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Age, Growth, and Movements of Westslope Cutthroat Trout, *Oncorhynchus clarki lewisi*, Inhabiting the Headwaters of a Wilderness River

Abstract

The purpose of our study was to document the age, growth, and movements of westslope cutthroat trout (WCT), a species of special concern inhabiting the upper South Fork of the Flathead River Drainage within the Bob Marshall Wilderness Complex. This is the largest, most secure WCT population in Montana. Using hook-and-line, usable scales from 843 WCT 144-470 mm in length were collected over 12 years. Back calculated length-at-age based on scales indicated that WCT averaged 57 mm at age-1, up to 435 mm at age-8. Back calculated lengths translated to annual growth of 60-90 mm for fish age-6 and younger. Once fish reached 400 mm, back-calculated lengths-at-age indicated that growth slowed to about 20 mm per year. Maximum ages of WCT (up to age-11) found in the upper South Fork were older than have been previously documented for WCT that inhabit streams or rivers. Based on recaptures of tagged fish during sampling, and reported by anglers, a number of WCT in the upper South Fork appear to reside as adults within our upper reach sampling area. Information from our study indicates that the upper South Fork supports a WCT population in which individuals are relatively long-lived, and grow to a larger average size than many other WCT populations residing in streams. The South Fork WCT population is important in conservation of the species particularly since individuals sampled have been found to be genetically pure.

Introduction

Westslope cutthroat trout (*Oncorhynchus clarki lewisi*; hereafter referred to as WCT) have declined in abundance and distribution throughout their historical range, which included the upper Columbia, Missouri, and South Saskatchewan river basins, as well as disjunct isolated populations in the John Day drainage of Oregon and Lake Chelan, Methow, Entiat, Yakima, and Wenatchee river drainages of Washington (Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995; Shepard et al. 2003). In a recent status assessment, Shepard et al. (2003) found that WCT currently occupy about 82% of their historical range within the upper Flathead River basin in northwest Montana. Genetically pure WCT currently occupy about 20% of this area. Levels of genetic introgression are less than 10% for almost all extant WCT populations from the upper Flathead River that have been tested, making this basin a major stronghold for this subspecies. The South Fork Flathead River (South Fork) is isolated from the rest of the Flathead River basin by the Hungry Horse Dam. Hence, the South Fork cur-

rently supports the largest genetically pure WCT population in Montana (Figure 1). Genetic testing in the upper portion of the South Fork of 29 WCT in 1989 and 25 WCT in 2000 indicated the population is genetically pure (Rob Leary, University of Montana, personal communication).

WCT in the upper South Fork are thought to live as adults in the main river or lower reaches of larger tributaries, and move into the smaller tributaries to spawn (Deleray et al. 1999). This migratory life-history strategy, where adult fish reside in main stem rivers and spawn in tributary streams, is a strategy that has been termed "fluvial" (Behnke 1979). WCT inhabiting streams and rivers feed mostly on invertebrates (Liknes and Graham 1988). Food habits studies of WCT in Hungry Horse Reservoir showed little difference in diet between juvenile and adult WCT, both sizes concentrating on terrestrial and aquatic insects (May et al. 1988). Less than 1% of the diet of adult WCT consisted of fish. However, in a review paper on salmonid food habits, Keeley and Grant (2001) noted that trout in streams can shift to at least partial piscivory at lengths over 270 mm, enabling them to reach maximum lengths similar to the fish in our study (450-479 mm).

