two species.

**Methods**

Perennial streams within the boundaries of each cutthroat trout population were sampled by backpack electrofishing during periods of low flow from July through September of 1994-1997. Progressing upstream in each river and from the mouth of each tributary, 100-m reaches were sampled at 1.0-km intervals until trout were not found in two consecutive reaches. The upstream boundary of fish occurrence was identified as the point halfway between the last occupied reach and first reach where cutthroat trout were not found. Average wetted stream width in each reach was measured with a tape perpendicular to stream flow at five transects equally spaced over each 100-m reach. Stream length was calculated from a digitized hydrologic coverage using a geographic information system.

Captured trout were identified and measured. To confirm that sampled cutthroat trout were genetically pure, eye, muscle, and liver tissue were taken from a sample of trout in each 100-m reach (N=20 for the entire tributary), frozen in liquid nitrogen, and analyzed at the Wild Trout and Salmon Genetics Laboratory, University of Montana, Missoula. Ten alleles were used to identify potential cutthroat trout and rainbow trout integration (Kruse 1998). In all cases, genetic analysis confirmed genetic purity of Yellowstone cutthroat trout.

To evaluate possible consequences of using barriers to protect segments of the existing Yellowstone cutthroat trout populations, we assumed that a barrier could be constructed at the mouth of each tributary stream where allopatric Yellowstone cutthroat trout were found and that a unique population could be isolated upstream from the barrier in each headwater tributary stream.

We converted the total number of fish captured (≥ 75 mm total length) with one electrofishing pass in each reach to an estimate of total abundance in the reach using the equation $A = -1.863 + 1.181 \text{ONE} + 0.797 W$; where $A$ is the estimate of total abundance in the reach, ONE is the number of fish captured with one electrofishing pass, and $W$ is the wetted stream width. Kruse et al. (1998) found that fish abundances using this
approach were highly correlated ($R^2 = 0.96$) with three pass depletion estimates done in a sample of 100-m reaches. Abundance estimates (number/100 m) for each reach in a tributary were averaged and extrapolated to the total number of 100-m reaches occupied by Yellowstone cutthroat trout in the tributary stream. The standard error of the population estimate for each stream was calculated as the standard error of the mean number of fish in the reaches sampled multiplied by the total number of 100-m reaches inhabited by fish (Krebs 1989). From this the 95% confidence interval was computed. We purposely did not correct our estimate of the standard error with the finite population correction factor in order to maintain conservative confidence intervals (Table 1). However, due to the nature of the sampling design (100-m reaches every km), including the finite population correction would have narrowed the confidence interval, modifying the upper and lower values approximately five percent.

The estimated population size within each tributary was converted to an effective population size or number of reproducing adults by multiplying the estimate by the proportion of individuals greater than 200 mm (total length) in the samples from each drainage. Although fluvial Yellowstone cutthroat trout spawners in higher order streams generally exceed 275 mm (Thurow et al. 1988), high-elevation populations may reproduce at lengths less than 200 mm (Downs 1997); thus, all fish greater than 200 mm were considered as part of the effective population. Others have reported that female spawners often out-number males (Thurow 1988; Gresswell 1995); however, a small sample of collected cutthroat trout indicated that the male to female ratio of mature pre-spawn fish was approximately equal (as was also shown by Byorh 1990) so our estimate of the effective population size assumed that the number of breeding males and females was equal. Therefore our estimate of the effective population size was equivalent to the estimated breeding population (Gall 1987).

The influence of population size on the likelihood of population persistence was assessed by comparing the effective population size of each isolated stream segment to minimum population levels considered necessary to prevent population extinction due to: 1) demographic stochasticity (20 to 30, as summarized in Rieman and McIntyre 1993, Young 1995), 2) excessive inbreeding (50), and 3) loss of long-term genetic variation (500, Franklin 1980; Soule 1987). We recognized that these criteria have not been confirmed for Yellowstone cutthroat trout and that there is debate regarding the accuracy of such criteria (Nelson and Soule 1987; Hildebrand and Kerschner in press), but we felt that these criteria provided reasonable guidelines for assessing potential viability of Yellowstone cutthroat trout populations isolated in individual streams relative to demographic, inbreeding, and long-term genetic considerations.

