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Westslope Cutthroat Trout in Montana: Life History, Status, and Management

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Abstract.—The historic range of westslope cutthroat trout *Salmo clarki lewisi* included western Montana, central and northern Idaho, a small portion of Wyoming, and portions of three Canadian provinces. The distribution and abundance of westslope cutthroat trout have drastically declined from its historic range during the last 100 years. Although previous studies in Montana identified strongholds of populations, the status of westslope cutthroat trout over its complete range is uncertain. Three life history forms are found within this range: (1) lacustrine–adfluvial stocks, (2) fluvial–adfluvial populations, and (3) fluvial fish. Migratory adults travel long distances during periods of high streamflow and spawn when water temperatures are near 10°C. Most migratory adults quickly leave the spawning grounds following the spawning act. Sexual maturity is attained at age 3 or older. In some drainages, repeat spawning occurs predominantly in alternate years. Westslope cutthroat trout are opportunistic in their food habits, but are not highly piscivorous; they tend to specialize as invertebrate feeders. The decline of westslope cutthroat trout has been attributed to overexploitation, genetic introgression, competition from or replacement by nonnative species, and habitat degradation. Westslope cutthroat trout occupy only 27.4% of their original range in Montana, and genetically pure populations are present in only about 2.5% of their historic range. As a whole, westslope cutthroat trout populations in Idaho and British Columbia, Canada, have fared better than in Montana. Management programs designed to protect the westslope cutthroat trout have helped to maintain or increase existing populations, and even to create new populations.

The decline in abundance and distribution of interior cutthroat trout *Salmo clarki* have been so dramatic that many subspecies are on the brink of extinction as genetically pure populations. It has been estimated that at least 99% of the original populations of interior cutthroat trout have been lost in the last 100 years (Behnke 1972). One of these subspecies, the westslope cutthroat trout *Salmo clarki lewisi* was once the dominant trout over a historic range that encompassed western Montana, central and northern Idaho, and a small portion of northwestern Wyoming in the USA and southwestern Saskatchewan, southern Alberta, and southeastern British Columbia in Canada (Figure 1; Behnke 1979). The Yellowstone cutthroat trout *S. c. bouvieri*, a subspecies found in adjacent drainages (Figure 1), has often been confused with the westslope cutthroat trout. Today the dominance of the westslope cutthroat trout has waned, and its present status is uncertain. Protection of the remaining populations is essential because, in addition to being uniquely adapted to a particular water, each population represents an exclusive source of genetic material for increasing diversity of brood stocks used for propagation and reintroductions.

The name "westslope" suggests a presence west of the Continental Divide, but a considerable portion of this subspecies' original range lies east of the Continental Divide. The current and historic ranges of the westslope cutthroat trout encompass the upper Missouri River drainage upstream from Fort Benton, Montana, as well as the headwaters of the Marias, Judith, Musselshell, and Milk rivers, which are tributaries that enter the Missouri River below Fort Benton (Behnke 1979). This subspecies is also found in the South Saskatchewan River system south of the Bow River in the Hudson Bay drainage (Behnke 1979). Cutthroat trout in the upper Missouri River drainage are often referred to as upper Missouri cutthroat trout, but they are essentially identical to the westslope cutthroat trout of the upper Columbia River and to those in the South Saskatchewan River drainage (Roscoe 1974; Phelps and Allendorf 1982). West of

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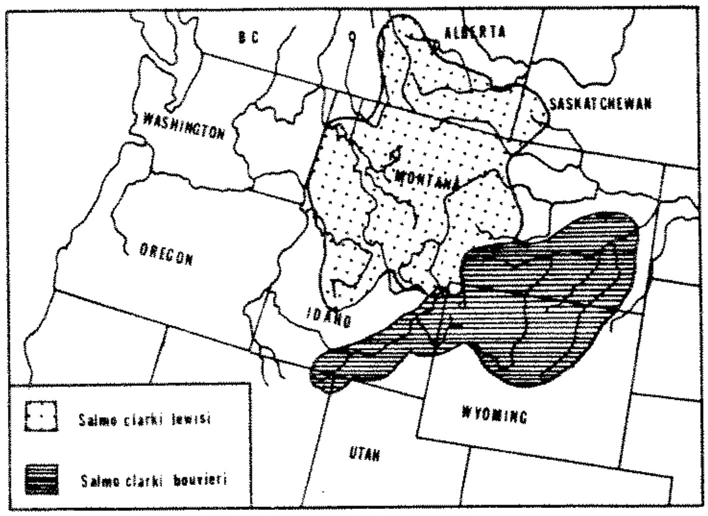

