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Status of Yellowstone Cutthroat Trout in Wyoming Waters

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Abstract.—Most subspecies of interior cutthroat trout *Oncorhynchus clarki* have suffered dramatic declines in range and number. We assessed the status of genetically pure Yellowstone cutthroat trout *O. clarki bouvieri* on predominantly public lands in three major watersheds of northwestern Wyoming (Greybull River and North and South Forks of the Shoshone River) between 1994 and 1997. These river basins encompass the majority of remaining habitat outside of Yellowstone National Park with potential to contain Yellowstone cutthroat trout, and little information on them was available. Only 26% of the 104 streams found to contain trout still support genetically pure Yellowstone cutthroat trout. Extant Yellowstone cutthroat trout occupied 245 of 822 km of the perennial streams that contained trout, suggesting native trout have been displaced by or hybridized with exotic salmonids in nearly three-quarters of the available habitat in these watersheds. The four remaining populations were widely separated in the watersheds and had populations that ranged from 900 to 23,000 age-1 and older individuals and that appeared genetically and demographically viable. However, because the threats of hybridization and competition remain, the current cutthroat trout populations cannot be considered secure or likely to persist over the long term. Yellowstone cutthroat trout have suffered larger than expected declines in their distribution in Wyoming outside of Yellowstone National Park largely because of nonnative salmonid introductions and invasions. We recommend immediate management intervention to control exotic salmonids and reestablish large, genetically pure, allopatric populations of Yellowstone cutthroat trout.

Before settlement of North America by Europeans, the Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* occupied the largest geographic range of any inland cutthroat trout subspecies (Varley and Gresswell 1988); however, there is evidence of population extinction and fragmentation due to anthropogenic perturbations throughout a large portion of its initial fluvial range (Varley and Gresswell 1988; Gresswell 1995). Recent qualitative estimates suggest that viable populations of Yellowstone cutthroat trout have declined approximately 60% (relative to May 1996). The American Fisheries Society has designated the Yellowstone cutthroat trout as a species of special concern (Johnson 1987), and the U.S. Forest Service considers the subspecies as ''sensitive'' (Gresswell 1995); both designations are recognized by state fish and game agencies. Conservation groups have recently petitioned the U.S. Fish and Wildlife Service to consider Yellowstone cutthroat trout for listing under the Endangered Species Act.

The Yellowstone cutthroat trout was indigenous to a large portion of the upper Yellowstone River drainage in Wyoming and Montana, and part of the Snake River watershed in Wyoming, Idaho, Utah, and Nevada. Approximately 65% of its historical range was in northwestern Wyoming. When managers began to respond to population declines, there was little information about the current distributions, genetic status, population size, and habitat conditions and requirements outside of Yellowstone National Park. Thus, knowledge of Yellowstone cutthroat trout status in Wyoming was critical to future management and definition of necessary conservation actions.

A primary agent in the decline of Yellowstone cutthroat trout appears to be hybridization and competition with nonnative salmonids (Leary et al. 1987; Allendorf and Leary 1988; Ferguson

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1990; Krueger and May 1991; Rieman and McIntyre 1995). Introduced rainbow trout *O. mykiss* and interior cutthroat trout lack reproductive isolating mechanisms and, with few exceptions, proliferate to produce hybrid swarms wherever there is overlap in distribution. Brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* have the potential to displace Yellowstone cutthroat trout through competitive interactions (Griffith 1972; Fausch 1988; Wang and White 1994). Habitat alterations from irrigation, logging, mining (Varley and Gresswell 1988; Gresswell 1995) also have displaced Yellowstone cutthroat trout and may exacerbate competitive interactions by favoring exotic species.

Remaining Yellowstone cutthroat trout populations were believed to be restricted to headwater environments where public ownership and relative inaccessibility have moderated detrimental anthropogenic impacts. Yellowstone cutthroat trout appear to be resistant to invasion in headwater habitats and may have a competitive advantage (probably due to physiological adaptations) over other salmonids in these habitats. Bozek and Hubert (1992) found that cutthroat trout in Wyoming were most likely to be found in small streams at high elevations, suggesting an ecological advantage over other trout species.

Although habitats in headwater streams are less likely to suffer extensive human modification, they are generally less diverse than those in higher-order, lower-elevation streams and more stochastic temporally and spatially, resulting in natural limitations on population size and sustainability. Even so, populations in headwater habitats are more likely to withstand the threat of extinction if connectivity is maintained among populations or segments of populations (e.g., individual streams). However, as populations are fragmented into isolated (defined as no access into a population from downstream habitats) headwater reaches, they are likely to have more variation in abundance, less genetic variation, and fewer refuges with no opportunity for demographic or genetic rescue (sensu Brown and Kodric-Brown 1977). They are also more likely to succumb to environmental events or reductions in genetic variation through inbreeding and genetic drift (Allendorf and Leary 1988; Rieman and McIntyre 1993; Rieman et al. 1993; Young 1995; Anders 1998; Guffey et al. 1998). Consequently, as exotic species force remaining Yellowstone cutthroat trout populations into smaller and disconnected enclaves their risk of extirpation will probably increase (Gilpin and Soule 1986; Rieman et al. 1993; as discussed for bull trout *S. confluentus* Rieman and McIntyre 1993).

Our goal was to define the distributions of genetically pure Yellowstone cutthroat trout in a large portion of their historical range in Wyoming outside of Yellowstone National Park where potential existed to find large (i.e., sustainable) populations. We also wanted to identify the factors governing the current distributions of these populations in order to focus future management of the subspecies. Within this framework we identified current distributions of genetically pure Yellowstone cutthroat trout in three major watersheds of northwestern Wyoming and evaluated potential threats to the survival of genetically pure populations. We hoped that this would enable us to provide perspectives on conservation that would help guide the future management of Yellowstone cutthroat trout in Wyoming waters.

