FEATURE

Resurrecting an Idaho Icon: How Research and Management Reversed Declines of Native Westslope Cutthroat Trout

Westlope Cutthroat Trout *Oncorhynchus clarkii lewisi*.
Photo credit: Ed Cannady.

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Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* (WCT), the dominant nonanadromous salmonid in central and northern Idaho, historically were extremely abundant and widely distributed. Despite restricted harvest methods and limits since 1899, many WCT populations declined and by the 1960s, populations in several major drainages were on the brink of collapse. In response, fisheries biologists began investigating WCT population dynamics, life histories, and habitat requirements and developed evidence-based regulations and habitat restoration alternatives. Here we describe fluvial WCT case histories that illustrate how research and management collaborated to rebuild populations. The sustained and successful effort to restore fluvial WCT in Idaho offers insights to assist WCT recovery efforts elsewhere. Today, populations in many watersheds have been rehabilitated and WCT currently inhabit about 80% of their historical stream range. Despite continued threats, many Idaho WCT populations are relatively secure, provide unique recreational opportunities, and remain an important ecological, cultural, and economic resource.

INTRODUCTION

Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* (WCT) were highly valued by Idaho's Indigenous people, subsequent Euro-American immigrants, and remain prized today. The species provides unique recreational opportunities and remains an important ecological, cultural, and economic resource. In 1808, David Thompson recorded WCT in the state (Trotter and Bisson 1988) and 50 years later, surveyor John Mullen described an abundance of WCT in Coeur d'Alene Lake (Ellis 1932).

The name "Westslope" originated with Montana biologists who recognized trout native to the westward-draining Clark Fork River differed from Yellowstone Cutthroat Trout *O. clarkii bouvieri* (YCT; Behnke 1992). Classification of WCT began with Richardson and Swanson (1836), who named the species *Salmo clarkii* (see Jordan and Evermann 1896; Schultz 1935, 1941; Behnke 1992 for subsequent changes culminating with today's classification). Idaho biologists similarly recognized differences in Cutthroat Trout north of the Salmon River and called them North Idaho Cutthroat Trout. Despite the name, WCT are the most widely distributed subspecies of Cutthroat Trout, residing on both sides of the Northern Rockies continental divide (Shepard and May 2005). Unlike YCT, WCT were sympatric with resident and anadromous Rainbow Trout *O. mykiss* (Simpson and Wallace 1978). The two species likely maintained low or no introgression by temporal and spatial reproductive isolation (Loxterman et al. 2014).

Early Idaho settlers referred to WCT as "natives" and large (>30 cm) Salmon River WCT continue to be called "redsides," the colloquial term for Cutthroat Trout (Carrey and Conley 1992). Evermann (1895) observed, "The trout caught in the Salmon River and Alturas Creek agree with those from Fish Lake in the red throat and rosy sides," Trueblood (1978) wrote: "They are a lovely trout with a pink sheen on their sides that has earned them the local name 'redside.' …they are strong and fast and take a fly well" (Figure 1). In 1990, the Idaho Legislature designated Cutthroat Trout the State Fish, "It is the sense of the legislature that the Cutthroat Trout is the fish best representing all Idaho waters and anglers. Cutthroat Trout can be a symbol of Idaho's natural heritage and high quality environment."

Cutthroat Trout express tremendous diversity and nine subspecies occur in the western United States (Behnke 1992), with four in Idaho: WCT, YCT, Bonneville Cutthroat Trout *O. clarkii utah*, and Snake River Finespotted Cutthroat Trout *O. clarkii behnkei*. Potamodromous WCT exhibit varied life histories (Thurow 2016) and three forms persist: resident, fluvial (spawn in tributaries and rear in flowing waters), and adfluvial (spawn in lake tributaries and rear in lakes; McIntyre and Rieman 1995). All forms may reside in a single watershed (Averett and MacPhee 1971).

Figure 1. A native Westslope Cutthroat Trout prior to release, South Fork Salmon River, Idaho. Photo credit: David C. Burns.

The species reside in relatively low productivity, cold environments and aggressive feeding developed there may influence its high vulnerability (Rieman and Apperson 1989). Westslope Cutthroat Trout were nearly twice as vulnerable to angling as Brook Trout *Salvelinus fontinalis* (MacPhee 1966), which are considered "highly vulnerable to angling" (Waters 1992). Paul and Post (2003) similarly reported that WCT catchability was 2.5-fold higher than Brook Trout, and higher catchability and older maturation caused WCT to be more susceptible to overexploitation. Behnke (1979) estimated that stream-dwelling WCT would be overexploited at angler effort levels less than 10% of the effort Brown Trout *Salmo trutta* survived. Their high catchability and surface feeding behavior make WCT ideal for fly fishing (Cleator et al. 2009).

Idaho supports six of the nine WCT lineages (Coeur d'Alene; St. Joe; North Fork Clearwater; Salmon; Clearwater headwaters; and Clearwater–eastern Cascades; Young et al. 2018). Idaho's Snake River populations display more genetic variation than WCT in other parts of their U.S. range, potentially because the drainage served as a refugium during the latest Pleistocene glaciations (Drinan et al. 2011).

Degradation and fragmentation of freshwater habitats, introduction of invasive species, and use of hatcheries were pervasive problems affecting the productivity and persistence of WCT (Liknes and Graham 1988; Rieman and Apperson 1989; Behnke 1992). Concerns about declining WCT led to two (1997, 2001) petitions for listing under the *U.S. Endangered Species Act of 1973* and subsequent evaluations determined their broad distribution did not warrant listing (U.S. Federal Register 1998, 2003; Shepard et al. 2005). The U.S. Forest Service and Bureau of Land Management list WCT as a Sensitive Species and the Idaho Department of Fish and Game (IDFG) recognizes it as "apparently secure, but with cause for long-term concern" (IDFG 2021). Concerns about future persistence of WCT prompted efforts to restore Idaho populations.

Here we focus on fluvial WCT and describe Idaho's collaborative approach to investigate and identify factors limiting fluvial WCT, develop management alternatives that addressed those factors, and implement restrictive harvest regulations and habitat rehabilitation to rebuild WCT populations. We share detailed case histories describing WCT response to restoration actions.

HISTORICAL ABUNDANCES, CONSERVATION EFFORTS, AND RESEARCH–MANAGEMENT COLLABORATION

Early accounts described WCT as extremely abundant (Trotter and Bisson 1988). Evermann (1895) wrote:

> [i]n the streams of the Upper Salmon Valley trout ranging from one-quarter pound up to 2 or 3 pounds (0.9–1.4 kg) were very plentiful. Near Redfish Lake is a small lake known as Fish Lake. On Aug 22, 100 were caught by Mr. Comstock of Hailey, and the next day I caught 45 trout from the same lake in less than an hour's time.

