STATUS OF WESTSLOPE CUTTHROAT TROUT IN THE MADISON RIVER BASIN: INFLUENCE OF DISPERSAL BARRIERS AND STREAM TEMPERATURE

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ABSTRACT

We evaluated the contemporary distribution and abundance of westslope cutthroat trout (*Oncorhynchus clarki lewisi*; WCT) in the Madison River basin, southwest Montana in relation to fish dispersal barriers and stream temperatures. Westslope cutthroat trout distribution boundaries were primarily shaped by natural fish dispersal barriers that excluded nonnative salmonids from upstream reaches. Most WCT populations occupied relatively short stream lengths ($\bar{x}$= 4.51 km, SE = 1.1), and densities ($\bar{x}$=21.9 fish >75 mm total length/100 m of stream, SE= 3.2) were generally much lower than in other drainages inside their range within Montana. Where WCT and nonnative salmonids segregated without the influence of dispersal barriers, distribution boundaries were related to stream temperature with WCT occupying colder stream reaches. Patterns of fish occurrence and stream temperature indicated that WCT have been displaced from warmer stream habitats and now occupy a narrower and colder range of stream temperatures than they did historically. Isolated populations of WCT encountered a higher and greater range of average summer stream temperatures and reached higher abundances than those populations in streams without dispersal barriers. This suggests that while colder stream temperatures may provide a competitive advantage for WCT relative to nonnative species, these habitats may be marginal due to lower individual fitness and reproductive success of WCT. Because low population sizes and isolation place many WCT populations at risk of extirpation, we recommend that WCT populations in the Madison Basin be replicated and expanded downstream to ensure their long term persistence.

Key words: competition, dispersal barrier, fish distribution, hybridization, *Oncorhynchus clarki, O. c. lewisi*, stream temperature, westslope cutthroat trout

INTRODUCTION

Because of their popularity as sport fish, many salmonid species have been transplanted outside their native ranges throughout North America. Introductions of nonnative salmonids have typically resulted in range constriction or elimination of native species as a result of predation, competition, or hybridization (Gresswell 1988, Behnke 1992). In some situations native salmonids have persisted in the presence of introduced species, but the mechanisms that regulate displacement, and the habitat conditions that provide refuges for native species are not well understood (Fausch 1988, Gresswell 1988, Bozek and Hubert 1992).

As with other interior stocks of cutthroat trout (*Oncorhynchus clarki*), populations of westslope cutthroat trout (*O. c. lewisi*; WCT) have declined throughout their historical range (Hanzel 1959, Liknes and Graham 1988, Behnke 1992). In

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Montana, declines of WCT have been most substantial within the Missouri River basin, with genetically pure populations occupying <5 percent of the historical range (Shepard et al. 1997). The original distribution of WCT within the Missouri River basin is thought to include the entire Missouri River drainage upstream from Fort Benton, Montana, including the Gallatin, Madison, and Jefferson drainages, as well as the headwaters of the Judith, Milk, and Marias rivers, which join the Missouri River downstream from Fort Benton (Behnke 1992). Prior to about 1900, the Madison River and its principal tributaries supported abundant populations of WCT upstream to barrier falls on the lower Firehole and Gibbon rivers in Yellowstone National Park (Jordan 1891). WCT abundance and distribution declined rapidly early in the 1900s (USDI Fish And Wildlife Service 1999) and by the early 1950's WCT no longer occurred in the Madison River or its principal tributaries within Yellowstone National Park (Benson et al. 1959), and were restricted to headwater habitats elsewhere in the drainage (Hanzel 1959).

Factors responsible for declines of WCT include habitat alterations caused by land and water use practices, overharvest, and introductions of nonnative fishes (Hanzel 1959; Liknes and Graham 1988, Behnke 1992, McIntyre and Rieman 1995). Interactions with nonnative species through predation, competition, or hybridization probably constitute the greatest contemporary factor responsible for the loss of WCT populations (Allendorf and Leary 1988, Liknes and Graham 1988, USDI Fish And Wildlife Service 1999).

Extant populations of WCT within the Madison River drainage are now restricted to headwater habitats, often above the upstream limit of nonnative salmonids (Sloat et al. 2000). In allopatry, WCT are capable of inhabiting a much broader range of habitats. Historically, WCT occupied small headwater streams and larger rivers, as well as mid- to low-elevation lakes (Shepard et al. 1984, Marnel 1988, Behnke 1992) and individuals are known to make extensive migrations between these habitats (Bjornn and Mallet 1964, Shepard et al. 1984, Schmetterling 2001). Interactive niche compression resulting from the influence of nonnative salmonids may partially explain the confinement of WCT to headwater habitats (Mullan et al. 1992). Fausch (1989) hypothesized that colder, higher gradient headwater habitats provide refuges for cutthroat trout, where nonnative salmonids either cannot persist or where environmental conditions tip the balance of interspecific competition to favor cutthroat trout. Behnke (1992) suggested that cutthroat trout might have a selective advantage over nonnative trout in headwater areas because they may function better in cold environments. Field and laboratory studies have demonstrated the importance of temperature in shaping cutthroat trout distribution (DeStaso and Rahel 1994, Mullan et al. 1992, Dunham et al. 1999). Cutthroat trout also have slightly lower thermal tolerances than nonnative salmonids (Heath 1963, Feldmuth and Erikson 1978, DeStaso and Rahel 1994). Even relatively small differences in salmonid thermal tolerances can reflect substantial differences in growth optima (Takimi et al. 1997), competitive ability (DeStaso and Rahel 1994), and regional distributions (Fausch et al. 1994). Consequently, the influence of temperature on the distribution of WCT has become a central concern in management for this subspecies. However, despite evidence that temperature is important, relatively little information is available to assess thermal regimes that provide suitable habitat for WCT or provide refuges from competition and hybridization with introduced salmonids.

Another factor potentially affecting the distribution of WCT in streams is the occurrence of dispersal barriers. Natural and anthropogenic dispersal barriers may restrict the distribution of salmonids (Kruse et al. 1997, Dunham et al. 1999) and in some cases protect native salmonids from potential displacement by nonnative species (Rinne and Turner 1991, Young et al. 1996).

Our goal was to explore how spatial patterns of fish dispersal barriers and stream temperature influenced the distribution of remnant WCT populations in the Madison River basin, Montana. Our specific objectives were to: 1) describe the contemporary distribution and abundance of WCT in the Madison River basin; 2) determine the influence of fish dispersal barriers on the distribution and abundance of WCT; and 3) determine the thermal characteristics of habitats occupied and unoccupied by WCT.

METHODS

Study Area

This study was conducted in the 906-km^2 Madison River Valley, a north-trending intermontane basin located in southwest Montana. The Madison River is formed at the confluence of the Firehole and Gibbon rivers in Yellowstone National Park and flows approximately 195 km northward before joining the Gallatin and Jefferson rivers to form the Missouri River near the town of Three Forks, Montana. Our study focused on tributaries to the 101 km section of the Madison River between Hebgen and Ennis reservoirs (Fig 1).

The study area was bordered by mountain ranges that differ in their morphology. The Madison Range forms the eastern boundary of the study area and rises sharply from the valley floor to peak elevations exceeding 3200 m. The Gravelly Range forms the western border of the study area and is less rugged than the Madison Range with elevations not exceeding 2900 m. Although the alluvial plain in the Madison River valley is predominantly in private ownership, the majority of the basin is public and managed by the USDA Forest Service (FS). The primary land use in the Madison Valley is livestock grazing with localized dryland and irrigated agriculture. Limited logging has occurred on FS land in the Gravelly Mountains. Land use is restricted in the Lee Metcalf Wilderness Area, which encompasses most of the Madison Range within our study area. Snowmelt drives flow regimes in tributary streams, and peak discharges occurred in May and June. Streams ranged from first to fourth-order (measured from 1:24,000-scale USGS topographic maps after Strahler [1957]) with drainage areas between 9.2 and 128.8 km^2. Mixed conifer stands dominated riparian vegetation adjacent to study streams in headwater reaches, except along unconstrained reaches where willows (*Salix* spp.) dominated. Willows, sedges (*Carex* spp.), and grasses typically dominated downstream reaches. Sloat et al. (2000) provide detailed descriptions of individual study streams.

The climate of the Madison River Valley is typical of high-elevation intermontane basins with mild summers and cold winters. The average annual precipitation is 33.7 cm, and the average annual air temperature is 6.4 °C on the valley floor (NOAA 1999).