Study Area

Headwaters of the Shoshone (North and South Forks) and Greybull rivers contain vast, relatively undisturbed wilderness areas, and were considered by fishery managers as likely to contain large populations of genetically pure Yellowstone cutthroat trout. These watersheds originate in the Absaroka Mountain Range (Figure 1) and eastwardly drain more than 4,400 km^2 of the Greater Yellowstone Ecosystem immediately east and southeast of Yellowstone National Park (Bighorn River drainage).

The Absaroka Mountains are erosional remnants of vast accumulations of volcanic material forming a steep, rugged landscape with uplifted peaks and deep valleys characterized by geologic instability (Keefer 1972; Nelson et al. 1980; Sundell 1993). Headwater streams are generally steep (average 6.5% channel slope and commonly exceed 8%) and torrential (large fluctuations in discharge) and have erosive, unstable substrates (Breckenridge 1975; Sundell 1993). Stream channels shift regularly and are predominately large angular bed material that limits the diversity and quality of instream habitat. Mass-wasting events (e.g., rock slides, earthflows, soil creep) are a ubiquitous and important geologic feature of the Absaroka Mountains (Sundell 1993). Elevations range from 1,660 m at the confluence of the North Fork (NF) and South Fork (SF) of the Shoshone River to 4,010 m at headwater divides. Climate is typical of high mountain environments, mean annual precipitation exceeding 50 cm, mostly as snowfall (Martner 1982).

The Greybull and upper portions of the NF and

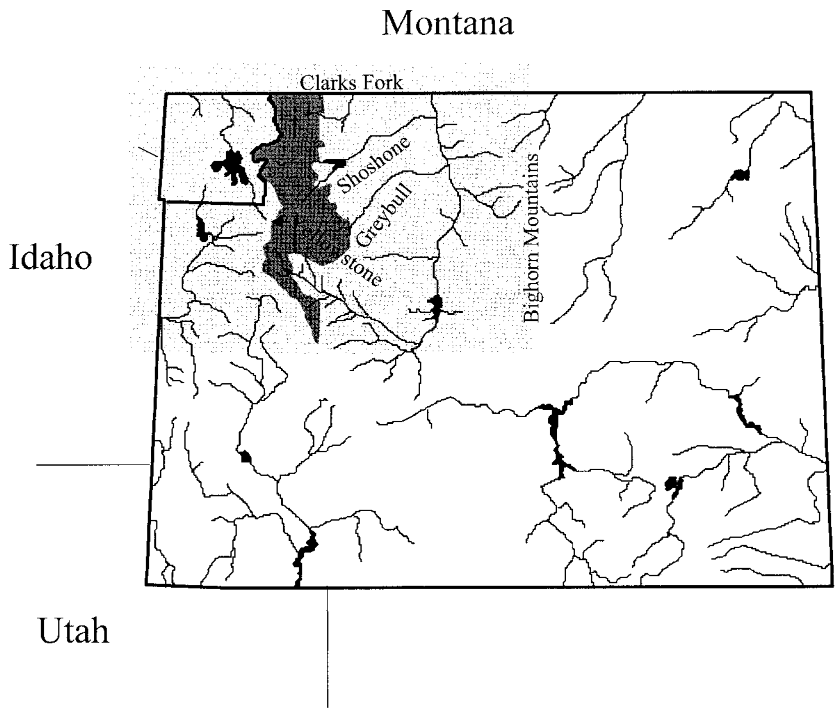

FIGURE 1.—Major drainage basins of Wyoming, showing the study area (light gray) and watersheds (labeled); the Shoshone National Forest is indicated in dark gray.

SF Shoshone river drainages are relatively inaccessible to humans and the habitat can be considered unaffected by human activity. Because of the rugged and unstable features of the area, the watersheds are part of the largest roadless area in the conterminous United States. The downstream portions of the NF and SF Shoshone rivers and the tributaries that flow into the lower portions of the watershed are affected by roads, agriculture, and irrigation withdrawals. Introductions of nonnative salmonids in the study area began about 1915. Brook trout, brown trout, and rainbow trout, which were commonly introduced until the 1970s, have established large, naturalized populations. Cutthroat trout from other basins were commonly stocked during this period. From 1972 to 1975 the nonindigenous finespotted form of cutthroat trout from the Snake River drainage was introduced into the three watersheds.

Methods

Perennial streams in the three watersheds were sampled with backpack electroshockers during low flow from July to September of 1994–1997. A single electrofishing pass was performed along a 100-m stream reach beginning at each tributary outlet and was repeated upstream, approximately every 1.0 km, until no fish were captured or visually observed in two consecutive reaches.

Locations (latitude, longitude) and elevations (m) of sampling sites were identified with global positioning units and 1:24,000 U.S. Geological Survey topographic maps. Wetted stream width (nearest 0.1 m) at five transects equally spaced through each 100-m reach was measured with a tape perpendicular to stream flow and averaged for the reach. Stream lengths (km) were measured with an electronic map wheel on the topographic maps and verified with digital hydrologic coverages derived from a geographic information system. Species distributions (km of stream occupied) in a given tributary were estimated assuming the species occupied one-half the distance between the last site the species was sampled and the next upstream site. Similarly, species sampled at a single site along the stream profile were assumed to occupy only that portion of the stream one-half the distance to the next downstream and upstream sites.