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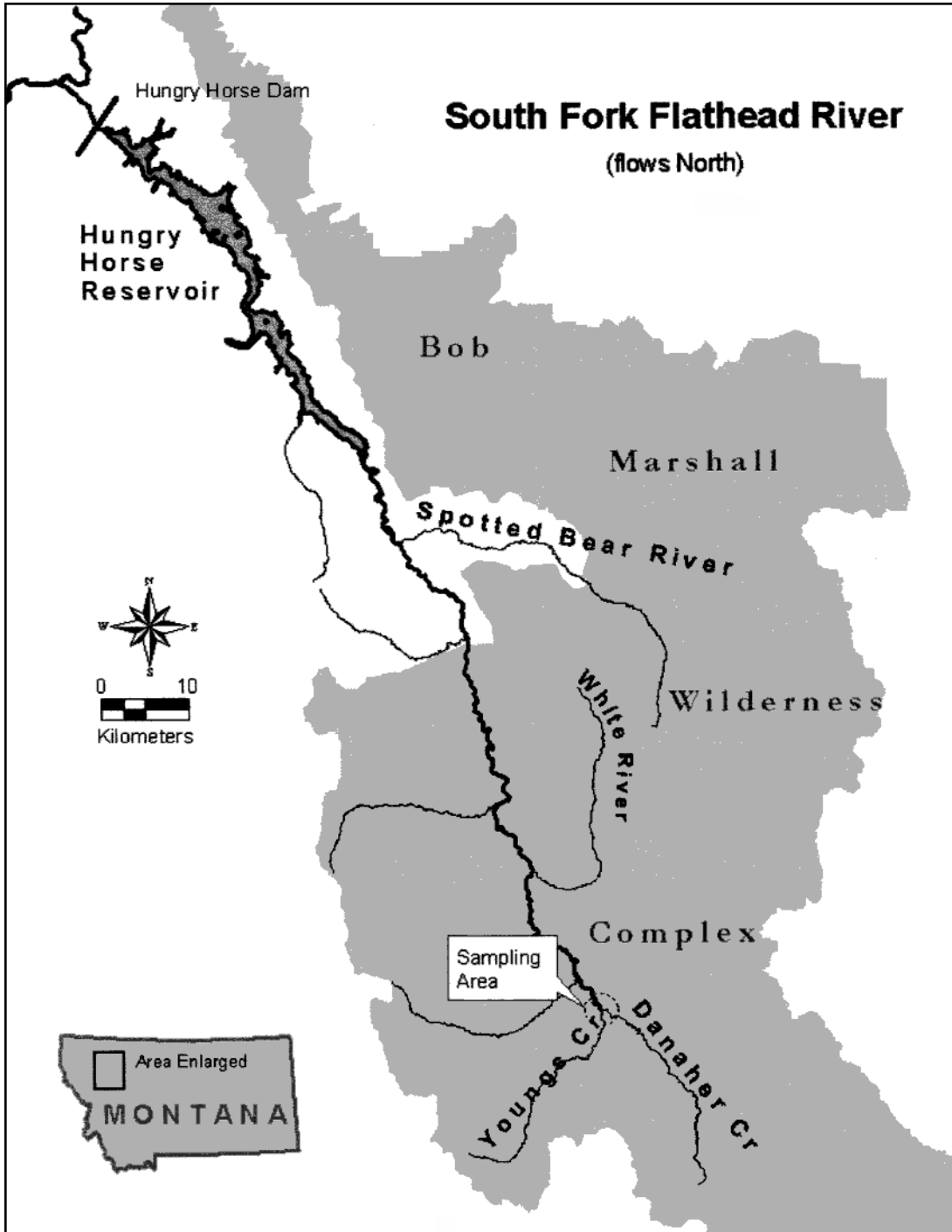


Figure 1. Map of the South Fork Flathead drainage and the sampling area.

Previous studies indicated that growth of WCT in the North and Middle Forks of the Flathead was slow, with most fish apparently requiring five to six years to attain lengths of 300 mm (total length, TL; Johnson 1963; Shepard et al. 1984). Relatively slow fish growth has been reported for other WCT populations (Purkett 1950; Bjornn 1961; Averett and MacPhee 1971; Lukens 1978; McMahon et al. 1994) and for other subspecies of cutthroat trout (Fleener 1951; Irving 1954; Cooper 1970).

Body lengths of WCT that inhabit the upper South Fork are often longer (>350 mm TL) than those found in other streams and rivers of the upper Flathead Basin. The purpose of the study was to describe the age and growth of WCT in the upper South Fork, and to determine if the larger size of these WCT was related to faster growth rates or greater longevity. We examined annual variations in age structure, growth rates, and growth increments in this WCT population. Estimating age and growth over a 12-year time-period accounted for effects that annual flow and climatic variations might have on annual growth.

Study Area

The South Fork originates at the confluence of Danaher and Youngs creeks and flows north for 95 km where it enters Hungry Horse Reservoir (Figure 1). Hungry Horse Reservoir is 56 km long and was created when Hungry Horse Dam impounded the river in 1952. No fish passage facilities exist at Hungry Horse Dam. The South Fork flows 8.0 km below Hungry Horse Dam before joining the North and Middle forks to form the Flathead River that then enters Flathead Lake 70 km downstream from the South Fork.

TABLE 1. Number of westslope cutthroat trout tagged with red floy tags in the South Fork Flathead River Study area from 1985-1991.