During the last 100 years, several nonnative salmonid species have been introduced into the Madison River (Montana Fish, Wildlife and Parks 2000). Rainbow trout (*O. mykiss*) and brown trout (*Salmo trutta*) were stocked periodically into the Madison River and its tributaries as early as 1889 (USDI Fish And Wildlife Service 1999) and were well established by the 1930's (USDI Fish And Wildlife Service 1954). Releases of hatchery-raised rainbow trout into the Madison River continued until 1974 (Vincent 1987). Yellowstone cutthroat trout (*O. c. bouvieri*) have been stocked in the Madison River drainage since the early 1950's, primarily in high mountain lakes, but also in many streams. Yellowstone cutthroat trout stocking in the Madison Range continued through the period of our study (Montana Fish, Wildlife and Parks 2000). Within the Madison River drainage the only native salmonids to co-occur with WCT were mountain whitefish (P*rosopium williamsoni*) and arctic grayling (*Thymallus arcticus*). The Madison River grayling population disappeared as early as 1920 (USDI Fish And Wildlife Service 1954), and only a vestigial population now inhabits Ennis Reservoir. Native nonsalmonid

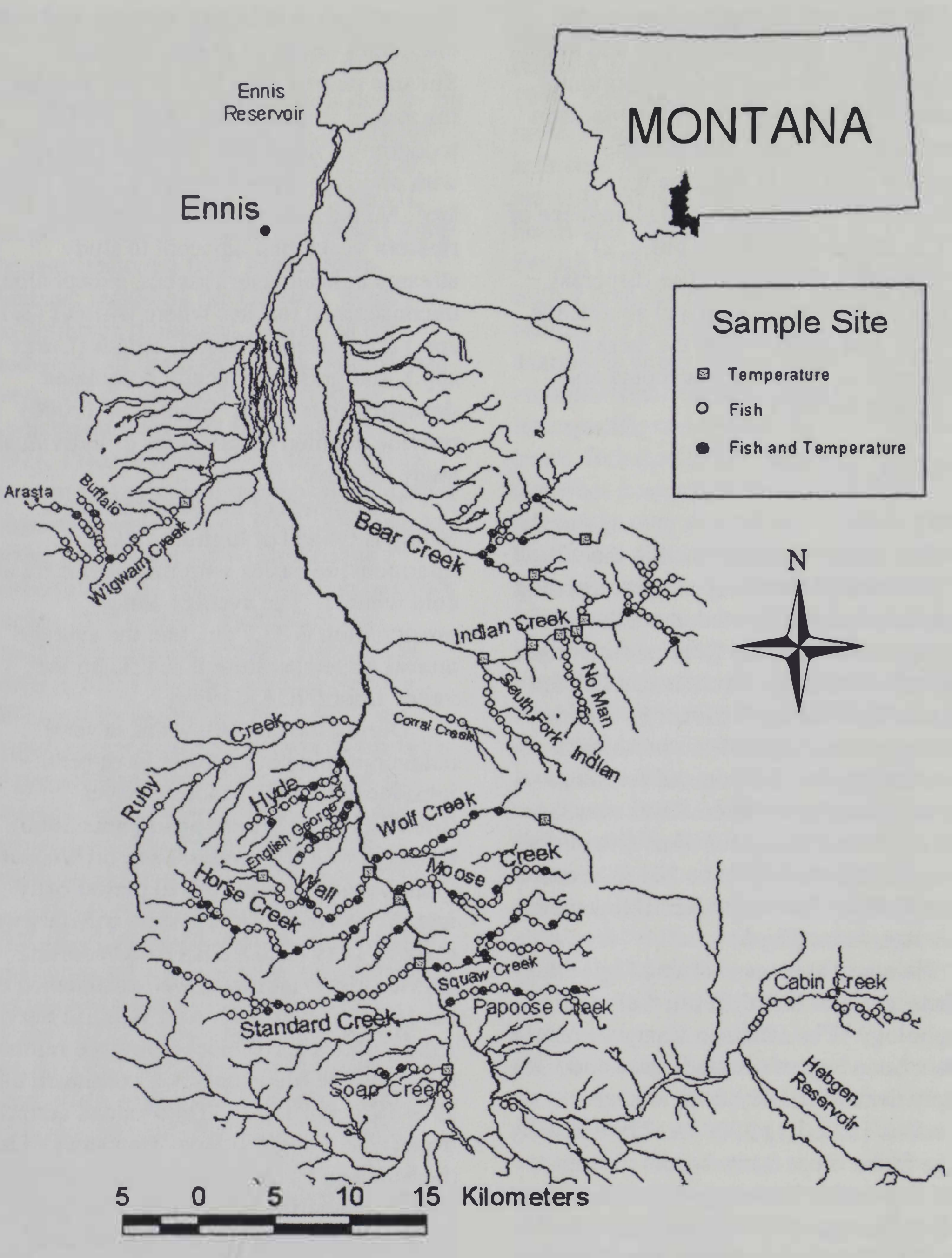

Figure 1. Map of Madison River drainage from Hebgen Reservoir to Ennis, Montana showing names of major streams sampled, and sample sites by type (Temperature = temperature recording site; Fish = electrofishing sample sites; Fish and Temperature = temperature recording and electrofishing sample site). Lower reaches of Bear, Corral, Indian, and Wigwam creeks were dry.

fishes present in the Madison River drainage include white sucker (*Catostomus commersoni*), longnose sucker (*C. catostomus*), mountain sucker (*C. platyrhynchus*), longnose dace (*Rhinichthys cataractae*), and mottled sculpin (*Cottus bairdi*) (Federal Energy Regulatory Commission 1997) but mottled sculpin was the only nonsalmonid species observed in Madison River tributaries.

Fish Distribution Sampling

We employed a systematic sampling

design to determine relative abundance and distribution of fishes. Our primary objective was to locate remnant WCT populations and we did not sample streams if previous inventories indicated that they contained only nonnative species. We sampled streams at 0.8 km (0.5 mi) intervals by single-pass electrofishing and at 3.2 km (2.0 mi) intervals, multiple-pass depletion population estimates were made (VanDeventer and Platts 1985). Smith-Root electrofishers (Models SR-15B, SR-12B) were used for all electrofishing. We slightly modified this protocol in some streams with more frequent sampling to document the upper and lower extent of distribution of each fish species. To help ensure that we captured all species present, sample section lengths were at least 35 times the average wetted stream width (Lyons 1992). Sample sites were referenced by stream kilometer starting at the mouth and by latitude and longitude obtained from a Global Positioning System (GPS). Sampling progressed upstream until trout were no longer present; then an additional upstream site was usually sampled to ensure fish absence. We recorded total length (TL) and weight for all captured salmonids. Most fish distributions were sampled during the summers of 1997, 1998, and 1999, but data for Soap Creek were collected in 1995.

When conducting multiple depletion population estimates, if field-calculated probabilities of capture (calculated as 1-[C2/C1]; where C1= number captured on the first pass, and C2 = number captured on second pass) were <0.80 after two passes, up to two additional passes were made until capture probabilities reached 0.80 (cf., Riley and Fausch 1992). Relative abundance was calculated by species as the number of fish ($\geq$75 mm TL)/100 m of stream captured in the first (or only) electrofishing pass. Population estimates were calculated using a maximum likelihood estimator within the MICROFISH program (Van Deventer and Platts 1985) and standardized as the number of fish/100 m of stream length.

Field identification of fish species was based on spotting pattern, body color, and presence/absence of an orange "cutthroat" slash below the lower mandible described for WCT in Behnke (1992) and was confirmed with genetic testing for most streams. Either whole fish or, most often, fin samples from fish identified as WCT were taken for genetic analysis. Genetic characteristics were determined by horizontal starch gel electrophoresis (whole fish) or by Paired Interspersed Nuclear DNA Element-PCR (PINE [fin clips]) by the University of Montana Wild Trout and Salmon Genetics Laboratory. Where possible, we sampled 25 field-identified WCT/stream, which provides a 95-percent chance of detecting as little as a 1 percent Yellowstone cutthroat or rainbow trout genetic contribution to a hybridized population of WCT (Spruell and Miller 1999). Often, however, the sample size was lower than 25 fish (Appendix A). Where possible, a portion of the 25-fish sample was captured at each of multiple sampling sites within a stream to test for longitudinal changes in genetic composition within a population. Fish were considered WCT if frequencies of alleles characteristic of WCT were ≥90 percent. This was based on management guidelines of Montana Fish, Wildlife and Parks that provide populations with >90 percent genetic purity the same protections afforded pure WCT because these populations indicate suitable habitat for WCT and may have genetic value for future conservation efforts (Montana Fish, Wildlife and Parks 1999). Hybridized populations of WCT with >10 percent introgression were classified as nonnative salmonids.

Potential barriers to fish movement, defined as structures with vertical drops at least 1.5 m high (Stuber et al. 1988, Kruse et al. 1997), were identified by surveying the entire length of each tributary. Barrier locations were referenced by latitude and longitude using a hand-held GPS unit and input into the geographic information system (GIS) computer program ArcView (Environmental Systems Research Institute 1999) and projected on 1:100,000 stream hydrography layers. Barriers consisted of waterfalls, decadent beaver (*Castor canadensis*) dam complexes, and irrigation diversion dams.