After electrofishing a reach, fish were identified, enumerated, measured (mm total length), and returned to the study reach. Fish in the *Oncorhynchus* genus were classified, based on morphological characteristics, as rainbow trout, cutthroat trout, or hybrids of rainbow trout and cutthroat trout. Genetically pure rainbow trout were identified by white pelvic fin margins, numerous spots on the head, and no red slash markings on the throat. Genetically pure Yellowstone cutthroat trout were identified by the characteristic red throat slashes, lack of white fin margins, and the presence of fewer, larger spots concentrated posteriorly. Fish with a combination of these character sets were classified as hybrids. If typical rainbow trout specimens were sampled at any given site, hybridization of cutthroat trout was assumed even if obvious hybrids were not collected. When only fish morphologically typical of genetically pure Yellowstone cutthroat trout were collected at a site, or identifications of possible hybrids were questionable, tissue samples were taken for electrophoretic verification of genetic purity. Eye, muscle, and liver tissue were removed from 20 specimens and frozen in liquid nitrogen within 1 h. Electrophoretic analysis was performed by the Wild Trout and Salmon Genetics Laboratory (WTSGL) at the University of Montana, Missoula. Analysis of 20 fish from a population or population segment provided a 99% probability of detecting introgression, which was indicated by the presence of alleles specific to rainbow trout at diagnostic loci.

When determining population size, a population was defined as a group of connected streams that contained genetically pure Yellowstone cutthroat trout and no rainbow trout or their hybrids. Contiguous distribution of trout was not required (i.e., patchy distributions were still considered a single population); however, enclaves of Yellowstone cutthroat trout that were isolated from other such groups by natural or artificial barriers or were interrupted by enclaves of nonnative trout were considered to be separate populations. By examining geographical distributions, we generally assumed that separated tributaries were part of a contiguous population if they were connected by the main stem and the distances between the tributaries were on the order of a few kilometers.

To assess genetic and demographic risks, abundance of trout in each 100-m reach was estimated by converting the number of fish captured during a single electrofishing pass (excluding age-0 fish) to an overall reach total. We did this with the equation $A = -1.863 + 1.181(\text{ONE}) + 0.797(W)$, where A is the estimate of total abundance in the 100-m reach, ONE is the number of fish captured with one electrofishing pass, and W is the wetted stream width (Kruse et al. 1998). To provide an estimate of total population size, abundance estimates (number/100 m) for each sampled reach in the tributary were averaged and extrapolated to the total continuously occupied stream length. Confidence intervals were estimated by multiplying the standard error of the estimated mean number of fish in each sampled reach by the total number of reaches occupied.

The total estimated population was converted to an effective population based on the proportion of the sampled fish in each watershed that were considered to be breeding adults. Thurow et al. (1988), summarizing several sources, reported that fluvial spawners generally exceeded 200 mm total length. Although fish less than 200 mm probably spawn, especially in high-elevation systems (Downs et al. 1997), we conservatively used 200 mm as our minimum total length for inclusion in the breeding population. We assumed that the number of breeding males and females were equal and therefore that the effective population was equivalent to the breeding population (Gall 1987).

We evaluated each remaining population of genetically pure Yellowstone cutthroat trout in terms of perceived threats to their continued existence: population size (genetic and demographic considerations), isolation, and the presence of nonnative salmonids in the watershed. Risks were assigned to each population to indicate possible extinction vulnerabilities and subsequent conservation priorities for each population. Risk levels were assigned, according to the literature and our experience, as high, moderate, low, or nonexistent, based on the most prodigious threats to Yellowstone cutthroat trout in the study area (Table 1). Although it is generally accepted that smaller, isolated populations are less likely to survive extinction pressures (Dunham et al. 1997), the threshold population size needed to resist demographic or genetic pressures is poorly understood and not based on empirical evidence (Nelson and Soule 1987). However, in our risk assessments we accepted literature-based population sizes needed to minimize population extinction: 20–30 effective individuals to minimize demographic stochasticity (summarized by Rieman and McIntyre 1993; Young 1995), 50 to minimize excessive inbreeding, and 500 to minimize loss of long-term genetic variation (Franklin 1980; Soule 1987). Remaining Yellowstone cutthroat trout populations were not considered secure, or to have a high probability of long-term persistence, unless effective population

TABLE 1.—Potential risks to the long-term persistence of remaining Yellowstone cutthroat trout populations based on effective population sizes. Risk ratings: high is of immediate concern for population persistence, moderate has potential to affect a population in the short term, low is of little concern in the short term but may have long-term consequences.

Effective population size	Demographic risk	Short-term genetic risk	Long-term genetic risk	Brook trout presence in watershed[a]	Brook trout presence in population[b]	Rainbow trout presence in watershed	Isolation
<30	High	High	High	High	High	High	High
31–50	Moderate	High	High	High	High	High	High
51–500	Low	Low	Moderate	Moderate	High	High or moderate[c]	Moderate[d]
>500	None	None	None	Low	Moderate	High or moderate[c]	None[e]

[a] Indicates that brook trout are present within the watershed where the Yellowstone cutthroat trout population is found, but not sympatrically.
[b] Indicates that brook trout are found sympatrically with Yellowstone cutthroat trout.
[c] Moderate risk when barrier is present.
[d] Moderate risk for the population directly but protects populations from exotic species.
[e] No risk for the population directly and protects populations from exotic species.

sizes exceeded the minimum value for all demographic and genetic risks (Table 1).

The presence of nonnative trout were considered a threat to Yellowstone cutthroat trout. Brook trout were considered on two levels: (1) presence in the watershed (i.e., not sampled within the defined boundary of the cutthroat trout population but with access to the population), and (2) presence in the population (sympatric with cutthroat trout). Because of their ability to outcompete Yellowstone cutthroat trout in some circumstances, brook trout within the geographical limits of a current Yellowstone cutthroat trout population were considered a high risk to all but the large populations. Large populations have a higher likelihood of sustaining themselves if brook trout are present; however, brook trout are still a moderate risk (threatening long-term survival), and any adverse effects (e.g., a decrease in Yellowstone cutthroat trout population size) could shift the risk from moderate to high. Presence of brook trout in the watershed outside the geographical extent of a small Yellowstone cutthroat trout population was considered a high risk for the population but less threatening to larger populations, which have the potential to withstand or overwhelm a brook trout invasion.

