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Status of Lahontan Cutthroat Trout in the Coyote Lake Basin, Southeast Oregon

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Abstract.—Lahontan cutthroat trout *Oncorhynchus clarki henshawi* occur in streams flowing north through the Trout Creek and Oregon Canyon mountains into pluvial Coyote Lake in southeast Oregon. The Coyote Lake basin has the only native population of Lahontan cutthroat trout in Oregon that is without threat of hybridization and is broadly distributed throughout a drainage. In October 1994, the number of Lahontan cutthroat trout in the basin was estimated at 39,500 fish, and fish were limited to 56 km of the potential 114 km of stream habitat available. Distribution was limited by dry channels and thermal and physical barriers to movement, which created two disconnected populations in the Willow Creek and Whitehorse Creek drainages and influenced population density, structure, and life history. Lahontan cutthroat trout in the Coyote Lake basin would be more secure if aquatic habitat were improved to allow the two populations to expand their current distributions and become more connected.

The Lahontan cutthroat trout *Oncorhynchus clarki henshawi,* which is on the federal list of threatened species (Coffin and Cowan 1995), occurs in the Willow Creek and Whitehorse Creek drainages in southeast Oregon (Williams 1991; Bartley and Gall 1991; Williams et al. 1992). These drainages flow north into the pluvial Coyote Lake and are no longer connected. Behnke (1992) suggests that Lahontan cutthroat trout may have emigrated from headwaters of the Quinn River system (Humboldt River basin) to the Coyote Lake basin 40,000–70,000 years ago. The Coyote Lake basin is unique compared with other basins with Lahontan cutthroat trout because the Lahontan cutthroat trout is the only fish species in the basin.

The Coyote Lake basin has the only remaining native population of Lahontan cutthroat trout in Oregon that is without threat of hybridization and is broadly distributed throughout its stream system. Remnant, isolated populations of cutthroat trout occurred in drainages adjacent to the Coyote Lake basin at the turn of the century. Alvord cutthroat trout (a cutthroat trout subspecies, *Oncorhynchus clarki* subsp.) existed in the Alvord Lake basin (Behnke 1992) but were extirpated or hybridized with introduced rainbow trout *Oncorhynchus mykiss.* Lahontan cutthroat trout also occurred in Trout Creek and Oregon Canyon basins but have hybridized with rainbow trout. Lahontan cutthroat trout presently occupy portions of two tributaries to McDermitt Creek in the Humboldt River drainage. Other streams in the McDermitt Creek drainage contain hybridized Lahontan cutthroat trout, brook trout *Salvelinus fontinalis,* and brown trout *Salmo trutta.*

Although the number of Lahontan cutthroat trout in the Coyote Lake basin as a whole remains high, the overall status is unknown. Riparian and upland habitats have been degraded by intensive grazing by cattle *Bos* spp. and sheep *Ovis aries* during the past 130 years. Drought and cold periods during the past decade have further affected the quantity and quality of the aquatic habitat.

Because of perennially or seasonally dry sections of channels, thermal barriers, and physical barriers (waterfalls), the ability of Lahontan cutthroat trout to disperse and migrate in the Willow Creek and Whitehorse Creek basins was believed to be limited. Our objectives were to (1) describe the distribution of Lahontan cutthroat trout throughout the Willow Creek and Whitehorse Creek drainages, (2) determine their age-class structures, (3) estimate the abundance of age-0 and age-1 and older (age-1+) fish in each drainage, and (4) discuss the potential changes in population dynamics given ecological restoration of the drainages.

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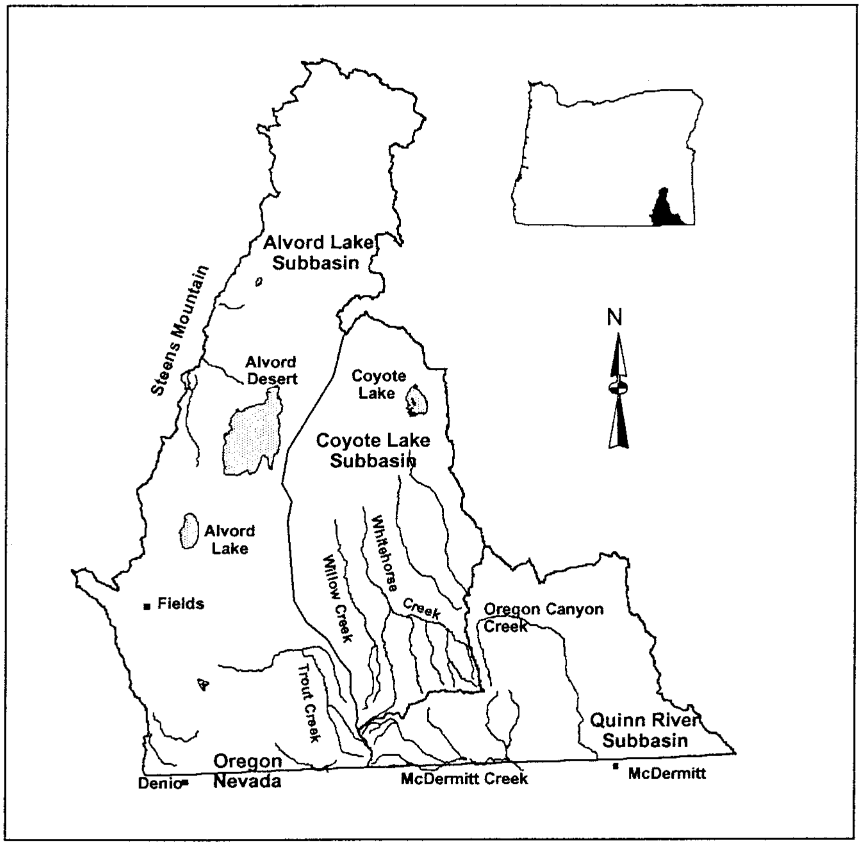