We derived length of habitat occupied by WCT and nonnative salmonids for each tributary drainage in ArcView using 1:100,000 stream hydrography layers and then made comparisons using Welch's modified t-test, which does not assume equality of group variances (Zar 1984). Occupied habitat lengths were defined as the total occupied stream kilometers in a drainage not interrupted by a dispersal barrier, and did not include the main stem of the Madison River.

Stream Temperature Sampling

Continuously recording digital thermographs ("Hobo" and "Stowaway" models, Onset Corp.; http://www.onsetcomp.com) were used to record water temperatures in first- to fourth-order streams (Strahler 1957) across the Madison River basin (Fig. 1). Thermographs were capable of measuring temperatures ranging from -5 to 37 °C with an accuracy of ± 0.2 °C. Prior to field deployment, thermographs were calibrated against a National Institute of Science and Technology hand held thermometer at 3, 9, and 20 °C.

Thermographs were deployed from early July to late September. Where trout distributions were known a priori, we placed thermographs at upper and lower distribution boundaries. For many streams where distributions were not known, thermographs were uniformly distributed along the stream's length. We placed a minimum of three thermographs from 1 to 7 km apart in principal study streams and at the mouths of smaller tributaries. Thermographs were placed in well-mixed run or pool habitats and were shielded from direct sunlight. Thermographs recorded hourly stream temperatures that we summarized into daily maxima, minima, and means.

Because of a limited number of thermographs available for this study and the extensive time involved in placing thermographs in the field, not all tributaries sampled for fish had thermographs. We collected stream temperature data from 71 sites in 1999 but also measured stream temperatures at six sites during 1998 and two sites in 1997.

The following temperature metrics were calculated for sites where both fish abundance and stream temperature data were collected: Maximum Average Daily Temperature (MDAT)—the maximum of all average daily temperatures within a year; Maximum Daily Maximum Temperature (MDMT)—the maximum of all maximum daily temperatures within a year; Maximum Weekly Average Temperature (MWAT)—the maximum seven-day average of daily average water temperatures; Maximum Weekly Maximum Temperature (MWMT)—the maximum seven-day average of daily maximum water temperatures; and Degree Days (DD): the sum of average daily temperatures over 0 °C. During 1999, not all thermographs were in place by 1 July. Therefore, to facilitate comparison, degree-days were calculated from 8 July to 15 September when all thermographs were in place and recording. We used t-tests and analysis of variance (ANOVA) ($\alpha = 0.05$) to test the hypothesis that stream temperatures were significantly colder at sites occupied by WCT than those occupied only by nonnative salmonids. We did not include sites if fish densities were <3 fish >75 mm TL/100 m of stream because extremely low densities of fish, indicating potential habitat limitations at some locations, may have biased the analysis. Fish sampling events were matched with temperature records corresponding most closely in time, but in some cases stream temperatures were not measured during the same year as the fish sampling event. For this analysis, we made two assumptions: 1) fish distribution boundaries did not change over the relatively short time period of this study; and 2) measured stream temperatures were representative of temperatures experienced by fish during the year fish distribution data were collected.

RESULTS

Fish Distribution

We determined the distribution of WCT in the Madison River drainage between Hebgen and Ennis reservoirs using samples from 318 locations in 58 streams within 18 different sub-drainages (Fig. 2). Except for Trail Creek from which data were unavailable, results for genetic testing of all field-identified WCT populations appear in Appendix A. Westslope cutthroat trout (>90% purity) were present in 79 (25 %) of 318 sites sampled—portions of 17 of 58 streams. We found nonnative trout species, including rainbow, brown, and Yellowstone cutthroat trout, as well as hybridized WCT with >10 percent introgression, in 133 (42 %) of 318 sample sites. Hybrid cutthroat trout were present in 48 of the 133 sample sites occupied by nonnative salmonids (15% of all sample sites). No fish were captured in 106 sample sites (Fig. 2).

Within the Madison River basin, distribution of WCT was concentrated in streams draining the Gravelly Range. In this range, we found WCT in six of nine sampled sub-drainages. Because some sub-drainages included more than one occupied stream, these six sub-drainages represented occurrence in 11 streams. All WCT populations but one (Arasta Creek) were isolated from nonnative species by dispersal barriers. Natural barriers to fish dispersal were found in eight of the nine sub-drainages sampled in the Gravelly Range. In six sub-drainages, nonnative salmonids were present up to the base of the barrier and only WCT were present upstream. Nonnative salmonids were present both above and below barriers (2-5 m high vertical falls) to fish migration in the two remaining sub-drainages (3 streams).

Except in Hyde Creek, where a large beaver dam complex prohibited upstream migration of nonnative salmonids, all dispersal barriers in streams draining the Gravelly Range consisted of waterfalls. Typically, fish dispersal barriers were located relatively low in streams draining the Gravelly Range. The average distance above the stream's mouth and mean elevation of dispersal barriers in the Gravelly Range were 3.9 km (SE= 1.7) and 1954 m (SE = 79), respectively.

Westslope cutthroat trout were found less frequently in streams draining the Madison Range. Only 4 of 10 sub-drainages (6 of 35 streams) sampled in the Madison Range supported WCT (Fig. 2), and in contrast to the Gravelly Range, we found only one WCT population (Cabin Creek; Fig. 2) above a natural fish migration barrier. Dispersal barriers were found on 10 of 33 streams supporting fish in the Madison Range (Fig. 2). In eight of these streams, fish were present up to the base of a waterfall barrier and absent upstream. We found introduced Yellowstone cutthroat trout above waterfall barriers in No Man Creek that contained a headwater lake regularly stocked by Montana Fish, Wildlife and Parks (2000). Additionally, a very small population (<50 individuals) of WCT was isolated above an irrigation diversion dam in Trail Fork Bear Creek. Fish dispersal barriers occurred significantly farther upstream ($\bar{x}$=12.5 km, SE=2.9) and at higher elevations ($\bar{x}$=2267 m, SE= 62) than in the Gravelly Range (*t*-tests, $P<0.05$).

Basin-wide, WCT were sympatric with nonnative trout in only two sample sites, one each in Standard and Hyde creeks (Fig. 2), each located directly below barriers which protected upstream WCT populations. The presence of WCT at these two sites may represent downstream migrants and not a healthy population since only 2 and 3 individuals were captured at these sites in Hyde and Standard creeks, respectively.

Relative abundance of WCT captured during a single electrofishing pass ranged from 1 to 40 fish/100 m of stream length ($\bar{x}$= 10.8, SE= 1, n =79), compared to a range of 1 to 84 for nonnative salmonids ($\bar{x}$=9.7, SE= 1, n=133). Mean relative abundance of WCT was not significantly different from nonnative salmonid species (*t*-test, P=0.43). Multiple depletion density estimates ranged from 3 to 40 fish/100 m of