Year	Number of fish floy-tagged	Size range (mm) of tagged fish
1985	60	235-430
1986	111	224-425
1987	101	221-400
1988	54	225-452
1989	65	228-441
1990	60	240-446
1991	62	243-442
Total	513	221-452

Major tributaries of the South Fork include Youngs, Danaher, Gordon, Bunker, Big Salmon, and Little Salmon creeks, and the White and Spotted Bear rivers. The South Fork drainage lies almost entirely within lands administered by the Flathead National Forest and the upper 65 km of the basin are within the Bob Marshall Wilderness area. Annual precipitation ranges from 75 cm around the reservoir to 230 cm on the highest ridge tops. Average annual flow into the reservoir is about $65 \text{ m}^3 \cdot \text{sec}^{-1}$ from the 4,403 km^2 drainage basin above the reservoir.

The reservoir and river system above Hungry Horse Dam support a native fish species assemblage that includes WCT, bull trout (*Salvelinus confluentus*), mountain whitefish (*Prosopium williamsoni*), and northern pikeminnow (*Ptychocheilus oregonensis*). WCT and bull trout are considered "Species of Special Concern" by Montana. Management objectives for WCT in the drainage are to: 1) maintain strong naturally reproducing populations, 2) protect older, larger fish, and 3) provide high quality recreation for anglers in terms of catch rates and fish size. Since 1984, the angling bag limit for cutthroat is three fish, and only fish smaller than 305 mm (12 inches) may be kept. In addition, no WCT can be harvested from an 18-km reach of the South Fork Flathead River between Meadow Creek footbridge to Spotted Bear footbridge (catch-and-release). We sampled 4.0 km of the South Fork Flathead River headwaters including the uppermost 2.0 km of the South Fork immediately below the confluence of Youngs and Danaher creeks, and the lowermost 1.0 km in each of Youngs and Danaher creeks. The mean July flow in the South Fork below the confluence of Youngs and Danaher creeks was $0.2 \text{ m}^3 \cdot \text{sec}^{-1}$ in 1986 (Zubik and Fraley 1988).

Methods

Collection

WCT were collected via hook-and-line using barbless flies as the terminal gear. The senior author collected all fish, except during 1995 when several volunteers helped collect fish. Hook-and-line sampling was used because the remote location (>38 km from the nearest road access) and wilderness designation precluded the use of other types of sampling gear. While this collection method may have introduced sampling bias, the method was consistent over the 12-year period

(1985-1996). Fish were sampled over a 3-5 day period from mid-July to early August each year. All 1,349 captured WCT were measured to the nearest mm (TL) using a metric tape. A total of 513 of these WCT ranging from 221-452 mm were tagged with individually numbered Floy anchor-type tags (Table 1). We relied on our sampling, sampling by other biologists within the basin, and anglers to recapture and return tag information from tagged fish.

All fish were released immediately after processing near their original locations of capture, except for 20 fish that were sacrificed in 1995 to collect otoliths. During the 1994 sampling, 104 WCT were weighed using a portable metric scale.

Age Determination

Scale samples were taken between the dorsal fin and the adipose fin and above the lateral line. This is the area on WCT where scales first form (Averett 1962; Shepard et al. 1984). No scale samples were collected in 1986 and 1987 and scales were only collected from fish under 250 mm in 1988. Cellulose acetate impressions were made of all scale samples and then examined at 72X magnification (Jearld 1983). Annuli were identified from scale impressions and ages were assigned for each fish by a single individual with over 25 years of experience interpreting annuli from WCT scale samples. Several studies have identified the phenomenon of a missing first-year annulus on a portion of WCT scales (Fraley et al. 1981; Shepard et al. 1984; Lentsch and Griffith 1987; Downs 1995), and while the scale reader attempted to classify and assign a first year annulus to all aged fish using past experience, we anticipated that ages assigned using scale samples would be under-estimates of true fish ages for many individuals.

Otoliths were collected from 20 fish during 1995 to validate ages assigned from scales and to provide an alternate method for determining longevity. Otoliths were analyzed by Dr. Ed Brothers of Cornell University, based on methods previously described (Stafford et al. 2002).

