AN ABSTRACT OF THE THESIS OF

Steven J. Starcevich for the degree of Master of Science in Fisheries
Science presented on December 1, 2005.
Title: Seasonal Movement Patterns and Habitat Use of Westslope Cutthroat
Trout in Two Headwater Tributary Streams of the John Day River.

Abstract approved:

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Robert E. Gresswell

Radiotelemetry was used to study the seasonal movements and habitat use

of adult westslope cutthroat trout *Oncorhynchus clarki lewisi* in Roberts

Creek and Rail Creek, headwater tributaries of the John Day River, Oregon,

from September 2000 to December 2001. The objectives were to (1)

describe adult cutthroat trout life history in headwater streams by

comparing seasonal movement patterns, and (2) assess seasonal habitat

selection by comparing habitat use to availability. For seasonal comparison,

only fish that survived with an active transmitter throughout winter, spring,

and summer were used in the analysis. Sample size was 17 (mean fork

length, 241mm) on Roberts Creek and 9 (mean fork length, 252 mm) on

Rail Creek. In winter and summer, radiotagged fish were relatively

sedentary on both Roberts Creek (median home ranges, 35 and 104 m,

respectively) and Rail Creek (median home ranges, 104 and 112 m). In

spring, 65% of fish in both streams moved over 100 m upstream to spawn;

upstream movements were as long as 1,138 m (median, 271 m) on Roberts Creek and as long as 3,771 m (median, 311 m) on Rail Creek. Postspawning movements downstream were common; 82% of fish on Roberts Creek and 57% on Rail Creek showed homing behavior, returning in summer to the same channel unit they inhabited in winter. Fish length was positively correlated to total movement distance in spring on Roberts Creek but not on Rail Creek. Over 86% of the surface area of both creeks consisted of fast-water channel units. Instream large wood created the majority of habitat heterogeneity in both streams and radiotagged cutthroat trout were strongly associated with large wood pools throughout the year, . Plunge pools were positively selected throughout the year on both streams. Headwater-resident populations of cutthroat trout are often considered nonmigratory; however, these radiotagged fish showed fluvial migratory behavior. These results demonstrate that habitat heterogeneity and connectivity are important life history requirements for fluvial headwater-resident cutthroat trout.

Seasonal Movement Patterns and Habitat Use of Westslope Cutthroat Trout
in Two Headwater Tributary Streams of the John Day River

by
Steven J. Starcevich

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APPROVED:

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Steven J. Starcevich, Author

ACKNOWLEDGEMENTS

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Introduction

Cutthroat trout *Oncorhynchus clarki spp.* are the most widespread and polytypic native trout in North America (Behnke 1992). Of the 14 subspecies of cutthroat trout described by Behnke (1992), two are thought to be extinct and three are listed as threatened under the Endangered Species Act. Although populations of extant subspecies still occupy most of their historical range, all have suffered dramatic declines from their historical distribution (Gresswell 1988; Young 1995; Duff 1996; Shepard et al. 2005).

Westslope cutthroat trout in Oregon only occur in the upper north fork and mainstem of the John Day River. These populations, and several occurring along the east side of the Cascade Mountains in Washington, are widely separated from the larger, contiguous distribution in Montana and Idaho (Liknes and Graham 1988). This unusual distribution, the lack of early historical references to westslope cutthroat trout presence in Oregon and Washington, and widespread stocking of cutthroat trout in this region, beginning around 1900, have lent plausibility to the hypothesis that humans may have introduced them to these basins (Gunckel 2002). In the John Day River basin, north fork populations are thought to be introduced because their distributions are still closely associated with known stocking sites. Westslope cutthroat trout in the upper mainstem, however, are widely distributed in at least 355 km of 41 tributary streams (Hemmingsen and Gray, pers. comm.), and preliminary results from a recent genetic analysis of these disjunct populations (Howell and Spruell 2003) and a stocking history of the John Day River basin (Gunckel 2002) suggest they are native to the upper mainstem John Day River.

Cutthroat trout populations in the John Day River are estimated to occupy about 21% of their historical distribution (Shepard et al. 2003). Decline in the distribution of cutthroat trout has been attributed to habitat degradation and fragmentation, genetic introgression, predation by, and competition with, introduced nonnative species, and angling pressure (Gresswell 1988; McIntyre and Rieman 1995; Young 1995). The riverine

environment in the John Day River basin, for example, has been altered by decades of livestock grazing, water diversion for irrigation, agricultural development, dredge mining, the decimation of beaver *Castor canadensis*, and timber harvest (Wissmar et al. 1994). Both hatchery rainbow trout *O. mykiss* and nonnative brook trout *Salvelinus fontinalis* have been introduced in the John Day River (Gunckel 2002), and there is evidence of hybridization between westslope cutthroat trout and rainbow trout (Howell and Spruell 2003).

About 70% of the current distribution of this subspecies is on federally managed lands that are frequently characterized by steep, high-elevation, forested headwater basins (Shepard et al. 2005), which are defined in this study as first and second order streams on a 1:24K scale. The importance of these headwater basins to the genetic integrity and persistence of westslope cutthroat trout throughout their diminished range was underscored by the recent U.S. Fish and Wildlife Service decision (U.S. Federal Register 2003) to reject a petition to list them as a threatened species. The U.S. Fish and Wildlife Service noted that headwater basins on federal property already provide significant protection from such threats as colonization by nonnative species and the adverse effects of human activities. Understanding how cutthroat trout populations have adapted to, and persist in, these headwater basins is important to the conservation and restoration of this subspecies.

Headwater streams in the range of most cutthroat trout experience extreme seasonal fluctuations in discharge and temperature. In a single year, fish are exposed to a prolonged period of stream temperatures at or near 0° C and dynamic instream ice conditions in winter, snow-melt driven peak discharge in spring, and temperature maxima and base flows in summer. Fish behavior also changes seasonally. Low stream temperatures (0-4° C) in winter produce a stressful period of acclimatization in winter, the time spent feeding and defending territories is expected to lessen or be eliminated, and minimizing energy expenditure and finding protection from

predators becomes paramount (Cunjak 1988, 1996). Adult cutthroat trout spawn in spring and also must find refuge from high flows. Summer is a time of maximizing growth by minimizing energy expenditure and maximizing access to invertebrate drift (Fausch 1984). These seasonal changes may lead to changes in seasonal habitat requirements of cutthroat trout. Because stream conditions are dynamic through time (Resh et al. 1988; Poff and Ward 1989) and stream habitat is patchy in space (Pringle et al. 1988), stream fish often must move to locate habitat required to maximize fitness (Northcote 1978; Warren and Liss 1980; Northcote 1997).

With the advent of radio telemetry, there has been greater recognition that cutthroat trout have evolved complex and diverse life histories in order to persist in these different stream environments. Westslope cutthroat trout are potamodromous; that is, they move and migrate entirely within freshwater habitats (Myers 1949). Based on reproductive migrations, Varley and Gresswell (1988) identified four categories of potamodromy, three of which have been associated with westslope cutthroat trout: fluvial, fluvial-adfluvial, and lacustrine-adfluvial. Fluvial fish confine spawning migrations to their natal stream or river, fluvial-adfluvial stocks migrate between main stem rivers and tributaries, lacustrine-adfluvial populations migrate from lakes to inlet tributaries. For westslope cutthroat trout, all three life histories may exist in a single basin (Liknes and Graham 1988; Rieman and Apperson 1989).

Because life history phenotypes are determined by the genotype interacting with the environment, including habitat availability, life history adaptations in headwater basins can be viewed from a habitat perspective (Southwood 1977; Warren and Liss 1980; Gross 1987). In potamodromous life history, migration evolves when optimal habitats are spatially, seasonally, or ontogenetically separated and moving to a new location improves fitness (Gross 1987; Northcote 1978, 1997).

Potamodromous salmonid migration has been defined by Northcote (1997) as movements that occur with regular, often seasonal, periodicity,

involve a large proportion of the population, are directed rather than random wandering or passive drift, and alternate between two (or more) usually well-separated habitats. Migration has been documented for many potamodromous salmonids (see Northcote 1997), including several species of char (West et al. 1992, Swanberg 1997, Curry et al. 2002) and cutthroat trout (Bjornn and Mallet 1964, Brown and Mackay 1995a, Schmetterling 2001, Schrank and Rahel 2004) and generally refers to riverine fish moving relatively long distances (up to 212 km) upstream to spawn in headwater tributaries and returning downstream after spawning. For cutthroat trout populations in headwater streams, movement is acknowledged, but their life history is often described as nonmigratory or resident, terms that are often used synonymously (see Shepard 1984; Northcote 1992; Rieman and McIntyre 1995; Rieman and Dunham 2000; Schmetterling 2001, Hilderbrand and Kershner 2004). Previous radiotelemetry studies of cutthroat trout generally have focused on movement and habitat use during a single season (e.g., Brown and Mackay 1995a; Young 1995) or sole seasonal transition (e.g., Jakober et al. 1998; Young 1998; Brown 1999), or on movement alone (e.g., Bjornn and Mallet 1964; Bernard and Israelson 1982; Brown and Mackay 1995b; Hilderbrand and Kershner 2000). Because adult cutthroat trout behavior and seasonal stream conditions change dramatically over the course of a year, studying potamodromous salmonid life history over this larger time scale may improve our understanding of how cutthroat trout have adapted to, and persist in, headwater streams. Understanding how adult cutthroat trout move and use habitat throughout a year and how behavior changes seasonally in headwater basins is critical for identifying important seasonal habitats and providing information that will enhance conservation and restoration of cutthroat trout populations.