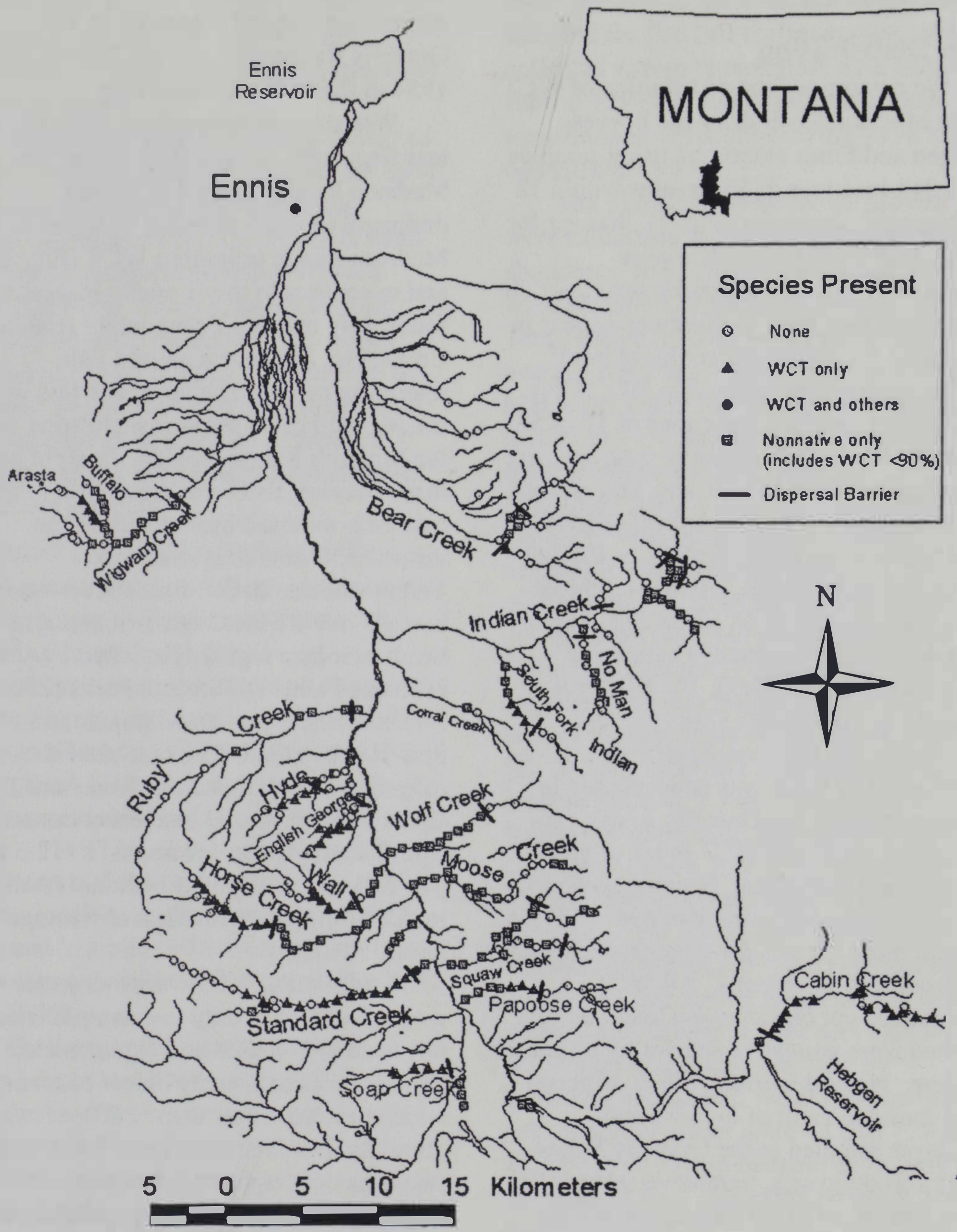

Figure 2. Map of upper Madison River drainage showing the distribution of westslope cutthroat trout with >90 percent genetic purity (WCT), nonnative salmonids and fish dispersal barriers

stream length ($\bar{x}$= 21.9, SE=3.2, n=20) for WCT, compared to 1 to 185 for nonnative salmonids ($\bar{x}$=25.6, SE=7.8, n=34). Estimated densities were not significantly different (t-test, P= 0.66). Based on capture probabilities derived from multiple depletion estimates, the efficiency of single-pass removals was approximately 80 percent for all species combined and was slightly higher for nonnative salmonids (82%) than WCT (79%), but this difference was not significant (t-test; P=0.79).

Non-isolated populations of WCT were found in only three streams: Papoose, South Fork Indian, and Arasta creeks (Fig. 2). Despite their strong association with dispersal barriers, the length of habitat occupied by WCT per sub-drainage ($\overline{x}$ = 4.51 km, SE= 1.1) did not differ from that occupied by nonnative salmonids ($\overline{x}$ = 4.99 km, SE= 1.2; *t*-test, *P*=0.77). However, when we compared occupied habitat lengths for only WCT populations, isolated WCT populations occupied longer stream lengths than did populations not isolated by fish barriers (*t*-test, *P*<0.05). Isolated WCT occupied an average stream length of 7.5 km (*n*= 8, SE= 2.2), whereas all three non-isolated populations occupied approximately 2.4 km of stream.

Westslope cutthroat trout also were more abundant (*t*-test, *P*<0.001) at sites above dispersal barriers. Mean WCT abundance at sites above physical dispersal barriers was 12.8 fish/100 m (SE=1.1) compared to 3.8 fish/100 m (SE=0.8) at sites not influenced by physical dispersal barriers. This difference in fish abundance was not made up by the presence of other species in the non-isolated cases and did not appear to be a function of limited physical habitat.

Stream Temperature

Water temperature patterns varied considerably both among and within streams. Trends in daily water temperatures at sites measured during multiple years were similar across years. Mean stream temperatures were highly correlated with daily maxima and minima. Stream temperatures fluctuated from as little as 2.3 to as much as 16.7 °C daily. Ranges of daily stream temperatures were weakly correlated with daily means but were more closely correlated with daily maxima. Average summer stream temperatures were colder in streams draining the Madison Range ($\bar{x}$ = 7.6 °C, SE=0.04) than the Gravelly Range ($\bar{x}$= 8.6 °C, SE=0.05) (*t*-test, *P*<0.001).

Westslope cutthroat trout were associated with habitats where average and maximum daily stream temperatures generally remained below 12 and 16 °C, respectively (1 Jul-15 Sep; Fig. 3). Maximum daily average temperatures (MDAT) ranged from 7.2 to 12.7 °C, and maximum daily maximum temperatures (MDMT) ranged from 9.9 to 16.5 °C at sites occupied by WCT during the summer sampling period (Table 1). Thermal regimes differed significantly between sites occupied by WCT and nonnative salmonids. Although there was considerable overlap, all stream temperature metrics tested were significantly lower at sites occupied by WCT than sites occupied solely by nonnative salmonids (Table 1).

All temperature metrics were lower for sites with WCT (*t*-tests, *P*<0.05) compared to sites occupied by rainbow trout. The distribution of rainbow trout coincided with a 1-3 °C warmer range of stream temperatures than those occupied by WCT. Rainbow trout occupied sites with maximum average daily stream temperatures between 9.2 and 13.1 °C, and maximum daily stream temperatures between 12.3 and 18.4 °C.

At the basin level, no statistical differences were found between sites occupied by rainbow x cutthroat trout hybrids and those occupied by WCT for any of the temperature metrics examined (*t*-tests, *P*>0.05). However, in at least one stream, temperature differences corresponded with distribution boundaries of WCT and nonnative species, including rainbow x cutthroat trout hybrids (Fig. 4). Westslope cutthroat trout segregated from nonnative salmonids without the influence of a dispersal barrier in Papoose Creek. In Papoose Creek, thermographs were placed at the upper distribution boundary of WCT, the upper distribution boundary of nonnative trout species, and at the stream's mouth. Average daily stream temperatures differed at all three sites (ANOVA, *P*<0.001) with average daily stream temperatures becoming progressively colder at upper stream sample sites. Average daily stream temperatures at the uppermost site in Papoose Creek were also lower than the "coldest" site where nonnative salmonids were captured (Horse Creek, km 8.8) in the Madison River drainage during this study (*t*-test, *P*< 0.001).

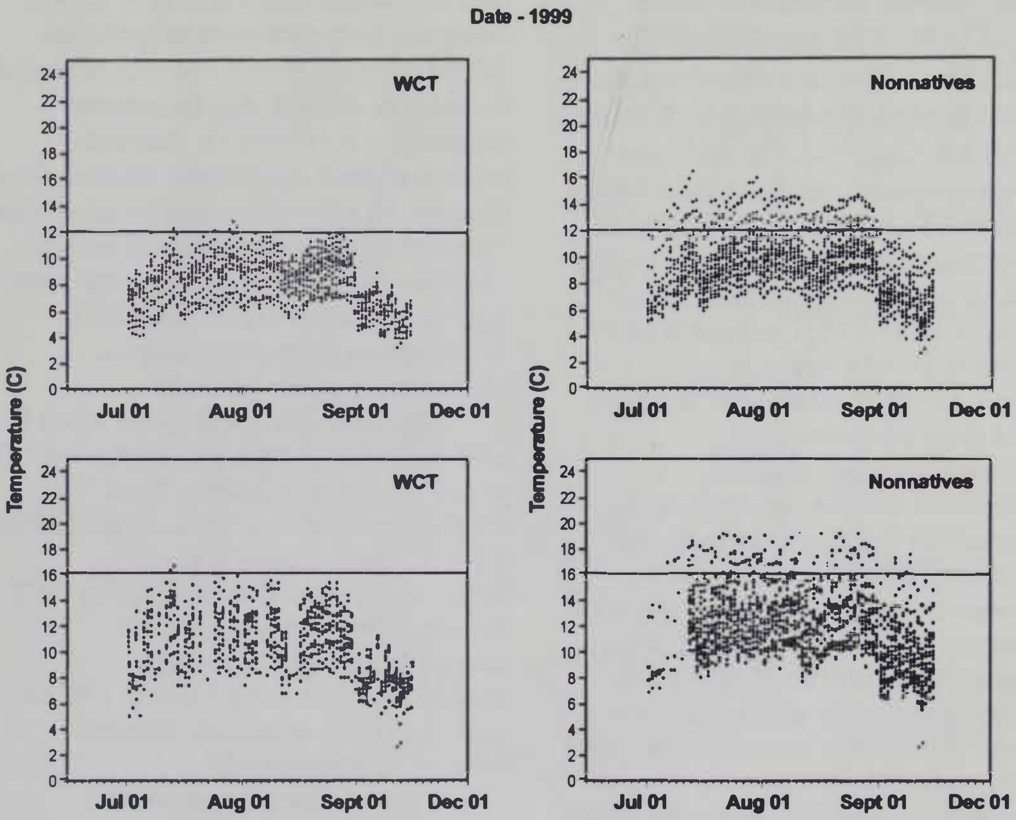

Figure 3. Average (upper) and maximum (bottom) daily stream temperatures at sites occupied by westslope cutthroat trout (WCT; n=16) and nonnative salmonids (Nonnatives; n= 25), with reference lines drawn at 12 and 16 °C, respectively

Populations of WCT above barriers encountered a greater range of average summer stream temperatures and slightly warmer stream temperatures (range= 6.6-11.8 °C, n=14) than those in streams without dispersal barriers (range= 5.9-8.4 °C, n=2). These slightly warmer thermal regimes translated into a higher number of degree days at sites above dispersal barriers ($\bar{x}$=694, SE=39) than non-isolated sites ($\bar{x}$ =564, SE= 98), but this difference was not significant (t-test, P>0.05).