Back-calculated Growth

Measurements (mm) were made from the scale's focus to each annulus and to the anterior edge of the scale. For otoliths, measurements to each annuli and the otolith's edge were made using a

video microscopy/image analysis system along the dorsal radius, a single axis that extends from a central primordium to the dorsal otolith margin. Since age structures were collected about halfway through the growing season, mid-July to early August, fish were actually a half-year older than the annuli counts. Back-calculations of fish lengths and growth from scales and otoliths were made using linear and curvilinear otolith or scale radii versus total fish length relationships.

For otolith back-calculation, previous otolith analysis data sets for WCT from Hungry Horse Reservoir were pooled and used to estimate equation parameters. These earlier data sets had larger sample sizes that included more young fish. Regression lines calculated from the South Fork sample of 20 otoliths and from earlier Hungry Horse samples were similar. The x-intercept estimated from these relationships was then used in a Lee back-calculation procedure (Hile 1970). Since the curvilinear otolith regression gave slightly better fits (especially at small fish sizes), the following equation form was used:

$$\ln Lt = C + (\ln Ot / \ln OT) (\ln LT - C);$$

where C = x-intercept of the ln transformation plot of dorsal radius to fish length (TL); Lt = TL at time t (mm); LT = TL at capture (mm); Ot = otolith radius at time t (um); OT = otolith radius at capture (um).

For scale annuli back-calculations we used the FIRE-1 program (Hesse 1977) to compute length-at-age from scales. Back-calculations were made using the Monastyrsky method (Hile 1970) and nomograph method (Carlander and Smith 1944; Hile 1948; Carlander 1981; Hile 1970). A Lee back-calculation procedure was used to set the x-intercept (Hile 1970), assuming that scales first formed when fish were 43 mm in length (Averett and MacPhee 1971; Shepard et al. 1984). Calculated lengths-at-age for all sampled fish were estimated and summarized using the nomograph technique by sample section and year after pooling sample sections.

Validation of Age Determination

We compared ages assigned from scales to ages assigned from otoliths for the 20 fish from which both structures were collected. We also used tagged fish to compare ages assigned at date of tagging and at date of recapture to validate ages determined from scale samples. Frequencies of

TABLE 2. Catch rates and fish lengths from westslope cutthroat trout caught by hook-and-line in the South Fork Flathead River headwaters from 1985-1996.

Year	n	Mean Length (mm)	Length Range (mm)	Proportion >305 mm (%)	Catch Rate (fish/hr)
1985	111	255	120-340	23	7.7
1986	142	268	190-425	24	8.8
1987	137	264	165-400	20	7.7
1988	106	243	179-452	12	6.0
1989	145	244	160-443	11	9.7
1990	133	263	140-446	20	9.2
1991	100	266	155-442	23	8.5
1992	132	272	180-442	23	11.0
1993	101	277	200-440	24	7.8
1994	104	289	170-445	40	8.3
1995	90	274	170-431	28	5.1
1996	48	265	165-470	27	4.6
Mean (1985-1996)	1349	265	120-470	23	7.9

length at date of capture were plotted and compared to length frequencies of ages assigned using annuli back-calculations from scales. However, since different individuals probably spent different lengths of time rearing within natal tributaries, it was difficult to segregate age-classes based on length frequencies.

Length-Weight Relationships

Fulton's condition factors (King 1995) and length-weight relationship models were computed for 104 WCT for which both lengths and weights were measured in 1994. Length-weight relationships were modeled using linear regression, exponential regression, and power function (Anderson and Gutreuter 1983), and model fit was compared using R² statistics.

Results

Catch Statistics

A total of 1,349 WCT were caught by hook-and-line from 1985 to 1996 (Table 2). Annual catch rates averaged 7.9 fish/hr (range: 4.6-11.0 fish/hr). Lengths of captured fish ranged from 120 to 470 mm (mean: 265 mm). Twenty-three percent of captured fish were longer than 305 mm, the maximum size that anglers can legally keep.

Age Validation

Ages assigned using scale and otoliths agreed for 11 of 20 WCT collected in 1995 (Table 3). Ages assigned by scales underestimated age for 8 of 20

fish, and overestimated age by one year for one fish. Tag-recapture information also indicated that ages assigned from scales may under-estimate true fish age, especially for older fish (Table 4).

The length-frequency plot for all fish aged by scales during this study shows a high degree of

TABLE 3. Comparison of ages assigned by otolith and scale readings for 20 westslope cutthroat trout collected in the South Fork Flathead River headwaters in July 1995.

