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[Article]

Status and Conservation of Westslope Cutthroat Trout within the Western United States

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Abstract.—We describe the historical and current distributions and genetic status of westslope cutthroat trout *Oncorhynchus clarkii lewisii* (WCT) throughout its range in the western United States using data and expert opinion provided by fish managers. Westslope cutthroat trout historically occupied 90,800 km and currently occupy 54,600 km; however, these are probably underestimates due to the large-scale (1:100,000) mapping we used. Genetic analyses found no evidence of genetic introgression in 768 samples (58% of samples tested), but the numbers of individuals tested per sample were variable and sample sites were not randomly selected. Approximately 42% of the stream length occupied by WCT is protected by stringent land use restrictions in national parks (2%), wilderness areas (19%), and roadless areas (21%). A total of 563 WCT populations (39,355 km) are being managed as ''conservation populations,'' and while most (457, or 81%) conservation populations were relatively small, isolated populations, large and interconnected metapopulations occupied much more stream length (34,820 km, or 88%). While conservation populations were distributed throughout the historical range (occupying 67 of 70 historically occupied basins), they were much denser at the core than at the fringes. From the information provided we determined that conserving isolated populations (for their genetic integrity and isolation from nonnative competitors and disease) and metapopulations (for their diverse life histories and resistance to demographic extinction) is reasonable. We conclude that while the distribution of WCT has declined dramatically from historical levels, as a subspecies WCT are not currently at imminent risk of extinction because (1) they are still widely distributed, especially in areas protected by stringent land use restrictions; (2) many populations are isolated by physical barriers from invasion by nonnative fish and disease; and (3) the active conservation of many populations is occurring.

Westslope cutthroat trout *Oncorhynchus clarkii lewisii* (WCT) is the most widely distributed subspecies of cutthroat trout *O. clarkii* (Allendorf and Leary 1988; Behnke 1992). Declines in the abundance and distribution of WCT have been related to introductions of nonnative fishes, habitat changes, and overexploitation (Hanzel 1959; Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995; Shepard et al. 1997; U.S. Fish and Wildlife Service 1999), while genetic introgression by nonnative fish has compromised many WCT populations (Allendorf and Leary 1988).

The U.S. Fish and Wildlife Service (FWS) administers the U.S. Endangered Species Act (ESA) to conserve native fauna deemed at risk of extinction. In 1997 the FWS received a formal petition to list WCT as ''threatened throughout its range'' under the ESA (U.S. Office of the Federal Register 1998). After conducting a status review the FWS concluded that a ''threatened'' listing was ''not warranted'' for WCT because of the currently wide distribution of this subspecies and ongoing conservation measures (U.S. Fish and Wildlife Service 1999; U.S. Office of the Federal Register 2000). Subsequently, a suit brought against the FWS argued there were numerous flaws in the rationale the FWS used for their determination. While the Court rejected some of the plaintiffs' concerns, the Court found that FWS's inclusion of hybridized WCT in the taxon considered for listing, while at the same time considering hybridization as a threat to WCT, was arbitrary and capricious. The Court also suggested that the FWS failed to adequately consider threats from disease, and remanded the ''not warranted'' listing decision back to the FWS (U.S. Office of the Federal Register 2002a).

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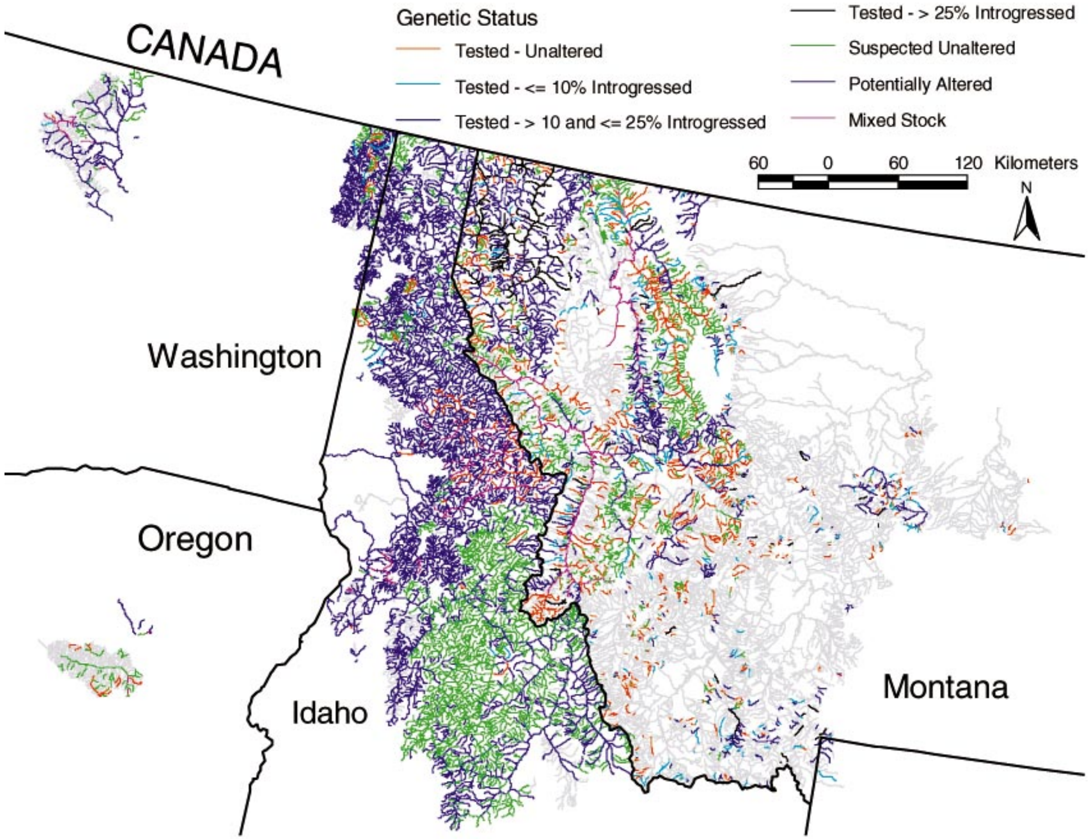

FIGURE 1.—Map delineating the distribution of westslope cutthroat trout throughout their range within the western United States. Colored lines indicate genetic status; gray lines indicate historical range.