Warm stream temperatures appeared to limit the lower distribution boundary of WCT in one sub-drainage. In English George and South Fork English George creeks, allopatric WCT located above a fish dispersal barrier were absent or rare (<1 fish/100 m) at sites where average daily stream temperatures warmed to 16 °C, and maximum daily stream temperatures warmed to 24 °C during the 1999 sampling season. In contrast, WCT were moderately abundant (mean abundance= 9 fish/100 m) in upstream sites where average daily water temperatures remained between 4 and 10 °C and maximum recorded stream temperatures remained below 12 °C during the summer sampling period.

DISCUSSION

Fish Distribution

Distribution of WCT in the Madison River drainage between Hebgen and Ennis reservoirs was concentrated in streams draining the Gravelly Range (Fig. 2) and was primarily shaped by natural fish dispersal barriers that excluded nonnative salmonids from upstream reaches. We hypothesized that barriers might isolate WCT from potential hybridization or competition with nonnative salmonids. This appeared to be the case in streams draining the Gravelly Range where most perennial streams supported isolated

Table 1. Mean and range of five temperature metrics (see text for definitions) at sites occupied by westslope cutthroat trout (WCT) and sites occupied by nonnative trout species.

Temperature metric	WCT	Nonnative trout	P-value[a]
MDAT	9.8 (7.2-12.7)	11.1 (8.1-16.3)	0.033
MDMT	13.2 (9.9-16.5)	14.5 (10.6-22.0)	0.050
MWAT	9.5 (7.1-11.7)	10.6 (7.8-15.1)	0.022
MWMT	12.3 (9.3-15.3)	13.8 (10.0-23.1)	0.027
DD	563.9 (414.5-693.2)	626.7 (465.7-882.6)	0.030

[a] Welch's modified t-test.

populations of WCT. However, except in Cabin Creek where a geologic barrier was located relatively close to the stream mouth, WCT did not occur above natural dispersal barriers in the Madison Range. Patterns of fish occurrence indicated that the location of dispersal barriers within a stream network was important in determining the presence or absence of WCT. Although dispersal barriers were equally common in the Gravelly Range (8 of 23 streams) and the Madison Range (13 of 35 streams), fish barriers occurred significantly closer to stream mouths and at lower elevations in the Gravelly Range, which may provide insight into WCT distribution patterns in the Madison River drainage.

Isolated populations of salmonids face a variety of extinction risks through environmental and demographic variation due to limited physical space and small population sizes associated with fragmented habitats (Rieman et al. 1993). Smaller, more isolated populations are less likely to persist because 1) small populations face a higher risk of extinction through demographic and environmental stochasticity, and 2) isolated populations have no possibility of demographic support or recolonization through dispersal from surrounding populations (Rieman and McIntyre 1995, Dunham et al. 1996). Flood flows, debris torrents, drought, and fires can locally extirpate trout populations (Propst et al. 1992). If WCT naturally occurred above barriers in streams draining the Madison Range, catastrophic events may have limited their persistence in these areas. However, for many streams we do not know if WCT ever had access to reaches above dispersal barriers. In Cherry Creek, a large isolated sub-drainage outside our study area but within the Madison River drainage, native fish were absent from all of the 90 km of contiguous stream habitat above an 8-m high barrier (Bramblett 1998). Because of the large size and hydrologic complexity of this sub-drainage (Bramblett 1998), the absence of native fish species above this barrier strongly suggests that WCT were historically absent above the falls rather than extirpated due to stochastic events. In our study fishless reaches above waterfalls >10 m high in several streams within the Indian Creek sub-drainage (Fig. 2) also may represent sites that were never colonized by WCT. Consequently, it is unlikely that all fishless reaches in the Madison Range have resulted from localized population extirpations.

Local extirpations of isolated salmonid populations as a result of catastrophic events have been documented elsewhere (e.g., Propst et al. 1992). Kruse et al. (1997) found that Yellowstone cutthroat trout were absent above natural dispersal

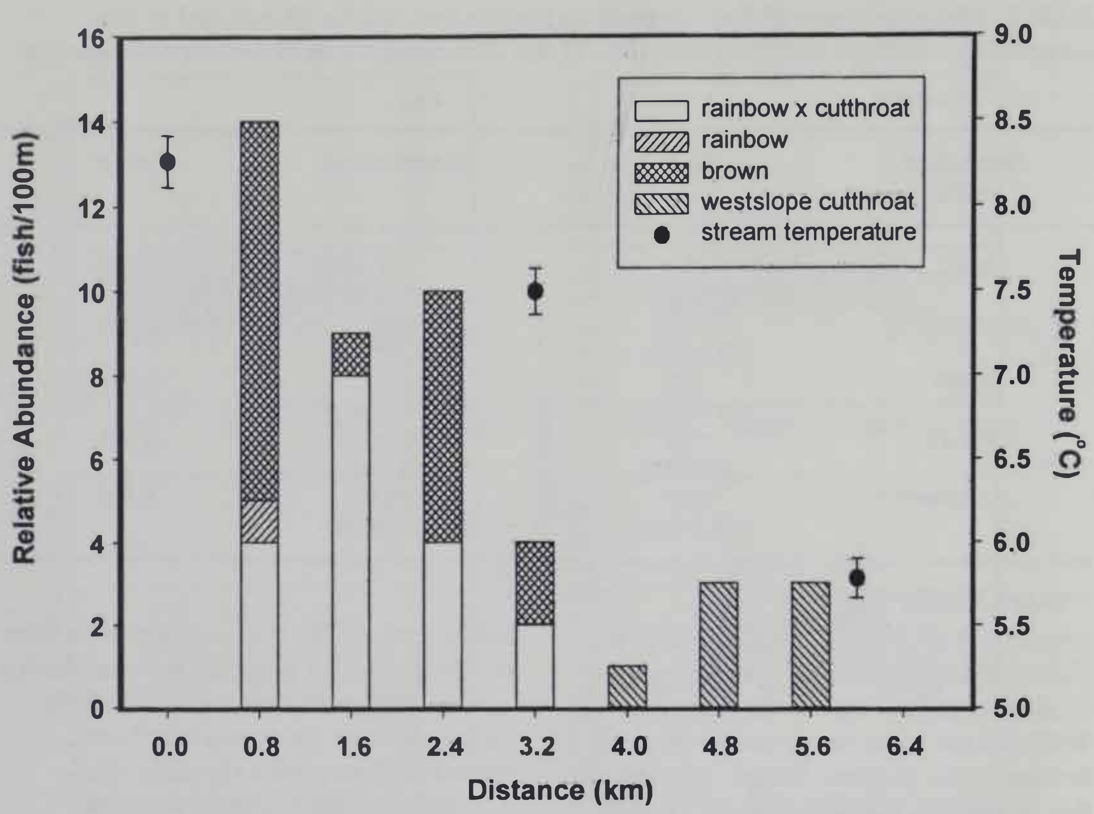

Figure 4. Relative abundance of rainbow, brown, rainbow x cutthroat hybrid, and westslope cutthroat trout greater than 75 mm (left axis) and average summer stream temperatures (right axis) in Papoose Creek by kilometer from stream mouth. Vertical lines represent standard errors.

barriers in the Wood and Greybull river drainages, Wyoming. They were unsure of historic presence, but if fish had access to these areas, they suggested that relatively short stream lengths above barriers, poor habitat conditions, and relatively common occurrences of catastrophic events could have limited their persistence. Similarly, Dunham et al. (1996) suggested that the general absence of Lahontan cutthroat trout populations above natural dispersal barriers was likely a byproduct of high extinction and low recolonization or population rescue probabilities in such small, isolated habitats. In our study, despite apparently suitable physical habitat (Sloat et al. 2000) fish were absent above a relatively recent barrier formed by a large debris jam in Wolf Creek (Fig. 2), suggesting that WCT had been eliminated from this historically accessible stream reach.