FIGURE 1.—The original ranges of the westslope cutthroat trout and the Yellowstone cutthroat trout in North America (Behnke 1979).

the Continental Divide, their range includes the Clark Fork River drainage upstream from the falls of the Pend Oreille River, the Kootenai River drainage from the headwaters to below the confluences of the Moyie and Elk rivers, the Spokane River basin above Spokane Falls, which includes the Coeur d'Alene and St. Joe river drainages and the Salmon and Clearwater river drainages (Behnke 1979).

The westslope cutthroat trout probably represents the first divergence of an interior cutthroat trout from the coastal cutthroat trout *S. c. clarki* ancestor (Behnke 1979). It evolved in sympatry with several other salmonids, including bull trout *Salvelinus confluentus* and mountain whitefish *Prosopium williamsoni*, throughout its range west of the Continental Divide. Below the barrier falls that isolated the upper Columbia basin, westslope cutthroat trout are found in waters containing Kamloops strain rainbow trout and steelhead *Salmo gairdneri* in some Idaho and British Columbia streams and chinook salmon *Oncorhynchus tshawytscha* in Idaho.

The presence of westslope cutthroat trout above barrier falls is indicative of a primitive dispersal pattern (Behnke 1979) and suggests that rainbow trout and chinook salmon expanded into the upper Columbia basin more recently than westslope cutthroat trout. The two native salmonids that coexisted with westslope cutthroat trout east of the continental divide were mountain whitefish and Arctic grayling *Thymallus arcticus*. Westslope cutthroat trout are thought to have crossed the Continental Divide from the west and expanded their range into the South Saskatchewan River and upper Missouri River systems about 7,000–10,000 years ago; the site of crossover from the Columbia River basin was probably in the vicinity of Glacier National Park, where the headwaters of all three drainages are adjacent (Roscoe 1987). It may have been relatively easy to move from one drainage to another during the Pleistocene when glacial lakes spanned drainage divides (Roscoe 1987).

The drastic decline of westslope cutthroat trout in portions of its historic range and its importance as a sport fish have resulted in efforts to prevent further loss of populations. Perturbations affecting some of these westslope populations include overexploitation, introgression, competition with introduced salmonids, and habitat degradation or loss. Each westslope cutthroat trout population is important because little genetic variation is present within a population but a large amount of variation occurs between populations (Leary et al. 1984). In the following discussion, we will examine (1) the life history patterns and habitat needs of various westslope cutthroat trout populations, (2) the present status of westslope cutthroat trout, (3) some of the ecological problems facing them, and (4) management programs designed to protect their remaining strongholds.

Life History

Three life history forms of westslope cutthroat trout are known to occur: lacustrine–adfluvial stocks, which migrate between lakes and streams; fluvial–adfluvial populations, which move between the main rivers and tributaries; and fluvial fish, which spend their entire lives in small headwater tributaries. Both lacustrine–adfluvial and fluvial–adfluvial fish will live from 2–3 years in tributary streams but they may spend as little as 1 or as long as 4 years the main water body prior to migration. Behavioral rather than morphological differences may separate lacustrine–adfluvial and fluvial–adfluvial fish (Averett and MacPhee 1971); however, the distinctive genetic and behavioral features of these forms have not been fully explored.

Westslope cutthroat trout migrations of considerable magnitude occur within some systems. These include spawning and smolt migrations, downstream movements from tributary streams to overwinter, or simply movements to other portions of lakes or rivers, which may be related to food availability. Upstream spawning movements of 212 km in 87 d (2.44 km/d) have been reported (Shepard et al. 1984).