FIGURE 1.—Lahontan cutthroat trout study area in southeast Oregon

Study Area

The Willow Creek and Whitehorse Creek basins are in southeast Oregon (Figure 1) between the Oregon Canyon Mountains to the east and the Trout Creek Mountains to the west. Both drainages flow northward into the pluvial Coyote Lake and are currently isolated from each other. The Whitehorse Creek watershed is 333 km^2, and the Willow Creek watershed is 130 km^2. Summer air temperatures in the basins exceed 38°C, and winter air temperatures drop to less than −18°C. Behnke (1992) suggested that these two drainages may have had intermittent connectivity through pluvial Coyote Lake several thousand years ago, but Coyote Lake has been dry in recent history. The Willow Creek basin includes small, intermittent tributaries, whereas the Whitehorse basin includes perennial Whitehorse, Little Whitehorse, Fifteenmile, Doolittle, and Cottonwood creeks (Figure 2). Several barriers to upstream fish migration are present in the Willow Creek and Whitehorse Creek drainages: a 3-m-high headcut in lower Willow Creek; falls in lower Cottonwood, Doolittle, and Fifteenmile creeks; and steep cascades in upper Whitehorse Creek.

Neither the Whitehorse Creek nor the Willow Creek drainage has stream gauges, although Trout Creek, the neighboring drainage (225 km^2) to the west has been gauged (1932–1991). Discharge has fluctuated dramatically during the past 15 years, with extremely high discharges during 1983–1984 and extremely low discharges during 1987–1988, 1990–1992, and 1994.

The Trout Creek and Oregon Canyon mountains rise from 1,200 m (above mean sea level) at the desert floor to 2,500 m. Streams flow through deep, rugged canyons of steep rimrock. The primary vegetation consists of sagebrush *Atemesia* spp., rabbit brush *Chrysothamnus* spp., and native bunchgrasses (e.g., *Agropyron spicatum, Festuca idahoensis, Stipa thurberiana, Sitanion hystri,* and *Poa sandbergii*) in the uplands and willow *Salix*