In 2002 a team of fisheries professionals was convened to conduct a consistent and comprehensive rangewide status assessment for WCT in the USA. Team members believed that it was mutually beneficial to work together to compile existing knowledge, evaluate risks to WCT populations, and summarize current conservation efforts so that the FWS would have the best scientific information to use in their listing determination (U.S. Office of the Federal Register 2002b). Information was compiled on historically occupied range, on current distribution and genetic status, and to assess risks for WCT throughout their range (Shepard et al. 2003). This assessment provided consistent and current information on WCT that helped the FWS review their initial listing determination and reach another ''not warranted'' listing conclusion (U.S. Office of the Federal Register 2003).

The objectives of this paper are to (1) better define the historical distribution of WCT by benchmarking to a more specific, and defensible, time period; (2) display the current distribution of WCT and associated federal land designations that afford various levels of habitat protections for this subspecies using a spatially explicit analysis; (3) define populations that fish managers are currently conserving, including the rationale fish managers used to define these populations; and (4) evaluate the risks to these defined conservation populations. The goal of this review was to determine the current status of and conservation efforts for WCT, especially as they relate to U.S. implementation of the ESA.

Analysis Area

The analysis area included all of the probable historical range of WCT within the United States. We relied primarily on Behnke (1992) to delineate likely historical range and then modified these boundaries based on more recent survey data and information (Figure 1). This area includes (from east to west) the upper portions of the Missouri, Saskatchewan, Columbia, and Snake river basins in Montana, Idaho, and Washington; the John Day

TABLE 1.—Genetic classes used for assessing genetic status of westslope cutthroat trout in the western United States during 2002. Contaminating species include any introduced species or subspecies, excluding native species (inland redband trout and steelhead [both variants of *O. mykiss*]), that could hybridize with westslope cutthroat trout.

Genetic status	Abbreviated status
Genetically unaltered (<1% introgression); tested via electrophoresis or DNA	Tested; unaltered
Introgressed ≥1% and ≤10%; tested via electrophoresis or DNA	Tested; ≤10% introgressed
Introgressed >10% and ≤25%; tested via electrophoresis or DNA	Tested; >10% to ≤25% introgressed
Introgressed >25%; tested via electrophoresis or DNA	Tested; >25% introgressed
Suspected unaltered with no record of stocking or contaminating species present	Suspected unaltered
Potentially hybridized with records of contaminating species being stocked or occurring in stream	Potentially altered
Hybridized and pure populations co-exist in stream (used only if reproductive isolation is suspected and testing completed)	Mixed stock; altered and unaltered

basin in Oregon; and the Methow and Lake Chelan basins in Washington. We did not include the Canadian portion of the WCT's range.

Methods

We convened 112 fisheries professionals from state, federal, and tribal agencies as well as private organizations and consulting firms in nine regional workshops to compile information on WCT within their respective geographical areas of responsibility and expertise. Twenty-one geographic information system (GIS) and data management specialists also participated in these workshops to enter data and display the information for real-time data editing. In a few cases, data editing took place following the workshops through phone contacts with individual biologists. Historical and current distributions of WCT and current genetic sampling results were entered into georeferenced databases (ARCVIEW version 3.2; ESRI 1999; Microsoft Access). A WCT interagency conservation team, consisting of state and federal agency representatives, developed a standardized approach and protocols that were consistently followed by all workshop participants (see Shepard et al. 2003 for details).

We delineated the probable historical distribution of WCT at the time of European expansion into the western United States (circa 1800) by modifying Behnke's (1992) description of historical range based on (1) the physical ability of stream and river reaches (we use the term ''stream'' to indicate both streams and rivers) to support WCT, (2) known geological barriers to upstream invasion and lack of WCT above these barriers, (3) historical accounts, and (4) current survey information. All streams identified on a 1:100,000-scale hydrography layer that were currently occupied by WCT were delineated and classified by genetic status (Table 1). We used 1:100,000-scale hydrography because this was the only scale for which hydrography coverage was available over the entire analysis area. While lake and reservoir habitats were not explicitly identified during this assessment, linear distances through any lake or reservoir that was bisected by any stream delineated on the 1:100,000-scale hydrography were included.

We recognized that there are issues related to mapping scale for which we did our assessment. Summaries based on this scale will underestimate ''true'' field lengths of stream habitats due to scale-based error. There are several potential sources of scale-based bias. First, map-derived stream lengths underestimate actual stream lengths. Firman and Jacobs (2002) found that while hip-chained measurements of Oregon coastal streams were significantly correlated to stream lengths computed using MapTech Terrain Navigator software and 1:24,000-scale maps, map lengths needed to be multiplied by about 1.14 to estimate measured stream lengths. Secondly, there are scale differences between 1:100,000- and 1:24,000-scale hydrography. Two types of scale differences potentially exist: differences in lengths of streams identified on both of these two scales, and identification of more streams on the 1:24,000 scale than on the 1:100,000 scale. We evaluated both these differences by (1) comparing the lengths of 30 streams identified on both scales from three different river basins (10 per basin), and (2) calculating and comparing the hydrographic density (kilogram of streams/ha) of both scales in two watersheds.