Juveniles emigrate downstream primarily at age 2 and 3 (Shepard et al. 1984). However, the number of age-1 outmigrants may also be substantial, and occasionally, individuals may be as old as age 4 before emigrating. Most juveniles move downstream during spring and early summer. Some juvenile westslope cutthroat trout may move out of natal streams, overwinter in a river, and then migrate to a lake (Shepard et al. 1984). Emigration has also been documented in the fall (Bjornn and Mallet 1964; May and Huston 1974, 1975) and may be a result of inadequate overwintering habitat. In such cases, early summer is a time of upstream migration for juveniles and adults that will reside in tributaries during the summer.

Fluvial westslope cutthroat trout and those juveniles that do not move out of small tributary streams may enter crevices in the substrate when water temperatures drop to 4–5°C. Summer is a time of little movement for westslope cutthroat trout; fish establish summer feeding stations which tend to define the primary behavioral pattern for that time period.

Timing of spawning activity is dependent on water temperature; adfluvial adults move into tributaries during high streamflows and spawn between March and July (Roscoe 1974), when water temperatures are near 10°C (Scott and Crossman 1973). Fluvial westslope cutthroat trout exhibit similar behavior. Most adfluvial adults spend little time in the tributaries, moving downstream shortly after spawning is completed. Spawning in some drainages occurs in the smaller tributaries, which may prevent mortality that associated with streambed scouring that occurs in larger streams during high water conditions (Johnson 1963).

Westslope cutthroat trout in the Flathead River basin attain sexual maturity at age 4 and older, and 5- or 6-year-old fish from Coeur d'Alene Lake spawn in Wolf Lodge Creek (Lukens 1978); elsewhere, they may mature as early as age 3 (Brown 1971). Size of westslope cutthroat trout at maturity varies widely, but adult lacustrine–adfluvial fish tend to be the largest, usually greater than 350 mm total length (TL) (Shepard et al. 1984). Fluvial–adfluvial forms vary from 250 to 350 mm TL, and fluvial fish are generally less than 250 mm with some as small as 150 mm TL (Shepard et al. 1984). Spawning populations of westslope cutthroat trout tend to have a high ratio of females to males; the sex ratio from three Montana waters and one Idaho stream was 3.4:1 (Huston 1972; Lukens 1978; Huston et al. 1984; Shepard et al. 1984). Fecundity of westslope cutthroat appears to be slightly higher than for other subspecies and varies from 1,000 to 1,500 eggs for females with a mean length and weight of 355 mm and 0.5 kg, respectively (Roscoe 1974).

The proportion of repeat spawners tends to vary greatly, accounting for 0.7% of the fish in the 1975 run into Young Creek, Montana (May and Huston 1975); in Hungry Horse Creek, 24 and 19% of the spawners in 1970 and 1971, respectively, had spawned previously (Huston 1972, 1973). Low numbers of repeat spawners are associated with high spawning mortality (Scott and Crossman 1973). In some drainages, repeat spawning predominantly occurs in alternate years.

Westslope cutthroat trout in the Flathead River drainage spawn in areas where gravel varies from 2 to 50 mm in diameter, mean depths range from 17 to 20 cm, and mean velocities range between 0.30 and 0.37 m/s (Shepard et al. 1984). Fluvial westslope cutthroat trout built smaller redds than adfluvial fish. Redds varied from 0.6 to 1.0 m in mean length and from 0.32 to 0.45 m in mean width (Shepard et al. 1984). Eggs require about 310 temperature units to hatch (temperature units

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equal the sum of the mean daily temperatures above 0°C). Yolk-sac larva remain in the gravel until the yolk sac is absorbed (Shepard et al. 1984).

Young westslope cutthroat trout tended to be evenly distributed along stream margins in low-velocity areas such as pools and runs, but larger, older fish displayed a preference for pools (Shepard et al. 1984). Dominance hierarchies were usually maintained in pools where westslope cutthroat trout aligned vertically in the water column (Shepard et al. 1984). Maintenance of position in the water column requires much more energy than bottom orientation by species such as the bull trout (Shepard et al. 1984); however, the midwater strategy may allow the westslope cutthroat trout to obtain more food. This advantage may more than compensate for the greater expenditure of energy.

Westslope cutthroat trout fry emerge from the gravel at approximately 20 mm TL and first form scales at lengths between 38 and 44 mm (Shepard et al. 1984). In some areas, fry do not grow sufficiently to form annuli or scales the first year. From 61–69% of the westslope cutthroat trout sampled in the North and Middle Forks Flathead rivers failed to form annuli in the first year (Shepard et al. 1984). In the Coeur d'Alene River drainage, Lukens (1978) found that all fish examined had formed the first annulus.