Early St. Joe River anglers caught up to 15.9 kg of WCT in 1 h (Crowell and Asleson 1980; Figure 2).

Soon, however, WCT and other species declined and in response, the IDFG was established in 1899 "To provide for the protection of fish and game." Its first director listed his major accomplishment as stopping market sale of game and trout (Arbuckle 1900). A June 24, 1899 *Idaho Statesman* articled titled "First arrest made under new fish and game law" reported two individuals had "between 400 and 500 pounds (181–227 kg) of trout in their possession which were caught in Hayden Lake and were intended for the Spokane markets." The IDFG established seasons, mandated hook and line angling, outlawed other methods, and prohibited sale of fish (Arbuckle 1900). To further conserve fisheries, Director Arbuckle petitioned for "restricting the taking of fish by any individual to a reasonable number of pounds per day" (Arbuckle 1900) and limits allowed 20 pounds (9.1 kg) per day and 30 pounds (13.6 kg) in possession.

Despite harvest restrictions, by the 20th century WCT populations were declining in several watersheds. The IDFG attempted to curb declines and protect WCT habitat by prohibiting sawmills from dumping waste into streams and requiring fish passage at all dams (Arbuckle 1900). Kemmerer and Bovard (1923) reported:

> [I]n 1911 the Milwaukee Railroad was building a grade up the St. Joe River and sluicing earth from the cuts into the water. The effects were noticeable 75 miles (120 km) below at the lower end of the lake (Lake Coeur d'Alene) where for years no trout had been caught, but this year the muddy water had driven them down to the head or source of the Spokane River where they were being taken. All trout fishing had ceased on the upper end of the lake and the St. Joe River as well, except above where the grade was being constructed.

By 1932, WCT were rarely caught near the Coeur d' Alene River confluence as Ellis (1932) reported:

> [T]he 50 miles (80.5 km) of the Coeur d'Alene River carrying mine wastes are essentially without fish fauna. Nearly all of the western lakes which in the early days supported large numbers of trout have been modified by deforestation, by the cultivation of land draining into them and by other conditions incidental to the advance of civilization.

Although localized problems existed, Idaho's human population was small (445,032 in 1930; U.S. Census Bureau 2020) and many areas remained inaccessible.

Access, angler harvest, and habitat changed after World War II. Idaho citizens had more leisure time, many roads were built, gasoline was unrationed, and boats and outboard motors became available (Mallet 2013). Advances in fishing tackle also contributed to increased fishing (Johnson and Orbach 1986). By the 1950s, Idaho's population exceeded 600,000 (U.S. Census Bureau 2020), resulting in more resource extraction and increasing angler harvest.

Opportunities to manage WCT improved with passage of the *Dingell-Johnson Act* of 1950 and its tax on fishing tackle, boats, and fuel (USFWS 2019). With *Dingell-Johnson Act* funds, Idaho increased fisheries biologists from two in 1950 to eight in 1952. Biologists soon identified declining WCT as a problem, yet their life history was poorly understood. By the 1960s, WCT populations in many major Idaho drainages were on the brink of collapse and anglers were dissatisfied (e.g., Ortmann 1969). Researchers responded by investigating WCT and collaborating with managers to develop alternatives, assess public preferences, and implement restoration actions.

Figure 2. The original photo caption reads: "Caught in one hour on the St. Joe River by Bob Clark, circa 1925." Courtesy of the Museum of North Idaho, Coeur d'Alene, Idaho.

CASE HISTORIES OF FLUVIAL WCT

Here we chronicle historic conditions, depict changes and declines, outline applied research, detail management changes, and describe WCT responses to illustrate how research collaborated with management to rebuild WCT populations. Case history watersheds met three criteria: (1) sufficient habitat to support robust WCT populations, (2) a management history of restoration actions, and (3) long-term research and datasets to assess limiting factors and monitor WCT responses to habitat rehabilitation and restricted harvest.

High-quality, connected habitat and restrictive angling regulations were important components of case histories. Intact habitat, largely within roadless and wilderness areas (Rieman and Apperson 1989), likely sustained WCT and enabled them to respond to regulation changes and rehabilitation of degraded habitats. Restrictive trout angling regulations originated in Great Smokey Mountains National Park (Stroud 1964) and Wisconsin (Hunt and Brynildson 1962) in the 1950s. By the 1960s, Idaho was evaluating restrictive regulations in several case history watersheds. These regulations allowed managers to maintain opportunity while reducing angling mortality.

Within each case history watershed, biologists monitored responses to management actions via hook-and-line angling and by counting WCT in established snorkel transects (hereafter, transects), annually or at longer intervals. Using snorkeling gear, biologists floated downstream or crawled upstream in transects, defined as linear segments of stream (Schill and Griffith 1984; Thurow 1994).

Salmon River Basin

The Salmon River drains a semi-arid region of central Idaho and is one of the largest undammed rivers in the United States. We highlight its tributaries, the Middle Fork Salmon River (Middle Fork) and South Fork Salmon River (South Fork). Segments of both rivers flow through the Frank Church River of No Return Wilderness (Figure 3). Most of the Middle Fork is designated as a Wild River (https://bit.ly/3jEHwos).

Middle Fork Salmon River

Initial studies of Idaho fluvial WCT began in response to declining Middle Fork populations and investigated mortality, distribution, and life history (Mallet 1960; Bjornn and Mallet 1964). Bjornn and Mallet (1964) were the first to describe fluvial WCT that seasonally migrate distances exceeding 160 km (Zurstadt and Stephan 2004). Historical accounts describe exceptional WCT fishing in the Middle Fork with common catches of 1.4–1.8 kg trout and 100 trout per day (Carrey and Conley 1992). Despite its remoteness, by 1960, excessive angler harvest threatened WCT persistence. A combination of slow growth, maturation in their sixth year, aggressive feeding, and vulnerability to anglers led to very high exploitation (Mallet 1961). Harvest was exacerbated by increasing floaters and anglers and liberal regulations (15 fish/day). In 1949, about 25 people floated the Middle Fork, and by 1969, 1,624 people annually floated the river (Thurow et al. 2018). With increasing angler effort, most WCT were harvested before they matured (Mallet 1961). Although anglers released many WCT, creel surveys documented increasing effort and declining WCT (Mallet 1961).