To gain insight about movement and seasonal habitat-use patterns, radiotelemetry was used to investigate adult cutthroat trout movement and habitat use throughout a year in two headwater streams in the upper John

Day River basin. This information was used to describe the potamodromous life history strategy of adult cutthroat trout in Roberts Creek and Rail Creek. As previous studies of adult cutthroat trout in headwater streams have shown movement patterns consistent with migration (sensu Northcote 1997), fish in Roberts Creek and Rail Creek were expected to show migratory behavior. Finally, seasonal habitat selection was assessed by comparing seasonal habitat use to habitat availability. Because of seasonal shifts in cutthroat trout behavior and stream conditions, we expected to see seasonal differences in habitat use.

Study Area

The study area was composed of Roberts Creek and Rail Creek, two second-order headwater streams in the John Day River basin, in northeast Oregon (Figure 1). Measuring upstream from the mouth of each stream to the most upstream location of a radiotagged fish, the extent of the study area was the first 5 km of Roberts Creek and 6.5 km of Rail Creek. The streams originate in the Strawberry Mountain and Blue Mountain ranges and flow through land owned in a public/private checkerboard pattern. Roberts Creek is steeper and has less basin area than Rail Creek (Table 1). Roberts Creek has a northeast aspect and Rail Creek faces west. The confluences of these streams and the John Day River are within 150 m of each other. Elevation ranged from 1,300 m to 1,700 m. Stream temperatures for both streams ranged from 0° to 3° C in winter and 7° to 14° C in summer. Tributaries of these creeks are steep, have relatively low discharge, and are not fish-bearing. Both streams have steep valley slopes vegetated primarily by ponderosa pine *Pinus ponderosa*, western larch *Larix occidentalis*, and lodgepole pine *P. contorta* on south-facing slopes and mixed conifer forest (grand fir *Abies grandis*, Englemann's spruce *Picea englemanii*, and Douglas fir *Pseudotsuga menziesii*) on north-facing slopes. Riparian vegetation consists of mature and second-growth conifers, red alder *Alnus rubra*, pacific yew *Taxus brevifolia*, red osier dogwood *Cornus stolonifera*, and currant *Ribes* spp. Sympatric salmonid species

include bull trout *Salvelinus confluentus* and native redband and steelhead trout and introduced hatchery rainbow trout. Spring Chinook salmon *O. tshawytscha* spawn and rear in Rail Creek near its confluence with the John Day River.
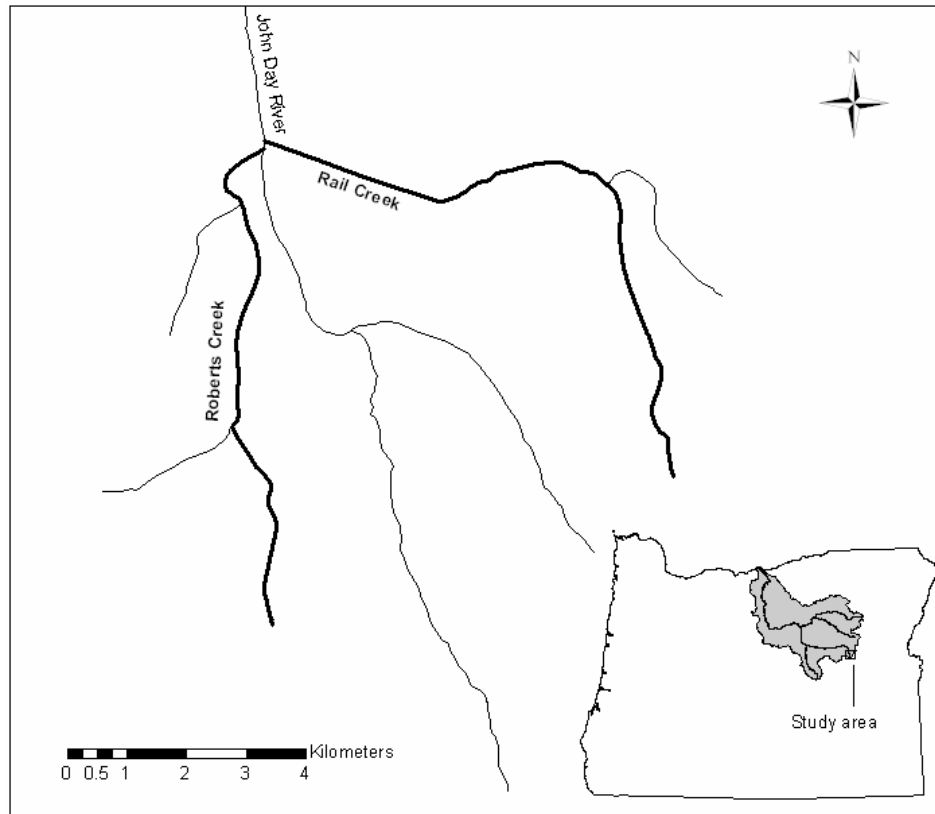
Figure 1. Upper John Day River basin in northeastern Oregon. Study streams in bold.

Table 1. Channel and basin characteristics of Roberts Creek and Rail Creek.

| Creek | Mean channel characteristics (m) | | | Pool density | Discharge (m^3/s) | | Gradient | Basin |
	Width	Depth	RPD*	(#/100m)	Base	Peak	(%)	area (km^2)
Roberts	3.0	0.19	0.25	4.5	0.10	0.43	4.9	22
Rail	3.4	0.23	0.33	4.3	0.30	0.94	4.1	27

*Residual pool depth is defined as the difference between maximum depth and tail crest depth.

Methods

Defining seasons

Seasons were defined by stream temperature thresholds, the snowmelt period, and spawning timing of cutthroat trout and bull trout. For this study, winter began in early November 2000 on both streams when the mean weekly stream temperature went below 4° C, a temperature threshold that is considered to be physiologically stressful to overwintering potamodromous fishes (Cunjak 1988). Spring began on 25 April on Roberts Creek and 16 April in 2001 on Rail Creek when mean weekly stream temperature exceeded 4 C and snowmelt began to influence discharge. Summer began when the spring snowmelt ended and cutthroat trout were no longer seen on or near redds, which occurred on 24 June on Roberts Creek and on 18 June on Rail Creek. Summer ended on Roberts Creek and Rail Creek on 12 September 2001 when bull trout were first seen spawning in the study streams. To monitor changes in stream discharge, a gauge was placed in each stream near the confluence with the John Day River. Gauge sites were located upstream of irrigation intakes and in glides of relatively laminar flow and uniform stream depth. Discharge was estimated using a gauge-discharge relationship (N=20), following methods described by Gore (1996). The relationship was based on 20 discharge estimates on each stream that were spread throughout the year and included peak flow. Gauge levels were recorded at least weekly. To monitor stream temperature, thermographs (Onset) were placed near the mouth and at 1-km intervals in both streams. Thermographs recorded stream temperature every hour and were downloaded every 3 months.

Radiotagging

Radio transmitters were used to monitor the movements of 28 cutthroat trout in Roberts Creek and 26 in Rail Creek from September 2000 to December 2001. Fish were radiotagged during 2 periods on both streams: 31 August to 9 September 2000 on Roberts Creek and 9-27 October 2000 on Rail Creek; and again during 20-28 February 2001 on both streams. Fish

greater than 200 mm were radiotagged because they were expected to have a high probability of maturity (McIntyre and Rieman 1995; Downs et al. 1997). Cutthroat trout were captured by fly-fishing. Transmitters were placed throughout the basin by moving 250m upstream of the previous tagging location before beginning to angle for another fish. After capture, fork length (nearest 1 mm) and body weight (nearest 1 g) were recorded. Scales were collected to estimate fish age and a small portion of the caudal fin was excised and stored in ethanol for genetic analysis. The interperitoneal radiotagging surgical procedures described by Young (1995) were followed. After surgery, fish recovered 10-25 minutes in an aerated and covered bucket before being returned to the capture location.

Interperitoneal transmitters (Advanced Telemetry Systems Inc., Isanti, Minnesota) with 200-day (4.5 g) and 140-day (3.6 g) battery lives were used. They emitted a unique frequency, 40 pulses/minute, at 150-151 mHz. Transmitters:fish weight ratio averaged 2.4% (range, 1.4-3.9%) on Roberts Creek and 2.3% (range, 1.1-3.8%) on Rail Creek. The "2% rule" (Winter 1983) of transmitter weight to fish weight was exceeded because recent laboratory evidence has suggested that radio-tagged coho salmon (150-211 mm, total length) swam and behaved normally when transmitters weighed less than 5% of fish weight (Moser et al. 1990). Results from a recent field study also suggested that violating the 2% rule does not affect seasonal movement patterns (Jakober et al. 1998).