Genetic status determinations were based on genetic testing or likely sympatry with potentially hybridizing species (Table 1). Fish tissue samples collected during 1,333 sampling events (representing over 22,500 individual fish) were genetically tested using either allozyme (n = 1,129 samples) or DNA (paired interspersed nuclear element

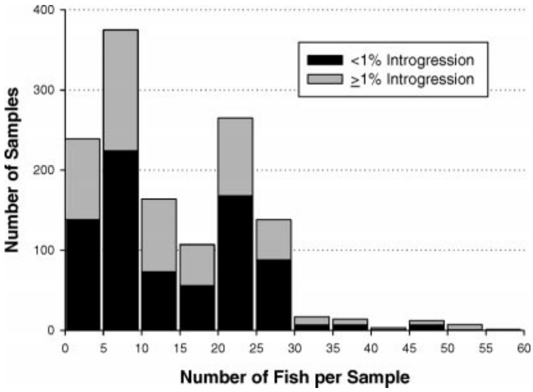

FIGURE 2.—Distribution of the number of samples taken for genetic analysis by the number of fish sampled classed by level of introgression detected (<1% or ≥1%).

[PINE] sequence analysis; $n = 204$) techniques. Most genetic sampling was not done randomly because most samples were taken from fish that phenotypically appeared to be WCT. Consequently, the available genetics information did not constitute a random sample taken from throughout the entire distribution of WCT.

Since the sample sizes for evaluating genetic status were variable, we evaluated the samples and found that of the 785 that detected less than 1% introgression, 234 (30%) consisted of 25 fish or more (Figure 2). Most genetic testing techniques have a 95% probability of detecting 1% introgression with a 25-fish sample, based on the number of diagnostic alleles. Thus, we can confidently (95% CI) classify only 30% of samples where genetic testing found no evidence of introgression as nonintrogressed based on an introgression detection level of 1%.

In some cases, particularly in larger streams, fish populations could comprise mixed stocks, a portion of stock made up of WCT that were not introgressed and another portion that contained individuals with varying levels of introgression. For these cases the population was considered a ''mixed-stock'' population, and a component of that population was considered to be nonintrogressed WCT only if ancillary evidence was available that indicated the WCT and any other potentially hybridizing nonnative species in the population were reproductively isolated, either temporally or spatially.

For much of the stream length analyzed no genetic sampling had been done, so we used the documented presence or absence of potentially hybridizing species to classify the likelihood of introgression. Where stocking records and field surveys indicated potentially hybridizing species were absent, WCT were classified as ''suspected unaltered,'' while they were classified as ''potentially altered'' if any information suggested that potentially hybridizing species had ever been present. Lengths of stream occupied, by genetic status, were summarized and spatial distribution was displayed.

Many populations of WCT receive additional conservation management emphasis and these were identified as ''conservation'' populations based on the genetic, life history, or unique habitat adaptation values represented by each population (Utah Division of Wildlife Resources 2000). While WCT populations generally have important recreational fishery values, if they did not meet at least one of the above conservation criterion, fish managers did not designate them as a conservation population. Any stream segment that supported WCT and met at least one of the above conservation criteria was designated by the fish managers as either an individual isolated conservation population, or aggregated as part of a larger conservation metapopulation (Hanski and Gilpin 1991), depending upon the isolation or connectivity and likely genetic exchange among spawning stocks. Where fish migration barriers were known to occur between stream segments that supported WCT, fish managers used these barriers to subdivide these stream segments into separate, isolated populations. We summarized information for designated conservation populations based on the length of stream occupied, number of populations, and geographical distribution.

Potential risks to conservation populations were identified as risks that could occur in the ''foreseeable future,'' which the WCT interagency conservation team considered to be two to three decades. Risks were stratified into genetic, disease, and demographic and stochastic population risk categories (Table 2). Genetic risk depended primarily on the distance from potential sources of anthropogenic introgression (Allendorf et al. 2001), and the presence of documented barriers between those sources and the conservation population. Diseases of concern were those that could cause severe and significant impacts to population health and included, but were not limited to, whirling disease, furunculosis, and infectious pancreatic necrosis. Disease risk was either directly assessed or reviewed by fish health professionals from each respective state's fish and wildlife agency. De-

TABLE 2.—Risks assigned to populations of westslope cutthroat trout (WCT) within the western United States designated as conservation populations by risk category (abbreviations used through the rest of the article are given parentheses). Genetic risk assumes hybridizing species includes any introduced species or subspecies, excluding native species (inland redband trout and steelhead), that could hybridize with westslope cutthroat trout. Population risks are broken into four subcategories (productivity, temporal variability, isolation, and size).