Results

We sampled 26 separate population segments (i.e., tributary or portion of mainstem), occupying 219 km of stream. Because we assumed that a non-native invasion of the remaining populations would occur via the mainstem rivers, ultimately displacing the Yellowstone in that portion of the habitat, we did not consider the mainstem population segment in our isolation analysis. Of the remaining 23 tributaries, thirteen tributaries (97.5 km of occupied stream length), were in the Greybull watershed, six (37 km) were located in the Wood watershed, and four (26.8 km) drained into the SF Shoshone River (Figure 1, Table 1). All the sampled tributaries contained Yellowstone cutthroat, while four streams contained brook trout, three in the SF Shoshone watershed and one in the Wood watershed (both the Wood and SF Shoshone mainstem rivers contained brook trout).

The mean abundance of Yellowstone cutthroat trout were highly variable (range 2.2–39.4 fish/100 m), as was the length of stream inhabited by Yellowstone cutthroat trout (range 0.8–19.5 km) in each tributary. Consequently, the estimated number of Yellowstone cutthroat trout (28–4,128) and the effective population size (range 15–2,175) varied widely among the tributaries. Estimates of abundance in individual reaches varied substantially within some tributaries and 95% confidence intervals were wide (Table 1). Thus, judgments regarding extinction probabilities must be made with recognition that estimates of potential population sizes in some tributaries have poor precision and that populations sizes are likely to vary over time.

If isolated by man-made barriers, we estimated that 21 of the 23 headwater tributaries would likely have (considering sampling error) an effective
population exceeding the 30 individuals needed to minimize the risk of extinction due to demographic instability. Similarly, 21 of the 23 would likely have effective populations of more than 50 individuals, lowering the short term risk of extinction due to inadequate genetic exchange and adaptability. Only seven tributaries could likely support effective Yellowstone cutthroat trout populations in excess of the 500 individuals needed to minimize all demographic and genetic risks. The breeding population of Yellowstone cutthroat trout would not exceed 2,500 in any of the intentionally isolated tributaries.

**Discussion**

Recent works regarding movement and meta-population structure of salmonids (Jakober et al. 1998; Dunham and Rieman 1999; among others) underscore not only the complexity of salmonid population structure and function in lotic systems, but also the importance of connectivity among habitats. As non-native salmonids, as well as habitat perturbations, continue to displace and fragment Yellowstone cutthroat trout, remaining populations are relegated to highly variable, peripheral habitats (when considering past historical distributions). Given the unstable nature of the Absaroka Mountains, which limits habitat complexity (Kruse 1998) and results in frequent torrential flows and mass wasting events (Sundell 1993), it is likely that Yellowstone cutthroat trout commonly experience severe reductions in abundance or local extinction in individual tributaries (e.g., Lamberti et al. 1991; Gresswell 1999). In the past, the affected areas were re-colonized by individuals connected through the mainstem rivers (sensu Pulliam 1988).
Once a tributary has been disconnected from the mainstream by some form of barrier (e.g., man-made, diverted flows, introduced salmonids), population functions such as movement of individuals, whether in a metapopulation framework (Hanski and Simberloff 1997) or seasonally related (e.g. spawning or wintering habitat; Brown and Mackay 1995; Jakober et al. 1991), are disrupted. Populations then face a higher probability of permanent extinction because individuals are lost from the population, genetic exchange is restricted, and rescue following a local reduction in abundance or extirpation is obstructed. Thus, if isolation is considered as a conservation strategy, managers must insure sufficient habitat is included to support the biological needs of a sustainable population (i.e., large), as well as provide sufficient refugia (i.e., connected habitats) to prevent complete population extirpation from a single stochastic event.