Typical westslope cutthroat trout streams are cold, nutrient-poor waters where conditions for growth tend to be less than optimal. For example, the average lengths of westslope cutthroat trout from the upper Flathead River basin at each age were: age 1, 55 mm; age 2, 100 mm; age 3, 146 mm; age 4, 194 mm; age 5, 251 mm; and age 6, 301 mm (Shepard et al. 1984). In other portions of the present range of the westslope cutthroat trout, annual growth is greater. In tributaries of the St. Joe River, Idaho, the total lengths at each annulus for migrating fish were: age 1, 71 mm; age 2, 135 mm; and age 3, 226 mm (Thurow and Bjornn 1978). This is substantially slower growth than for the Yellowstone cutthroat trout (Varley and Gresswell 1988, this volume). Growth rates increase after fish emigrate from their natal tributaries; fish that moved from headwater streams in the Flathead River basin grew an average of 89–119 mm in the year after emigration but grew only 40–60 mm during years spent in tributaries (Shepard et al. 1984).

Westslope cutthroat trout tend to be opportunistic in their food habits and are not highly piscivorous; instead they tend to specialize as invertebrate feeders (Roscoe 1974; Behnke 1979). This dependence on invertebrates for food is attributed to their sympatric evolution with two highly piscivorous species, the bull trout and northern squawfish *Ptychocheilus oregonensis*. Utilization of aquatic insects in their diet may have prevented direct competition (Roscoe 1974; Behnke 1979) or may have been the result of competition.

Dipterans and ephemeropterans are the most important dietary components for westslope cutthroat trout; trichopterans are also an important dietary constituent for larger fish (110 mm long or longer; Shepard et al. 1984). Winged insects are not important in the diets of smaller fish (less than 110 mm) but become prominent as the fish increase in size. The diversity of food items used increases as the fish become larger. The most important food item for westslope cutthroat trout in Flathead and Priest lakes, which have large populations of planktivorus kokanee *Oncorhynchus nerka*, is terrestrial insects. Elsewhere, studies have shown that westslope cutthroat trout feed primarily on zooplankton as well as on terrestrial and aquatic insects (Jeppson and Platts 1959; Carlander 1969).

Population Status

The first report of westslope cutthroat trout by Europeans came from the journal of Lewis and Clark on 13 June 1805, when six cutthroat trout were caught while camped near the Great Falls of the Missouri. More recent surveys (Hanzel 1959) in Montana documented westslope cutthroat trout as the only or the predominant game fish in 230 streams and 130 lakes, but this effort was concentrated in the portion of the range east of the Continental Divide.

The historic range of the westslope cutthroat trout in Montana was conservatively estimated at 25,547 stream kilometers (Liknes 1984). The majority of this range, 54.4%, was west of the Continental Divide, 44.7% was east of the Continental Divide, and 0.9% was in the South Saskatchewan River system. Westslope cutthroat trout are currently known to be present in 655 streams and 6,993 stream kilometers in Montana or 27.4% of the historic range (Liknes 1984). These data include waters containing introgressed westslope cutthroat trout populations.

In 1984, 25 streams, consisting of 290 stream kilometers were known to contain genetically pure westslope cutthroat trout populations. Since

1984, 47 additional genetically pure populations have been documented; 30 were upgraded, previously classified streams, and 17 were previously unclassified and included many small first-order streams. These additional streams boost the proportion of genetically pure westslope cutthroat trout waters to over 2.5% of their historic range and 9.0% of their current range in Montana. Streams known to contain and those that potentially could contain genetically pure populations represented slightly more than 2,000 stream kilometers or about 29% of the current and 8% of the historic range (Liknes 1984).

Pure westslope cutthroat trout populations are known (or thought) to be present in nine river drainages in Montana. The upper Flathead River basin is the largest stronghold; westslope cutthroat trout are still present in 85% of their historic range in the upper Flathead River basin. The South Fork Flathead River is the largest and most secure portion within this area.