In response, the IDFG adopted a three-fish limit in 1963 as the first restrictive WCT regulation in Idaho. Subsequent research led to progressively more restrictive angling regulations. Floaters and angler effort tripled from 1960–1969, and an estimated 2,000 WCT were harvested, many prior to spawning (Ortmann 1969, 1971). In 1969, IDFG further reduced the limit to two trout per day, prohibited bait, and required barbless hooks. In 1971, biologists began

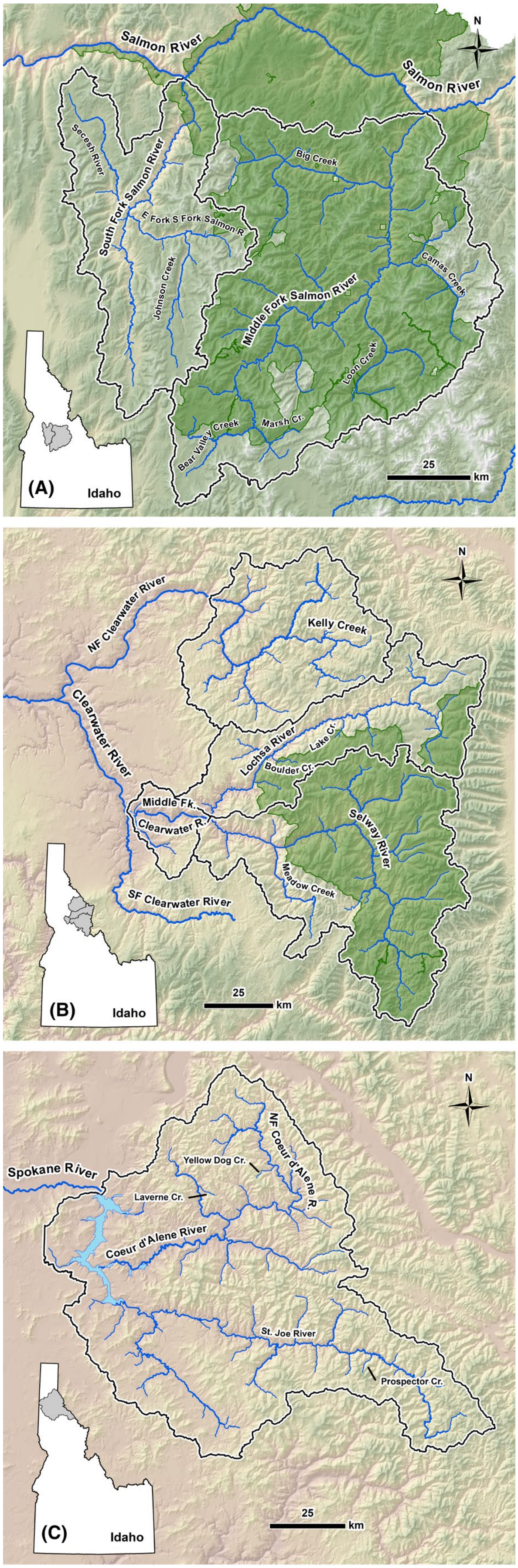

Figure 3. Map of the sixth level hydrologic units denoting Idaho case history watersheds in the Salmon River basin **(A):** Middle Fork Salmon River and South Fork Salmon River; Clearwater River basin **(B):** Lochsa River, Selway River, and Kelly Creek; and the Spokane River basin **(C):** St. Joe River and Coeur d'Alene River. Dark green shading outlines designated wilderness.

monitoring WCT trends in transects (Corley 1972). Catch-and-release for all trout was adopted on the mainstem in 1972 with a tributary limit of 10 trout, no more than 2 WCT. An anticipated public backlash never occurred. Reingold (1979) observed, "Fishermen were beginning to accept the fact that resources were limited and one didn't necessarily have to kill and eat wildlife to enjoy it."

The initial response of WCT to restricted harvest was dramatic. By 1978 transects contained more than twice as many WCT as in 1971 (Corley 1972; Jeppson and Ball 1979). Reduced harvest likely allowed more trout to mature and large WCT rapidly increased. Densities of WCT and large WCT (>30 cm) increased nearly threefold and sixfold, respectively, from 1971 to 1984; densities have fluctuated since 1984 (Figure 4). Estimated total annual survival nearly doubled from 1959 (Mallet 1963) to 2015 (Messner et al. 2017).

Although abundance and size of WCT has remained above pre-catch-and-release levels, scale-derived growth rates have declined (Messner et al. 2017; Messner and Schoby 2019) as have large (>30 cm) WCT caught by IDFG personnel. In 1981, 50% of IDFG caught WCT exceeded 30 cm and in 2017, 30% exceeded 30 cm (Thurow 1983; Messner et al. 2017; Messner and Schoby 2019). Local habitat conditions and observer error may affect variance in trout density estimates (Copeland and Meyer 2011). However, reduced growth and declines in large WCT may be linked to severe declines in marine-derived nutrients. Salmon abundance is related to growth and fitness of resident fish (Wipfli and Baxter 2010). Thurow et al. (2020) estimated potential returns of 48,000 adult Chinook Salmon *O. tshawytscha* to the Middle Fork in the 1950s–1960s compared to 322 adults (0.7%) in 2019. Kennedy and Meyer (2015) reported no causative effect of recent salmon redd counts on WCT abundance and suggested recent salmon returns are so diminished that a nutrient delivery signal may be undetectable.

Middle Fork WCT illustrated that, even in excellent and remote habitat, very restrictive angling regulations were necessary to sustain populations. As the public and outfitters enjoyed improved WCT fishing, they endorsed catch-and-release angling (Thurow et al. 2018), which sustains a quality fishery (Messner and Schoby 2019). Today, despite more than 11,000 people annually floating the river (Leuzinger 2015), native WCT remain secure. Achieving full productivity of WCT and other native species, however, may ultimately also depend on restoring anadromous fish.

South Fork Salmon River

Like the Middle Fork, WCT were abundant in the South Fork. Anglers who fished there since the 1920s reported "common" catches of WCT up to 40 cm (Thurow 1987). In contrast to the Middle Fork, aquatic habitat in the upper South Fork was degraded by historical mining, road construction, and logging (Megahan and Platts 1980; Platts and Martin 1980) and by the 1950s, WCT were uncommon (Thurow 1987). Severe erosion of granitic sediments filled pools, embedded spawning areas, and reduced rearing capacities (Corley 1976). In 1965 logging and road construction were suspended and extensive rehabilitation efforts began to decommission and revegetate roads, install erosion controls, and establish annual sediment monitoring (Zurstadt 2017).