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a barrier despite the occurrence of apparently suitable habitat. However, Yellowstone cutthroat trout were commonly found immediately downstream from the barriers in areas accessible from the mainstem rivers. It is unknown whether Yellowstone cutthroat trout were ever present above any of the natural barriers, but their distribution in tributaries with barriers (i.e., present below, absent above) underscores not only the effectiveness of barriers in preventing the movement of unwanted species, but also their role in preventing initial or re-colonization of usable, but fishless habitats.

Other researchers have addressed the issue of salmonid population viability by considering population size along with the additional probability of extinction associated with catastrophic events (i.e., disturbances of such a magnitude that the size of the affected population(s) are reduced quickly and substantially; Allendorf et al. 1997). It has been assumed that smaller populations, in general, are at higher risk of extinction from catastrophic events (Shaffer 1987; Lande 1988, Propst et al. 1992; Rieman and McIntyre 1993; Dunham et al. 1997). Some attempts have been made to quantify the risk of stochastic catastrophic events when assessing risks of extinction of cutthroat trout populations (Allendorf et al. 1997; Dunham et al. 1997; Shepard et al. 1997), but all involved speculation as to the frequency of occurrence of future catastrophic events. We could not predict the frequency, intensity or effects of these events (see Siegfried and Knight 1977; Lamberti et al. 1991; Rieman and McIntyre 1993), but could assume that the geologic instability of the Absaroka Mountains leads to catastrophic floods and debris torrents at a much higher frequency than in other mountain ranges (Sundell 1993; Knuse 1998). It appears that such events occur in the Absaroka Mountains with frequencies measured in decades, whereas frequencies are much less in most other mountain ranges in Wyoming with occurrences measured in centuries or millennia. Shepard et al. (1997) considered lotic populations of westslope cutthroat trout to be at high risk if the frequency of occurrence of catastrophic events was in the range of 20-70 years. Such frequencies of occurrence are probable among populations of Yellowstone cutthroat trout in the Absaroka Mountains.

While generally discussed in the scientific literature (Rieman et al. 1997; Dunham et al. 1997; Shepard et al. 1997), the wholesale extinction of a salmonid population as a result of a catastrophic environmental event has rarely been documented. Localized extirpations have resulted from fires and debris flows (Lamberti et al. 1991; Rieman et al. 1995; Gresswell 1999), but the loss of fish in these cases was rapidly mitigated by re-colonization from adjacent habitats. It could be argued that cutthroat trout populations are resilient to environmental disturbance and concerns over small, isolated populations are overstated; however, there has been little opportunity to observe the real effects of small population size and isolation on native, extant Yellowstone cutthroat trout populations, which are now approaching levels where demographic and genetic processes or localized disturbances could impact an entire population.

Construction of barriers on individual tributaries might be considered to preserve portions of the current Yellowstone cutthroat trout populations in the study area if only risks associated with population size, such as demographic viability and genetic stability, are considered. While most of the tributaries either already support non-native trout (see Table 1) or would not support adequate numbers of breeding adults to warrant a long-term isolation management program, seven tributaries might support populations with an effective size substantially greater than 500. None of these seven currently contain brook trout; however, because each of these streams has a relatively limited geographical extent (< 20 km; Table 1) with few connected habitats, we argue that their potential to support an isolated Yellowstone cutthroat trout population is limited when faced with environmental stochasticity.

Construction of large barriers on the mainstem of the rivers to prevent upstream movement of non-native trout into an entire watershed or a complex of tributaries may be considered. However, the rivers downstream from current Yellowstone cutthroat trout populations are sizable (> 50 - 100 m wide at bank-full flows), requiring large structures with high fluctuations in discharge and unstable stream channels creating a high risk of structural failure. One option to consider is a barrier at the mouth of the South Fork Wood River, which would isolate, in complex, the South Fork Wood
River and Chimney Creek. However, other opportunities to isolate multiple tributaries with a single barrier are limited in the study area. Additionally, artificial barriers are expensive to install and maintain, and commonly fail, either through loss of physical integrity or unsuccessful inhibition of upstream movement by undesired fishes (Young et al. 1996; Thompson and Rahel 1998). It is probable that artificial barriers would have very high failure rates in the Absaroka Mountains due to the geologic instability in the region. Construction of barriers requires accessibility to sites with stable stream banks (Novotny and Binns 1990), sites which are difficult to find in these highly variable, wilderness streams.