In Montana, 265 lakes are believed to contain westslope cutthroat trout populations; 8.3% of these lakes are known to contain genetically pure populations. Nineteen of the 22 genetically pure populations are in Glacier National Park (Marnell 1988, this volume); other lakes are in the Flathead River drainage. Only four lakes or reservoirs east of the Continental Divide in Montana were found to contain westslope cutthroat trout populations.

A status evaluation similar to that done in Montana has not been conducted in Idaho or Canada, but a greater proportion of the populations in those areas appears to have remained intact. Westlope cutthroat trout have been lost completely from some streams in Idaho, but many populations are genetically pure. In Idaho, important populations are found in the Middle Fork Salmon, North Fork Clearwater, Lochsa, Selway, St. Joe, and Coeur d'Alene rivers. However, the subspecies is presnt only in small numbers in most other streams of the Salmon River drainage and the South Fork Clearwater River.

Factors Affecting Population Abundance

Of all the factors threatening westslope cutthroat trout populations, hybridization with rainbow trout, golden trout *Salmo aguabonita*, and Yellowstone cutthroat trout represents the biggest problem. Because the westslope cutthroat trout was isolated and evolved separately from rainbow trout, it lacks an innate isolating mechanism which would allow the two species to coexist without hybridization.

Although a westslope cutthroat trout population may have undergone introgression, phenotypically it can still appear pure. Leary et al. (1983) demonstrated that identification by means of morphological characteristics does not accurately reflect the genetic composition of individuals or of a population of westslope cutthroat trout. Other tests using Yellowstone cutthroat trout and Alvord cutthroat trout have met with the same results (Tol and French, 1988, this volume; C. Clancy, Montana Department of Fish, Wildlife and Parks, personal communication).

Even though hybridization has occurred in westslope cutthroat trout populations, any population that closely resembles and has the same characteristics as the pure westslope cutthroat trout is still of considerable importance for management purposes. The trophy fishery of Ashley Lake in the Flathead River drainage is sustained by a rainbow trout × cutthroat trout hybrid population. Genetically pure populations of westslope cutthroat trout are still needed to reestablish or increase genetic variation in broodstocks maintained for propagation and reintroductions. Without genetic input from wild stocks, the highly selected hatchery fish could become increasingly vulnerable to disease, competition, predation, and changes in the physical environment. Wild, genetically pure populations also maintain the unique genetic-behavioral adaptations found in each individual population which have evolved in response to different environmental factors.

Although introgression has been widespread over most of the westslope cutthroat trout's historic range, there are several areas where populations of rainbow trout and westslope cutthroat trout coexist. The lower portion of the Flathead River above Flathead Lake contains rainbow trout, and at times, the same area is important in the life history of migratory westslope cutthroat trout. Rainbow trout have not greatly expanded their range within the drainage, and they have not hybridized extensively with westslope cutthroat trout. Evidently, spawning by the two species is both spatially and temporally isolated, and the drainage may be only marginal habitat for rainbow trout. In the Kootenai River drainage, different flow and temperature patterns of the Tobacco River tributaries and a difference in the timing of westslope cutthroat trout and rainbow trout spawning runs from Lake Koocanusa (Huston et al. 1984) tend to limit hybridization. Hybridization between the two species is widespread throughout the rest of the Lake Koocanusa system (Huston et

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al. 1984). Westslope cutthroat trout and steelhead in the Clearwater and Salmon river drainages have evolved sympatrically without significant hybridization. Mechanisms that limit the potential for hybridization between these species include aggressive spawning behavior and spatial separation of spawning sites.

The protection of high-quality habitat is essential for the continued existence of westslope cutthroat trout populations in streams. Habitat degradation is probably the second greatest influence (after hybridization with other salmonids) on westslope cutthroat trout populations. Human activities that can have detrimental effects include overgrazing by livestock, poor timber harvesting practices, oil and gas exploration, mining (placer operations in particular), water diversions, subdivisions and development of riparian zones, and construction of dams. Platts (1974) reported that cutthroat trout were common only in undisturbed reaches of streams in the Salmon River drainage of Idaho. Behnke (1979) described how clear-cutting along two streams in the Smith River drainage of Montana increased erosion, sediment loads, and water temperatures; the westslope cutthroat trout population was eliminated in the disturbed area, and brook trout *Salvelinus fontinalis* was the principle species. A small area in the headwaters of one stream was not logged, and an indigenous westslope cutthroat trout population still dominated that reach. While each individual habitat perturbation may affect only a small portion of the historic range, the total of these habitat alterations have contributed greatly to the range reduction of the subspecies.