Risk	Risk attribute
Genetic	
Low	Hybridizing species cannot interact with existing WCT population. Barrier provides complete blockage to upstream fish movement.
Med–low	Hybridizing species are in same stream, drainage further than 10 km from WCT population, or both but not in same stream segment as WCT or within 10 km where a barrier currently exists (though that barrier may be at risk of failure).
Med–high	Hybridizing species are in same stream, drainage within 10 km of WCT population and no barrier exists, or both; however, hybridizing species not yet found in same stream segment as WCT population.
High	Hybridizing species are sympatric with WCT population in same stream segment.
Disease	
Low	Significant diseases and the pathogens that cause them have very limited opportunity to interact with existing WCT population. Significant disease and pathogens are not known to exist in stream or watershed associated with WCT population.
Med–low	Significant diseases, pathogens, or both have been introduced, identified, or both in stream, drainage further than 10 km from WCT population, or both but not in same stream segment as WCT or within 10 km where existing barriers exist (though barriers may be at risk of failure).
Med–high	Significant diseases, pathogens, or both have been introduced, identified, or both in same stream, drainage within 10 km of WCT population, or both, and no barriers exist between disease, pathogens, or both and diseased fish species and WCT population.
High	Significant disease, pathogens, or both and disease-carrying species are sympatric with WCT in same stream segment.
Population productivity (Pop prod)	
Low	Population is increasing or fluctuating around an equilibrium that fills available habitat that is near potential. No nonnative competing or predating species present. Represents high population productivity.
Med–low	Population has been reduced from potential but is fluctuating around an equilibrium (population relatively stable and either habitat quality is less than potential or another factor—disease, competition, etc.—is limiting the population).
Med–high	Population has been reduced and is declining (year-class failures are periodic; competition may be reducing survival; habitat limiting population).
High	Population has been much reduced and has either been declining over a long time period or has been declining at a fast rate over a short time period (year-class failures are common; competition or habitat dramatically reducing survival). Represents low population productivity.
Population temporal variability (Pop var)	
Low	At least 75 km of connected habitats—good connectivity
Med–low	25–75 km of connected habitats
Med–high	10–25 km of connected habitats
High	$<$10 km of connected habitats—poor connectivity
Population isolation (Pop iso)	
Low	Migratory forms must be present and migration corridors are open (connectivity maintained)—not isolated.
Med–low	Migratory forms are present, but connection with other migratory populations disrupted at a frequency that allows only occasional spawning.
Med–high	Questionable whether migratory form exists within connected habitat; however, possible infrequent straying of adults from other populations into area occupied by population.
High	Population is isolated from any other population segment, usually due to a barrier, but may be related to lack of movement or distance to nearest population—isolated.
Population size (Pop size)	
Low	$>$2,000 adults
Med–low	500–2,000 adults
Med–high	50–500 adults
High	$<$50 adults

mographic and stochastic population risks were ranked using criteria established by Rieman et al. (1993). Both empirical evidence and professional judgment were used to rank these risks. We rated risks to 539 of the 563 designated WCT conservation populations by both number of populations and length of stream occupied. We were unable to rate extinction risk for 24 conservation popula-

TABLE 3.—Criteria used to rate relative size of streams within the range of westslope cutthroat trout in the western United States and number of streams that fell in each category.

Relative size	Criteria for length of stream	Number of streams
1	≤5 km	9,921
2	>5 and ≤10 km	5,118
3	>10 and ≤15 km	1,629
4	>15 and ≤25 km	1,012
5	>25 and ≤40 km	489
6	>40 km	202

tions because one tribal government considered this information proprietary.

Habitat loss (which we define as loss of capacity to support WCT over a length of stream) is a key threat to the continued persistence of many species (Diamond 1984; cited in Caughley 1994), and the FWS specifically addressed this threat in their status review (U.S. Fish and Wildlife Service 1999; U.S. Office of the Federal Register 2000). While this assessment did not specifically evaluate habitat loss, we determined the spatial extent and distribution of stream reaches that currently support WCT and also have high levels of habitat protection. This type of analysis is similar to gap-type analyses for vegetation (Caicco et al. 1995). We did this by overlaying a land management GIS layer that delineated National Parks, Forest Service Wilderness Areas, Forest Service ''roadless'' areas, and all federally managed lands onto hydrography layers that delineated stream segments currently occupied by WCT and stream segments occupied by conservation populations. U.S. Bureau of Land Management (BLM) designated wilderness and roadless area GIS maps were not readily available for our entire analysis area, so these areas were not included. We used a GIS to compute the length of hydrography currently occupied by WCT and occupied by conservation populations within each of the above land management designations.

We summarized the stream lengths occupied by each genetic class and by designated conservation populations, stratified into isolates or metapopulations, by relative stream size based on 1:100,000-scale hydrography. Since we had no measurements of stream width or other standardized stream size metric, we used the total length of each stream identified on the 1:100,000-scale hydrography as an indicator of relative stream size (Table 3). Relative stream sizes were ranked from smallest (1) to largest (6), the smallest ranks generally representing short headwater tributaries and the largest ranks representing rivers. We evaluated conservation efforts by determining whether various types of conservation activities had been implemented for any part of each conservation popu-

TABLE 4.—Number and percentage (based on the 539 conservation populations that were evaluated) of designated westslope cutthroat trout conservation populations in the western United States that have had various types of conservation, restoration, and management actions applied as of 2002.

Conservation action	Number	Percentage
Angling regulations	298	55
Bank stabilization	39	7
Barrier construction	21	4
Barrier removal	24	4
Channel restoration	39	7
Chemical removal of competing–hybridizing species	3	1
Culvert replacement	50	9
Diversion modification	18	3
Fish ladder installation	11	2
Fish screen installation	21	4
Grade control	11	2
Instream cover habitat	16	3
Irrigation efficiency	9	2
Physical removal of competing–hybridizing species	27	5
Pool development	27	5
Population restoration–expansion	23	4
Public outreach (interpretive site)	31	6
Riparian fencing	48	9
Riparian restoration	53	10
Spawning habitat enhancement	13	2
Water lease–flow enhancement	9	2
Watershed under protective management (wilderness or park)	54	10
Woody debris addition	30	6

TABLE 5.—Length of stream or river (km) occupied by westslope cutthroat trout by genetic status and relative size of stream or river (1 = smallest and 6 = largest). Refer to Table 1 for more complete descriptions of genetic status codes and to Table 3 for relative sizes of streams or rivers.

Genetic status	Relative size 1	2	3	4	5	6	Total
Tested; unaltered	315	1,376	1,127	1,423	907	450	5,598
Tested; >25% introgressed	25	207	228	303	219	498	1,480
Tested; ≤25% to >10% introgressed	27	126	236	213	191	14	807
Tested; ≤10% introgressed	84	434	341	459	601	66	1,985
Suspected unaltered	3,281	5,696	2,590	1,374	1,022	842	14,805
Potentially altered	5,561	7,683	3,852	4,088	2,907	4,110	28,201
Mixed stock; altered and unaltered	27	138	144	217	209	950	1,686
Total	9,320	15,660	8,517	8,078	6,056	6,931	54,561

lation (Table 4). We did not segregate these conservation activities by stream length so could not report the length of stream for which each of these activities was applied. Angling restrictions were included as an appropriate conservation measure (Gresswell and Liss 1995).