Radiotracking

Radiotagged fish were tracked using a Lotek receiver and hand-held two-element Yagi antenna. The average time between observations was 7 days in spring and summer and 9 days in winter. When the transmitter signal was located, the tracker triangulated the fish location 5-10 m from the stream and approached carefully in an attempt to gain a visual location of an undisturbed fish. When a fish was observed in a location different from the previous observation, the distance between the two points was measured with a 50 m tape. The shortest distance recorded was 2 m. At the

beginning of the study, flagging was hung at 100 m intervals (measured by hip string box) along the stream from the mouth to the top of the study area and these flags were referenced to measure long distance movements.

Movement patterns

The seasonal movement patterns measured were total distance, seasonal range length, directional distance, and location persistence. Total distance was defined as the sum of individual movement distances (upstream and downstream) during a season. An individual movement was recorded when a radiotagged fish was tracked to a channel unit or sub-unit (i.e., a non-channel spanning area of greater depth and lower velocity within a fast-water channel unit) different from its previous location. Seasonal range length was defined as the distance between the most upstream and downstream locations of a fish during an individual season (sensu Young 1994). Directional distance was defined as the difference between the modal location of a fish during one season and its modal location during another season. Modal fish location in spring was considered its spawning location; and when spawning was not observed, its most upstream or downstream location. Positive directional distance meant the fish moved upstream during a season and a negative number meant the fish moved downstream. Location persistence represented the number of times a fish was observed in the same location as it was previously observed compared to all observations (sensu Ramsey and Usner 2004).

Only fish that survived with an active tag February through mid-August were used in the seasonal analysis. To avoid including observations of an ejected transmitter in the sample, when a transmitter showed extended persistence in a single location, it was included in the analysis only if the the fish and its trailing transmitter antenna was seen before the signal stopped or the radiotagged fish showed directed movement.

Habitat use and availability

In order to quantify seasonal habitat use, when a radiotagged fish was tracked to a new location, the habitat of the new location was

inventoried following a modified protocol of Moore et al. (2000). At the channel unit scale, channel unit type was recorded and unit length, width, modal depth of fast-water units (sensu Hawkins et al. 1993) were measured, and residual depth (difference between maximum and tail crest depth) of pools with a 2-m graduated staff. Within fast-water channel units, we recorded use of sub-unit habitat and the primary structure type producing the sub-unit. Pool-forming structure type was also recorded and consisted of instream large wood, riparian vegetation, boulder, and meander. Structure types for sub-units were the same except that stream bank was used instead of meander.

In order to estimate habitat availability at the channel-unit scale, the habitat of the entire study area was inventoried, following the protocol described above for habitat use. To estimate the availability of sub-unit types, stream transects were evaluated at each 100 m reference flag. Each transect was divided into five 1-m long cells of equal width. When a transect cell included a sub-unit, maximum depth and structure type were recorded. To account for seasonal changes in availability (see Hilderbrand et al. 1999), the study area was inventoried three times: 18 August to 2 November 2001, and 7 to15 February and 27 May to 13 June in 2002. Inventories in 2002 were completed the year following the tracking period. Stream discharge during the freshet was similar during both years and it appeared habitat availability was consistent among years. Stream conditions in February were substantially different from the previous year. Because extensive instream ice altered habitat, and shelf ice prevented the measurement of a large proportion of the streams in February, summer channel unit dimensions were substituted. Summer and winter dimensions were similar because base flows were the same and the channel unit dimensions in ice-free sections of the streams closely matched those of summer.

Analysis

Movement patterns

Seasonal range length, directional distance, and location persistence were described by medians, range, and graphs. Seasonal differences in movement patterns were examined using Friedman repeated measures of analysis of variance on ranks for non-normal data and Dunn's multiple contrast test for post hoc comparisons. Spearman rank correlation was used to evaluate relationships between total movement distance in spring and fish length and transmitter:fish weight ratio. All analyses were done with SigmaStat and were considered significant at $P < 0.05$.

Habitat use

An independent multinomial selections (IMS) model (McCracken et al. 1998) was used to estimate seasonal habitat use at the channel unit and sub-unit scales. A statistical assumption of this model is that repeated observations of the same fish represent independent habitat selections. This assumption has been questioned in habitat association studies because of the tendency of a radiotracked animal to be observed in the same location as it was previously observed and observations may therefore be temporally autocorrelated (Thomas and Taylor 1990; Manly et al. 1993). Violation of this assumption can adversely affect measures of uncertainty (Neter et al. 1985) so it is important to account for this potential lack of independence.

A Markov chain extension of the IMS model, proposed by Ramsey and Usner (2004) for use on radio telemetry studies, was used to account for the tendency of an animal to be sighted in the same habitat as it was previously sighted. We found substantial evidence of this type of location persistence in this study, especially in winter and summer (Figure 2). Ramsey and Usner (2004) suggest that although the location persistence parameter does not necessarily model all dependence between observations; however, the model detects and quantifies the lack of independence and provides reasonable protection when this assumption fails. This location persistence model was used to calculate habitat use probabilities for channel

unit and sub-unit types and their structure types. The use probability for a particular variable was compared to the proportion available in the stream using simultaneous Bonferroni confidence intervals (Byers and Steinhorst 1984). Significant positive differential use of a variable occurred if the use probability and its confidence interval were greater than the proportion available. Significant negative differential use occurred when the selection probability and its confidence interval were below the proportion available.

Results

Because of failed transmitters, tag ejections, and transmitter battery expiration before the end of the study period, only 17 fish on Roberts Creek and 9 on Rail Creek were successfully tracked throughout February through mid-August (Table 2). Mean fork length of radiotagged fish in Roberts Creek was 241 mm (range, 201-280) and 252 mm (range, 208-298) in Rail Creek. Estimated median age of radiotagged fish in both Roberts Creek and Rail Creek was 4 (range, 3-5). In both streams, cutthroat trout from a variety of habitats were radiotagged. On Roberts Creek, 2 cutthroat trout (12%) were captured in faster-water units, 7 (41%) in scour pools, 6 (35%) in plunge pools, and 1 each in a dam pool and glide. Twelve fish (71%) were caught in habitats formed by instream large wood, 4 (24%) in meander pools, and 1 in a boulder pool. On Rail Creek, 3 fish (33%) were caught in fast-water units, 3 (33%) in scour pools, 2 (22%) in plunge pools, and 1 in a glide. Seven (78%) came from pools and sub-units formed by large wood and 2 (22%) from boulder pools.

Seasonal movement patterns

There were significant differences in movement patterns of radiotagged cutthroat trout among the seasons in both streams ($P < 0.01$) with the exception of directional distance on Rail Creek ($P < 0.06$). There was also substantial variation in movement patterns within seasons (Table 3). Dunn's multiple comparison test showed that on Roberts Creek, in spring, radiotagged cutthroat trout moved greater median total distance (644 m) and median range (446 m) than in winter (60 and 35 m, respectively)

and summer (183 and 104 m, respectively). Median directional distance in spring (271 m) was only significantly greater than summer (-210 m).

Radiotagged fish on Roberts Creek also showed significantly less median location persistence in spring (44%) compared to winter (63%) and summer (67%). On Rail Creek, cutthroat trout showed significantly greater median total movement in spring (1,574 m) than in winter (208 m) but not in summer (240 m). There were no significant differences in median directional distance on Rail Creek in winter (0 m), spring (311 m), and summer (-183 m). Median range length in spring (898 m) was significantly greater than in winter (104 m) but not in summer (112 m) on Rail Creek. Radiotagged cutthroat trout showed less median location persistence in spring (22%) than in summer (50%) but did not differ from winter (33%). Summer and winter movement patterns on both streams were not significantly different.

There was a significant positive correlation between fork length of fish and the total distance moved in spring (Figure 4) on Roberts Creek (r = 0.55; *P* = 0.02) but not on Rail Creek (r = 0.42; *P* = 0.243). There was no significant negative correlation between the transmitter:fish weight ratio and total distance moved in spring on Roberts Creek (r = -0.38; *P* = 0.075) or Rail Creek (r = -0.34; *P* = 0.204).

Table 2. Characteristics of cutthroat trout tracked throughout winter, spring, and summer 2000-01. Tag weight ratio represents the transmitter weight relative to the fish body weight.