It is important to note that the 30, 50, and 500 levels we have used to assess demographic, short-term genetic, and long-term genetic risks, respectively, are less conservative guidelines than those suggested by others. Nelson and Soule (1987) suggested that minimizing short- and long-term genetic risks would require 500 and 5,000 individuals, respectively. McIntyre and Rieman (1995) speculate that extinction risks are substantially higher for cutthroat trout populations with less than 2,000 individuals. Only two populations in the entire study area that could be isolated would likely to exceed 2,000 effective individuals and none would be greater than 2,500.

Another factor to consider when purposefully isolating Yellowstone cutthroat trout populations in headwater streams is recruitment to the population. Shepard et al. (1997) considered habitat availability, incubation success, and survival of fry and juveniles in their analysis of extinction risks among populations of lotic westslope cutthroat trout. Similarly, spawning habitat and survival likely affect recruitment of Yellowstone cutthroat trout in the headwater streams of the Absaroka Mountains. Spawning and nursery habitat was relatively common in the mainstem portions of the study area, but was infrequently and patchily distributed throughout the steeper, erosive headwater tributaries. One fishless tributary in the Greybull watershed was stocked upstream from a natural barrier in 1988 and 1993. We evaluated the population and found that Yellowstone cutthroat trout numbers decreased 30-fold in three years (8.0/100 m to 0.25/100 m) with no evidence of natural reproduction. Three other tributaries stocked with genetically pure Yellowstone cutthroat trout above natural barriers showed a similar lack of recruitment. This observation suggests an intimate tie between the spawning habitat in the mainstem rivers and the persistence of fish in tributaries. Lack of recruitment in headwater streams, whether from absence of adequate spawning and rearing habitat, catastrophic or chronic year-class failures, or some other factor, may be a substantial limitation to establishment of sustainable Yellowstone cutthroat trout populations upstream from artificial barriers in headwater habitats.

Although there has been debate on the relative importance of various factors that can contribute to the extinction of salmonid populations (Fausch and Young 1995; Waples 1995; Hanski and Gilpin 1997; Jakobar et al. 1998), most researchers agree that conservation strategies that restrict movements (e.g., dispersal, genetic exchange, habitat needs) or reduce the sizes of populations increase the risks of localized population extinctions. As Wilcox and Murphy (1985) point out, habitat fragmentation is one of the greatest threats to species survival. Yet faced with the alarming decline of Yellowstone cutthroat trout, among others, we are forced to consider just such a strategy to preserve a species. For long-term survival, isolated habitats must provide the resources necessary to sustain a population, as well as the area and diversity necessary to withstand environmental stochasticity (Propst et al. 1992). Isolation of Yellowstone cutthroat trout populations in individual headwater streams to preserve Yellowstone cutthroat trout in the Absaroka Mountains does not seem to be a viable long-term strategy for preservation. If used, barriers should be applied cautiously and only to prevent complete extirpation of Yellowstone cutthroat trout populations in the short-term, with a goal of long-term stability through reconnection of isolated fragments. If populations extending over several tributaries and a portion of a mainstem river can be protected by isolation, long-term conservation of Yellowstone cutthroat trout in the Absaroka Mountains could have a higher probability of success. However, construction and maintenance of large barriers on the mainstems of these rivers would be necessary, an alternative that is expensive and difficult due to the instability and remoteness of the watersheds. In this context, continued isolation of the relatively large, allopatric Yellowstone cutthroat trout population in the Greybull River drainage should be a high priority in the
conservation of Yellowstone cutthroat trout in the Absaroka Mountains.

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