Results

We found that the lengths of streams derived from 1:100,000-scale hydrography were only about 1% shorter than estimates of that same stream using 1:24,000-scale hydrography. However, differences in the number of streams identified on the two different scales were much more of a problem as 35% higher stream densities were found on the 1:24,000-scale hydrography than on the 1:100,000-scale hydrography for some river basins.

We estimated that WCT historically occupied 90,800 km and currently occupy 54,600 km (59% of historical) of lotic habitats within the western United Statea (Figure 1). Genetic sampling (n = 1,333 samples) of putative WCT found no evidence of genetic introgression in 768 samples (58%), indicating that WCT in about 5,600 km of stream length were not introgressed (Table 5). Westslope cutthroat trout that were likely part of a mixed-stock population with no evidence of introgression occupied almost another 1,700 km (mostly in larger streams and rivers), and approximately 14,500 km of streams were occupied by WCT that were suspected to be (but not tested) genetically unaltered (Figure 1).

A total of 563 WCT populations, occupying 39,355 km of stream length (72% of occupied stream length), were being managed as conservation populations (Figure 3; Table 6). Conservation populations were spread throughout the historical range, occurring in 67 of the 70 river basins historically occupied by WCT, though more of these populations were concentrated near the core than near its fringes (Figure 3). Individual conservation populations occupied from 0.5 to over 9,780 km of lotic habitats (median = 8.6 km). The distribution of stream length occupied by conservation populations was skewed as most of the populations occupied less than 20 km. Most conservation populations were isolated; however, conservation populations that were defined as metapopulations occupied much more stream length (Table 6). Most (60%, or 339) of the designated conservation populations had at least one genetic sample that found no introgression, and we suspected that 172 (30%) WCT conservation populations were not introgressed based on both genetic sampling and physical isolation. These 172 sus-

TABLE 6.—Number and kilometers of designated westslope cutthroat trout conservation populations by rationale used for so designating populations and whether those populations consist of single isolated populations (isolates) or connected groups of subpopulations (metapopulations).

Rationale for designation	Isolates Number	Isolates Km	Metapopulations Number	Metapopulations Km	Total Number	Total Km
Core conservation population	254	2,457	34	1,927	288	4,384
Unique life history	142	1,496	46	29,449	188	30,945
Ecological adaptation	2	9	1	19	3	29
Other	59	573	25	3,425	84	3,998
Total	457	4,535	106	34,820	563	39,355
(%)	81%	12%	19%	88%		

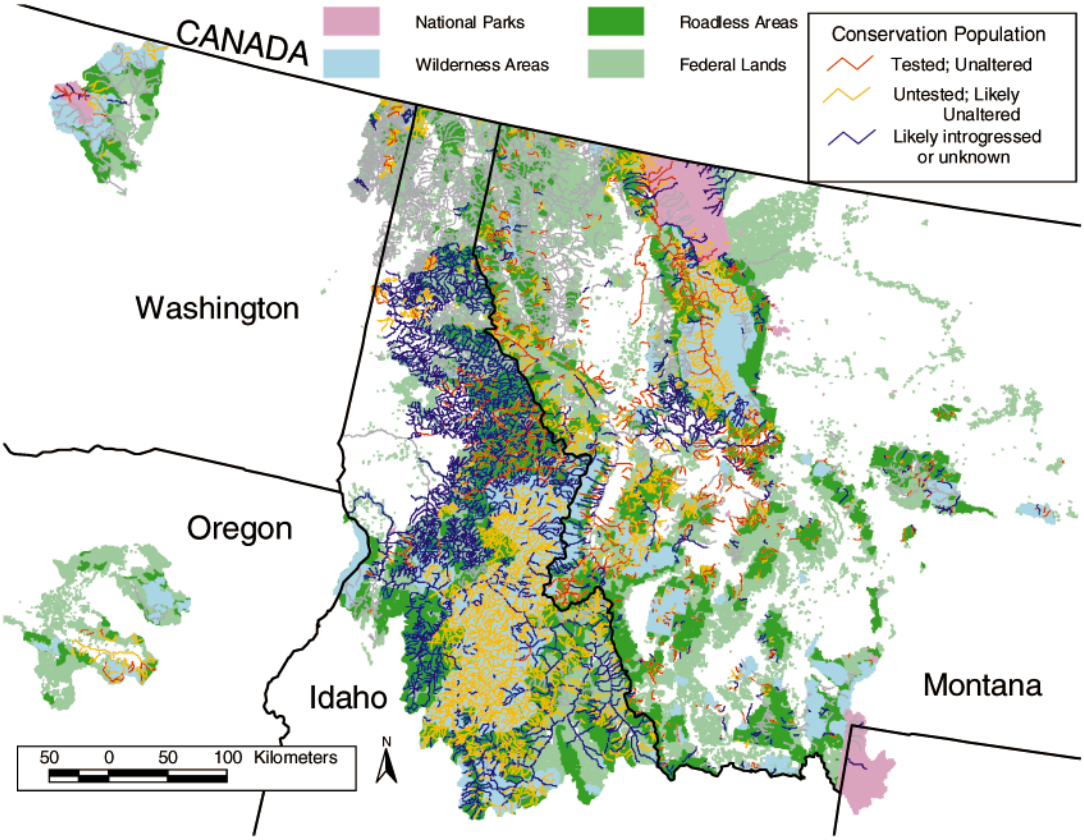

FIGURE 3.—Map showing the current distribution of westslope cutthroat trout vis-à-vis federal lands, designated wilderness areas, roadless areas, and national parks. Colored lines indicate conservation populations; gray indicates populations not designated as conservation populations.

pected genetically pure conservation populations occupied from 0.6 to 20.6 km of stream length (Table 7).