Creek	N	Fork Length (mm)		Weight (g)		Age (y)		Tag weight ratio (%)	
		Mean (SD)	Range	Mean (SD)	Range	Median	Range	Mean (SD)	Range
Roberts	17	241 (20)	201-280	160 (44)	92-250	4	3-5	2.4 (0.70)	1.4-3.9
Rail	9	252 (30)	208-298	177 (69)	94-314	4	3-5	2.3 (0.85)	1.1-3.8

Table 3. Sample size and median movement patterns of radiotagged cutthroat trout during individual seasons on Roberts Creek and Rail Creek. Negative numbers signify downstream directional trend. For comparison between seasons, medians (and range values) followed by the same letter were not significantly different based on Dunn's multiple comparison test.

	Winter	Spring	Summer
Roberts Creek			
Sample size (observations)	17 (244)	17 (144)	17 (121)
Total distance (range) (m)	60 (0–469) a	644 (88–2,891)	183 (0– 4,165) a
Directional distance (range) (m)	-4 (-50– 393) ab	271 (-1,424–1,138) a	-210 (-1,531–1,378) b
Range length (range) (m)	35 (0– 393) a	446 (30–1,531)	104 (0–1,378) a
Location persistence (range) (%)	63 (43–100) a	44 (0–62)	67 (22–100) a
Rail Creek			
Sample size (observations)	9 (109)	9 (79)	9 (86)
Total distance (range) (m)	208 (5–1,446) a	1,574 (160–3,933) b	240 (0–3,326) ab
Directional distance (range) (m)	0 (-133–322) ab	311 (-1,867–3,771) ac	-183 (-1,411–3,389) bc
Range length (range) (m)	104 (5–522) b	898 (30–3,852) a	112 (0–3.326) ab
Location persistence (range) (%)	33 (0–94) ab	22 (12–44) a	50 (39–100) b
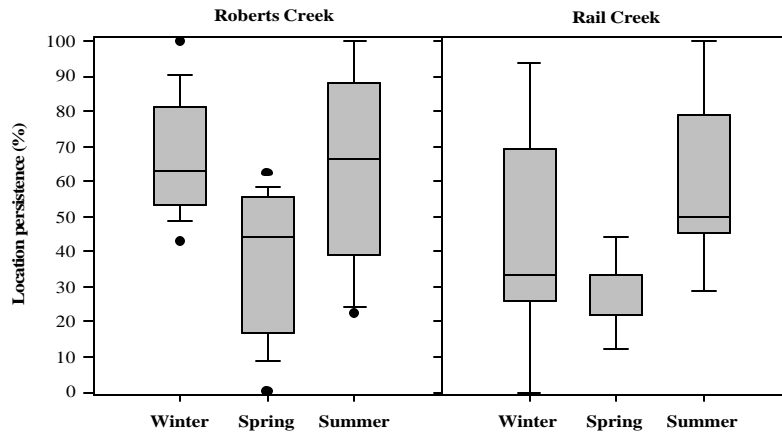
Figure 2. Seasonal boxplots of location persistence for Roberts Creek and Rail Creek. Location persistence is defined as the likelihood of observing a radiotagged fish in the same location as the previous tracking observation.
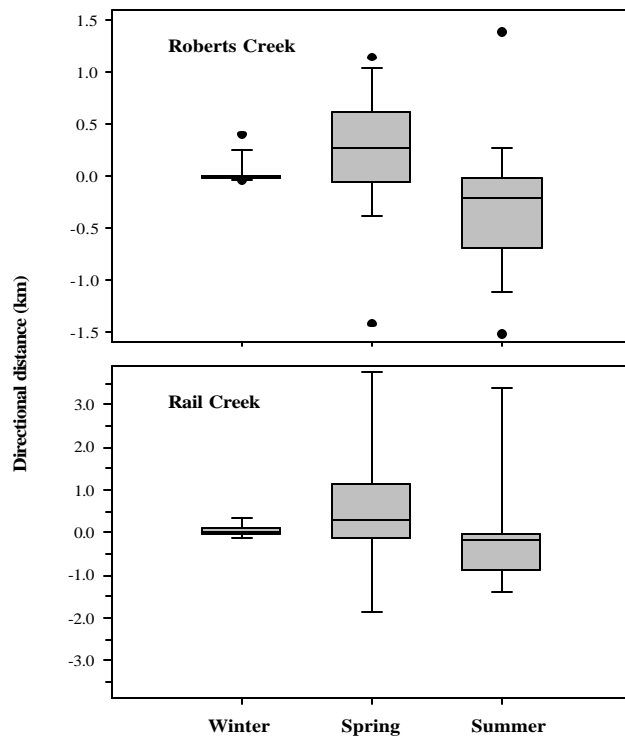
Figure 3. Seasonal directional distance for radiotagged cutthroat trout on Roberts Creek (N=17) and Rail Creek (N=9). Creeks are on different scales. Boxplots consist of the median and inter-quartile range; whiskers represent 95% confidence intervals, and all outliers are shown.
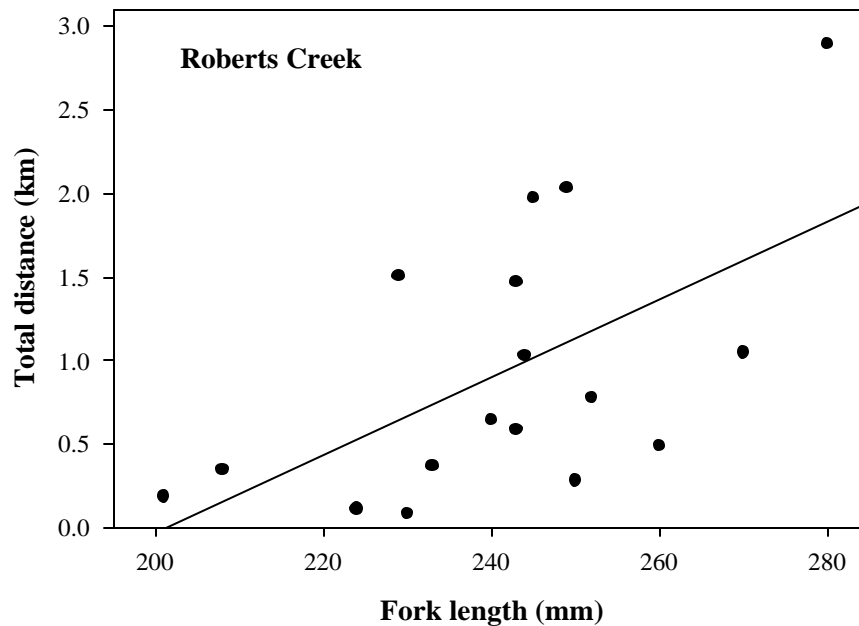
Figure 4. Scatter plots with a best-fit line respresenting the correlation of fork length to total distance moved in spring. Roberts Creek showed a positive correlation (Spearman rank correlation coefficient=0.553; p=0.021) and Rail Creek did not show a significant relationship (p=0.243).

Seasonal habitat availability

Radiotagged cutthroat trout were generally found in slow-water habitats (pools, glides, and sub-units) so only these habitats were used in the calculation of habitat availability (Table 4, Figures 5, 6, and 7). Fast-water units were more prevalent than slow-water channel units, constituting over 86% of the total stream area in both Roberts Creek and Rail Creek (numbers in parentheses in Table 4). As a result, sub-units were the slow-water habitats most available to radiotagged cutthroat trout, providing over 56% of the total slow-water habitat surface area in Roberts and Rail Creek. Plunge pools and scour pools were the most common pool types, and dam pools and glides made up relatively small proportions of slow-water habitat surface area. Instream large wood was the dominant structure type in both streams, accounting for over 23% of pools and 32% of sub-units in both streams. Stream bank protrusions and riparian vegetation were relatively rare structure types.

Table 4. Seasonal habitat availabilities on Roberts Creek and Rail Creek. Availability of individual slow-water habitat types (pools, glides, and sub-units) is expressed as a percentage of the total surface area of slow-water habitats in the channel unit type section. Availability of slow-water habitats created by individual pool and sub-unit structure types is also expressed as a percentage of the total surface area of slow-water habitats. (In parentheses are the availabilities of different channel unit types expressed as percentages of the total stream surface area.)

	Roberts Creek		Rail Creek	
	Winter/summer	Spring	Winter/summer	Spring
Channel unit type				
Fast-water units	61 (87)	63 (89)	56 (86)	63 (88)
Dam pool	4 (1)	6 (2)	9 (3)	8 (3)
Plunge pool	14 (5)	15 (4)	11 (3)	10 (3)
Scour pool	14 (5)	14 (4)	18 (6)	13 (4)
Glide	7 (2)	3 (1)	7 (2)	6 (2)
Pool structure type				
Large wood	25	27	27	23
Boulder	4	4	4	3
Stream bank	4	3	5	3
Riparian vegetation	1	1	2	2
Sub-unit structure type				
Large wood	36	41	32	42
Boulder	29	21	25	16
Stream bank	0	0	1	3
Riparian vegetation	1	3	4	8

Seasonal habitat use

     Among slow-water channel units, radiotagged cutthroat trout showed significant positive differential use of plunge pools in all seasons but summer on Roberts Creek and winter on Rail Creek, in which they were used in proportion to their availability (Figure 5). Scour pools were used in greater proportion to their availability in summer on Roberts Creek and less than the proportion available in winter on Rail Creek. Otherwise, scour pools were used in proportion to their availability. Dam pools and glides were used in proportion to their availability in all seasons.