While not all fish-less stream reaches above barriers represent sites where cutthroat trout have been extirpated, this does not diminish the risk of extinction for small, geographically restricted populations. Where WCT currently exist above barriers in the Madison River drainage, low population sizes and isolation may place many of these populations at risk. Although abundances of WCT were not significantly lower than those of nonnative salmonids, relative abundances of all salmonid species in the Madison River drainage were generally much lower than in tributaries from other drainages in the upper Missouri and upper Clark Fork river basins in Montana (Sloat et al. 2000). Low abundance of trout in Madison River tributaries may be related to the relatively high elevation of this river basin, inherent geologic instability that translates into somewhat unstable stream channels, and moderate to low productivity of its watersheds (Sloat et al. 2000).

In most streams, WCT populations existed in relatively short stream reaches (mean occupied length= 4.5 km). Based on an empirical evaluation of translocation success, Harrig (2000) suggested that stream segments <5.7 km long may have insufficient space to sustain adult and juvenile greenback cutthroat trout (*O. c. stomias*). Hilderbrand and Kershner (2000) developed a simple relationship between observed cutthroat trout abundances, the proportion of individuals leaving a population through emigration and mortality, and desired population sizes to estimate the minimum stream length (MSL) necessary to maintain viable cutthroat trout populations. Following earlier work by Allendorf et al. (1997), they recommended a population benchmark of 2500 individuals >75 mm long to insure the long-term persistence of isolated populations. Based on a target population size of 2500 individuals, and assuming no proportional loss of individuals, only two streams sampled in this study have occupied MSL's that meet criteria for long term persistence presented by Hilderbrand and Kershner (2000) (Table 2).

Limited space does not necessarily mean that a population will become extinct (Hilderbrand and Kershner 2000). Some fish populations have persisted for extended periods in small habitat patches isolated by natural barriers and may have adapted to restricted space (Northcote et al. 1970, Northcote 1981, 1992). Northcote (1981) reported that heritable differences in rheotaxis between rainbow trout populations above and below a waterfall were genetically coded. Similarly, Shepard et al. (1998) found that the proportion of stream dwelling WCT moving 0.5 km or longer was negatively correlated to the level of isolation experienced by the population. While these local adaptations may be advantageous for individuals in restricted habitats, adaptations to stochastic events such as extreme floods, debris flows, or droughts may be unlikely because either the intensity or the time between such events is too great (Poff 1992). Additionally, traits that confer the greatest advantages to species occupying marginal habitats, such as high mobility and multiple life histories (Thorpe 1994), may actually be selected against in isolated habitats. Consequently, without the chance for recolonization, population extinctions in fragmented stream systems may proceed in a "ratchet-like" manner, increasing the chances of basin-wide extinction (Dunham et al. 1996).

Translocation of trout into fish-less reaches above natural barriers is a common management action to increase the range of native fishes (Harig 2000). The general absence of fish from high elevation reaches above fish barriers found in this and other studies of cutthroat trout (Dunham et al. 1996, Kruse et al. 1997) indicate that this action may not assure the long-term viability of cutthroat trout populations (e.g., Harig 2000). However, our results also indicate that dispersal barriers may effectively protect WCT populations when located relatively low within stream networks. While isolation carries risks associated with low population sizes and limited physical space, it is often the only factor preventing displacement by nonnative salmonids through competition and hybridization. For example, Hanzel (1959) found that most pure cutthroat trout populations in Montana occurred above fish dispersal barriers. Young et al. (1996) reported that 20 of 27 allopatric populations of genetically pure Colorado River cutthroat trout considered indigenous, and in a drainage not recently stocked, were located above fish migration barriers. Distribution patterns we observed in the Gravelly Range illustrate the importance of natural barriers to remaining WCT populations in the Madison River drainage. Primarily because of their association with barriers occurring relatively low within stream networks, isolated populations of WCT occupied greater stream lengths and reached significantly higher abundances than non-isolated cutthroat trout populations. However, based on minimum habitat requirements suggested by other researchers (e.g., Harig 2000, Hilderbrand and Kershner 2000) the viability of most WCT populations in the Madison River drainage remains tenuous and, where possible, these

Table 2. Mean fish abundance (>75 mm total length) per linear meter of stream used for the minimum stream length estimator (MSL), and observed occupied stream lengths (including inhabited tributaries) for WCT populations sampled in this study. Bold streams meet the MSL recommended by Hilderbrand and Kershner (2000).

Stream	Mean abundance[a] fish/m	Occupied length km	MSL km
Arasta Creek	<0.10*	2.4	>25.0
Cabin Creek	**0.31**	**20.0**	**8.1**
English George Creek	0.25	9.0	10.0
Horse Creek	0.20	7.1	12.5
Hyde Creek	0.36	2.7	6.9
Papoose Creek	0.10	2.4	25.0
South Fork Indian Creek	<0.10*	2.4	>25.0
Soap Creek	0.21	3.4	11.9
Standard Creek	**0.28**	**12.1**	**8.9**
Trail Fork Bear Creek	<0.10*	<1.0	>25.0
Wall Creek	0.20	4.8	12.5

[a] From multiple pass depletion estimators except * where no estimates were made because very few fish were captured.

populations should either be expanded further downstream or replicated in larger drainages provided that potential hybridizing and competing species are first removed.

Unfortunately, in Madison River tributaries even some populations isolated by dispersal barriers were slightly introgressed, indicating that nonnative trout have been widely introduced into headwater habitats throughout the drainage. The degree of genetic introgression that can occur before the unique characteristics of WCT are no longer diagnostic for the subspecies is unknown (USDI Fish and Wildlife Service 1999). We adopted guidelines of Montana Fish, Wildlife and Parks and considered all WCT populations with 90 percent or greater purity (Montana Fish, Wildlife and Parks 1999). We feel this is an appropriate approach to analysis of fish distributions in the Madison River basin for two reasons. First, populations identified as slightly introgressed from a genetic sample may contain significant numbers of genetically pure individuals due to the nature of genetic sampling (Montana Fish, Wildlife and Parks 1999). This can result because genetic samples contain a few hybrid individuals mixed with genetically pure individuals or from testing problems related to low sample sizes (Appendix A). Consequently, slightly hybridized populations can indicate suitable habitat for WCT and may have genetic value for future conservation efforts (Montana Fish, Wildlife and Parks 1999). Secondly, the genetic status of many WCT populations in the Madison River drainage remains somewhat uncertain due to the possibility that some of these populations may contain a "deviant allele" that is a diagnostic allele characteristic of rainbow or Yellowstone cutthroat trout but that may simply be a rare WCT genetic variation (Appendix A). This situation likely exists for populations in upper English George, Cabin, Papoose and Wall creeks, and may exist for Soap Creek (Appendix A). Additional genetic sampling will be necessary for some of these populations to clarify their genetic status before population expansion or replication efforts are undertaken.

STREAM TEMPERATURE

In addition to dispersal barriers, stream temperature also influenced WCT distribution in the Madison River drainage. The association of most WCT populations with fish dispersal barriers in the Madison River drainage obviously confounds our ability to make direct temperature or species interaction inferences. Overall temperature relationships would become clearer and stronger in areas where WCT and other salmonids segregated without the influence of barriers. However, in at least one stream, longitudinal temperature patterns coincided with fish distribution boundaries. Genetic data from Papoose Creek suggest that WCT segregated from nonnative salmonids without the presence of a fish dispersal barrier. Stream temperatures in Papoose Creek were significantly lower in the reach occupied by WCT than in downstream reaches occupied by nonnative salmonids. Stream temperatures in the reach of Papoose Creek occupied by WCT also were significantly lower than the coldest site occupied by nonnative salmonids in the Madison River drainage. This situation also may occur in South Fork of Indian Creek (see Fig. 2), where genetically pure WCT were observed upstream from reaches occupied by nonnative species. Unfortunately, the remote locality and lack of a priori knowledge of fish distribution and genetic status precluded temperature measurement in this stream.

Similar to our findings, Mullan et al. (1992) found that in naturally sympatric populations, rainbow trout excluded the first two or three age classes of WCT up to a point where stream temperatures decline to about 1600 annual thermal units (sum of average daily temperatures [°C]). These distribution boundaries may be attributable to temperature-mediated competitive differences between cutthroat trout and nonnative salmonids or temperature mediated growth differences. For example, Destaso and Rahel (1994) found that a 1 °C difference in Critical Thermal Maxima between brook trout (*Salvelinus fontinalis*) and cutthroat trout correlated with greater competitive ability of brook trout at warmer temperatures. Adams (1999) found that lower growth and fecundity, and greater female age-at-maturity resulting from cold stream temperatures limited upstream invasions of brook trout in some Rocky Mountain streams. In addition to brook trout, thermal tolerances of cutthroat trout are generally lower than other nonnative species such as rainbow and brown trout (Feldmuth and Erikson 1978, Eaton et al. 1995).