Of the nearly 54,600 km of stream length currently occupied by WCT, 2% was in national parks, 19% was in designated Forest Service wilderness areas, 21% was in Forest Service−designated roadless areas (excluding wilderness areas), and 30% was in other federally managed lands (Figure 3). Designated wilderness areas and national parks supported 1,000 km of the stream length occupied by genetically tested WCT populations with no evidence of introgression (representing 1–2% of all occupied length). Of the over 39,000 km of

TABLE 7.—Length of stream or river (km) that was occupied by conservation populations of westslope cutthroat trout in the western United States by genetic status and relative size of stream or river (1 = smallest and 6 = largest). Refer to Table 1 for more complete descriptions of genetic status codes and to Table 3 for relative sizes of streams and rivers.

Genetic status	Relative size						Total
	1	2	3	4	5	6	
Tested; unaltered	315	1,318	1,091	1,392	897	450	5,463
Tested; >25% introgressed	2	21	12	53	22		110
Tested; ≤25% to >10% introgressed	5	9	38	9	82		144
Tested; ≤10% introgressed	73	345	277	399	526	66	1,685
Suspected unaltered	3,056	5,230	2,413	1,244	975	820	13,738
Potentially altered	2,995	4,978	2,307	2,294	1,824	2,618	17,016
Mixed stock; altered and unaltered	23	138	139	207	193	499	1,199
Total	6,468	12,039	6,278	5,599	4,518	4,453	39,355

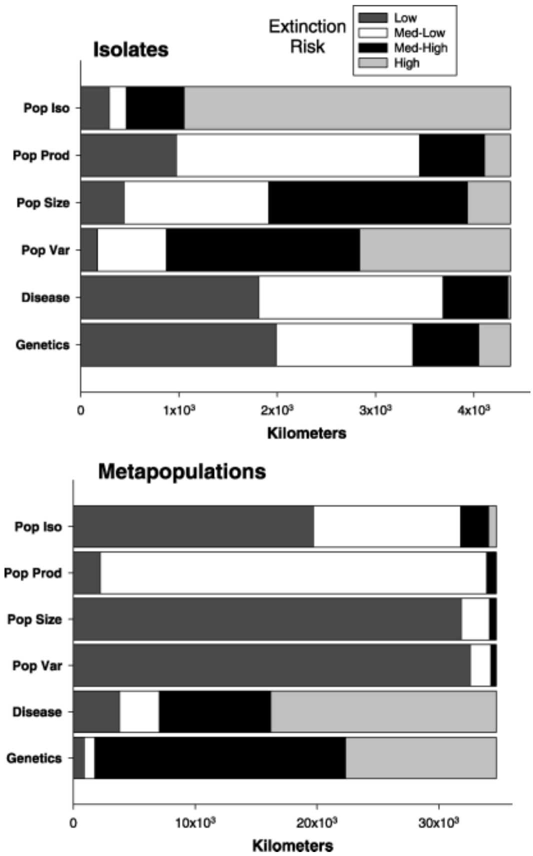

FIGURE 4.—Relative extinction risk (low to high) due to six factors (vertical axes; see Table 2 for detailed descriptions of each risk factor) by length of stream within designated westslope cutthroat trout conservation populations that were isolated (top panel) and connected (metapopulations; bottom panel).

stream length occupied by conservation populations, 76% was located within federally administered lands, 49% was in roadless areas, 24% was in designated wilderness areas, and 1.6% was in national parks.

In general, fish managers considered isolated conservation populations to be at higher risk than metapopulations due to temporal variability, population size, and isolation but at lower risk due to genetic introgression, disease, and population demographics (Figure 4). Some type of restoration activity has occurred, or is currently occurring, in some portion of 435 of the 563 identified conservation populations (77%), and many conservation populations had more than one conservation activity occurring for at least part of its occupied length (Table 4). Since fish managers consider WCT a game fish over all their range within the western Unites States, angling regulations apply to all WCT populations. Implementation of angling restrictions that were more stringent than the general angling regulation was the most common conservation action, affecting over half of the designated conservation populations. These more stringent restrictions often consisted of catch-and-release fishing for WCT, but other restrictions such as reductions in daily limits, size limits, and gear restrictions were also included. Habitat restoration activities—such as culvert replacement, channel restoration, bank stabilization, and riparian fencing—have each been implemented for 5–10% of the conservation populations. Projects to remove potential hybridizing or competing nonnative species, either by chemical or physical techniques, have occurred for over 5% of the conservation populations.

Discussion

The use of 1:100,000-scale hydrography for this analysis resulted in underestimate (downward) biases for both historical and current WCT distributions. However, these biases should be consistent. We have found that some streams not shown on 1:100,000-scale hydrography but appearing on 1:24,000-scale hydrography actually supported WCT (in fact, we have also found WCT in streams not identified on 1:24,000-scale maps), but these streams were not included in our assessment.

Historical Distribution

The length of the streams that we estimated to be within the WCT historical range in the western United States was less than previous estimates (Hanzel 1959; Behnke 1979; Liknes and Graham 1988; Behnke 1992; Van Eimeren 1996; Lee et al. 1997; Shepard et al. 1997; Thurow et al. 1997; U.S. Fish and Wildlife Service 1999). There are several reasons for these differences. First, we defined the historical time period as the time of European expansion into the western United States (circa 1800), later than the time period defined by most other authors. Secondly, we eliminated stream reaches above barriers (geological falls or thermal) or where habitats were unsuitable (i.e., extremely high channel gradient, intermittent streamflow), and there was no evidence suggesting WCT ever occupied the reach. Most previous assessments lumped relatively large geographical areas as being wholly within the historical range and assumed all reaches within these areas were historically occupied. We believe it is appropriate to benchmark historical range occupancy to a specific time period and used a more contemporary time period than some previous authors because we believed it was important to have some level of documentation for delineating historical range.