Despite aggressive habitat restoration, research to assess WCT status and distribution confirmed they remained uncommon. In 1984 and 1985, Thurow (1987) counted few WCT in transects (Table 1). Westslope Cutthroat Trout were

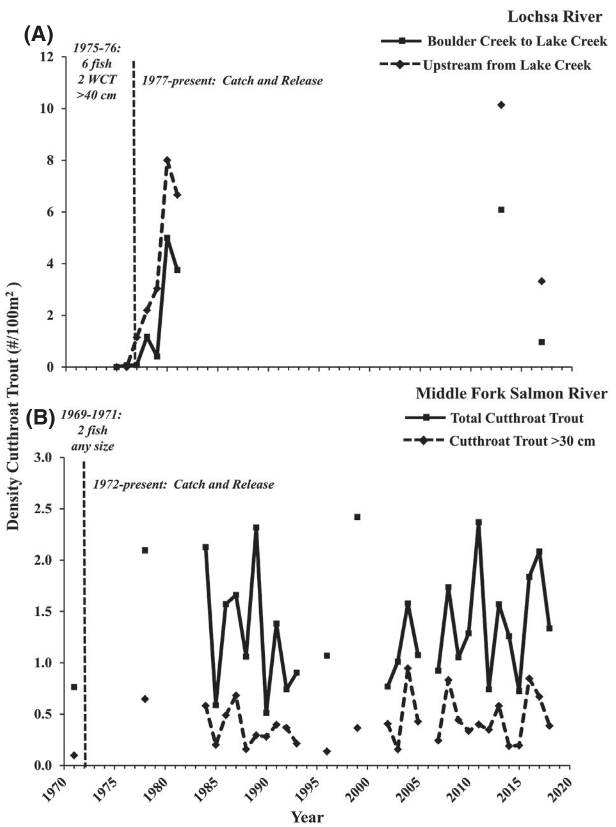

Figure 4. Westslope Cutthroat Trout (WCT) observed in snorkel transects within the Middle Fork Salmon River, Idaho, 1971–2018 (**B**) and in two reaches of the Lochsa River, Idaho 1975–2018 (**A**). In the bottom graph, the solid line illustrates the total number of WCT observed and the dashed line the number of WCT larger than 30 cm. Adapted and updated from Messner and Schoby (2019). In the top graph, the solid line illustrates the density of WCT observed from Boulder Creek to Lake Creek and the dashed line illustrates WCT density upstream from Lake Creek. Adapted from Hand et al. (2021).

Table 1. The number of Westslope Cutthroat Trout (WCT) observed in snorkel transects, South Fork Salmon River, Idaho, 1984 to 2012 (Anderson et al. 1987; Thurow 1987; Roth et al. 2021).

Year	Total transects surveyed	Number of WCT observed	Total repeatedly surveyed transects	Number of WCT observed	Number of WCT >30 cm
1984	25	14	11	14	7
1985	28	17	11	14	3
1986	14	16	11	16	6
2012	11	72	11	72	16

most common in inaccessible, roadless reaches, suggesting angler exploitation was also limiting WCT.

In 1986, scarce WCT, potential overexploitation, and WCT responses in other watersheds prompted managers to adopt catch-and-release in the South Fork (Anderson et al. 1987). By 1994, increasing WCT prompted the Outfitters and Guides Licensing Board of Idaho to approve guided angling trips. From 1997 to 2000, client catch rates doubled, percentages of WCT >30 cm nearly doubled, and some WCT exceeded 45 cm (Janssen et al. 2000).

By 2012, WCT abundance increased more than fivefold, densities increased nearly fourfold, and the percentage of WCT >30 cm more than doubled compared to 1984–1986 (Table 1). Roth et al. (2021) suggested reduced WCT harvest was the biggest contributor to population recovery; however, decades of habitat improvements have also likely contributed.

In contrast to the Middle Fork, habitat rehabilitation was an essential component of WCT recovery in the South Fork. Repeated substrate monitoring since 1966 revealed improving trends in most sites (Zurstadt 2017). Habitat restoration began in the 1960s and is still in progress after nearly 6 decades, as Beechie et al. (2000) similarly observed in logged, coastal watersheds. South Fork habitat improvements to date, coupled with reduced angler harvest after less than a decade, substantially improved WCT size and abundance. Although the rebuilding WCT population is encouraging, densities of WCT in Middle Fork transects are six times larger compared to the South Fork (Roth et al. 2021), suggesting WCT in the South Fork remain below their potential.

Clearwater River Basin

The Clearwater River forms at the confluence of the Middle Fork and South Forks and we highlight the Lochsa and Selway rivers and Kelly Creek, all world-renowned for WCT fishing (Figure 3). In contrast to the Salmon River basin, Pacific maritime western red cedar *Thuja plicata* and western hemlock *Tsuga heterophylla* forests occur along the Lochsa and Selway rivers that form the Middle Fork Clearwater River. Kelly Creek is tributary to the North Fork Clearwater River. In 1936, the Selway–Bitterroot Primitive Area was established (Space 1981) and in 1964, the area was formally protected as wilderness (Figure 3). Reaches of the Lochsa and Selway rivers are designated as Wild, Scenic, or Recreational Rivers (https://bit.ly/3jEHwos).

Lochsa River. Like the Salmon River basin, formerly abundant WCT declined with human development. In the 1940s, historic trails were rapidly converted to roads (Space 1981). By 1956, roads paralleled one-third of the Lochsa River (43 km) and creel surveys reported 5,948 WCT harvested (Corning 1957). In 1962, U.S. Highway 12 was constructed along the entire 125 km of the Lochsa River. Hatchery-reared Rainbow Trout (HRbt) were stocked to supplement the declining WCT fishery. In 1966, repeated creel surveys documented a 70% decline in WCT harvest and a fourfold reduction in catch rates since 1956 (Keating 1968). Keating (1968) cautioned that construction of campgrounds and advertised recreation "promises a steady increase in fishing pressure in the future."

Concerns over the downward trend in abundance of Lochsa River WCT prompted investigations to estimate harvest, monitor abundance, and assess angler preferences. Lindland (1977) reported harvest of WCT had declined to 30% and 10% of 1966 and 1956, respectively. Multiple snorkel surveys were unable to locate WCT (Lindland 1977), leading to changes in regulations and management strategies. In 1977 catch-and-release was adopted on 83 km upstream from Boulder Creek (with termination of HRbt stocking); while general harvest regulations (six fish, two >40 cm) were maintained in the lower 43 km with continued HRbt stocking (Figure 3).

Response of WCT to reduced harvest was swift. Within the catch-and-release section, WCT densities, angler effort, and catch rates increased dramatically (Lindland 1978, 1979; Figure 4; Table 2). In contrast, effort in the general regulation area decreased the second and third years as WCT catch and catch rates remained much smaller compared to the catch-and-release section (Table 2). By 1980, angler attitudes also changed in the general regulation area as anglers released 90% more WCT than in previous years (Lindland and Pettit 1981).

As fishing improved, more Lochsa River anglers supported catch-and-release. In 1994, IDFG adopted catch-and-release year-round in the upper river and from December 1 to Memorial Day downstream. Trophy harvest regulations (two trout >40 cm) were adopted on the lower river during the remainder of the season.