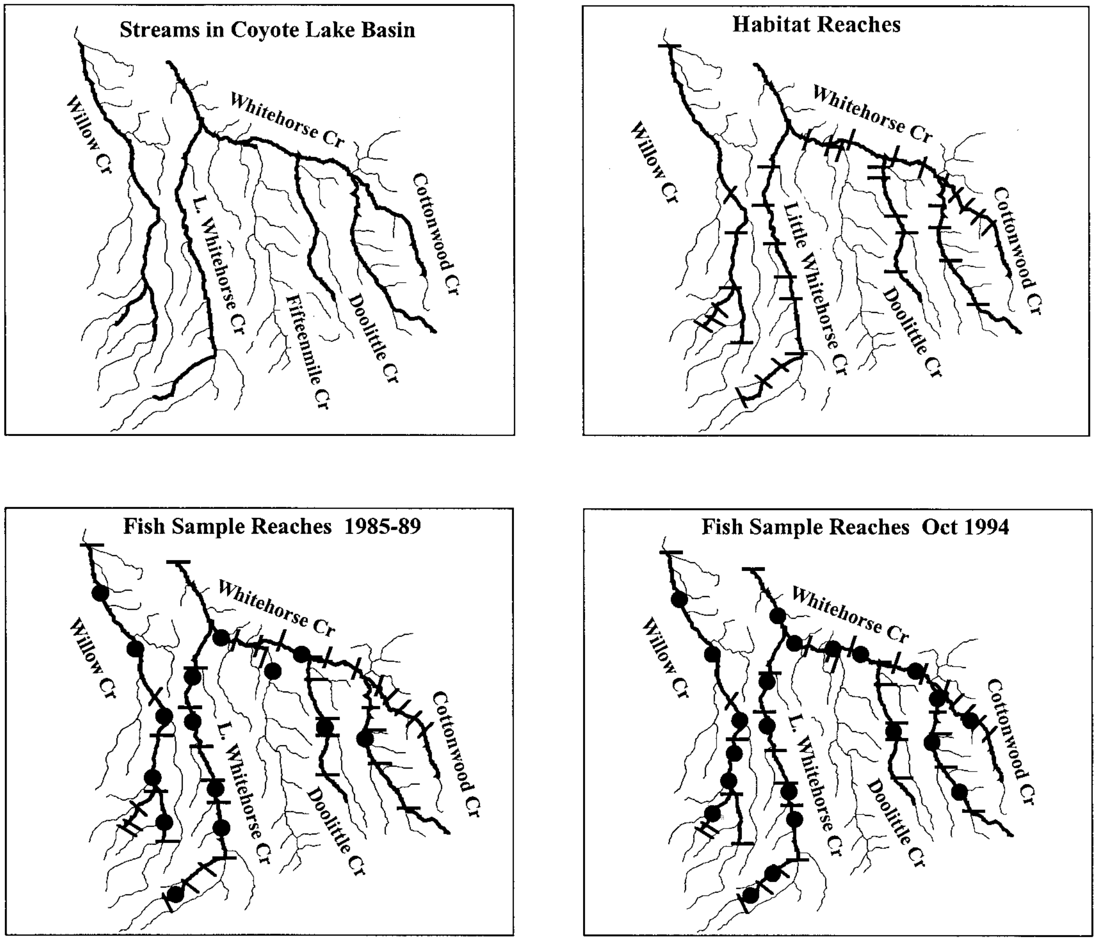

FIGURE 2.—Potential fish-bearing streams in the Willow Creek and Whitehorse Creek drainages of Coyote Lake basin in southeast Oregon. Habitat reach breaks are shown with a straight line and fish sample sites in 1985–1989 and 1994 are depicted by a solid circle.

spp., wild rose *Rosa gymnocarpa*, sedges *Carex* spp., and sagebrush along streams. Mountain mahoganies *Cerocarpus ledifolius* cover some of the high-elevation areas, scattered quaking aspens *Populus tremuloides* occur on hillsides and riparian areas and some cottonwoods *Populus angustifolia* remain in the basin. The lowest elevations contain irrigated hay fields where the streams empty onto flat valleys. The portion of the basin above the valley floor is managed by the U.S. Bureau of Land Management (BLM), and the primary uses are cattle grazing and recreation. The basin has been used for sheep and cattle grazing since the late 1800s, and cattle grazing continues in the basin with a management strategy initiated in 1989 (BLM 1990).

Methods

Habitat surveys.—The Oregon Department of Fish and Wildlife (ODFW) assessed habitat conditions (channel and valley morphology, riparian characteristics and condition, and instream features) in the Willow, Little Whitehorse, and Whitehorse subbasins following Moore et al. (1997). Habitat data were collected and analyzed on a hierarchical system of basins, stream, reach, and habitat units (Frissell et al. 1986; Hankin and Reeves 1988; Gregory et al. 1991).

Two-person crews surveyed streams from their mouths to headwaters. Reaches were defined with similar valley and channel geomorphology (Gregory et al. 1989; Moore and Gregory 1989), stream gradient, land use, riparian characteristics, and stream flow (Figure 2), and the stream channel was described as a sequence of habitat units within each reach. Each unit was longer than one active channel width and represented an area of homogeneous slope, depth, and flow. The channel was classified into a series of hierarchically organized habitat units of pools, glides, riffles, rapids, cascades, and steps (Bisson et al. 1982; Hawkins et al. 1993). In each habitat unit, the depth and water surface slope was measured, and the length and width were visually estimated and adjusted by calibration (Hankin and Reeves 1988) from actual measurements in a 1-in-10 sample of habitat units. Substrate, woody debris, shade, features of in-stream cover, and bank stability were measured or classified at each unit.

Fish population estimates.—Fish were surveyed in October 1994 with a stratified, systematic design to determine the abundance of the Lahontan cutthroat trout populations in three basins: Willow Creek, Little Whitehorse Creek, and Whitehorse Creek (including Fifteenmile, Doolittle, and Cottonwood creeks; see Figure 2). Sample sites were selected in all reaches that had wetted channels, and some were selected to replicate sampling in 1985 and 1989 (Buckman 1989; Perkins et al. 1991).

Previous sampling indicated that a confidence interval of ±50% of the estimated size of the fish population could be achieved with a minimum sample size of 40 habitat units in each basin, and we considered this level of precision to be acceptable.

Fish abundance was determined with removal–depletion estimates (White et al. 1982). Each habitat unit (pools and fast water) was blocknetted and a backpack electrofisher was used to collect fish. We required a 50% reduction in a subsequent pass for an adequate depletion estimate for both age-0 fish and age-1+ fish. Usually two passes were required, but up to four passes were occasionally necessary. Age-0 fish were distinguished from older fish based on length. Ponds formed by beavers *Castor canadensis* that were too deep to electroshock effectively were censused separately by snorkeling. Two snorkelers swam up each side of beaver pools and counted age-0 and age-1+ fish. Snorkel counts were considered as minimum estimates because the inability to verify by another method (Hankin and Reeves 1988) precluded estimation of fish not observed.

Estimates of population size and confidence limits were calculated for age-0 and age-1+ fish with equations in Bohlin (1981). Subbasin estimates of total population size were extrapolated, based on the wetted-channel length or area at the time of sampling. Fish of each age-class (age-0 and age-1+) were expanded separately for each habitat unit type (pool, fast water, and beaver pond) and summed. Counts of fish in beaver pools were added to subbasin totals without any contribution of sampling variance.