     The most important pool-forming structure type to radiotagged cutthroat trout was instream large wood, showing significant positive differential use in all seasons on both streams (Figure 5).   Boulder and

meander pools were used in proportion to their availability in all seasons, with the exception of meander pool in Roberts Creek in winter, which fish showed significant positive differential use.

Within faster-water channel units, radiotagged cutthroat trout generally showed significant negative differential use of large wood and boulder sub-units and no differential use of stream bank and riparian vegetation sub-units (Figure 6). Large wood sub-units were used in proportion to their availability only in winter on Rail Creek and boulder sub-units were used similarly in spring on Roberts Creek. Sub-units created by stream bank protrusions were used in proportion to their availability. On Rail Creek, cutthroat trout showed positive differential use of sub-units formed by riparian vegetation in winter, negative differential use in spring, and did not use them in summer. Radiotagged fish in Roberts Creek used riparian sub-units in proportion to their availability in all seasons.
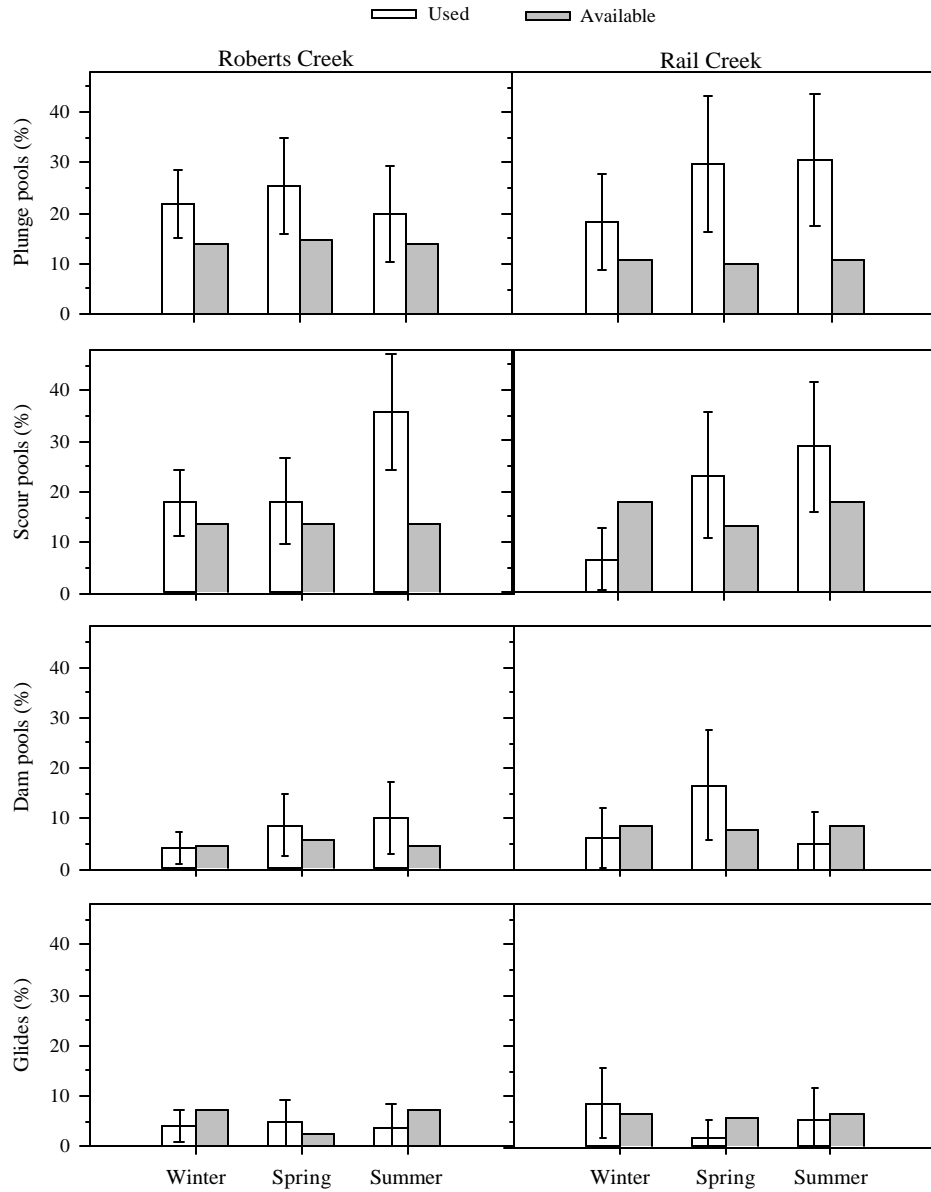
Figure 5. Habitat selection probabilities and availability of slow-water channel units on Roberts Creek and Rail Creek. Error bars represent 95% Bonferroni confidence intervals.
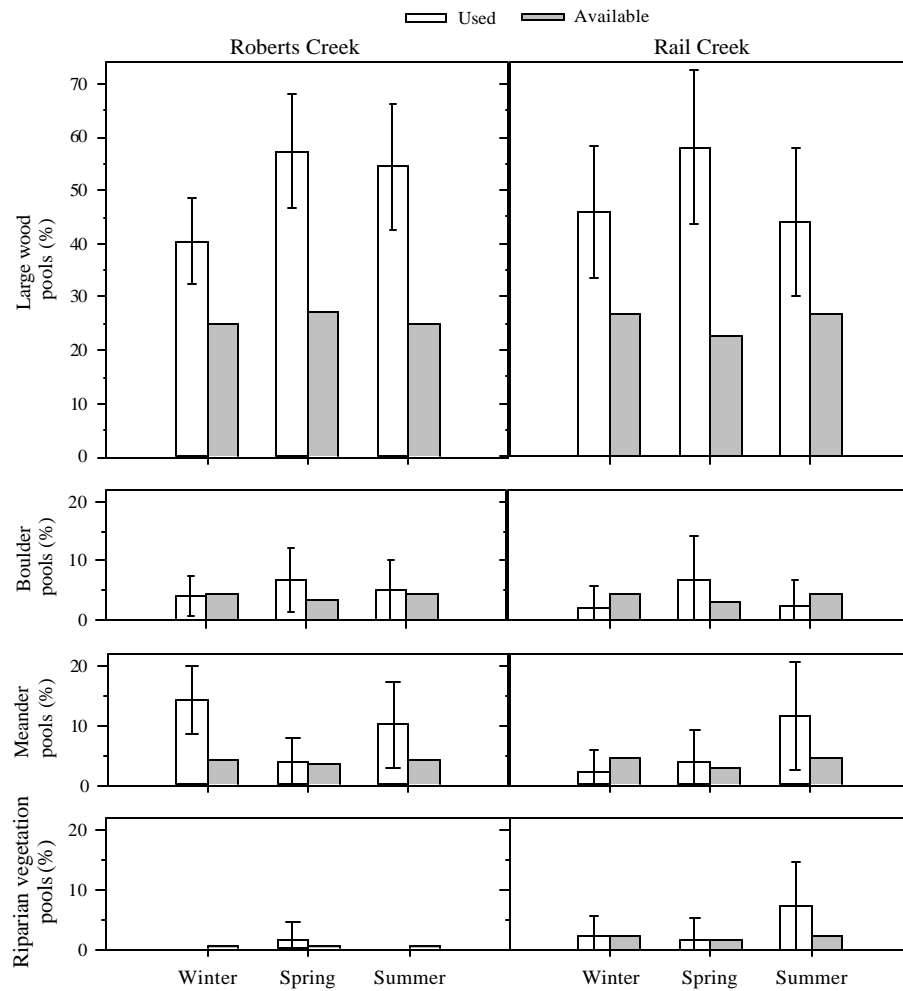
Figure 6. Habitat selection probabilities of pool-forming structure types and their availabilities. Error bars represent 95% Bonferroni confidence intervals.
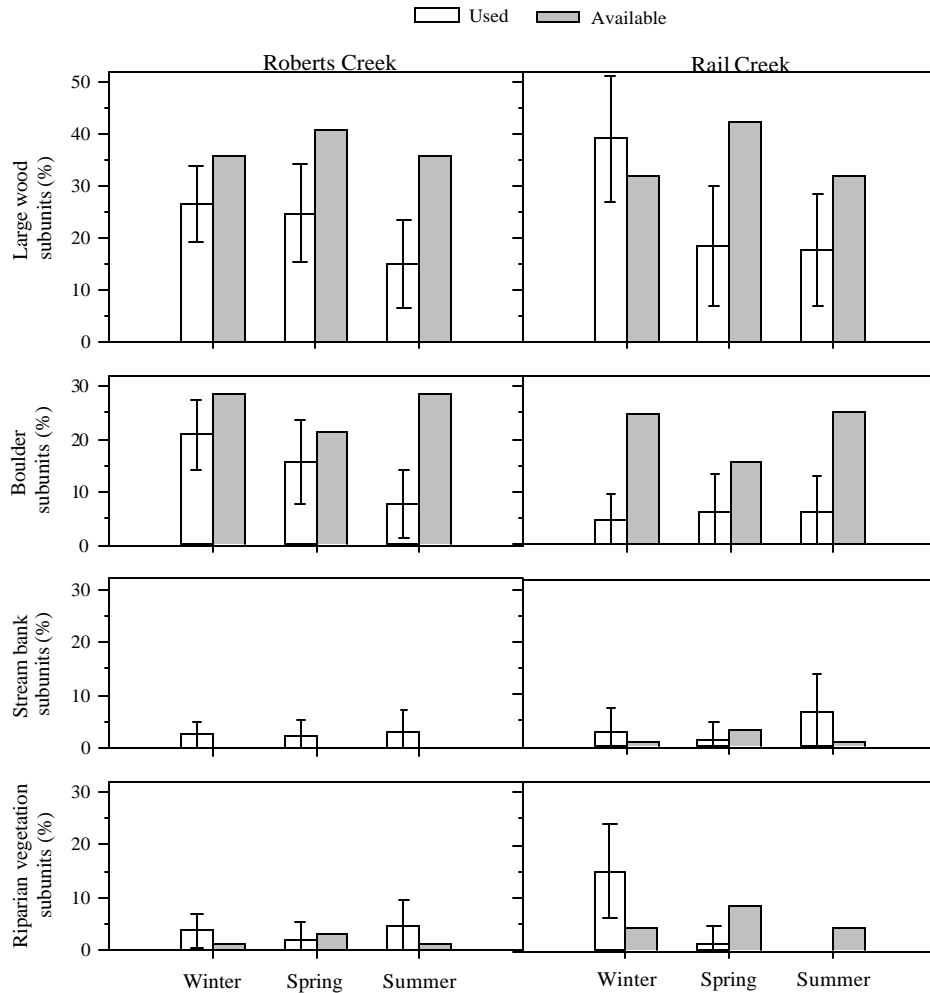
Figure 7. Habitat selection probabilities and availability for fast-water units and subunit-forming structure. Error bars represent 95% Bonferroni confidence intervals.