Transects were not re-surveyed until 2013 and 2017, when WCT densities remained higher compared to the 1980s (Hand et al. 2021; Figure 4). By 2017, densities declined to their lowest levels since 1979 and biologists were unsure if recent declines represent natural fluctuations or were influenced by other factors (Hand et al. 2021; Figure 4). However, Hand et al. (2016) reported that water temperatures are an important driver of WCT distributions in the Lochsa River; as summer temperatures increased, WCT sought optimal temperatures and moved upstream. The authors observed a strong correlation between WCT density and elevation and concluded that density fluctuations were likely influenced by temperature.

Lochsa River investigations confirmed that, with quality habitat, WCT responded to restrictive harvest (Figure 4), even in a highly accessible river paralleled by roads. Although densities of Lochsa River WCT have fluctuated, the river has maintained a productive fishery (Hand et al. 2021).

Selway River. Despite the Selway River's protected status and remoteness, as in the Middle Fork Salmon River, WCT

Table 2. A comparison of angler effort and Westslope Cutthroat Trout (WCT) catch and catch rates in catch-and-release and general regulation sections, Lochsa River, Idaho, 1977 to 1980 (Lindland 1978, 1979; Lindland and Pettit 1981).

	Catch and release section			General regulation section		
Year	Angler effort (h)	Number WCT caught	WCT catch rate (#/h)	Angler effort (h)	Number WCT caught	WCT catch rate (#/h)
1977	984	541	0.55	8,785	210	0.02
1978	1,363	2,377	1.75	7,278	513	0.07
1979	1,369	1,269	0.93	5,878	467	0.08
1980	2,491	2,065	0.83	7,302	886	0.12

abundance declined as harvest increased. Lindland (1974) investigated abundance and size structure and reported an average of 4.40 WCT per transect with 18% exceeding 30 cm in roadless areas, while roaded reaches held 0.05 WCT per transect and no fish >30 cm. The declining abundance of WCT led to a three-fish limit in 1974 that was further restricted to catch-and-release in 1975.

Abundance of WCT increased as transects were periodically re-snorkeled from 1976 to 1986 (Table 3). After peaking in 1986, abundance has fluctuated, yet remained higher than pre-catch-and-release levels. More large WCT were also observed in transects and caught by IDFG angling. The percentage of WCT (>30 cm) exceeded 20% in 5 of 8 years after 1975 (Table 3), and large WCT caught by IDFG increased 4-fold, WCT >35 cm increased 15-fold, and WCT >40 cm remained uncommon (Hand et al. 2021; Figure 5).

As in the Middle Fork, catch-and-release was necessary for WCT to recover, even in roadless reaches with high quality habitat. In contrast, the Middle Fork has more and larger tributaries, including eight streams with cumulative drainage areas >300 km^2 and its largest (Big Creek) drains 1,543 km^2; compared to the Selway River, which has four streams >300 km^2 and its largest (Moose Creek) drains 944 km^2. Despite its smaller and fewer WCT production areas, as in the Middle Fork, WCT abundance and size increased rapidly with reduced harvest in the Selway River. Today, Selway River WCT are considered abundant and stable (Hand et al. 2021). Hand et al. (2021) suggested recent fluctuations are in response to drought, temperature extremes, flooding, and observer variability.

Kelly Creek. Increasing roads improved angler access and formerly abundant WCT similarly declined in Kelly Creek (Chapman et al. 1972). Anecdotal accounts by loggers in the 1940s–1950s described how camp cooks fished Kelly Creek and the North Fork Clearwater River and fed the entire camp with WCT.

Kelly Creek was selected as the first Idaho stream to investigate catch-and-release as an alternative for maintaining angler opportunities, while reducing WCT mortality (Chapman et al. 1972). In 1969, Ball (1971) established transects to collect baseline data under general angling regulations (15 fish limit). He observed an average of five WCT per transect and 3.5% exceeded 30 cm.

Catch-and-release was adopted in 1970 and WCT response was dramatic. After 2 years, WCT abundance increased 3- to 6-fold (Chapman et al. 1972; Chapman et al. 1973), and 13-fold after 5 years (Johnson and Bjornn 1978). Larger WCT (>25 cm) increased from 4 to 160 and WCT >30 cm increased from 1 to 45 (Johnson and Bjornn 1978). Abundance of WCT per transect increased from 9.41 in 1989 to 15.59 in 2015 (Hand et al. 2021). Since 2015, WCT abundance has fluctuated, yet remained higher than pre-catch-and-release levels (Hand et al. 2021).

Kelly Creek investigations were the first to confirm that catch-and-release was effective in increasing WCT abundance and size, while maintaining angling opportunities. In contrast to the larger mainstem Lochsa (111 km) and Selway (161 km) rivers, Kelly Creek is unique in being wadable with one major tributary entering its 42 km.

Table 3. Comparison of the mean number of Westslope Cutthroat Trout (WCT) and WCT >30 cm observed in Selway River snorkel transects in roadless stream reaches, 1973–1988 (Lindland 1987; Bowler and Lindland 1989).

Year	Mean WCT per transect	Percent WCT >30 cm
1973	4.4	18
1974	5.5	10
1975	5.7	13
1976	7.1	21
1977	15.4	20
1978	13.0	19
1980	17.0	14
1982	16.1	16
1984	18.3	23
1986	21.5	20
1988	17.1	20

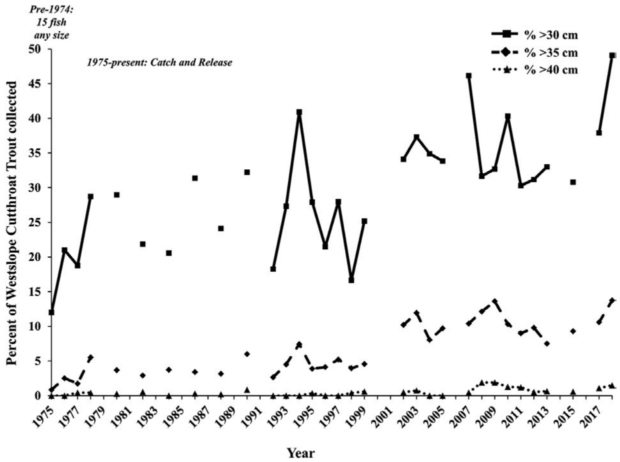

Figure 5. The percent of Westslope Cutthroat Trout exceeding total lengths of 30, 35, and 40 cm that were collected by Idaho Department of Fish and Game angling in the Selway River, Idaho, 1975–2018. Updated and adapted from Hand et al. (2021).

Spokane River Basin

We highlight the St. Joe and Coeur d'Alene rivers, tributaries to the Spokane River. Segments of the St. Joe River are designated as Scenic and Recreational Rivers (https://bit.ly/3jEHwos; Figure 3).