Although there was considerable overlap, and despite the confounding influence of dispersal barriers, all stream temperature metrics tested were significantly lower at sites occupied by WCT than at sites occupied by nonnative salmonids (Table 1). When sites occupied by rainbow trout, a potential hybridizing and competing species, were compared to sites with WCT all temperature metrics remained significantly lower for sites with cutthroat trout. The distribution of rainbow trout coincided with a 1-3 °C warmer range of stream temperatures than occupied by WCT. Magnuson et al. (1978) considered the "fundamental thermal niche" for fishes to encompass 4 °C, and Christie and Regier (1988) suggested this niche ranged from –3 to +1 °C around a species optimal growth temperature. For rainbow trout, maximum growth occurs at approximately 17.2 °C (Hokanson et al. 1977), and thus the range of maximum daily temperatures occupied by rainbow trout in the Madison River drainage (12.3-18.4 °C) corresponded closely with their fundamental thermal niche (14.2-18.2 °C). Conceivably, competitive advantages of rainbow trout at higher temperatures near their optimal growth range may account for the absence of WCT where rainbow trout were found.

Contrary to patterns for rainbow trout, no statistical differences were found between sites occupied by rainbow x cutthroat trout hybrids and those occupied by WCT at the basin level. The influence of genetic introgression of both rainbow trout and Yellowstone cutthroat trout on the thermal response of WCT has not been studied. In laboratory experiments, Ihssen (1973) found that two reciprocal first-generation hybrids of brook trout and lake trout (*Salvenlinus namaycush*) had similar times to death upon exposure to several lethal high temperatures for a series of acclimation temperatures. Second generation hybrids were intermediate to the parent species in resistance and the backcrossed offspring were intermediate between the second generation hybrids and their respective parents. This suggests that differences in thermal responses between potentially hybridizing species may quickly break down when hybrid swarms develop. If these patterns are similar for rainbow x cutthroat trout hybrids, there is a need to differentiate relatively pure from hybridized populations when investigating relationships between cutthroat trout distribution and stream temperature. Some populations with relatively high (but <90%) proportions of WCT genetic material were classified as nonnative salmonids, which may have weakened relationships between stream temperatures and fish distribution.

Basin-wide, WCT were associated with habitats where average daily stream temperatures generally remained below 12 °C and maximum daily stream temperatures remained below 16 °C. Bell (1984) reported a preferred temperature range of 9-12 °C for cutthroat trout. Dwyer and Kramer (1975) reported the greatest scope for activity in cutthroat trout occurred at 15 °C when tested at 5, 10, 15, 20, and 24 °C. Assuming that the scope for activity was a better measure of optimal temperature than temperature preference tests, Hickman and Raleigh (1982) selected 12 to 15 °C as an optimal temperature range for cutthroat trout. Average and maximum daily water temperatures at sites occupied by WCT generally corresponded with these reported ranges of preferred and optimal temperatures for cutthroat trout.

While WCT were associated with habitats where stream temperatures seldom exceeded 16 °C, this should not be construed as the upper thermal tolerance limit for this subspecies. Although warm stream temperatures approaching 25 °C appeared to limit the downstream distribution of WCT in the English George sub-drainage, temperatures in most reaches now occupied by nonnative species were well below reported critical thermal maxima of 27-28 °C for cutthroat trout (Feldmuth and Eriksen 1978, DeStaso and Rahel 1994). The patterns of fish occurrence and stream temperature we observed indicate that WCT have been displaced from warmer stream habitats and that WCT now occupy a narrower and colder range of stream temperatures than they did historically. In our study, isolated populations of WCT encountered a higher and greater range of average summer stream temperatures than in streams without dispersal barriers, indicating that without the influence of fish barriers the range of stream temperatures occupied by WCT would be substantially narrower and colder due to the influence of nonnative salmonids.

While many researchers have focused on the role that maximum stream temperatures play in regulating salmonid distribution (e.g., Dunham et al. 1999, Haas, in press), few have explicitly addressed the ecological costs for salmonids in habitats where stream temperatures remain below thermal optima. Several WCT populations sampled in this study inhabited streams where water temperatures remained below optimal temperature ranges (Hickman and Raleigh 1982) for most of the summer season (Fig. 4). Low WCT densities in Papoose Creek and Trail Fork of Bear Creek (range= 3 to <1 fish/ 100 m) may be attributed to low stream temperatures, because maximum stream temperatures remained below 10 °C throughout the summer at sites where WCT were captured in these two streams.

The two major external factors controlling fish growth are water temperature and food availability (Weatherly and Rogers 1978). Averett (1963) documented higher growth rates for WCT from lower versus higher elevation tributaries of the St. Joe River, Idaho, presumably a result of differences in stream temperatures. Body size is strongly related to fecundity in WCT (Downs 1995). Cold stream temperatures can delay cutthroat trout spawning, prolong egg incubation (Behnke 1992, USDI Fish And Wildlife

Service 1998, Harrig 2000), and reduce embryo survival (Hubert et al. 1994, Stonecypher et al. 1994). Late hatching fry risk winter starvation if they cannot grow enough to withstand metabolic deficits at low winter temperatures (Cunjak and Power 1987, Shuter and Post 1990, Harrig 2000). Consequently, WCT probably experience lower individual fitness and reproductive success in habitats where temperatures remain well below optimal ranges. The low abundances of WCT we observed at sites not physically isolated from nonnative species suggest that, while colder stream temperatures may provide a competitive or demographic boost for WCT relative to nonnative species, sub-optimal thermal regimes may also limit a population's ability to buffer environmental and demographic stochasticity in headwater habitats.

In addition to fish dispersal barriers, other local factors may affect the correspondence between fish distributions and temperature within streams, including variability of habitat quality, disease, food availability, and water quality and quantity (Dunham 1999). The potential for seasonal migrations may also add noise to data relating fish distributions directly to stream thermal characteristics (Dunham 1999). Northcote (1992) noted that the most extensive movements in resident salmonid populations were associated with spawning migrations. However, Downs (1995) reported that WCT living in headwater habitats did not appear to have extensive spawning migrations. Similarly, Shepard et al. (1998) found that while some individual WCT move relatively long distances, little movement was observed for most resident WCT inhabiting headwater streams in Montana.

A potential problem with our study is a lack of temporal concordance between fish distribution and temperature data. We matched fish sampling records with temperature records corresponding most closely in time. Because fish were sampled over a 3 year period, while most temperature data were collected in 1999, stream temperatures were not measured during the same year as the fish sampling event in some locations. For the temperature associations presented in this study to be valid, two assumptions must be met. First, fish distribution boundaries did not change during the study period. Other studies have found that distribution limits of cutthroat trout were relatively constant across a 20-year period (1977-1997) despite fluctuations in densities (Dunham et al. 1999). Similarly, brook and rainbow trout showed no net change in distribution limits over a similar time period in eastern Tennessee streams (Strange and Habera 1998). We expect this to be true in the Madison River drainage as well, especially considering the relatively short time period of our study and the strong influence of dispersal barriers on fish distribution. The second assumption is that measured stream temperatures are representative of temperatures experienced by fish during the year fish distribution data were collected. This assumption also seems reasonable because stream temperature is highly correlated with air temperature (Stefan and Preud'homme 1993) and published air temperature records for the period of our study indicate that annual and summer air temperatures from 1997-1999 corresponded closely with long term average air temperatures (NOAA 1997, 1998, 1999).

CONCLUSION AND RECOMMENDATIONS

This study provided important information on the distribution and abundance of WCT in the Madison River drainage. Identifying and protecting existing populations is the first step in an effective conservation plan for WCT (Montana Fish, Wildlife and Parks 1999). Because of the inherent risks associated with the restricted distribution and small sizes of many WCT populations, simply maintaining the status quo will probably not be sufficient to ensure the long-term persistence of all populations. Due to the limited number of genetically pure populations of WCT in the Madison River drainage, we believe it would be worthwhile to replicate pure populations from Cabin and Papoose creeks. We recommend that further genetic testing be completed in English George, upper South Fork Indian, and Wall creek sub-drainages to confirm the presence of genetically pure populations in these areas. Should any of these populations prove to be genetically pure, they should be replicated, preferably somewhere within the Madison River drainage, as soon as technically feasible to conserve these unique genetic resources. When WCT populations are to be expanded, results from our study agree with others (Montana Fish, Wildlife and Parks 1999, Harrig 2000, Hilderbrand and Kershner 2000) suggesting that translocation sites be located relatively low within stream networks to ensure that habitat space and quality are sufficient to maintain the long-term viability of cutthroat trout populations. Additionally, we recommend that existing genetically pure populations of WCT be expanded downstream, where possible, to incorporate larger habitat areas. We also recommend that slightly introgressed (<10% introgression) WCT populations be managed with the same protection given to genetically pure WCT, because such populations may have genetic value and their presence indicates suitable habitat for WCT (Shepard et al. 1997, Montana Fish, Wildlife and Parks 1999).