Westslope cutthroat trout populations are highly vulnerable to angling. MacPhee (1966) found that cutthroat trout were caught twice as easily as brook trout, and Behnke (1979) estimated that fishing pressure of 124 h/hectare per year will result in overexploitation of stream-dwelling westslope cutthroat trout populations. In contrast, brown trout *Salmo trutta* populations were not overexploited even with 1,235–1,976 h of fishing pressure per hectare per year (Behnke 1979). Because of their vulnerability to angling, westslope cutthroat trout populations depressed by overexploitation respond rapidly to special regulations, such as smaller bag limits, size restrictions, or catch-and-release fishing (Johnson and Bjornn 1978; Thurow and Bjornn 1978; Peters 1983). Five years after catch-and-release regulations were implemented on Kelly Creek, 13 times more cutthroat trout were counted in snorkeling transects (Johnson and Bjornn 1978). If the limiting factor is habitat-related, however, special regulations may cause a decrease of mortality due to angler harvest, but natural mortality will increase (Johnson and Bjornn 1978). Also, if anglers do not comply with regulations, depressed populations may not recover.

Competition with introduced salmonids is often listed as a major reason for the decline of cutthroat trout populations; however, there is a lack of detailed accounts and descriptions of the mechanisms involved (Liknes 1984; Griffith 1988, this volume). Although introduced salmonids may have actively displaced westslope cutthroat trout from some waters, brook trout and perhaps other introduced salmonid competitors may have simply replaced westslope cutthroat trout populations that had been depressed by other factors, such as high fishing pressure or habitat degradation (Griffith 1988). However, westslope cutthroat trout populations in high gradient areas at the heads of many streams may be able to remain essentially unaffected by introduced salmonids (Griffith 1988).

Management

The decline of westslope cutthroat trout in a specific water is usually not due to a single factor but rather to a combination of factors such as introgression, habitat degradation, exploitation, and competition or replacement. Each of these factors differs in importance for specific populations, and land managers and fisheries professionals must identify which management techniques can be best utilized to increase population levels.

Management steps taken for many waters include implementation of special regulations which maintain a resilient fishery resource and provide a quality fishing experience where catch rates, angler success, and satisfaction are high, and the mean length of fish caught is considered large. Species-specific fishing regulations that conserve westslope cutthroat trout populations but encouraging harvest of introduced salmonids may benefit populations in some waters. Stream closures protect spawning areas of fluvial, fluvial–adfluvial, or lacustrine–adfluvial forms (Liknes 1984). After the implementation of special regulations or closures, monitoring must continue to verify that the measures taken are effective.

Informed management decisions regarding land and fishery use can be made only if the status of a westslope population is known. This information can be provided by a systematic program of

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electrophoretic analysis to identify genetically pure and introgressed populations. Other protective measures for westslope cutthroat trout populations include chemical rehabilitation to eliminate nonnative fishes, installation of physical fish barriers to prevent the expansion of nonnative fishes into westslope cutthroat trout waters, and acquisition of property, conservation easements, or water rights.

Management should emphasize the protection of existing strongholds, and policy decisions affecting those areas should be conservative and minimize uses that may adversely affect westslope cutthroat trout populations. The largest and most secure westslope cutthroat trout refuges in Montana are within wilderness areas and within Glacier National Park, where habitat degradation associated with human activities has been minimized. Maintenance of the wilderness system at present or expanded levels would prove beneficial to the westslope cutthroat trout.

Native salmonids such as the westslope cutthroat trout are often labeled "stupid" because their aggressive feeding behavior increases their vulnerability to angling. Such labels are counterproductive and should be avoided. Instead, a positive attitude, emphasizing high catch rates (which provide angler satisfaction) and the unique adaptations of a westslope cutthroat trout population for a particular water, should be stressed.

The current status of the westslope cutthroat trout appears more secure than several of the other interior cutthroat subspecies. Although the westslope cutthroat trout has disappeared from much of its historic range, we can maintain existing populations if we utilize wise conservation measures and manage with foresight.

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