Population structure.—The fork lengths of fish captured by electroshocking were measured to the nearest millimeter, and scale samples were taken from a subset of the fish collected from mid- and high-elevation sites to determine length at age. Age-0 fish were distinguished from older fish by length frequency analysis (MacDonald 1987) and confirmed with scale analysis (L. Borgerson, ODFW, personal communication), as were the proportions of age-1, age-2, and age-3 and older fish in the populations. We tested the length frequency plots to determine if fish lengths at age were similar at different elevations. The sampled fish were placed into three elevation classes: <1,500 m, 1,500–1,800 m, and >1,800 m. A Kruskal–Wallis test was used to test for differences ($P < 0.001$) in length distribution among the three elevation classes for age-0 and for age-1 fish (Neter and Wasserman 1974). A pairwise multiple-comparison procedure (Dunn 1964) was used to test ($P < 0.05$) for differences in length distributions between classes.

Results

In all, 205 habitat units were sampled across the three basins: 91 pools, 91 fast-water units (riffles, rapids, cascades), and 23 beaver ponds. Approximately 4% of the total habitat area was sampled, including 3.5% of fast water, 12% of the pools, and 65% of the beaver ponds.

Age-0 and age-1 fish were significantly smaller ($P < 0.001$) at higher elevations (Figure 3). The median lengths of age-0 fish were 72 mm at elevations below 1,500 m; 64 mm at 1,500–1,800 m; and 51 mm at elevations above 1,800 m. Age-1 fish had median lengths of 123 mm, 118 mm, and 95 mm, respectively. Of the age-1+ fish sampled, an average of 73% were age 1, 20% were age 2, and 7% were age 3+.

The number of fish was estimated at 39,472 (95% confidence interval = ±7,893 fish) over 56 km of stream habitat during autumn of 1994 in the Willow and Whitehorse basins. Population size in Willow Creek basin was estimated to be 5,400 age-0 and 9,300 age-1+ fish (Table 1). Population size in Little Whitehorse Creek subbasin was estimated

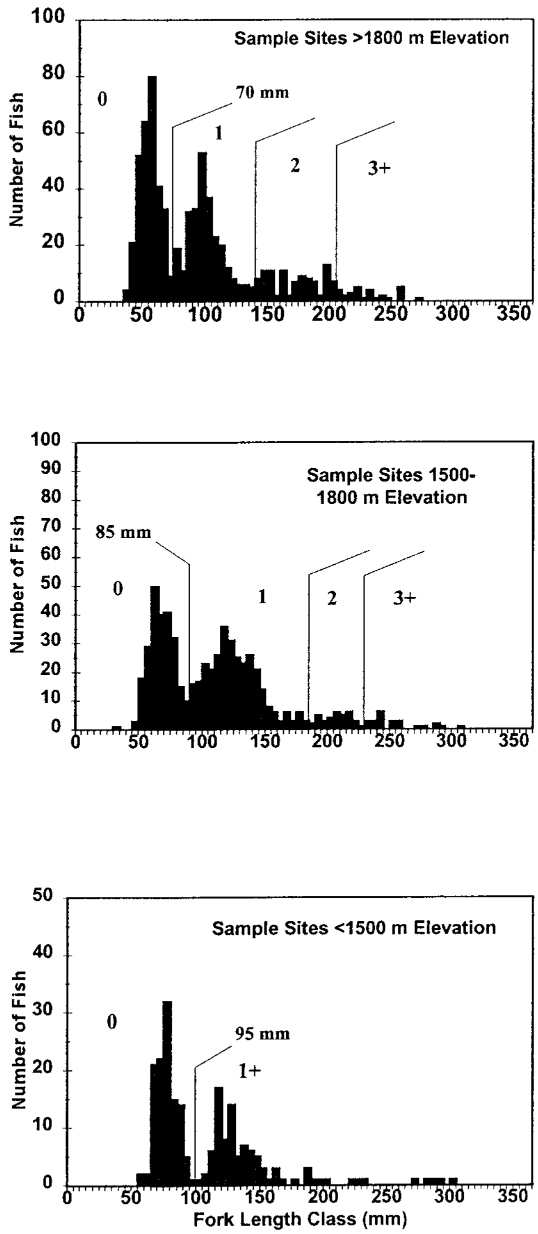

FIGURE 3.—Length frequency of Lahontan cutthroat trout at different elevations in the Willow Creek and Whitehorse Creek drainages. Ages are estimated from scale analysis for the high- and mid-elevation sites.

to be 3,500 age-0 and 2,800 age-1+ fish. Fewer than 200 age-1+ fish occupied the lowest five reaches in October 1994. Population size in Whitehorse Creek subbasin was estimated to be 8,600 age-0 and 9,900 age-1+ fish.

Low-elevation reaches had the lowest densities of fish (0.00–0.25 fish/m^2) in both pools and fast-water units (Figure 4; Table 2). Headwater reaches consistently held the highest densities of age-1+ fish in all streams (0.54-1.09 fish/m^2 in pools and 0.19–0.48 fish/m^2 in fast-water units). The distribution and density of age-0 fish differed from that of age-1+ fish (Figure 4). While the densities of age-0 fish were also highest in headwater reaches, age-0 fish also had densities of 0.25 fish/m^2 in pools in some of the low-elevation reaches.

The densities of age-1+ fish sampled in 1985 and 1989 (Buckman 1989; Perkins et al. 1991) with a representative reach approach are presented in Figure 5. In 1985, following 2 years of extremely high flow discharge, fish populations extended to the lower reaches of the drainages. In 1989 during an average water year that followed two drought years and an extremely cold winter, the densities of age-1+ fish were much lower than in 1985 or 1994, and fish were limited in distribution or absent in the lower reaches, similar to the situation in 1994.