Current Distribution

We estimated that WCT currently occupy more stream length than earlier estimates for analogous areas. For example, Liknes and Graham (1988) estimated WCT occupied 6,900 km of lotic habitats in 1986 within Montana, Van Eimeren (1996) estimated 17,400 km were occupied in 1995, and we estimated that WCT occupied 20,900 km in 2002. Similar differences were also found among lengths these authors estimated were occupied by WCT with no evidence of introgression. These differences could easily be attributed to additional sampling that was done from 1986 (217 genetic samples and 2,224 fish surveys) to 1995 (1,232 and 6,586), and then to our summary in 2002 (1,994 and 10,299), and to the more detailed assessment we conducted. In contrast, Lee et al. (1997) and Thurow et al. (1997) estimated that WCT occupied 85% of their historical range in the upper and middle Columbia River basin using subwatershed areas (mean = 7,800 ha), a finding similar to ours for this basin (82%), though we used stream length. We caution that while over half of the genetic samples found no evidence of introgression, only 30% of these samples had enough individuals sampled to detect 1% introgression at the 95% level of confidence. Thus, we can only say that about 15% of all genetic samples had no evidence of introgression (<1%) with a high degree of confidence.

Westslope cutthroat trout currently occupy a higher proportion of the core of their historical range and display sparser occupancy near range fringe areas, particularly in the Missouri River system of Montana and disjunct habitats in Washington and Oregon (Figure 1). Several studies, both theoretical and empirical, have suggested a decline in the proportion of sites occupied and in population densities from the center to the fringe of a species range for many vertebrate species (e.g., Brown 1984; Caughley et al. 1988; Lawton 1993).

Habitat Protection

Our finding that wilderness and roadless areas provide important strongholds for WCT was similar to findings from other assessments (Liknes and Graham 1988; Marnell 1988; Rieman and Apperson 1989; Thurow et al. 1997). Since we did not assess BLM wilderness or roadless areas in this assessment because compatible GIS layers for BLM-administered lands were not readily available, our estimates of the proportions of habitat currently occupied by WCT within lands managed as wilderness and roadless are underestimates.

Designation of Conservation Populations

We found that state, tribal, and national park fish managers designated genetically pure, slightly introgressed, and genetically untested WCT as conservation populations (Utah Division of Wildlife Resources 2000). Fish managers generally did not include WCT populations with introgression levels of 10% or higher as conservation populations unless they made up part of a larger, interconnected metapopulation that was designated to conserve migratory life history characteristics. We found that only 5% of conservation populations had one or more stream reaches where introgression higher than 10% was documented by genetic testing.

The decision to conserve hybridized fish is subject to debate. However, we believe the inclusion of slightly hybridized fish may be prudent because (1) much of the genetic variation within WCT results from unique alleles (often occurring at relatively high frequencies) found in only one or two local populations (Allendorf and Leary 1988; Taylor et al. 2003), and (2) several authors have suggested that conserving slightly introgressed populations was a reasonable strategy to ensure the conservation of local phenotypic, genotypic, and behavioral variation but should be based on local considerations (Dowling and Childs 1992; Allendorf et al. 2001; Peacock and Kirchoff 2004). Dowling and Childs (1992) recommended that ''extreme care must be exercised when considering elimination of any (genetically) contaminated population lest the unique genetic identity of the native taxon be lost forever.'' In contrast, others have recommended that only genetically pure WCT should be protected under ESA (Allendorf et al. 2004). We do not believe that eradicating slightly introgressed populations is a reasonable or prudent conservation strategy.

Conservation Efforts

The potential vulnerability of WCT to both displacement (MacPhee 1966; Griffith 1972; Behnke 1979; Liknes and Graham 1988; Griffith 1988; Shepard et al. 2002; Dunham et al. 2003) and hybridization (Allendorf and Leary 1988; Allendorf et al. 2001, 2004) by nonnative trout has caused a dilemma for fish managers charged with conserving this subspecies. Metapopulation theory (Hanski and Gilpin 1991; Doak and Mills 1994; Hanski and Simberloff 1996) suggests that maintaining groups of connected local populations reduces long-term risks of extinction, and many researchers and managers have called for universally applying this theory in the conservation of native salmonids (Rieman and McIntyre 1993; Bisson 1995; Li et al. 1995; Reeves et al. 1995; Schlosser and Angermeier 1995; Independent Scientific Group 1996; National Research Council 1996; Lee et al. 1997; Policansky and Magnuson 1998; Rieman and Dunham 2000). However, maintaining or establishing connectivity among local populations of WCT may place these populations at high risk of invasion, and subsequent displacement or introgression, by nonnative trout (Allendorf and Leary 1988; Adams 1999; Allendorf et al. 2001; Adams et al. 2000; Adams et al. 2001; Rubidge et al. 2001; Dunham et al. 2003; Hitt et al. 2003; Weigel et al. 2003).

There were two types of conservation strategies inherent in how fish managers designated WCT conservation populations. One strategy emphasized conserving genetic integrity by isolating WCT populations that have no evidence of genetic introgression to prevent introgression. Isolating nonintrogressed WCT populations also reduces the risks associated with competition by nonnative fish and diseases. Isolated conservation populations accounted for 168 (98%) of the 172 conservation populations with no evidence of introgression, and the designation of 161 (94%) of these populations as conservation populations was based on conserving their genetic integrity. Of these 168 conservation populations, 56 (33%) were genetically ''secured'' by the presence of a fish migration barrier. Fish managers believed that while smaller, isolated WCT populations would be more susceptible to population-level risks due to isolation, small population size, and temporal variability, their isolation would make them less susceptible to risks from genetic introgression and disease. The assumption made in rating population risks as high for these isolated conservation populations was based on theoretical population dynamics, which assumes that groups of populations occupying relatively large connected habitats are at a lower risk of extinction than smaller, isolated populations.