Presence of rainbow trout was considered an eminent threat to a Yellowstone cutthroat trout population because of the additive effects of hybridization and competition. Because Yellowstone cutthroat trout and rainbow trout readily hybridize, individual Yellowstone cutthroat trout sampled among sympatric rainbow trout and hybrid swarms were not considered genetically pure populations, and risks were not evaluated. The presence of rainbow trout in a watershed containing a genetically pure population of Yellowstone cutthroat was considered a high risk if connectivity between the species was apparent.

Population isolation was not considered an independent threat and was evaluated in the context of genetic, demographic, and invasion risks. For example, isolation was considered highly risky for small populations that are potentially more susceptible to genetic, demographic, or environmental extinction risks because isolation exacerbates the situation by not allowing rescue or genetic input from other populations or population segments. On the other hand, isolation can be beneficial for large populations if it prevents invasion by exotic salmonids. We considered an enclave of Yellowstone cutthroat trout to be effectively isolated if it was above a barrier to upstream movement or separated from other such enclaves by segments of river (i.e., tens of kilometers in length) occupied by nonnative salmonids.

Results

We sampled 414 sites on 172 streams (including main-stem rivers) throughout the Greybull and NF and SF Shoshone river drainages and obtained information on 10 additional tributaries in the NF Shoshone drainage (Wyoming Game and Fish Department [WGFD] records). These data provided information regarding Yellowstone cutthroat trout distributions for 182 of 188 streams and 1,705 km of the 1,751 km of perennial tributaries and main-stem rivers in the study area. It is unlikely that Yellowstone cutthroat trout exist in the unsurveyed streams (all of which are in the NF Shoshone watershed) because pure Yellowstone cutthroat trout were not found in nearby streams and all unsurveyed streams were connected to other streams with

TABLE 2.—Distributional extent of Yellowstone cutthroat trout (YSC) in the study area by drainage. Greybull River (GRB), North Fork Shoshone River (NFS), and South Fork Shoshone River (SFS).

Stream length and number	GRB	NFS	SFS	Total
Total stream kilometers	362	834	555	1,751
Stream kilometers surveyed	362	788	555	1,705
Total number of perennial streams	53	82	53	188
Total number streams sampled	53	76	53	182
Stream kilometers above barriers	73	95	172	340
Stream length (km) occupied by trout	192	432	198	822
Stream length (km) occupied by YSC	192	0	53	245
Streams with trout	22	58	24	104
Streams with only brook trout	0	5	6	11
Streams with brown trout	0	3	11	14
Streams with only *Oncorhynchus*[a]	20	29	2	51
Streams with pure YSC	22	0	5[b]	27
Streams with only pure YSC	20	0	1	21
Steams with brook trout and *Oncorhynchus*	2	27	8	37
Streams with brook trout and pure YSC	2	0	4[b]	6

[a] *Oncorhynchus* indicates cutthroat trout, rainbow trout, or their hybrids.
[b] Indicates that one of the streams containing pure YSC populations was in the main stem; however, genetically pure YSC were not found throughout the entire main-stem river.

populations of rainbow trout and hybrids of rainbow trout and cutthroat trout.

Native or introduced salmonids were found in 104 streams (57%), 51 of which contained only *Oncorhynchus* (Table 2). Genetically pure Yellowstone cutthroat trout were found in segments of 27 streams, 21 allopatrically. All 22 streams occupied by salmonids in the Greybull River watershed contained genetically pure cutthroat trout with no indication of rainbow trout introgression. The remaining five streams containing genetically pure Yellowstone cutthroat trout were in the SF Shoshone River drainage. In the NF Shoshone River watershed, all 58 occupied streams supported populations of rainbow trout or *Oncorhynchus* hybrid swarms. A few individual, genetically pure Yellowstone cutthroat trout were sampled in these streams but always within a sample that contained hybridized fish. Brook trout were found in all three drainages, but only rarely in the Greybull drainage (2 of 22 streams). Brown trout were most common in the SF Shoshone watershed (11 of 24 streams; Table 2). Assuming total salmonid (native and exotic) distributions at the time of the survey approximated the proportion of streams historically occupied by Yellowstone cutthroat trout, native trout appear to have been extirpated from 74% (77 of 104 streams) of suitable streams.

Yellowstone cutthroat trout were found in 245 km of stream habitat over the 1,751 km in the study area: none in the NF Shoshone drainage, 53 km (27% of total occupied habitat in the drainage) in the SF Shoshone drainage, and 192 km (100%) in the Greybull drainage (Table 2). Considering all perennial stream lengths in the three watersheds as potential Yellowstone cutthroat trout range, only 14% contained genetically pure Yellowstone cutthroat trout. A more likely estimate, considering only the habitat currently occupied by all trout species as potentially useable, suggests that portions or entire populations of genetically pure Yellowstone cutthroat trout have been lost from 70% of the perennial stream lengths in the study area.

The 27 tributaries and portions of three main-stem rivers containing genetically pure Yellowstone cutthroat trout were allocated into four populations. The 22 streams in the Greybull drainage were distributed between two populations: the Greybull River watershed (15 streams) and its primary tributary, the Wood River watershed (7 streams). These two populations are separated by a segment of river containing large populations of exotic salmonids and affected by irrigation withdrawals and diversion dams that effectively isolates the two populations. Four of the five SF Shoshone tributaries containing Yellowstone cutthroat trout were connected and formed a headwater population, whereas the fifth stream, Marquette Creek, near the mouth of the SF Shoshone River, was isolated by irrigation diversion structures and separated from the headwater population by a 50-km river segment.

All four populations had estimated breeding populations that appear to be large enough to withstand demographic and genetic pressures (Table 3). The Greybull at 12,300, Wood at 5,300, and Marquette at 1,600 individuals each exceeded an effective population of 1,000 individuals. The

TABLE 3.—Effective population sizes for the four genetically pure Yellowstone cutthroat populations.