Discussion

In 1994, about 25,000 Lahontan cutthroat trout occupied the Whitehorse Creek drainage and about 15,000 cutthroat trout occupied the Willow Creek drainage. Less than 21 of the 33 km of stream habitat in the Willow Creek drainage and 35 of the 81 km of stream habitat in the Whitehorse Creek drainage supported Lahontan cutthroat trout because many of the channels were dry or had very high water temperatures.

The ability of local populations to interact is important to the long-term viability of a metapopulation (Hanski and Gilpin 1991). The population of Lahontan cutthroat trout in the Whitehorse Creek subbasin has been fragmented by numerous barriers (Figure 6) into four discreet local populations that occupy Little Whitehorse, Doolittle, Cottonwood, and Whitehorse creeks. Fish in these local populations can migrate downstream (some only during high streamflows), but upstream migration can occur only in the main stem of Whitehorse Creek and Little Whitehorse Creek. Populations in Cottonwood and Doolittle are isolated by falls, Fifteenmile Creek is uninhabited above a 3-m-high falls located 1 km upstream of the mouth, and a cascade in a mid-elevation reach of Whitehorse Creek may restrict the upstream movement of fish. The Willow Creek subbasin is largely free of migration barriers, except for a 2-m-high headcut in its lower floodplain that is probably passable at high flows. Seasonally, all streams in the drainages have disjunct populations because of high

TABLE 1.—Estimated sizes and ±95% confidence intervals (CI) of Lahontan cutthroat trout populations for age-0 and age-1 and older (age-1+) fish in the Willow Creek, Little Whitehorse Creek, and Whitehorse Creek subbasins and the length of stream habitat occupied in October 1994.

	Age 0		Age 1+		All ages		Length of occupied stream habitat
Streams	Estimate	CI	Estimate	CI	Estimate	CI	(km)
Willow Creek	5,441	±3,903	9,273	±4,269	14,714	±5,784	21
Little Whitehorse Creek	3,483	±2,391	2,773	±1,639	6,256	±2,900	14
Whitehorse Creek	8,612	±3,922	9,890	±2,245	18,502	±4,519	21
Total	17,536	±6,028	21,936	±5,094	39,472	±7,893	56

summer temperatures (>26°C) or dry channels (Figure 6).

The isolated populations in Doolittle and Cottonwood creeks occupied a small amount of habitat and had few adult fish in 1994. We estimated that 1,500 age-1+ fish and 100 age-3+ fish occur in Cottonwood Creek and that 55 age-1+ fish and fewer than 10 age-3+ fish occur in Doolittle Creek.