Our study also provided important information on the thermal regimes associated with suitable habitat for WCT as well as evidence that distribution boundaries between WCT and nonnative salmonids are related to stream temperatures. However, relationships between WCT distribution and abundance and stream temperature need to be clarified through both laboratory experiments and more extensive field studies. Because thermal gradients are important determinants of species distributions and because temperature data acquisition can be costly and time consuming in remote or expansive study areas, numerous regional- or basin-scale stream temperature models have been developed recently (e.g., Keleher and Rahel 1996, Isaak and Hubert 2001, Sloat 2001). When the thermal requirements of WCT are better known, these stream temperature models can be used to prioritize WCT conservation efforts at broad scales by 1) predicting WCT occurrence in areas where their distributions are unknown, 2) identifying stream reaches where translocations of WCT have a high probability of success, and 3) predicting effects of land use and global warming on WCT distribution and abundance.

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Appendix A. Genetic testing results for sites in the Madison River drainage by date, location (legal or stream kilometer), sample size (*n*), and analysis method (E = allozyme electrophoretic and P = PINE DNA), showing species code (RB = rainbow trout; WCT = westslope cutthroat trout; and YCT = Yellowstone cutthroat trout) and proportion of sample estimated to contain alleles characteristic of each species (NA = proportions not available), and, where applicable, number of individuals that were pure WCT. Information from the Montana Resource Information System database (http://www.nris.mt.us) unless otherwise denoted.

STREAM				Genetic Results (species code and %)				Number pure WCT
Date	Location	*n*	Analysis method	Code %	Code %	Code %		
ARASTA CR								
7/26/1995	07S03W36[1]	5	E	WCT 100				5
7/20/1999	08S02W06[2]	1	P	WCT NA		YCT NA		0
BUFFALO CR								
7/26/1995	07S02W31[1]	4	E	WCT 100				4
7/20/1999	08S02W05[2]	7	P	WCT 84	RB 4	YCT 12		0
7/20/1999	07S02W31[2]	7	P	WCT 84	RB 4	YCT 12		0
CABIN CR								
8/31/1997	11S04E05	7	E	WCT 100				7
11/15/1998	11S03E15	8	E	WCT 0	RB 71	YCT 29		0
4/19/1999	11S03E14	10	P	WCT 93	RB 7	YCT 0		0
7/26/1999	Km 3.2-9.3	27	P	WCT 96	RB 4	YCT 0		0
7/27/1999	11S04E14[3]	6	P	WCT>90	RB<10			5
CABIN CR, M FK								
6/01/1993	11S04E11	10	E	WCT 100				10
7/27/1999	Km 0-8.0[3]	58	P	WCT 98	RB 2	YCT 0	0	
CORRAL CR								
7/8/1998	Km 9.7[4]	21	P	WCT 86	RB 8	YCT 6		0
ENGLISH GEORGE CR								
8/1/1992	09S01W36	15	E	WCT 95	RB 5	YCT 0		0
6/8/1999	10S01W02[5]	10	P	WCT>90	RB<10			*NA*
HORSE CR								
8/10/1995	10S02W19[1]	8	E	WCT 100	RB 0	YCT 0		8
7/28/1998	Km 7.2-11.3[6]	70	P	WCT 88	RB 3	YCT 9		0
7/28/1998	Km 12.1-13.7[6]	29	P	WCT 98	RB 0	YCT 2		*NA*
HYDE CR								
7/21/1995	09S01W34[2]	3	E	WCT 96	RB 4	YCT 0		0
7/13/1999	09S01W33[3]	16	P	WCT 96	RB 0	YCT 4		0
MIDDLE FORK BEAR CR								
7/27/1994	07S02E06[7]	2	E	WCT 87	RB 13	YCT 0		0
NORTH FORK BEAR CR								
7/26/1994	07S01E36[7]	4	E	WCT 70	RB 25	YCT 5		0
PAPOOSE CR								
7/26/1994	11S02E06[7]	4	E	WCT 100	RB 0	YCT 0		4
7/27/1999	Km 0-5.6[8]	24	P	WCT NA	RB NA	YCT NA		6

Appendix A. (continued)

STREAM Date	Location	*n*	Analysis method	Genetic Results (species code and %) Code %	 Code %	 Code %	Number pure WCT
QUAKING ASPEN CR							
6/30/1998	Km 1.6	16	P	WCT 77	RB 23	YCT 0	0
SOAP CR							
9/19/1991	11S01E29	12	E	WCT 99	RB 0	YCT 1	0
9/01/1992	11S01E29	16	E	WCT 99	RB 0	YCT 1	0
SOUTH FORK ENGLISH GEORGE CR							
6/8/1999	10S01W02[9]	9	P	WCT NA	RB NA	YCT NA	*NA*
SOUTH FORK INDIAN CREEK							
8/05/1998	Km 1.6-4.0[10]	22	P	WCT 79	RB 15	YCT 6	0
8/05/1998	Km 4.0-5.6[10]	12	P	WCT >90	RB NA	YCT NA	*NA*
STANDARD CR							
8/11/1997	11S01E05[11]	13	E	WCT NA	RB NA	YCT NA	0
TEPEE CR							
8/01/1995	10S02W 13[1]	5	E	WCT 100	RB 0	YCT 0	5
7/28/ 1998	Km 1.6	13	P	WCT 98	RB 0	YCT 2	0
WALL CR							
7/13/1999	Km 5.6	7	P	WCT 97	RB 0	YCT 3	0
WIGWAM CR							
7/20/1999	08S02W 07[2]	7	P	WCT 82	RB 1	YCT 17	0

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[1] Information from letter to Jim Brammer, Montana Fish Wildife and Parks (MFWP), from Robb Leary, University of Montana Wild Trout and Salmon Genetics Laboratory (WTSL) dated May 6, 1997.

[2] Information from letter from Naohisa Kanda, WTSL, to Brad Shepard, MFWP, dated March 27, 2000. Samples from locations in Buffalo Creek combined. An individual trout collected from Arasta Creek possessed PINE markers characteristic of both westslope and Yellowstone cutthroat trout but proportions were not available.

[3] Information from letter to Brad Shepard, MFWP, from Naohisa Kanda, WTSL, dated August 21, 2000. A single allele characteristic of rainbow trout was present in one fish from Cabin Creek at T 11, R S04E, SEC 14, indicating either slight genetic introgression or a pure westslope cutthroat trout with a single deviant allele similar to rainbow trout.

[4] Information from letter to Brad Shepard, MFWP, from Naohisa Kanda, WTSL, dated November 8, 1999.

[5] In English George Creek a single allele characteristic of rainbow trout was present at low frequencies. This could indicate a small amount of hybridization or it could simply be a rare westslope cutthroat trout genetic variation. Information from letter from Naohisa Kanda, WTSL, to Brad Shepard, MFWP, dated March 27, 2000.

[6] Within the Horse Creek drainage (Horse and Tepee creeks) all fish were hybridized between westslope cutthroat, Yellowstone cutthroat, and rainbow trout, however, the population above a waterfall near stream mile 7.5 did not contain any rainbow trout alleles, had what may have been a few pure westslope cutthroat trout individuals, and had a higher proportion of westslope cutthroat trout alleles than the population below the falls. Information from letter to Brad Shepard, MFWP, from Naohisa Kanda, WTSL, dated November 8, 1999.

[7] Information from letter to Jim Brammer, MFWP, from Robb Leary, WTSL, dated May 23, 1995.

[8] Information from letter from Naohisa Kanda, WTSL, to Brad Shepard, MFWP, dated March 27, 2000. Proportions not available. Some fish that were pure WCT (6 of 9) were sampled at 4.0, 4.8, and 5.6 km. All fish below 4.0 km were either rainbow (3 of 15) or hybrids. The three hybrids above 4.0 km contained a single allele characteristic of RB.

[9] In the South Fork English George Creek, a single allele characteristic of Yellowstone cutthroat trout was present in one individual. It may be a pure westslope cutthroat trout population with a single deviant allele that is similar to Yellowstone cutthroat trout. Additional sampling is necessary. Information from letter from Naohisa Kanda, WTSL, to Brad Shepard, MFWP, dated March 27, 2000.

[10] Fish from the South Fork Indian Creek were all classified as hybrids between westslope cutthroat, rainbow, and Yellowstone cutthroat trout. However, fish from stream kilometer 4.0 to 5.6 contained over 90% westslope cutthroat trout alleles, while fish from lower in the drainage contained much lower westslope cutthroat trout allele frequencies. Information from letter to Brad Shepard, MFWP, from Naohisa Kanda, WTSL, dated November 8, 1999.

[11] Information from letter to Brad Shepard, MFWP, from Naohisa Kanda and Robb Leary, WTSL, dated November 2, 1998. While westslope cutthroat trout genes were dominant, some Yellowstone cutthroat trout introgression was documented. A freezer malfunction made it impossible to determine the extent of introgression with either Yellowstone cutthroat or rainbow trout.