Population	Mean number of cutthroat trout per 100-m reach	Total stream length (km) containing cutthroat trout	Estimated population size[a]	95% confidence interval	Estimated effective population size
Greybull River	12.9	145.0	23,200	19,960–26,450	12,300
Wood River	17.6	46.7	10,100	7,500–12,680	5,300
South Fork Shoshone River	9.2	11.3	900	400–1,390	500
Marquette Creek	18.6	15.5	2,900	460–5,300	1,600

[a] Estimated population size and effective population size cannot be exactly calculated based on the mean number of cutthroat trout and the total stream length (km) containing trout (as shown here) because the actual values are based on weighted averages (occupied length × number per 100 m) for each tributary sampled. The mean number of cutthroat trout per 100-m reach is the average for all the tributaries that make up each population.

smallest effective population (500) was in the upper SF Shoshone population. It was underestimated, however, because numbers of Yellowstone cutthroat trout in the main-stem river, which connected the other three tributaries, could not be estimated because of high discharge. Regardless, the sampled portion of the population indicated that population size was adequate to preserve long-term genetic variation and adaptability.

Because of its large population size and the presence of an irrigation diversion dam on the main stem that acts as a fish migration barrier, the Yellowstone cutthroat trout population in the Greybull River drainage had the lowest overall extinction risk of the four remaining populations (Table 4). Although the presence of rainbow trout in the watershed downstream of the barrier is a potential risk, they provide a moderate risk to the Yellowstone cutthroat trout because of the barrier. Marquette Creek, also protected by irrigation diversions, was threatened by the presence of brook trout (low risk) and rainbow trout (moderate risk) downstream of the barrier. The populations in the Wood River drainage and the SF Shoshone drainage appear to be at high risk due to the presence of rainbow trout and brook trout and the lack of barriers. None of the four populations can be considered secure because of the presence of at least a moderate risk to their continued existance.

Discussion

This watershed-scale survey exemplifies the impact of nonnative salmonids on native Yellowstone cutthroat trout. Although the competitive mechanisms are poorly understood, it is generally suspected that in many circumstances exotic salmonids will displace cutthroat trout over time when found in sympatry (Hearn 1987; Fausch 1988; Fausch 1989; DeStaso and Rahel 1994). Based on the distributions of salmonids in the study watersheds, it appears Yellowstone cutthroat trout have succumbed to competitive pressures from exotic salmonids over the majority of the three watersheds. Although Yellowstone cutthroat trout and brook trout are commingled, brook trout appear to have displaced cutthroat trout from a vast area of the SF Shoshone River headwaters. Similarly, rainbow trout have extensively hybridized with native cutthroat trout throughout the NF and SF Shoshone drainages and in most cases have replaced the Yellowstone cutthroat trout completely. In some tributaries in the NF and SF Shoshone watersheds, genetically pure Yellowstone cutthroat trout individuals were found among rainbow trout

TABLE 4.—Risks for the four genetically pure Yellowstone cutthroat trout populations, based on population size, isolation, and the presence of nonnative salmonids in the watershed. Populations with moderate or high rankings (see Table 1) should be considered unsecure (i.e., long-term persistence is threatened).

	Assessed risk						
				Brook trout			
Population	Demographic	Short-term genetic	Long-term genetic	Watershed	Population	Rainbow trout, watershed	Isolation
Greybull River	None	None	None	None	None	Moderate	None
Wood River	None	None	None	Low	Moderate	High	None
South Fork, Shoshone River	None	None	None	Low	Moderate	High	None
Marquette Creek	None	None	None	Low	None	Moderate	None

and hybrid (cutthroat trout and rainbow trout) swarms, but these individuals were not considered to represent viable populations. Although inclusion of these fish in our assessment would moderate the outcome, we considered these genetically pure fish to be insignificant in terms of value to a population or the status of Yellowstone cutthroat trout as a subspecies. Individual fish may represent a valuable component of genetic variation (Allendorf and Leary 1988; Ryman 1991; Leary et al. 1993) and should not be discounted in conservation strategies, but when found within a swarm of hybrids they cannot contribute to maintenance of genetically pure populations unless removed and used in captive breeding programs. In our samples, these individuals were generally adult fish, indicating that reproduction among pure fish has been limited, that they were migrants from pure populations in the watershed, or that they were uncharacteristic hybrids. That is, through several generations of backcrossing, individual hybrid fish could appear as genetically pure cutthroat trout at the diagnostic loci, and if the appropriate diagnostic loci are not selected, detection of hybridization in individual fish is virtually impossible. It is probable that fish appearing as pure were actually undetected hybrids.

This genetic assessment provides critical conservation information (e.g., distributions, population sizes, and genetic purity) regarding Yellowstone cutthroat trout, clarifies the status of the subspecies in Wyoming, and identifies future management needs. The Greybull and Shoshone rivers, as watersheds that remain relatively pristine and inaccessible, were considered the most likely to support expansive populations of native trout of the major watersheds within the historical range of the subspecies. However, our results indicate that habitat occupied by cutthroat trout in the watersheds has declined by almost three quarters and Yellowstone cutthroat trout have been virtually eliminated from the NF and SF Shoshone River watersheds (96% reduction). Yellowstone cutthroat trout in other river systems have suffered a similar fate. The Clark's Fork watershed, a portion of which may have been historically fishless due to barrier falls (Jordan 1891), has been extensively stocked with nonnative salmonids including hatchery raised Yellowstone cutthroat trout. Systematic sampling has found only a single, introduced population of genetically pure Yellowstone cutthroat trout (Kruse 1998; WGFD records) in approximately 1,500 km (estimated by May 1996) of perennial stream. On the west slope of the Bighorn Mountains (i.e., Bighorn River drainage) in north-central Wyoming, only three widely separated, first-order streams harbor genetically pure Yellowstone cutthroat trout (Kruse 1998); however, cutthroat trout from other sources have been introduced in all three streams. These streams compose a small portion (<1%) of the total stream habitat currently supporting trout fisheries in the western Bighorn Mountains. The estimate that Yellowstone cutthroat trout remain in only 4% of available habitat within their native range in the entire Bighorn mountain range (eastern and western slopes) appears reasonable (Steve Kozel, U.S. Forest Service, personal communication). Consequently, in northwestern Wyoming, only the Greybull River (this study) and the upper Yellowstone River drainage (contains a robust population of genetically pure cutthroat trout in 250 km of stream supported by an adfluvial link to Yellowstone Lake; Kruse 1998), still support appreciable numbers of native cutthroat trout outside of Yellowstone National Park.