Discussion

Seasonal movement

The movement patterns of radiotagged westslope cutthroat trout in Roberts Creek and Rail Creek were consistent with the four criteria for migration, as defined by Northcote (1978, 1997). Using the categories proposed by Varley and Gresswell (1988) for potamodromous populations, these radiotagged fish can be classified as fluvial migrants: fish whose feeding, refuge, and spawning migrations occurred within a headwater stream or river home range (Northcote 1997). These radiotagged cutthroat trout, generally four years old and between 200-300 mm fork length, spent

the entire year in the headwater stream in which they were captured. Similarities with the movement patterns reported for other cutthroat trout populations suggest fluvial migration within headwater basins may be common throughout the current distribution of westslope cutthroat trout.

Consistent with the first migration criterion, movements of cutthroat trout in this study occurred with seasonal periodicity similar to other headwater-resident cutthroat trout populations (Shepard et al. 1984; Liknes and Graham 1988; Varley and Gresswell 1988; Hilderbrand and Kershner 2000; Brown and Mckay 1995; Gresswell and Hendricks, in revision). These movements began as the hydrograph began to rise: April 15 on Rail Creek and May 1 on Roberts Creek (Figures 8 and 9). Most of the spring upstream movement occurred during the second half of May on both streams, which was immediately after peak flow and throughout the descending limb of the hydrograph. Downstream movements in early summer was similar to seasonal periodicity patterns reported in other cutthroat trout studies (Gresswell et al. 1994; Young 1996; Schmetterling 2001; Schrank and Rahel 2004). Because more than 40% of the radiotagged fish were observed on or near redds, displaying courtship behavior, or showing spawning coloration, it appeared that movements during spring were associated with spawning. Fish that were not visually observed during spring also moved relatively longer distances, a response that is probably not related to high discharge alone. There are several examples of a modest response to high discharge by adult stream fishes (e.g., Jowett and Richardson 1994; Swanson et al. 1998; Harvey et al. 1999), but, typically, fish moved to nearby stream margins, or behind nearby obstructions, where water velocities were relatively lower.

Movement to overwintering refugia is another pattern with seasonal periodicity reported for headwater-resident cutthroat trout. Radiotagged cutthroat trout in Roberts Creek and Rail Creek showed relatively little movement in winter. These two creeks experienced no anchor ice and very little frazil ice, and we found no warm water springs in winter that had a

measurable effect on stream temperature. One fish was observed making short upstream refuge movements to the nearest ice-free pool to avoid frazil ice accumulation behind a temporary ice dam. These extreme cold air conditions occurred twice during the winter, and each episode lasted about 10 days. The fish returned to its previous location when frazil ice disappeared. The results on Roberts Creek and Rail Creek were similar to the winter movement patterns for radiotagged cutthroat trout in headwater streams in southeast Idaho (Hilderbrand and Kershner 2000), southwest Wyoming (Lindstrom and Hubert 2004), and Montana (Jakober et al. 1998), where instream ice was not an important factor. Harper and Farag (2004) observed similar short refuge movements in response to dynamic streams condition in the upper Snake River, Wyoming, where Yellowstone cutthroat trout *O. c. bouvieri* moved to off-channel habitats influenced by groundwater discharge during periods when the water temperature fell below 1.0° C and returned to main channel habitats when the temperature rose above 1.0° C. In two headwater streams in southeast Alberta that experienced prolonged, habitat-altering, instream ice conditions, radiotagged westslope cutthroat trout showed relatively more substantial (>1 km) multi-stage winter refuge movements, with no directional tendency, in response to changing winter stream conditions (Brown and Mackay 1995a; Brown 1999).

Consistent with the second migration criterion, a large percentage of the population (>65%) on Roberts Creek and Rail Creek moved more than 100 m upstream in spring, and 71% and 56%, respectively, moved more than 100 m downstream in summer. Other radiotracking studies of headwater populations of adult cutthroat trout also report high percentages of the population moving relatively long distances in spring (Brown and Mackay 1995b, Hilderbrand and Kershner 2000) and early summer (Young 1996) with similar seasonal directionality.

Third, these results suggest that at least some movements were directed rather than a result of random wandering or passive drift.

Moreover, substantial percentages of radiotagged cutthroat trout on Roberts Creek (53%) and Rail Creek (33%) showed post-spawning homing behavior (Figure 8A and 9A); that is, fish left their relatively short winter range to spawn in locations of varying distances upstream (and downstream, for one fish on Roberts Creek) and then returned in June or July to one of the same channel units used frequently during the previous winter. Although relatively few fish were tracked in fall, the low occurrence of movement in fall of 2000 and 2001 suggests that the use of approximately the same summer and winter range by adult cutthroat trout in Roberts Creek and Rail Creek was not a single year occurrence. Only two other studies track headwater-resident cutthroat trout movement patterns in spring, but transmitters expired too early to monitor potential post-spawning movement (Hilderbrand and Kershner 2000), or they were implanted after pre-spawning movements may have already begun (Brown and Mackay 1995b). Post-spawning homing behavior in headwater streams may partly explain why earlier researchers using mark and recapture methods and sampling in consecutive summers concluded that a great proportion of cutthroat trout inhabited short home ranges (<20 m), often a single channel unit, for their entire lives (Miller 1957; Gerking 1959; see Gowan et al. 1994 for other examples).

The fourth criterion for migration is that the movements result in an alternation between two "well-separated" habitats (Northcote 1997). Few radiotagged fish were seen actively digging or guarding a redd so determining spawning location was often impossible, and the adjective "well-separated" is not defined by Northcote (1997). However, most radiotagged cutthroat trout in Roberts Creek and a substantial portion in Rail Creek literally alternated between downstream summer and winter locations and upstream locations in spring (Figures 8A and 9A). Movement distances of this study (and most other radiotracking studies) should be considered minimum estimates because tracking methods usually contain a substantial temporal interval between observations during which relatively

long-distance movements may be missed by the tracker (Horton et al. 2004; Gresswell and Hendricks, in revision). In this study, the average interval between observations in spring was 7 days, the longest movement recorded over this interval was 2.3 km, and radiotagged cutthroat trout often spent less than two weeks at or near their spawning or upstream-most location.

There was substantial variation in westslope cutthroat trout behavior within a season and between Roberts Creek and Rail Creek. Movement patterns on both streams varied from no directional movement, and upstream movement in spring with no post-spawning movement downstream in summer, to active relatively long-distance movement through out summer (Figures 8B and 9B). Some of the seasonal variation in spring may be the result of tagging some immature individuals and potential alternate year spawners (Schmetterling 2001) that did not seek spring spawning habitat, or some fish simply did not need to move long distances to successfully spawn. The variation within a season and the extent of separation between an overwintering location and a spawning site is difficult to predict for an adult cutthroat trout because it may be the result of many interacting factors, including fish size.