St. Joe River. Like many other Idaho river basins, construction of roads improved angler access and increased harvest coupled with localized habitat degradation reduced formerly abundant WCT. Historically, the Coeur d'Alene Tribe fished the St. Joe River and associated waters; in the mid-19th century, Mullan observed natives fishing for what Corsi and Corsi (2018) judged were adfluvial WCT in the St. Joe River near Coeur d'Alene Lake. Steamboat expeditions later provided access and trout fishing became a major tourist activity (Corsi and Corsi 2018). By the early 20th century, the St. Joe River was recognized as one of the finest trout streams in the United States (Crowell and Asleson 1980). From 1901 to 1905, anglers caught 3.2–4.1 kg WCT and the *St. Maries Courier* reported anglers catching 50–100 trout averaging 1.4–2.3 kg in a few hours (Rankel 1971). In the early 1930s, the Civilian Conservation Corp began building roads (Crowell and Asleson 1980). Similar to the Lochsa River, most of the St. Joe River was paralleled by a road. By the 1960s, anglers were dissatisfied and believed fishing had deteriorated (Rankel 1971).

In response, researchers began investigating WCT. Averett (1963) identified two "races," adfluvials that migrated to Coeur d'Alene Lake before returning to natal streams and residents that remained in tributaries. As WCT continued to decline, IDFG estimated angler effort and harvest, and then supplemented the fishery with HRbt and YCT (Mallet 1968). In 1969, Rankel (1971) assessed WCT status and confirmed that excessive harvest was responsible for WCT declines. The modal length of harvested WCT was <18 cm in 1969 and 1970, with some creeled fish <9 cm (Rankel 1971). Most (88%) anglers preferred to catch native WCT and accepted reduced harvest to restore them (Rankel 1971).

The IDFG applied diverse regulations to provide harvest opportunities in the lower river and improve angling in the upper river. Trout abundance, habitat quality, scenic values, and angler preferences were considered in establishing boundaries (Rankel 1971). A daily limit of three WCT >30 cm was adopted with bait prohibited and termination of HRbt releases upstream from Prospector Creek (Figure 3), while HRbt releases continued downstream with a 15-fish limit.

Anglers also favored restrictive regulations in tributaries and requested closures to increase WCT in the mainstem (Thurow and Bjornn 1978). In 1973, four St. Joe River tributaries were experimentally closed to fishing. Researchers contrasted closures with streams open to general angling and with "trophy trout" regulations (three fish >30 cm; Thurow 1976). Most WCT in tributaries, particularly at higher elevations, were resident fish maturing at small sizes (10–15 cm), few exceeded 30 cm, and they retained limited home ranges (Thurow 1976). In contrast, WCT <20 cm in lower reaches were primarily fluvial or adfluvial progeny (Thurow and Bjornn 1978). Closure of tributaries increased abundance and densities of resident and migratory WCT, especially in accessible reaches (Thurow 1976; Thurow and Bjornn 1978).

Reduced harvest led to more WCT and increased angler effort and catch rates. In 1975, 3–5 times more WCT were counted in transects compared to 1970 (Johnson and Bjornn 1978). Although angler effort initially decreased, within 3 years effort annually exceeded 10,000 h and from 1968 to 1975, catch rates improved 12-fold (Johnson and Bjornn 1978).

In 1988, catch-and-release was adopted in the upper St. Joe River. In the lower river, general regulations became progressively more restrictive in 1972 (10 fish bag limit), 1977 (6 fish, 2 > 40 cm), 1988 (1 fish >35 cm), and 2000 (2 fish, either <20 or >40 cm). In 2002, HRbt stocking was terminated and in 2008 catch-and-release was adopted for WCT in the entire watershed (Hardy et al. 2010).

Despite extensive mainstem road access, eliminating WCT harvest and liberally harvesting Rainbow Trout and Brook Trout has restored WCT in the basin (Watkins et al. 2018). Although a lack of annually replicated surveys limits our understanding of WCT trends from 1977 to 1992, large WCT (>30 cm) increased nearly 10-fold from 1971 to 1990 (Figure 6). Since 1993, densities of large WCT have fluctuated, yet remained higher than pre-trophy trout regulations (Figure 6).

Coeur d'Alene River. Similar to the South Fork Salmon River, portions of the Coeur d'Alene River were severely degraded by mining and logging that decimated once abundant WCT. While touring the watershed in 1888, General William Tecumseh Sherman wrote, "Gold was discovered there, a railroad is built, and the beautiful forests are being swept away, and the virgin lakes and streams robbed of their trout." (Royster 1991). Like the St. Joe River, the Coeur d'Alene River was considered one of the nation's finest trout streams (Dupont and Horner 2008). By the 1930s, Ellis (1932) was unable to collect fish in virtually the entire mainstem Coeur d'Alene River.

In the 1960s, WCT remained at low abundances (Dupont and Horner 2008). Researchers observed few WCT in the 1970s (Bowler 1974), and studies by Rabe and Sappington (1970), Mink and Williams (1971), and Lewynsky (1986) concluded that excessive harvest, degraded habitat, and toxic mine waste were contributing factors (Dupont and Horner 2008).

After passage of the *U.S. Clean Water Act* in 1972, state and federal agencies enforced water quality standards and implemented remediation efforts to remove toxic floodplain deposits and cap toxic mine waste. As water quality improved, WCT began recolonizing reaches. By the 1980s, WCT, albeit with elevated contaminants, were recolonizing the formerly barren Coeur d'Alene River. Subsequently, reaches of the South Fork Coeur d'Alene River that were devoid of fish in the 1990s began to support WCT (C. E. Corsi, IDFG, personal

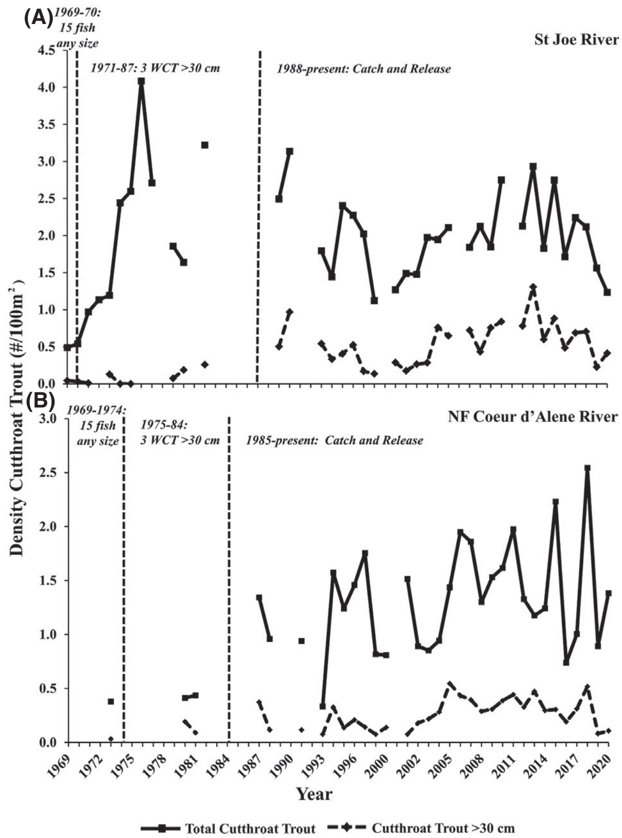

Figure 6. Westslope Cutthroat Trout (WCT) observed in snorkel transects within the St. Joe River, Idaho (**A**), 1969–2020 and the Coeur d'Alene River, Idaho (**B**), 1973–2020. Solid line illustrates the total number of WCT observed and the dashed line the number of WCT larger than 30 cm. Updated and adapted from Watkins et al. (2018).

communication). Recently, the Coeur d'Alene Tribe, state, and federal agencies developed an agreement to fund restoration of resources damaged by mining-related contaminants (Coeur d'Alene Basin Natural Resource Restoration Trustees 2018).