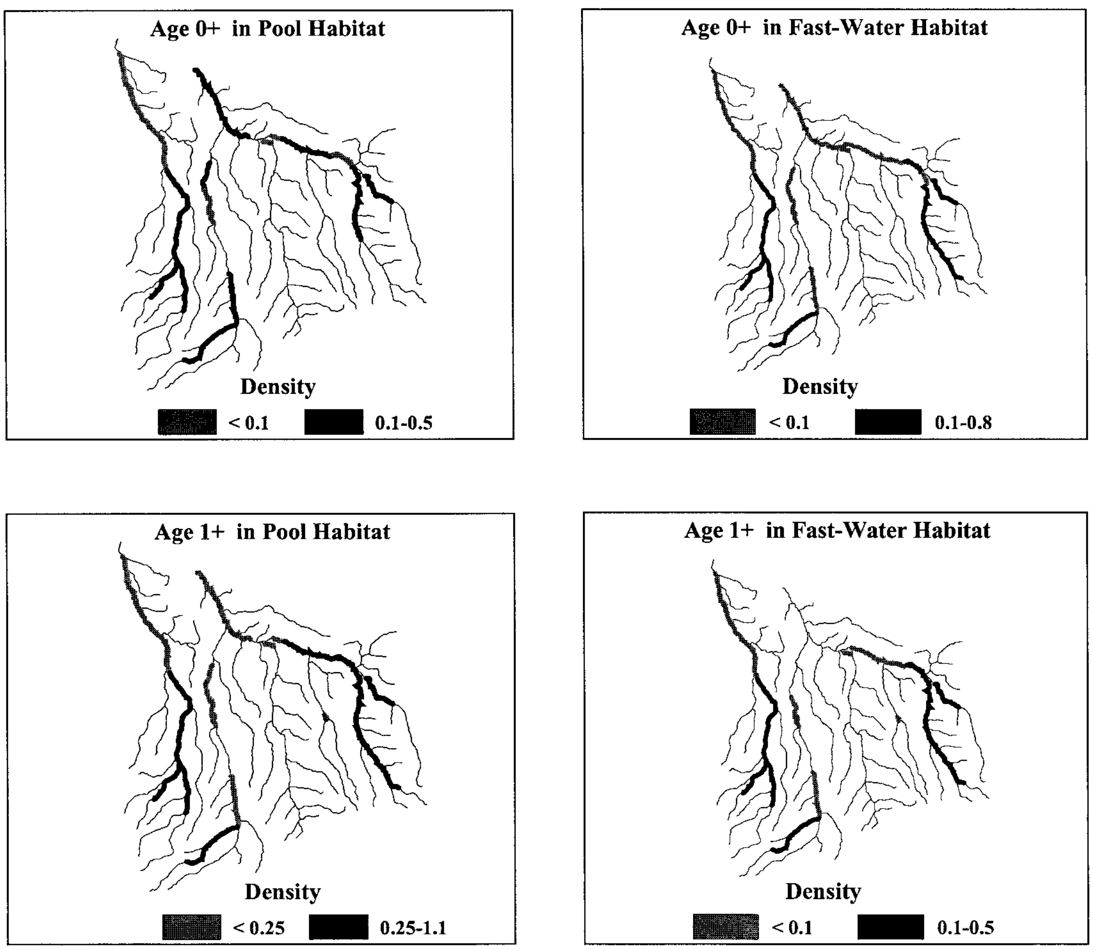

FIGURE 4.—Average densities (fish/m^2) by reach of age-0 and age-1+ Lahontan cutthroat trout in pools and fast-water habitat units in the Willow Creek and Whitehorse Creek drainages.

TABLE 2.—Average densities (ranges in parentheses) of age-0 and age-1 and older (age-1+) Lahontan cutthroat trout in fast-water (fast) and pool habitats for all reaches sampled in the Willow Creek, Little Whitehorse Creek, and Whitehorse Creek watersheds in 1994.

Stream	Number of reaches sampled	Habitat	Density (number/m^2) of	
			Age-0 fish	Age-1+ fish
Willow Creek subbasin				
Willow Creek	4	Fast	0.21 (0.03–0.41)	0.21 (0.05–0.38)
		Pool	0.20 (0.09–0.28)	0.40 (0.05–0.71)
Willow Creek tributary[a]	3	Fast	0.10	0.24
		Pool	0.39	1.09
Little Whitehorse Creek subbasin				
Little Whitehorse Creek	6	Fast	0.07 (0.00–0.30)	0.01 (0.00–0.03)
		Pool	0.07 (0.00–0.26)	0.06 (0.00–0.12)
Cow Camp tributary	3	Fast	0.40 (0.29–0.46)	0.30 (0.19–0.36)
		Pool	0.26 (0.21–0.35)	0.83 (0.54–0.98)
Whitehorse Creek subbasin				
Whitehorse Creek	10	Fast	0.14 (0.00–0.79)	0.10 (0.00–0.30)
		Pool	0.11 (0.00–0.27)	0.54 (0.00–0.97)
Fifteenmile Creek	3	Fast	0.01 (0.00–0.01)	0.10 (0.00–0.10)
		Pool	0.03 (0.00–0.04)	0.13 (0.00–0.20)
Doolittle Creek	6	Fast	0.00 (0.00–0.00)	0.01 (0.00–0.05)
		Pool	0.00 (0.00–0.00)	0.04 (0.00–0.23)
Cottonwood Creek	7	Fast	0.25 (0.00–0.35)	0.34 (0.00–0.48)
		Pool	0.34 (0.00–0.47)	0.34 (0.00–0.48)

[a] Three reaches were sampled as one fish sample site.

Lacustrine and resident Lahontan cutthroat trout mature at ages 3–5 (Gerstrung 1988; Downs et al. 1997); thus, the spawning populations in Doolittle and Cottonwood creeks are very small. Small local populations may have an increased probability of extinction because of environmental instability (Schlosser 1982; Hanski 1991), low recolonization potential (Rieman and McIntyre 1995), and loss of genetic variation (Allendorf and Phelps 1980).

Densities of Lahontan cutthroat trout in both the Willow and Whitehorse drainages were high in the high-elevation reaches because of consistent flows of cool water during the summer. Densities of fish (>0.25 fish/m^2) in the high-elevation reaches were similar to cutthroat trout and rainbow trout densities in other streams in eastern Oregon and Nevada (Platts and McHenry 1988; ODFW, unpublished data).

Understanding the spatial structure of metapopulations is essential in developing meaningful conservation strategies that protect and restore fish populations (Schlosser and Angermeier 1995) and maintain core populations necessary for long-term persistence of stream fish populations (Li et al. 1995; Schlosser and Angermeier 1995). In the Willow Creek and Whitehorse Creek drainages we define core populations for Lahontan cutthroat trout to be those populations that persist in a reach of stream year-round, during both favorable conditions (wet climate) and unfavorable conditions (dry climate). The spatial variation in population density during 1985, 1989, and 1994 implies that core populations existed in the high-elevation reaches in Willow, Little Whitehorse, Whitehorse, Doolittle, and Cottonwood creeks (Figure 7). The distribution of the population appears to expand during favorable conditions, as in 1985, and contracts during unfavorable conditions, as in 1989 and 1994. Core populations identified in Cottonwood and Doolittle creeks have falls or dry-channel sections near their stream mouths; downstream migration can occur only during high stream flows, and upstream migration is totally blocked by falls. Isolated population segments are more at risk of extinction after localized disturbances, such as extreme flood or intensive grazing, and recolonization from adjacent populations cannot occur.