Greater fish length confers stronger swimming ability (Alexander 1982) and may allow larger fish to move upstream faster, taking advantage of peak flows in spring, and pass over instream obstructions that may act as a barrier to smaller fish. This study provides some evidence that size may influence the distance a fish migrates to spawn. Fish length was positively correlated with total movement distance in spring on Roberts Creek, but the relationship was not significant on Rail Creek. Fish length has been positively correlated with movement distance for many other species (brown trout, Clapp et al. 1990, Young 1994; Bonneville cutthroat trout *O.c. utah*, Schrank and Rahel 2004; and potamodromous coastal cutthroat trout, Gresswell and Hendricks, in review), but some studies have found a negative correlation (for cutthroat trout, Schmetterling 2001) or no

significant relationship (westslope cutthroat trout, Hilderbrand and
Kershner 2000).

Figure 8. Movement patterns (A and B) of individual radio-tagged
cutthroat trout in relation to discharge and stream temperature (C) in
Roberts Creek. Fish in box A showed directional movement in spring and
post-spawning homing to the same channel unit inhabited in winter. Other
movement patterns are depicted in box B. In box C, solid line represents
discharge and dotted lines represent the mean weekly minima and maxima
stream temperature in box C. Y-axis represents stream kilometers measured
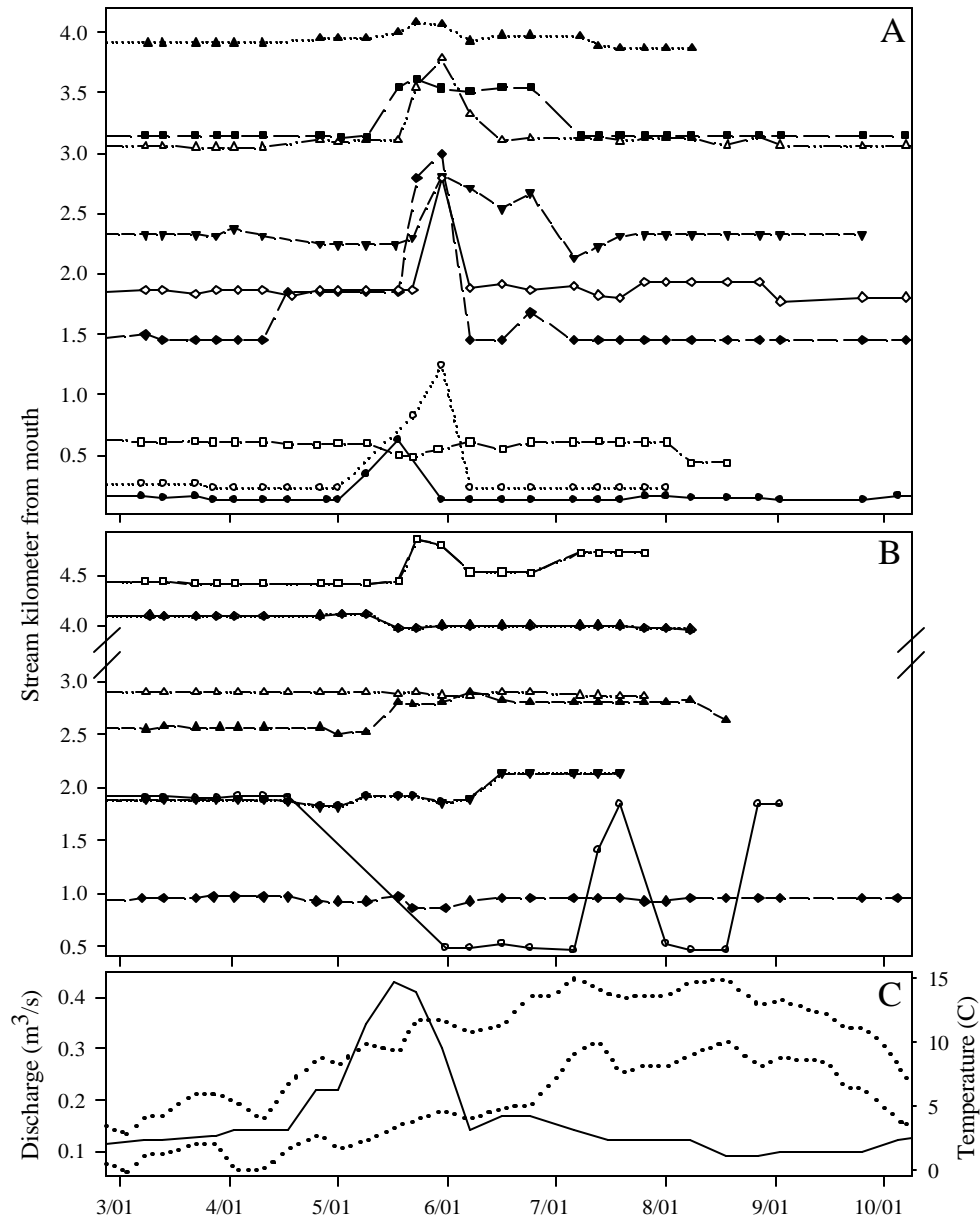upstream from the mouth.

Figure 8. Movement patterns (A and B) of individual radio-tagged cutthroat trout in relation to discharge and stream temperature (C) in Rail Creek. Fish in box A showed directional movement in spring and post-spawning homing to the same channel unit inhabited in winter. Other movement patterns are depicted in box B. In box C, solid line represents discharge and dotted lines represent the mean weekly minima and maxima stream temperature in box C. Y-axis represents stream kilometers measured upstream from the mouth.
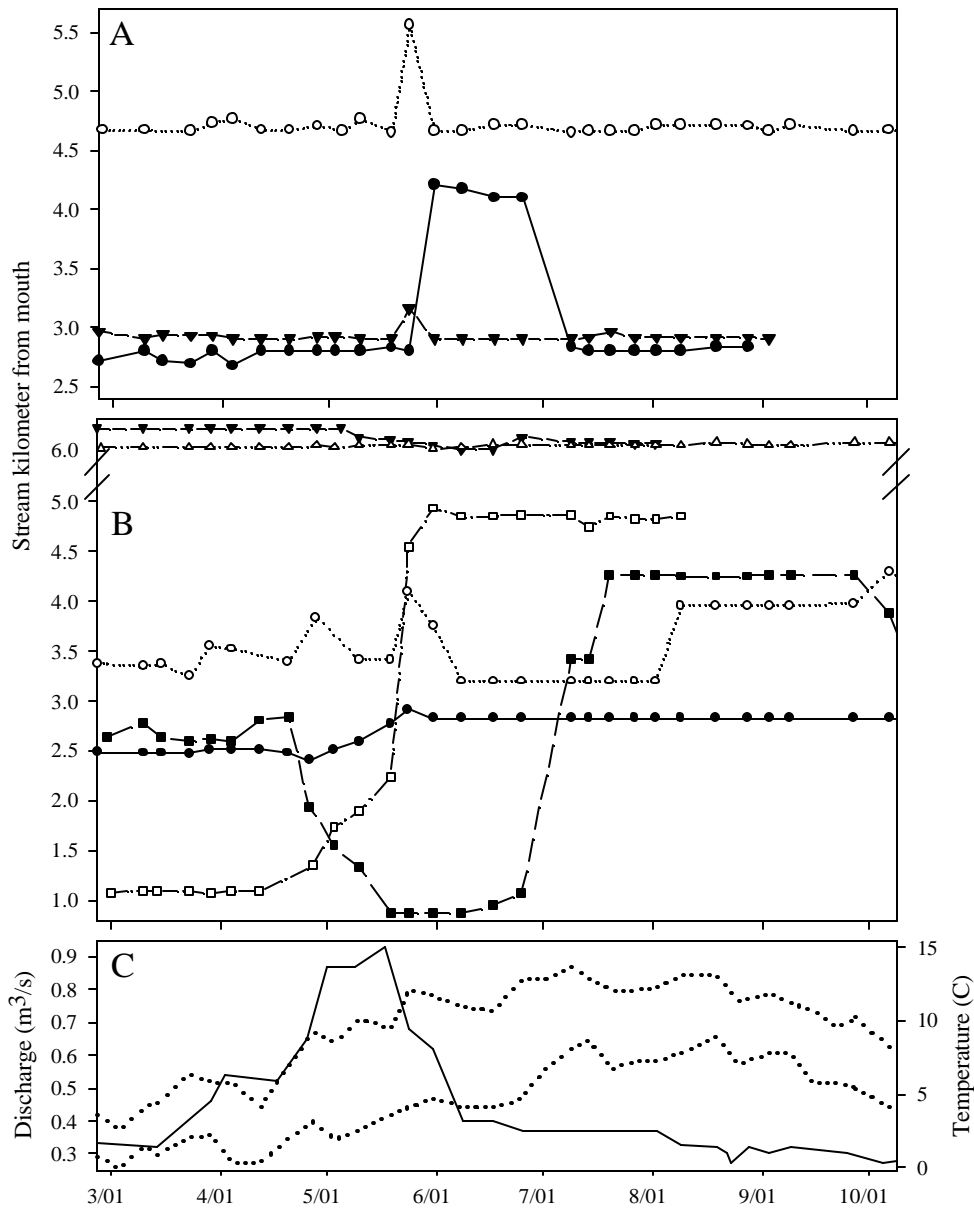
Seasonal habitat use

In other studies of adult potamodromous salmonids in headwater streams, overwintering habitat usually consisted of relatively deep pools often with instream large wood cover (Peters 1988; Cunjak and Power 1986, 1987) but varied depending on the availability of pool types, instream ice formation during especially cold periods (Chisolm et al. 1987; Jakober et al. 1998; Jakober 1998; Lindstrom and Hubert 2004), or the presence of areas influenced by winter warm water discharge (Brown and Mackay 1995).