Fish Length (mm)	Otolith Age	Scale Age (years)	Age Difference
190	2	2	0
208	3	2	1
220	2	2	0
225	4	3	1
230	5	3	2
240	2	2	0
240	3	2	1
252	3	3	0
256	3	3	0
260	4	3	1
275	3	3	0
276	3	3	0
280	4	4	0
285	3	4	-1
288	5	4	1
304	4	4	0
322	5	5	0
350	5	5	0
362	6	5	1
431	10	6	4
Mean Age: Agreement	3.95	3.40	0.65 55%

TABLE 4. Capture date, fish length, and age assigned from a scale sample at time of tagging and time of recapture and annual fish growth (mm/yr), for westslope cutthroat trout tagged and subsequently recaptured in the upper South Fork Flathead River. The difference in age assigned by scales and time between capture events (in years) is given where available.

Tag Number	Tagging Information			Recapture Information				Age Difference (yr-Scale)
	Date	Fish Length (mm)	Scale Age	Date	Fish Length (mm)	Age Age	Fish Growth mm/yr	
5803	7/18/1985	275	5	7/14/1986	318		43	
5822	7/18/1985	253	5	7/14/1986	310		57	
7929	7/15/1986	288		7/28/1987	310		22	
7756	7/27/1987	295		7/12/1988	336		41	
7774	7/28/1987	256		7/12/1988	300		44	
7837	7/29/1987	340		7/11/1988	358		18	
5677	7/12/1988	384		8/9/1990	410	7	13	
				7/16/1994	445	9	9	2
5648	7/10/1988	300		8/10/1990	377	7	38.5	
5656	7/10/1988	277		7/30/1989	338		61	
9278	8/9/1990	272	4	7/26/1991	336	6	64	-1
8159	7/27/1991	370	6	7/22/1992	382	7	12	0
				7/16/1994	408	7	13	2
8124	7/26/1991	308	5	7/22/1992	373	7	65	-1
				7/21/1993	402	7	29	1 ^a
9282	8/9/1990	318	5	7/22/1992	370	7	26	0
9425	8/9/1990	255	4	7/22/1992	346	6	46	0

^aA probable incorrect age assignment for this fish in 1992 of age-7 led to this difference. If the 1992 age assignment had been age-6, there would have been “0” age difference in 1993.

overlap among lengths of fish assigned different ages using scales (Figure 2). This high level of overlap was also observed when these data were analyzed by site.

Age

Lengths of 900 WCT from which scales were taken averaged 265 mm (range: 144-470 mm). Scales from 57 fish could not be aged due to scale regeneration. Ages assigned using scales ranged from 2 to 9 years (n=843; Figure 2), while ages assigned from 20 otolith samples ranged from 2 to 10 years. Based on scale analyses, slightly over 7% of aged WCT were at least seven years old. Since ages interpreted from scales probably under-estimated true ages, it is likely that a higher proportion of this population is at least 7 years of age.

Recapture information for tagged and recaptured WCT also indicated this population contained many fish older than age-7. One fish probably reached at least 11 years of age and was first captured and tagged on 12 July 1988 at

a length of 384 mm. No scales were taken from this fish, so it was not possible to estimate its age at the time it was tagged. However, based on size, it seems reasonable that this fish was at least age-5. A scale sample was taken when it was recaptured on 9 August 1990 at a length of 410 mm and it was estimated to be age-7. Assuming the age-7 assignment made in 1990 was accurate, this WCT was 11 years old in 1994 when it was subsequently recaptured.

Growth

Back calculated length-at-age based on scales indicated that WCT averaged 57 mm at age-1, up to 435 mm at age-8 (Table 5). Back calculated lengths translate to annual growth of about 60-90 mm for fish age-6 and younger. Once fish reach 400 mm, back-calculated lengths-at-age indicated that growth slowed to about 20 mm per year (Table 5). Empirical lengths of WCT captured during July and August, and aged from scales, averaged from 213 mm at age-3, to 441 mm at age-10 (Table 6). The mean empirical length for age-4 WCT, for