Researchers evaluated WCT status and angler preferences, concluded that overexploitation reduced WCT to remnant status (Bowler 1974), and collaborated with managers to develop regulatory options for restoring the fishery (Dupont and Horner 2008). Trophy regulations (three WCT >40 cm) were adopted in 1975. From 1975 to 1984 there was no detectable change in WCT abundance, mortality, or size and extensive angler noncompliance was observed (Lewynsky 1986). In 1985, managers adopted catch-and-release on the North Fork Coeur d'Alene River upstream from Yellow Dog Creek (Figure 3) and retained general regulations on the lower river (Horner and Rieman 1984).

North Fork Coeur d'Alene River WCT responded to reduced harvest slower than WCT in the St. Joe River (Dupont and Horner 2008). In 1981, an estimated 51, 39, and 10% of anglers illegally used bait, harvested undersized WCT, and exceeded the daily limit, respectively, within the special regulation zone (Lewynsky 1986). From 1980 to 1987, WCT abundance increased 2–5-fold, although WCT >30 cm did not (Horner et al. 1988). The lack of >30 cm fish suggested continued angler noncompliance and IDFG launched an information campaign and increased enforcement (Horner et al. 1988). Legal harvest in downriver areas also hampered recovery; creel surveys estimated >1,700 WCT averaging 32 cm were harvested within 1 month (Horner et al. 1988). In the 1990s, anglers in the North Fork Coeur d'Alene River were seven times more likely to illegally harvest WCT and twice as likely to exceed creel limits compared to St. Joe River anglers (Schill and Kline 1995). Dupont and Horner (2008) suggested high angler effort, illegal harvest, and degraded habitat continued to suppress WCT in the Coeur d'Alene River. Although a lack of annually replicated surveys limits our understanding of WCT trends, densities of large WCT (>30 cm) increased 10-fold from 1971 to 1994 and since 1994, have remained higher than pre-trophy trout regulations (Figure 6).

Unlike other Idaho basins, restrictive regulations did not immediately enhance WCT or improve angler satisfaction within the Coeur d'Alene River. Lewynsky (1986) suggested extensive angler noncompliance likely contributed to delayed recovery of WCT in the heavily roaded Coeur d'Alene River drainage. In contrast, low rates of noncompliance were observed in the St. Joe River (Schill and Kline 1995) and its roadless areas provide angling refugia (Lewynsky 1986). Like the South Fork Salmon River, the legacy of degraded habitat in the Coeur d'Alene River continues to limit WCT recovery. Catch-and-release was also recently adopted (2008) in the entire drainage (Hardy et al. 2010; Watkins et al. 2018). Managers concluded habitat rehabilitation, protected WCT, liberal Rainbow and Brook Trout harvest, and increased angler education and acceptance have and will contribute to improve WCT abundance and size structure (Watkins et al. 2018).

CONTEMPORARY IDAHO WCT STATUS

Although WCT have declined from historical levels (Rieman and Apperson 1989), Idaho case histories illustrate how sustained efforts since the 1960s have improved the species abundance and distribution. Within Idaho, WCT maintained or increased during the previous 15–34 years and estimated 100-year population persistence ranged from moderate to high for 9 of 10 populations (Schill et al. 2004). A decade later, Kennedy and Meyer (2015) concluded that most WCT populations were stable or increasing. Schill et al. (2004) postulated that the secure status of WCT may be a result of their widespread distribution in high-quality watersheds and extensive movements that suggest local subpopulations function as a metapopulation. Rieman and Apperson (1989) reported that WCT in Idaho seem to have fared better than those in other states (e.g., Liknes and Graham 1988). About 37% of historical WCT stream habitat in the USA lies within Idaho (34,661 km; May 2009). In Idaho, WCT currently occupy an estimated 27,784 km, persisting in approximately 80% of the state's historic range (IDFG 2013). Furthermore, a large percentage of the historical range of WCT in Idaho occurs within federally protected wilderness, roadless areas, or national forests (IDFG 2013).

In contrast to fluvial WCT, myriad factors limit lacustrine WCT recovery: degraded natal tributaries and lentic habitats, toxic mining pollution, overharvest, and invasive Brook Trout, Rainbow Trout, kokanee *O. nerka*, Chinook Salmon, Lake Trout *S. namaycush*, and mysis shrimp *Mysis relicta* (IDFG 2013). Large northern Idaho lakes formerly supported abundant and large (3.2–4.1 kg) WCT (Rankel 1971) with daily catches of 30 WCT (Mauser et al. 1988). By the 1950s many lake anglers were dissatisfied and Bjornn (1957) began restoration efforts by removing Brook Trout in tributaries, opening migration barriers, reducing the WCT limit from 15 to 3 fish, and closing tributary fishing. Rebuilding lacustrine WCT to historical levels remains a daunting task (IDFG 2013); despite continued restoration efforts, introduced species still support the bulk of contemporary lake fisheries. However, adfluvial WCT persist in both Pend Oreille and Priest lakes, are relatively widespread, and contribute to fisheries (Ransom et al. 2021). Tributary rehabilitation to restore trout life history diversity and metapopulation function (Pierce and Podner 2013), combined with Brook Trout reduction and excluded WCT harvest, continue in north Idaho lakes (IDFG 2013).

FUTURE THREATS TO WCT PERSISTENCE

Habitat Fragmentation and Degradation

Idaho is one of the fastest growing states in the nation and its expanding population may increase threats of habitat fragmentation and degradation. From 1990 to 2010, Idaho's population grew by 55% and in 2018, nearly 80,000 people immigrated (U.S. Census Bureau 2020). A growing population will likely increase development, road construction, and disturbances that have the potential to degrade and fragment WCT habitat. An extensive body of literature documents the adverse effects of such habitat fragmentation and degradation (Meehan 1979; Rieman and Apperson 1989; IDFG 2013). Idaho resource management agencies will be challenged to enforce existing habitat protection laws and abate detrimental effects of an expanding human population.