Radiotagged cutthroat trout in this study were strongly associated with wood in all seasons (Figure 9), especially large wood pools. Overwintering fish in this study were visually observed relatively rarely in winter, which suggests that they were using instream cover relatively more often than in other seasons. However, shorter days and the contrast between snowy stream banks and dark stream bottom may have impaired visual detection. Winter in the upper John Day River basin during the study period was relatively mild and no use of thermal refugia by radiotagged fish was observed. Hanging ice dams formed on instream large wood and frazil ice accumulated in slow-water habitats at least twice. This phenomenon directly affected only one of the radiotagged fish. Twice during winter on Roberts Creek, an ice dam formed on a piece of instream large wood, raising the depth of the pool and lowering flow velocities. When frazil ice accumulated in the pool, the fish moved 30 m upstream to an ice-free meander (or lateral scour) pool with no instream large wood.

Several other studies found beaver ponds, when they were present in the study area, were important habitat for potamodromous salmonids in winter (Chisolm et al. 1987; Jakober et al. 1995; Lindstrom and Hubert 2004). There were small signs of beaver activity in Roberts Creek and Rail Creek but no dams were constructed and stream habitat was not altered by beavers during the study period. One local resident recalled seeing a long series of beaver dams on lower Rail Creek over 40 years ago so it is possible that in the past beaver ponds provided important winter habitat for

cutthroat trout in the upper John Day River headwater tributaries. It is also possible that beaver ponds will play an important habitat-forming role in these streams in the future. Nearby tributaries of the John Day River are experiencing a relatively recent increase in beaver dam construction, and I saw an 8 m wide beaver dam blocking a meandering side channel on Rail Creek two years after the field work for this study ended.

Subunits

Because pools are widely reported as important winter habitat, extensive use of sub-units in winter in Roberts and Rail Creek was surprising. Several fish did not move throughout the entire winter from sub-units of such low habitat volume that it was believed the signal was coming from ejected transmitters. After these fish migrated upstream in spring, these sub-units were examined and relatively deep pockets (20-35 cm) underneath the sub-unit structure were found. Rimmer et al. (1984) and Cunjak (1988b) noted similar winter sheltering behavior beneath boulders for juvenile Atlantic salmon and found boulder diameter and size of the fish using the boulder to be directly proportional. Muhlfeld et al. (2001) also reported substantial early winter use of sub-units (which they called non-channel spanning "side pools" formed by large wood or boulders and "pocket water" created by boulders) by radiotagged redband trout in a Rocky Mountains stream. They found trout inhabiting sub-units in 31% of tracking observations in October; however, use of sub-units decreased to 19% in November and December. They suggested movement out of sub-units was related to lower stream temperatures and the prevalence of instream ice in November and December, but did not report if ice affected the sub-units directly. Because fast-water channel units usually constitute the vast majority of surface area in steep headwater streams, and non-channel spanning habitats probably represent a substantial proportion of potential fish habitat, perhaps rivaling the availability of pool habitats as they did on Roberts Creek and Rail Creek, their lack of mention in the fish habitat use literature (but see Young [1994] for summer use of sub-units) is

surprising and may be related to differing criteria in the classification of channel units.

Spring habitat is generally considered to consist of spawning habitat and refuge from high stream flows. Describing spawning habitat was difficult because only 15% (4/26) of fish were seen paired up on redds. Most fish were seen spawning in sub-unit tailouts formed by instream large wood (1/4) or boulder (3/4). One of the fish observed on a sub-unit redd was paired up a week later with another fish on a redd in the tailout of a large wood plunge pool. Schmetterling (2000) found fluvial-adfluvial westslope cutthroat trout in the upper Blackfoot River, Montana, used mainly channel units for spawning: 75% of redds were found in the tailout of glides. Only 21% of redds were found in riffles; possibly in sub-units created by instream structure, but structure was not explicitly mentioned. Comparing the results of this study with those on Roberts Creek and Rail Creek, there is suggestive evidence of segregation of spawning habitats between fluvial headwater-resident populations and the fluvial-adfluvial form.

Refuge habitat has often been described in terms of structure that reduces cutthroat trout movement (e.g., during winter bankfull flood, Harvey [1998]; or seasonal immigration rates without distinguishing between ontogenetic life stage, Harvey et al. [1999]). Other studies have reported short movements during floods to stream margins or nearby structure (Jowett and Richardson 1994; Swanson et al. 1998). Many observations in this study occurred during the spring freshet when fish were migrating between their generally downstream winter location and their upstream spawning location. During spring, cutthroat trout in Roberts Creek and Rail Creek were strongly associated with instream large wood pool in general and plunge pools in particular. There are very few studies of adult potamodromous salmonid habitat use during spring en route to spawning locations. Schmetterling (2000) found that fluvial-adfluvial cutthroat trout, after entering their spawning tributary, used almost

exclusively channel units formed by instream large wood even though they used other channel units for spawning.

Conclusions

Adult westslope cutthroat trout in Roberts Creek and Rail Creek showed complex migratory behavior. Similar migratory behavior appears to be common in headwater streams among many potamodromous salmonids (Schrank and Rahel 2004), which suggests that the commonly used terms "resident" and "nonmigratory" do not describe precisely the migratory life history of headwater-resident populations of salmonids (Gresswell 1997). The use of more precise terms that reflect the diverse life histories of potamodromous salmonids is suggested (see Varley and Gresswell 1988; Northcote 1997).

Many interacting factors may influence migration distance and likely will result in substantial variation, as was seen on Roberts Creek and Rail Creek. The capacity for movement during or after stochastic events, such as in response to dynamic instream ice conditions, or to recolonize areas after debris flows and flash floods, also contributes to long-term persistence of a population. Because movement allows a fish to improve reproductive fitness and survival, managing for habitat connectivity and migration leads to greater population abundance and persistence of potamodromous salmonids in headwater streams.

In these two steep forested headwater basins, instream large wood played the primary role in creating habitat heterogeneity and these radiotagged cutthroat trout were strongly associated with instream large wood pools throughout the year. These results highlight the importance of healthy riparian zones to creating habitat for adult headwater-resident cutthroat trout.
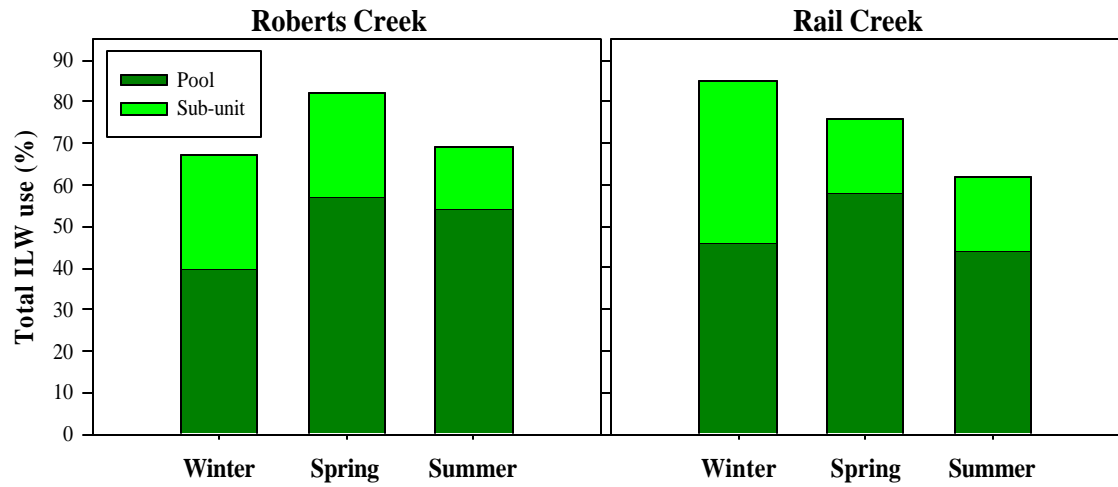
Figure 9. The summed habitat use probabilities of instream large wood
pools and subunits on Roberts and Rail Creek.

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