The distinction of the finespotted form of cutthroat trout endemic to the Snake River drainage is a major problem when assessing Yellowstone cutthroat trout status. Conventional assessments (Varley and Gresswell 1988; May 1996) have considered trout native to the Yellowstone (which includes the Greybull, NF and SF Shoshone, and Bighorn rivers) and Snake (above Shoshone Falls) river watersheds as the Yellowstone subspecies because they lack genetic, meristic, or ecological differences (Loudenslager and Kitchen 1979; Loudenslager and Gall 1980; Leary et al. 1987). However, Behnke (1992) described the finespotted form as a separate subspecies, based on morphological (primarily spotting pattern) and geographical differences. The finespotted cutthroat trout is found throughout most of its historical range in the Snake River watershed of Wyoming (approximately 2,500 km of perennial streams; May 1996). If considered a form of Yellowstone cutthroat trout, the inclusion of the present-day finespotted cutthroat trout range (as in May 1996) lessens the decline in the overall distribution of the Yellowstone cutthroat trout subspecies. Finespotted cutthroat trout were extensively stocked into the study watersheds from 1972 to 1975. Visual field assessments and genetic analysis have confirmed the integration of the finespotted form in the Greybull and Marquette populations. If the finespotted cutthroat trout is a unique subspecies, its integration with endemic cutthroat trout of the Greybull and Marquette populations eliminates them from consideration as genetically pure Yellowstone cutthroat trout. Subsequently, the upper Yellowstone River may be the only secure population of pure Yellowstone cutthroat trout in Wyoming outside of Yellowstone National Park.

The decline of many native species due to population fragmentation caused by habitat loss or nonnative species invasions has provided insight into the viability and long-term persistence of isolated populations (Boyce 1992; Emlen 1995; Young 1995; Dunham et al. 1997; Guffey et al. 1998). It is likely that extinction probabilities for stream salmonids increase, because of deterministic, genetic, and stochastic processes, as population connectivity and size decrease (Harrison 1991; Rieman and McIntyre 1993). Because Yellowstone cutthroat trout populations have declined in both size and numbers, we developed a risk assessment protocol to evaluate the status of each remaining population in the study watersheds. The evaluation was not intended to provide a measure of population viability but rather an assessment of potential risks to the persistence of each population.

Once a population has become fragmented or reduced in size, remaining population fragments may not be large enough to maintain evolutionary processes and demographic needs. Although some small (e.g., <100 individuals) salmonid populations have considerable perseverance (see Young et al. 1996), genetic and demographic concerns are increasingly important as population size decreases to a threshold below which population recovery on its own would be unlikely (Schaffer 1987; Harrison 1991; Boyce 1992). Additionally, healthy populations may quickly become at risk if stochastic environmental perturbations decimate a population. Rieman and McIntyre (1993), summarizing several sources addressing bull trout, suggested that demographic risks are minimal until effective populations are reduced to around 20 individuals. Young (1995) suggested 30–50 individuals. The minimum number of individuals needed to mitigate genetic loss is difficult to estimate (Rieman and McIntyre 1993; Rieman et al. 1993), but Soule (1987) proposed the ''50/500 rule'' as a guide. Under this rule, an effective population size of 50 is needed to circumvent excessive inbreeding in isolated populations, whereas 500 individuals will maintain genetic variation in the long-term and preserve adaptive ability. Others have suggested more conservative guidelines for minimizing genetic and demographic risks. Nelson and Soule (1987) suggest a ''500/5,000 rule'' to alleviate genetic risks, whereas Rieman and McIntyre (1993) speculate that salmonid populations of less than 2,000 individuals may experience much higher extinction probabilities. Appropriate population sizes can be expected to vary among species and groups of species (Boyce 1992). The effective sizes of all four populations in our study suggest that demographic or genetic constraints are currently a minimal risk to population persistence.

A more obvious risk to remaining Yellowstone cutthroat trout populations is the invasion of nonnative salmonids. Whereas most evaluations of native stream salmonids (e.g., bull trout, cutthroat trout, brook trout) suggest that nonnative introductions and invasions are at least partially responsible for their decline (Rieman and McIntyre 1995; Dunham et al. 1997; Guffey et al. 1998), we suggest that nonnatives are the single most important reason that Yellowstone cutthroat trout have declined in the study area. We found no evidence to indicate that habitat alteration had significantly affected the remaining populations. Additionally, habitat segregation among brook, rainbow, and cutthroat trout was not apparent (Kruse 1998), suggesting that habitat refugia or areas having characteristics unique to cutthroat trout are unavailable within the narrow range of habitats we observed across the study watersheds. Thus, nonnative salmonids will probably invade and affect all remaining cutthroat trout populations, given the opportunity. Because brook trout were present within the boundaries of two of the four populations and rainbow trout were found in all the watersheds, we consider all four populations to be at least moderately threatened by competition or hybridization. The Greybull and Marquette populations were protected by irrigation structures that prevent the upstream movement of brook trout and rainbow trout, which were both found immediately downstream from the structures.