Lahontan cutthroat trout can exhibit resident, fluvial, adfluvial, and lacustrine life histories. A key factor for rearing of fluvial fish is the deeper habitat available in low-gradient meadow reaches (Gerstung 1988). A fluvial life history in the Willow Creek and Whitehorse Creek drainages is currently limited because rearing in downstream reaches, which have high amounts of deep-scour pools and beaver ponds, is limited by lethal water temperatures (>26°C). Recovery and connectivity of downstream habitats would increase the pro-

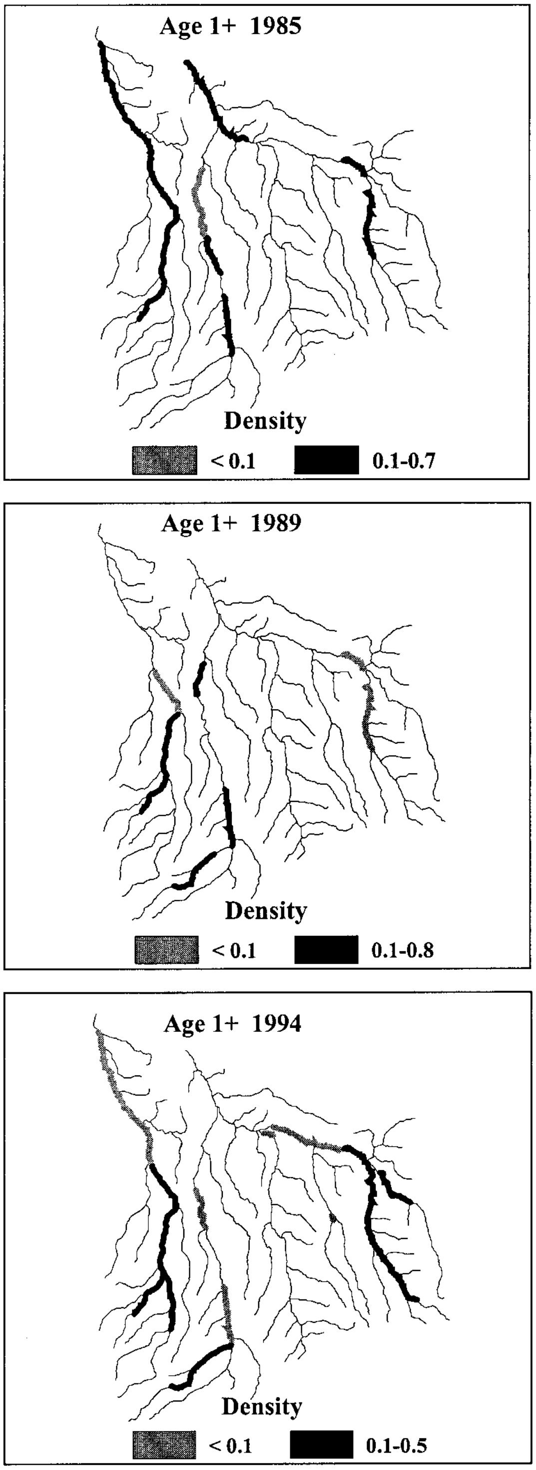

FIGURE 5.—Average densities by reach of age-1+ Lahontan cutthroat trout in 1985, 1989, and 1994.

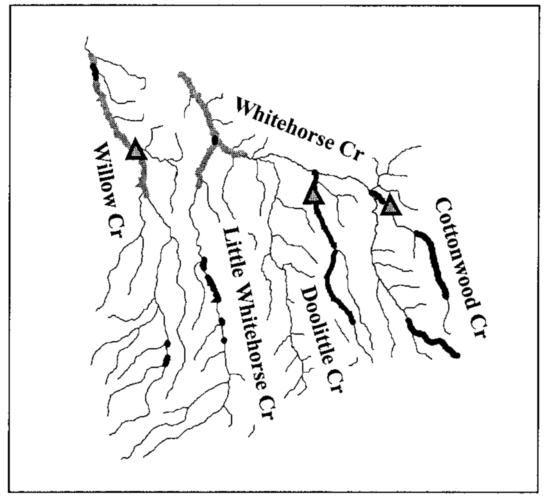

FIGURE 6.—Locations of dry channel (heavy black river sections), water temperatures above 26°C (gray), and physical barriers (triangles) in the Willow Creek and Whitehorse Creek drainages.

duction potential of Lahontan cutthroat trout and support a greater diversity of life histories in the two basins.

This study was conducted to support management objectives of ecological restoration (Kauff-

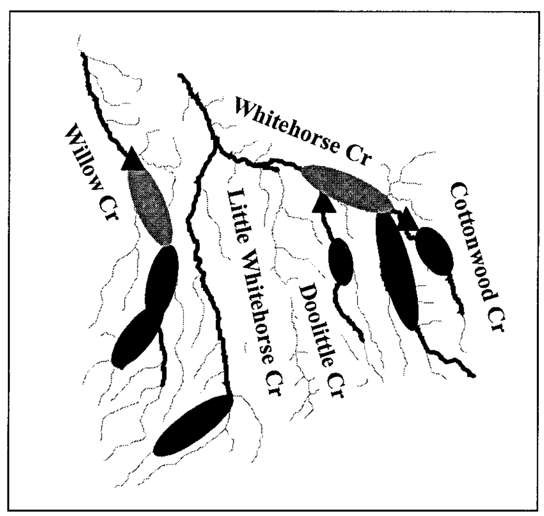

FIGURE 7.—Location of Lahontan cutthroat trout high-density population centers. Black ellipses represent all years (1985, 1989, 1994); gray ellipses represent high-density areas in a wet year (1985). Population centers are restricted to upper portions of basins during dry years and expand to lower reaches in wet years. Triangles show the location of barriers in the Willow Creek and Whitehorse Creek drainages.