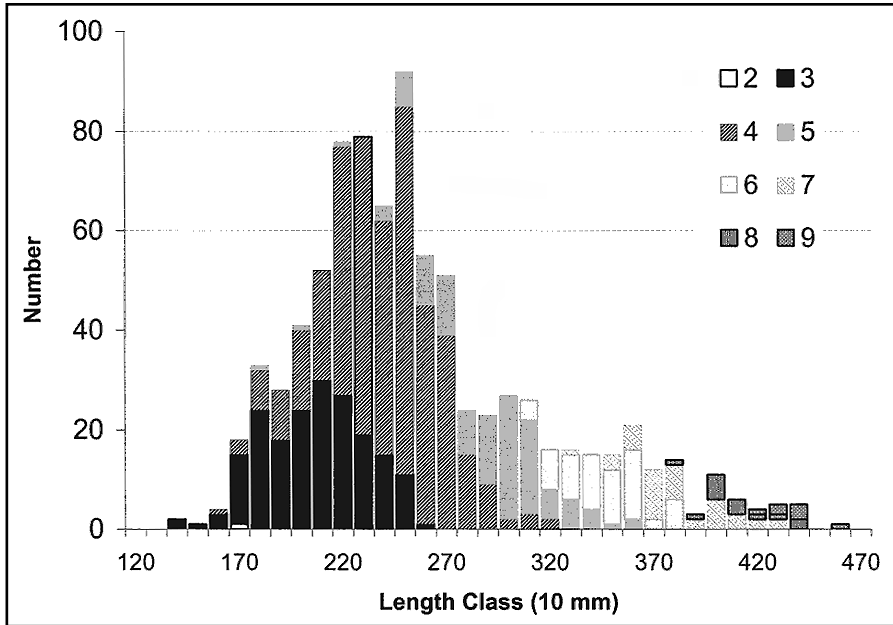


Figure 2. Length frequency by age (ages represented by different bars shown on legend) for 843 westslope cutthroat trout captured by angling in the South Fork Flathead River and two main tributaries from 1985 to 1996.

TABLE 5. Back-calculated length (mm) at annulus from scale samples for 843 westslope cutthroat trout captured from 1985 to 1996 in the upper South Fork Flathead River.

	Age (yr)							
	1	2	3	4	5	6	7	8
Mean	57	119	188	274	338	377	409	435
n	843	843	652	248	127	62	21	7
Min	31	74	116	162	255	321	384	417
Max	92	208	303	347	391	428	449	470

TABLE 6. Mean empirical lengths, length range (95% C.I.), and sample size for westslope cutthroat trout sampled during July and August in the upper South Fork Flathead River study area for the period of 1985-1996.

Age	3	4	5	6	7	8	9	10
Mean Length (mm)	213	247	297	352	382	415	445	441
Range (mm) (95% C.I.)	209-216	244-249	292-302	347-357	379-395	406-424	425-464	371-510
Number of Fish	191	404	121	65	41	14	5	2

which the largest sample size exists ($n=404$), ranged from 229-256 mm ($\bar{x}=247$ mm) for the 12-year period. This variation could be due to annual growth differences and varying lengths of time juvenile WCT spent in natal tributaries.

Annual growth increments estimated empirically for 17 WCT tagged and recaptured at least one year later ranged from 9-65 mm (Table 4). Annual growth averaged 41 mm for fish recaptured

at lengths less than 400 mm, and 16 mm for fish recaptured at lengths greater than 400 mm.

Weight-length Relationships

Weights of the 104 WCT collected in 1994 ranged from 50-994 g, while lengths ranged from 170-445 mm. Fulton's condition factors for these weighed WCT averaged 1.004 (range: 0.789-1.114). All three tested regression models provided reason-

ably good fits for describing the length-weight relationship, but the power function appeared to provide the best fit with an R^2 of 0.99 ($Wt = 6^{-06(L)-3.0766}$).

Movement

A total of 513 WCT were tagged from 1985-1991. Of these, 14 (2.7%) were recaptured (Table 4). Three of those 14 were recaptured more than once for a total of 17 recaptures (3.3% total recapture rate). For example, WCT #5677 was captured and tagged in 1988, and then recaptured in 1990 and 1994. All 17 WCT that were recaptured at least one year after tagging were found close to their original tagging site within the 4.0 km study area. One WCT (#8124) was captured in exactly the same location within the upper South Fork in 1991, 1992, and 1993, indicating long term residence as a fluvial fish in the study section.

Anglers reported 24 recaptures of tagged fish marked during our study (Table 7). Of these recaptures, 12 were recaptured within the 4 km study area, while 6 moved less than 4 km from the study area. Six fish moved significant distances

downstream; these fish were all less than 300 mm in length when tagged.