Isolation was considered as a risk to remaining Yellowstone cutthroat trout populations; however, we recognize that an assessment of isolation is inherently tied to other risks. Isolation may be harmful because it prevents genetic exchange or rescue after catostrophic events, but when isolation prevents invasion of nonnative salmonids, presumably a more immediate and prodigious threat, the harmful effects of isolation are moderated. Population structure (e.g., metapopulation, source-sink; Harrison 1994; Hanski and Gilpin 1997) is an important consideration when assessing isolation. Individual movement or dispersal (highlighted in recent works by Brown and MacKay 1995;

Young 1996; Jakober et al. 1998) may be important for population maintenance in light of extinction risks presented by stochastic environmental events and limited habitat diversity in headwater areas of the Absaroka Mountains. Although we have little information on movements of Yellowstone cutthroat trout in the study area, we speculate that the small streams in headwater habitats may not support large, permanent Yellowstone cutthroat trout populations. Rather, small headwater populations may need an influx of individuals from more secure, lower-elevation habitats during favorable conditions, a process that has been eliminated in many portions of the watersheds by population fragmentation and isolation. We believe all four populations were isolated from each other, either by a physical barrier or distance; however, they may be large enough to withstand the harmful effects of isolation, unless population size is suddenly reduced by unpredictable events.

Environmental stochasticity is an important consideration with fragmented and isolated populations because catastrophic events (environmental disturbance of sufficient size to impact a population) can affect population survival regardless of population size. Environmental events can disrupt aquatic communities (Siegfried and Knight 1977; Reice et al. 1990; Lamberti et al. 1991; Bozek and Young 1994). However, the unpredictability of both the event (timing and level of effect) and the population's response has precluded development of estimates of minimum population sizes needed to withstand catastrophic events. Some researchers have attempted to quantify the risk presented by catastrophic events to cutthroat trout populations (Lande 1988; Probst et al. 1992; Rieman and McIntyre 1993; Dunham et al. 1997). We did not attempt to predict the frequency, intensity, or effect of catastrophic events but point out that because of the geologic instability and climate of the Absaroka Mountains, flood flows, severe droughts, and debris torrents are frequent events and are likely to cause local extirpations of cutthroat trout populations. For example, one tributary stocked by WGFD in the Greybull watershed, which was isolated from upstream migrants by a geologic barrier, experienced a 30-fold decrease in abundance over 3 years of the study—a result putatively attributed to abnormally high spring flows (Kruse, unpublished data). Because habitat diversity was low (predominately boulder step-pool) in the watersheds and environmental conditions are more variable in high-elevation systems, trout densities in the study area are lower than statewide averages (Kruse 1995). Thus, it will probably be more difficult for the remaining Yellowstone cutthroat trout populations to overcome catastrophic population reductions. Conservation strategies need to consider the ramifications of catastrophic events and provide for instream refugia (Hawkins and Sedell 1990; Sedell et al. 1990) and population connectivity (Wilcox and Murphy 1985; Taylor et al. 1993).

Headwater population segments of Yellowstone cutthroat appear resilient to demographic, genetic, and environmental influences when main-channel and lower-elevation refugia are available. However, the ability of nonindigenous salmonids to hybridize and compete with Yellowstone cutthroat trout has fragmented the remaining fish into four smaller populations and eliminated them from most of the main-stem, lower-elevation habitats. It appears that Yellowstone cutthroat trout have been eliminated from about 90% of fluvial habitat in the state of Wyoming. Only two watersheds outside of Yellowstone National Park support populations with high probabilities of persistence without substantial management intervention, and only one watershed (the upper Yellowstone River drainage) should be considered to support truly endemic Yellowstone cutthroat trout. Although habitat alterations may have had substantial effects on native trout in higher-order rivers, we found little evidence of habitat degradation in the study area. Rather the presence of introduced, hybridizing, and competing salmonid species has been the primary causal agent of Yellowstone cutthroat trout declines. Nonnative fishes will continue to exert pressures on the few remaining Yellowstone cutthroat trout populations and will exacerbate genetic and demographic risks of population extinctions. It is likely that the few remaining genetically pure enclaves found in Wyoming will be eliminated within decades without intense management to control exotic salmonids and to reestablish large, genetically pure, allopatric populations of Yellowstone cutthroat trout. Consequently, conservation of Yellowstone cutthroat trout will require control of nonnative fishes and reconnection of vast areas of headwater streams and main-stem river systems—a daunting challenge.

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References

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170–184.

Anders, P. J. 1998. Conservation aquaculture and endangered species: can objective science prevail over risk anxiety? Fisheries 23(11):28–31.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481–506.

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

Bozek, M. A., and M. K. Young. 1994. Fish mortality resulting from delayed effects of fire in the greater Yellowstone ecosystem. Great Basin Naturalist 54: 91–95.

Breckenridge, R. M. 1975. Quaternary geology of the Wood River area, Wyoming. Pages 45–54 *in* R. A. Exum and G. R. George, editors. Geology and mineral resources of the Bighorn basin. 27th Annual Field Conference. Wyoming Geological Association, Cheyenne, Wyoming.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Brown, R. S., and W. C. Mackay. 1995. Spawning ecology of cutthroat trout (*Oncorhynchus clarki*) in the Ram River, Alberta. Canadian Journal of Fisheries and Aquatic Sciences 52:983–992.

DeStaso, J., III, and F. J. Rahel. 1994. Influence of water temperature on the interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Transactions of the American Fisheries Society 123:289–297.

Downs, C. C., R. G. White, and B. B. Shepard. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. North American Journal of Fisheries Management 17:85–92.

Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North American Journal of Fisheries Management 17:1126–1133.

Emlen, J. M. 1995. Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 52:1442–1448.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences 45:2238–2246.

Fausch, K. D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? Physiology and Ecology Japan Special Volume 1:303–322.

Ferguson, M. M. 1990. The genetic impact of introduced fishes on native species. Canadian Journal of Zoology 68:1053–1057.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–149 *in* M. E. Soule and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Massachusetts.