man et al. 1997) of the Coyote Lake basin. The Willow Creek and Whitehorse Creek drainages represent a key component of Lahontan cutthroat populations in the Great Basin, and they are part of the overall restoration and protection of fish species and populations in the Pacific Northwest (Watershed Subcommittee 1993; Li et al. 1995). These data on the status of Lahontan cutthroat trout are being used to monitor and improve a basinwide restoration plan (Hanson et al. 1993; Coffin and Cowan 1995). The restoration strategy for the basin is designed to emphasize not only the core habitats and populations, but also the marginal habitats and local populations (Scudder 1989). Security of the Lahontan cutthroat trout population in the Coyote Lake basin ultimately depends on the restoration of fragmented aquatic habitat.

Acknowledgments

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References

Allendorf, F. W., and S. R. Phelps. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. Transactions of the American Fisheries Society 109: 537–543.

Bartley, D. M., and G. A. E. Gall. 1991. Genetic identification of native cutthroat trout (*Oncorhyncus clarki*) and introgressive hybridization with introduced rainbow trout (*O. mykiss*) in streams associated with the Alvord basin, Oregon and Nevada. Copeia 1991:854–859.

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

Bisson, P. A., J. A. Nielsen, R. A. Palmasono, and E. L. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low stream flow. Pages 62–73 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

BLM (U.S. Bureau of Land Management). 1990. Whitehorse Butte allotment final environmental assessment. BLM, R-030-90-08, Vale, Oregon.

Bohlin, T. 1981. Methods of estimating total stock, smolt output and survival of salmonids using electrofishing. Institute of Freshwater Research Drottningholm Report 59.

Buckman, R. C. 1989. Trout Creek Mountains wild trout investigations. Oregon Department of Fish and Wildlife, Special Report, Hines, Oregon.

Coffin, P. D., and W. F. Cowan. 1995. Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon.

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

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6:241–252.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification; viewing streams in a watershed context. Environmental Management 10:199–214.

Gerstung, E. R. 1988. Status, life history, and management of the Lahontan cutthroat trout. Pages 93–106 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Gregory, S. V., G. A. Lamberti, and K. M. Moore. 1989. Influence of valley floor landforms on stream ecosystems. U.S. Forest Service General Technical Report PSW-110:3–8.

Gregory, S. V., F. J. Swanson, and W. A. McKee. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

Hankin, D. G., and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834–844.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17–38.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: a brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Hanson, M. L., W. Bowers, and R. Perkins. 1993. Lahontan subbasins fish management plan. Oregon Department of Fish and Wildlife, Portland.

Hawkins, C. P., and ten coauthors. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18(6):3–12.

Kauffman, J. B., R. L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. Fisheries 22(5):12–24.

Li, W. H., and twelve coauthors. 1995. Safe havens: refuges and evolutionarily significant units. Pages 371–380 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystems: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

MacDonald, P. D. M. 1987. Analysis of length–frequency distributions. Pages 371–384 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Moore, K. M., and S. V. Gregory. 1989. Geomorphic and riparian influences on the distribution and abundance of salmonids in a Cascade Mountain stream. U.S. Forest Service General Technical Report PSW-110:256–261.

Moore, K. M. S., K. K. Jones, and J. M. Dambacher. 1997. Methods for stream habitat surveys. Oregon Department of Fish and Wildlife, Information Report 97-4, Portland.

Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Irwin, Homewood, Illinois.

Perkins, R. R., R. C. Buckman, and W. E. Hosford. 1991. Trout Creek Mountains wild trout investigations. Oregon Department of Fish and Wildlife, Special Report, Hines.

Platts, W. S., and M. L. McHenry. 1988. Density and biomass of trout and char in western streams. U.S. Forest Service General Technical Report INT-241.

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

Schlosser, I. J. 1982. Fish community structure and function along the habitat gradients in a headwater stream. Ecological Monographs 52:395–414.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Scudder, G. G. E. 1989. The adaptive significance of marginal populations: a general perspective. Canadian Special Publication of Fisheries and Aquatic Sciences 105:180–185.

Watershed Subcommittee. 1993. Oregon critical watershed database. American Fisheries Society, Oregon Chapter Natural Production Committee, Corvallis, Oregon.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, UC-11, Los Alamos, New Mexico.

Williams, R. N. 1991. Genetic analysis and taxonomic status of cutthroat trout from Willow Creek and Whitehorse Creek in southeastern Oregon. Boise State University, Evolutionary Genetics Laboratory Report 91-3, Boise, Idaho.

Williams, R. N., D. K. Shiozawa, and R. P. Evans. 1992. Mitocondrial DNA analysis of Nevada cutthroat trout populations. Boise State University, Evolutionary Genetics Laboratory Report 91-5, Boise, Idaho.

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