Reduced Life History Diversity

Life history diversity tends to increase production and buffer population fluctuations (Greene et al. 2010; Schindler et al. 2010). Increasing habitat degradation and fragmentation will escalate the risk of losing spatial and life history diversity and contribute to declining productivity and long-term persistence (Lichatowich and Mobrand 1995).

Persistence and adaptation in variable environments will require maintenance or rehabilitation of a network of well-connected, high-quality habitats essential to support the full expression of life histories, dispersal mechanisms, and genetic diversity (Thurow et al. 1997). Idaho WCT have generally persisted best in areas least altered by humans (Thurow et al. 1997). It will be crucial to maintain diverse life history and genetic portfolios to ensure resilience and adaptability in an uncertain future (Battin et al. 2007; Haak and Williams 2012; Al-Chokhachy et al. 2018).

Genetic Introgression

Introgression with nonnative Rainbow Trout and other Cutthroat Trout subspecies poses a serious threat to WCT (Allendorf et al. 2001) and is extensive across their range (Drinan et al. 2011). Nonnative Rainbow Trout occupy approximately 6,199 km (36%) of currently occupied WCT streams in Idaho and nonnative Cutthroat Trout reside in about 118 km of currently occupied habitat (May 2009). Fortunately, expanded genetic surveys in the Coeur d'Alene (Campbell and Cegelski 2005), Moyie (Walters 2006), Kootenai (Paragamian et al. 2008), Pend Oreille (Campbell et al. 2013), and Salmon rivers (Loxterman et al. 2014) reported relatively low introgression levels. The South Fork and Middle Fork of the Salmon River were highlighted as WCT core areas because of minimal nonnative trout introductions (Loxterman et al. 2014). Despite nonnative trout introductions in lakes, most surveys also reported low introgression levels (Kozfkay et al. 2007).

Management agencies have a portfolio of options to reduce WCT introgression: cessation of stocking, stocking sterile fish, suppression of invasives, enhancement of migratory WCT life histories, and habitat restoration (Young et al. 2016). Conserving hybridized WCT also continues to be debated (Shepard et al. 2005; Kozfkay et al. 2007). Since much of the genetic variation within WCT results from unique alleles found in one or two local populations, conserving slightly introgressed populations is a reasonable strategy to conserve local phenotypic, genotypic, and behavioral variation (Shepard et al. 2005). Shepard et al. (2005) however, clearly prioritized conservation of genetically pure populations. Although the U.S. Fish and Wildlife Service considers WCT a single conservation unit (U.S. Federal Register 2003), molecular studies provide support for delineating additional conservation segments (Drinan et al. 2011; Young et al. 2018).

Climate Change

Climate change is altering connectivity and thermal conditions for WCT, raising concerns that freshwater biodiversity is at disproportionate risk (Dudgeon et a. 2006; Isaak and Rieman 2013). Climate change will likely interact with other stressors (i.e., habitat fragmentation), to render some habitats unsuitable (IDFG 2013). Consequently, the size and number of habitats supporting WCT are expected to shrink (Young et al. 2016). However, because WCT endure warmer water than species like Bull Trout *S. confluentus* and persist in large and small habitats, their less restrictive thermal niche may enable some populations to expand (Isaak et al. 2015).

Although potential habitat gains will not counterbalance losses at lower elevations, the largest climate-related risk for WCT may be warming that will enhance the spread of nonnative salmonids (Isaak et al. 2015). The probability of occurrence and extent of Rainbow × Cutthroat Trout hybridization increased in warmer locations with less precipitation (Muhlfeld et al. 2017). Nevertheless, the ability of WCT to occupy isolated, small (0.2–1.7 km) habitats for generations (Peterson et al. 2014) and selection against invasive alleles (Kovach et al. 2016) suggests genetically intact populations are likely to persist. Genetically intact populations without invasion barriers are more likely to maintain migratory life histories, however, they may be at higher risk of introgression.

SUMMARY AND CONCLUSIONS

The sustained and collaborative effort by Idaho researchers and managers to rehabilitate WCT is a success story that offers insights to assist recovery efforts in other portions of the species' range. By the 1960s, WCT populations in many major Idaho drainages were on the brink of collapse. Populations in many watersheds have been rehabilitated and WCT inhabit about 80% of their historical stream habitat, an estimated 27,784 km (IDFG 2013). Despite continued threats from a changing climate, habitat degradation, invasive species, genetic introgression, and declines in marine-derived nutrients, many Idaho fluvial WCT populations are relatively secure, especially in intact watersheds within roadless areas.

The Middle Fork Salmon River, Selway River, and Kelly Creek illustrate how WCT in high quality habitats with limited access responded swiftly to reduced harvest, regardless of stream size and cumulative tributary drainage area. Despite far more extensive road access, WCT in high-quality habitats within the Lochsa and St. Joe rivers also dramatically increased after reduced harvest. In degraded habitats within the South Fork Salmon and Coeur d'Alene rivers, habitat restoration efforts and restricted harvest were both necessary and WCT are rebuilding more slowly. The Coeur d'Alene River further illustrates the importance of sociological considerations in fisheries management. Where a majority or large minority of anglers oppose a special regulation or perceive no benefits, use will either decrease substantially, or if no change in the user group occurs, noncompliance may be extensive and difficult to control by enforcement alone (Lewynsky 1986).

Idaho's research and management experiences suggest high-quality habitat coupled with very restrictive angling regulations may be necessary to sustain WCT populations (Rieman and Apperson 1989). Angling effort of 100 to 200 h/km overexploited WCT in the St. Joe, Lochsa, and Coeur d'Alene rivers and Kelly Creek (Lewynsky 1986). Johnson and Bjornn (1978) believed unrestricted harvest would ultimately have fished many WCT populations, including those in high-quality habitats, to extinction. Allowing harvest of even two WCT of any size proved inadequate to sustain these highly vulnerable fish (Johnson and Bjornn 1978). Ultimately, catch-and-release or trophy trout regulations were deemed necessary to reduce exploitation.

Acknowledging the rich, collaborative history of recovery efforts by fisheries researchers and managers across the native range of WCT, we endorse recommendations to prioritize existing strong populations (Rieman and Apperson 1989), efforts to rehabilitate watersheds and develop more ecologically compatible land use policies (Thurow et al. 1997), and frameworks to identify and rank conservation actions (Al-Chokhachy et al. 2018). The Western Native Trout Initiative (available: https://bit.ly/3meP4zL) is a collaborative effort among multiple state, federal, and local agencies, private organizations, tribes, and landowners to protect and restore WCT and other native salmonids and improve recreational opportunities for these iconic species. Such focused efforts will be essential to restore WCT and boost their resiliency and adaptation to an uncertain future.

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