During the study period, 534 WCT were tagged downstream in the lower South Fork (Deley et al. 1999) and 1,085 WCT were tagged in Hungry Horse Reservoir (May et al. 1988). Neither we nor anglers recaptured any of these fish in our upper South Fork sampling area during the 1985-96 sampling period, possibly indicating limited upstream movement of fish into our study section from downstream areas, at least during our July sampling periods.

Discussion

Maximum ages of WCT in the South Fork were older than have been previously documented for any other WCT that inhabit streams or rivers in any literature we could find. One WCT in the South Fork was determined to be age-10 based on its age interpreted from an otolith sample, while another fish was likely at least age-11 based on tag recaptures over a seven-year period. Downs (1995) reported stream-resident WCT up to age-8 in a Montana study. We found that 15% of the fish

TABLE 7. Tag returns reported by anglers from 1985-1988 (data are available only from these four years) from fish tagged in the study area. Movement is reported in km from the 4 km study area; "+" designates movement upstream, "-" designates movement downstream.

Tag Number	Length (mm)	Date Tagged	Date Recaptured	Movement (km)
5814	284	7/18/85	8/15/85	0
5819	253	7/19/85	8/15/85	0
5825	344	7/19/85	8/15/85	0
5830	246	7/19/85	8/15/85	-4
5821	250	7/19/85	7/13/86	-20
5846	320	7/19/85	7/15/86	0
5874	305	7/18/85	7/12/86	0
7885	285	7/16/86	8/12/86	-30
7892	300	7/16/86	6/26/87	+3
7906	295	7/15/86	6/12/87	-4
7912	270	7/15/86	10/1/89	0
7915	340	7/15/86	8/8/86	-2
7931	270	7/15/86	7/28/86	0
7936	288	7/15/86	10/8/86	0
7968	234	7/14/86	5/24/87	-60
7752	252	7/27/87	7/2/88	-60
7755	315	7/27/87	8/8/87	0
7765	230	7/28/87	8/10/89	-25
7788	294	7/28/87	8/8/87	0
7823	270	7/29/87	8/4/87	-2
7845	240	7/30/87	9/15/87	0
5629	230	7/10/88	8/14/89	-20
5636	225	7/10/88	10/16/89	-4
5638	254	7/10/88	7/31/88	0

in the population were age-6 and older, while 7.4% were age-7 or older. Only two of 12 WCT populations in Idaho and Montana reported in Rieman and Apperson (1989) contained any individual fish that were at least 7 years old.

Discrepancies between ages assigned using otoliths and scales were probably related to the failure of some fish to form a first-year scale annulus and/or erosion of the scale edge. These discrepancies indicated that scale-age assignment was negatively biased and highlighted the previously documented difficulties in accurately assigning ages of cutthroat trout using only scales (Fraley et al. 1981; Shepard et al. 1984; Lentsch and Griffith 1987; Downs 1995).

WCT in the upper South Fork were longer at a given age than WCT from the North and Middle Forks of the Flathead River. WCT in the upper South Fork attained lengths of 300 mm prior to age-5, while WCT in other portions of the basin often did not reach 300 mm until age-5 or age-6 (Johnson 1963; Shepard et al. 1984). Back calculated growth of WCT in our study also exceeded growth in the St. Joe River, Middle Fork of the Salmon River, and 10 other waters in Idaho and Montana as reported in Rieman and Apperson (1989). The larger size of WCT in our study area could be related to one or more of the following factors: 1) fishing regulations imposed in 1984 that allow only three WCT less than 305 mm (12 inches) to be kept, 2) the older age structure of the WCT population in our study area, 3) habitat factors that we did not measure, 4) a shift in food habits of adult WCT to piscivory, or 5) movements of larger fish into our study area from Hungry Horse Reservoir (we believe this to be the least likely factor, and it hasn't been documented in downstream sections). Sampling and tag return

data (multiple summer period recaptures of adult WCT) indicate that some WCT in our study area reside in the upper South Fork as adults. The low rate of recapture could be reflective of some migration of tagged fish out of our study area. However, no tagged adult fish from our study section were recaptured by anglers or by sampling downstream, and no tagged adult fish from downstream were captured in our study section. The low recapture rate could also be related to sample size and the time (one year) between annual 4-day sampling periods.

In summary, information from our study indicates that the upper South Fork supports a strong WCT population in which individuals are relatively long-lived, and grow to a larger average size than other WCT populations residing in streams. The South Fork WCT are important in conservation of the species particularly since individuals sampled have been found to be genetically pure.

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