Gall, G. A. E. 1987. Inbreeding. Pages 47–88 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. Pages 13–34 *in* M. E. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinuaer, Sunderland, Massachusetts.

Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pages 36–54 *in* M. K. Young, editor. Conservation assessment for inland cutthroat trout. U.S. Forest Service, General Technical Report RM-GTR-256.

Griffith, J. S. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265–273.

Guffey, S. Z., G. F. McCracken, S. E. Moore, and C. R. Parker. 1998. Management of isolated populations: southern strain brook trout. Pages 247–265 *in* J. D. Peine, editor. Ecosystem management and sustainability. CRC Press, Boca Raton, Florida.

Hanski, I. A., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics and evolution. Academic Press, San Diego, California.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73–88.

Harrison, S. 1994. Metapopulations and conservation. Pages 111–128 *in* P. J. Edwards, N. R. Webb, and R. M. May, editors. Large-scale ecology and conservation biology. Blackwell, Oxford, UK.

Hawkins, C. P., and J. R. Sedell. 1990. The role of refugia in the recolonization of streams devastated by the 1980 eruption of Mount St. Helens. Northwest Science 64:271–274.

Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream dwelling trout and salmon: a review. Fisheries 12(5):24–31.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127: 223–235.

Johnson, J. E. 1987. Protected fishes of the United States and Canada. American Fisheries Society, Bethesda, Maryland.

Jordan, D. S. 1891. A reconnaissance of the streams, and lakes of the Yellowstone National Park, Wyoming, in the interest of the United States Fish Commission. U.S. Fish Commission Bulletin 9:41–63. (Not seen; cited *in* May 1996)

Keefer, W. R. 1972. The geologic story of Yellowstone National Park. U.S. Geological Survey Bulletin 1347.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48(Supplement 1):66–77.

Kruse, C. G. 1995. Genetic purity, habitat, and population characteristics of Yellowstone cutthroat trout in the Greybull River drainage, Wyoming. Master's thesis. University of Wyoming, Laramie.

Kruse, C. G. 1998. Influence of non-native trout and geomorphology on distributions of indigenous trout in the Yellowstone River drainage of Wyoming. Doctoral dissertation. University of Wyoming, Laramie.

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

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flows. Canadian Journal of Fisheries and Aquatic Sciences 48:196–208.

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

Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conservation Biology 7:856–865.

Leary, R. F., F. W. Allendorf, S. R. Phelps, and K. L. Knudsen. 1987. Genetic divergence and identification of seven cutthroat trout subspecies and rainbow trout. Transactions of the American Fisheries Society 116:580–587.

Loudenslager, E. J., and G. A. E. Gall. 1980. Geographic patterns of protein variation and subspeciation in cutthroat trout, *Salmo clarki.* Systemic Zoology 29: 27–42.

Loudenslager, E. J., and R. M. Kitchen. 1979. Genetic similarity between two forms of cutthroat trout, *Salmo clarki,* in Wyoming. Copeia 1979:673–678.

Martner, B. 1982. Wyoming climate atlas. University of Nebraska Press, Lincoln.

May, B. 1996. Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*). Pages 11–43 *in* D. A. Duff, editor. Conservation assessment for inland cutthroat trout. U.S. Forest Service, Intermountain Region, Ogden, Utah.

Nelson, K., and M. E. Soule. 1987. Genetical conservation of exploited fishes. Pages 345–368 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Nelson, W. H., H. J. Prostka, and F. E. Williams. 1980. Geology and mineral resources of the North Absaroka wilderness and vicinity, Park County, Wyoming. U.S. Geological Survey Bulletin 1447.

Probst, D. L., J. A. Stefferud, and P. R. Turner. 1992. Conservation and status of Gila trout, *Oncorhynchus gilae.* Southwestern Naturalist 37:117–125.

Reice, S. R., R. C. Wissmar, and R. J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14:647–659.

Rieman, B., D. Lee, J. McIntryre, K. Overton, and R. Thurow. 1993. Consideration of extinction risks for salmonids. U.S. Forest Service, Technical Bulletin 14.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of various size. Transactions of the American Fisheries Society 124:285–296.

Ryman, N. 1991. Conservation genetics considerations in fishery management. Journal of Fish Biology 39(Supplement A):211–224.

Schaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 69–86 *in* M. E. Soule, editor. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Sedell, J. R., G. H. Reeves, R. R. Hauer, J. A. Stanford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711–724.

Siegfried, C. A., and A. W. Knight. 1977. The effects of washout in a Sierra foothill stream. American Midland Naturalist 98:200–207.

Soule, M. E. 1987. Where do we go from here? Pages 175–183 *in* M. E. Soule, editor. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Sundell, K. A. 1993. A geologic overview of the Absaroka volcanic province. Pages 481–506 *in* A. W. Snoke, J. R. Steadman, and S. M. Roberts, editors. Geology of Wyoming, memoir no. 5. Geologic Survey of Wyoming, Laramie.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Thurow, R. F., C. E. Corsi, and V. K. Moore. 1988. Status, ecology, and management of Yellowstone cutthroat trout in the upper Snake River drainage, Idaho. Pages 25–36 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Varley, J. D., and R. E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. Pages 13–24 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout.

American Fisheries Society, Symposium 4, Bethesda, Maryland.

Wang, L., and R. J. White. 1994. Competition between wild brown trout and hatchery greenback cutthroat trout of largely wild parentage. North American Journal of Fisheries Management 14:475–487.

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

Young, M. K. 1995. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-256.

Young, M. K. 1996. Summer movements and habitat use by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences 53:1403–1408.

Young, M. K., R. N. Schmal, T. W. Kohley, and V. G. Leonard. 1996. Conservation status of Colorado River cutthroat trout. U.S. Forest Service General Technical Report RM-GTR-282.