The other strategy emphasized maintaining connectivity among WCT populations by protecting large areas of continuous habitat, thus allowing WCT to express all life history traits, especially migratory life histories. While metapopulations were believed less vulnerable to population risks such as temporal variability, isolation, and small population size, their connectedness made them more susceptible to risks from genetic introgression, competition, and disease. Thus, the risks inherent in these two different conservation strategies are dramatically different.

Some authors have indicated that cutthroat trout populations need to be supported by an effective population of 500 reproducing adults based on the 50/500 ''rule'' (Franklin 1980; Soulé 1980); thus, they have considered extinction risks to be high for most isolated, small populations of cutthroat trout (Shepard et al. 1997; Kruse et al. 2001; Hilderbrand and Kershner 2000). Harig and Fausch (2002) found that cutthroat trout translocations were most successful when the drainage area was at least 15 km^2, which translates to inhabited habitat lengths of about 5 km. Hilderbrand and Kershner (2000) estimated that cutthroat trout needed at least 9 km of habitat at moderately high densities to persist under the 500 rule. Rieman and Dunham (2000) provided data that indicated small, isolated populations of WCT might not be as prone to extinction as other vertebrates, and even other salmonids, based on their evaluation of the persistence of isolated headwater populations of WCT in the Coeur d'Alene basin of Idaho.

Since genetic introgression and nonnative competition threats may outweigh stochastic risks over the short term for many extant WCT populations, we suggest that isolating the remaining nonintrogressed WCT populations is a prudent, short-term conservation strategy (Novinger and Rahel 2003). Replicating and refounding existing isolated, nonintrogressed WCT populations that have high extinction risk due to stochastic or demographic pressures has been recognized as a viable conservation strategy (e.g., Montana Fish, Wildlife, and Parks 1999; Young and Harig 2001), and we recommend this strategy, where feasible. Applying this conservation management strategy implies that humans must act as the dispersal agent, via conservation stocking, to refound WCT populations that are lost from isolated habitats due to stochastic processes.

Evaluation of Workshop Approach

We suggest that the regional workshop approach used for simultaneously collecting both data and expert opinion provided consistent information across the range of this subspecies; however, we have several observations on why this worked and recommendations to improve this process. First, we believe that the consistent protocol that was developed and agreed upon prior to beginning workshop sessions was an integral reason for the success of this effort. Quality control and assurance was maintained by using a few facilitators who attended each workshop. Secondly, there was a strong commitment by each management agency that made attendance mandatory for their respective staffs. Thirdly, having baseline data available at each workshop in both electronic and hard copy format—displayed both in databases and on maps—allowed workshop participants to start from a common baseline. Fourthly, having data entry and GIS technicians at each workshop to enter and edit the data in real time and then display the new data on a GIS was invaluable. However, we strongly recommend that all final editing be completed at these workshops to avoid having to recontact individuals to verify or edit the information later.

We identified several weaknesses that were modified for subsequent assessments. While overall data quality was rated for each WCT population, we recommend rating data quality for each estimated parameter (i.e., upper distribution bound, lower distribution bound, abundance, genetic status, barrier status, barrier location). Participants did not explicitly include estimates of population size, relative abundance, or stream width, so it was impossible to assess abundance or density of remaining WCT populations. Participants attributed various conservation activities and human impacts to individual conservation populations, but not to specific stream segments occupied by that conservation population. While this generalization limited our ability to analyze these types of data, we found from an earlier assessment for Yellowstone cutthroat trout *O. c. bouvieri* that fish managers had difficulty directly linking human impacts to spatially explicit reaches because these data were usually not available. We suggest conservation activities might be linked to specific reaches but are unsure whether human impacts could be determined with currently available information.

Conclusions

Shepard et al. (2003) provided a baseline of information that can be used to assess future conservation progress and to prioritize and plan WCT conservation efforts. Updating this database with data from well-designed field monitoring programs will serve as a barometer to monitor the status of WCT over time. This monitoring should provide empirical evidence for testing and contrasting the success of isolation versus connection conservation strategies.

We found that WCT currently occupy significant portions of their historical range within the western United States, that they are well distributed across that range, and that fish managers are actively conserving many remaining WCT populations. Over 20% of the current length of streams occupied by WCT in the western United States are located within lands with very stringent land use restrictions that should adequately protect these aquatic habitats. Fish managers are working to reduce threats to WCT from genetic introgression, nonnative fish competition and predation, diseases, habitat loss, and angler harvest, while concurrently trying to maintain some WCT populations with migratory life histories.

Fish migration barriers are being used to isolate some WCT populations from threats of genetic introgression, nonnative fish competition and predation, and diseases. However, this strategy may increase potential extinction risks due to stochastic environmental and demographic processes. Fish managers are trying to address these risks by replicating some of these isolated populations, thereby having the potential to use these replicates to refound populations that go extinct. Maintaining WCT metapopulations in relatively large connected systems will likely increase risks of introgression, nonnative fish competition, and disease for some of these connected populations, but this will be a necessary trade-off in some systems in order to maintain populations with migratory life histories and to reduce stochastic environmental and demographic risks.

We conclude that while the distribution and abundance of WCT have declined dramatically from historical levels, as a subspecies WCT are not currently at imminent risk of extinction because (1) they are still widely distributed, especially within lands that have stringent habitat protection measures in place, (2) many populations are isolated by physical barriers from invasion by nonnative fish and disease, and (3) the active conservation of many populations is occurring. However, this conclusion does not reduce the need for continued aggressive conservation of this subspecies throughout its range, and particularly for populations located at the fringes of its historical range.

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