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Use of Similar Habitat by Cutthroat Trout and Brown Trout in a Regulated River During Winter

Abstract

Few differences in habitat use were observed between cutthroat trout and brown trout during winter in the Shoshone River, a regulated river in northwestern Wyoming. Radio-tagged fish of 20-30 cm total length were found in pool habitat five to six times more frequently than would be expected if they were using pools in proportion to pool availability. Nevertheless, run habitat was most frequently used by both species. The microhabitat characteristics at locations of each species were similar when in both pools and runs, however, habitat use was variable suggesting that a variety of microhabitats were suitable over-wintering habitat. Brown trout were more frequently associated with boulder cover than were cutthroat trout. Cutthroat trout used large pools that provided refuge from high water velocities more frequently that brown trout. Cutthroat trout and brown trout were found at similar distances from the bank except in late February when cutthroat trout were farther from the bank. Both species moved frequently during the winter, but cutthroat trout showed a greater propensity than brown trout to move long distances. This study suggests that during a mild winter in a stable environment, these species were able to overwinter successfully in a variety of habitats.

Introduction

In regulated rivers of western North America, discharge from upstream impoundments is often reduced to annual lows during fall and winter after the irrigation season. The habitat constriction associated with decreased discharge may reduce habitat segregation among multiple populations of introduced salmonids. Rainbow trout (*Oncorhynchus mykiss*) or cutthroat trout (*O. clarki*) are often reared in hatcheries and stocked into regulated rivers (Wiley et al. 1993) where brown trout (*Salmo trutta*) have been introduced and have become naturalized (Heidinger 1993). While studies have been conducted on habitat preferences and competition among native and introduced salmonids, little comparative research has been conducted in regulated rivers among combinations of non-natives, especially during winter when habitat limitation may be most severe. The purpose of our study was to examine one combination of non-natives, sympatric populations of cutthroat trout and brown trout, in a regulated river during winter.

The physiological constraints placed on fish at low water temperatures are reflected in their habitat use and movement during winter. Pools are important areas for stream-dwelling salmonids during winter that provide decreased water velocities and protection from harsh environmental conditions and predation (Swales et al. 1986, Heggenes et al. 1993, Brown and Mackay 1995, Jakober et al. 1998, Simpkins et al. 2000a). Use of cover by salmonids appears to increase in the winter. Several studies have reported that salmonids suspend diurnal activity and conceal themselves when temperatures drop below 8-10°C (Rimmer et al. 1983, Griffith and Smith 1993, Fraser et al. 1995, Valdimarsson et al. 1997). However, salmonids may not cease activity entirely as they have been observed feeding during the day when water temperatures were substantially less than 8°C (Needham and Jones 1959, Pirhonen et al. 1997, Simpkins et al. 2000b).

Most studies of salmonid movement in winter have shown that mobility is decreased when compared to other times of year (Hilderbrand and Kershner 2000) and is most often related to changes in environmental conditions (Brown and Mackay 1995, Simpkins et al. 2000a). However, the bulk of previous research was conducted in natural-flowing streams that maybe subject to greater environmental variability and potentially harsh environmental conditions, such as river ice formation.

Despite similar body forms, there are contrasts in habitat use between cutthroat trout and other

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salmonids when in sympatry. When cutthroat trout and bull trout (*Salvelinus confluentus*) were studied in Montana (Nakano et al. 1992) and cutthroat trout and brook trout (*Salvelinus fontinalis*) were assessed in Idaho (Griffith 1972), cutthroat trout were more frequently found at locations farther from structures than either bull trout or brook trout.

While there have not been any direct comparisons of cutthroat trout and brown trout in a natural setting, studies of habitat use by brown trout suggest there may be differences between the species. Brown trout are a highly cover-oriented species often occupying positions downstream from structures that create feeding stations, areas with slow water in close proximity to fast water (Chapman and Bjornn 1969, Fausch and White 1981, Bachman 1984, Greenberg et al. 1996, Haugen and Rygg 1996, Quinn and Kwak 2000). This contrasts with the open-water, swift-flowing environment often used by cutthroat trout.

We wanted to know if there would be detectable differences in habitat use by cutthroat trout and brown trout that are placed in unnatural sympatry in a regulated river during winter. Our objective was to assess the similarity and differences in winter habitat use between cutthroat trout and brown trout in a regulated river where these two introduced species dominate the salmonid community. No research has been conducted during winter when lower water temperatures and habitat limitations could result in substantial overlap in habitat use between the species (Chapman 1966). Because of the environmental stability and higher water temperatures associated with river regulation, we expected to observe habitat-use patterns and spatial segregation similar to previous research.

Study Area

This research was conducted in the Shoshone River, a regulated river in northwestern Wyoming. Discharge is controlled by Buffalo Bill Dam, located ~11 km west of Cody, Wyoming (Figure 1). Discharge during winter 1997-1998 was relatively stable at 13.8-14.8 m^3/s.

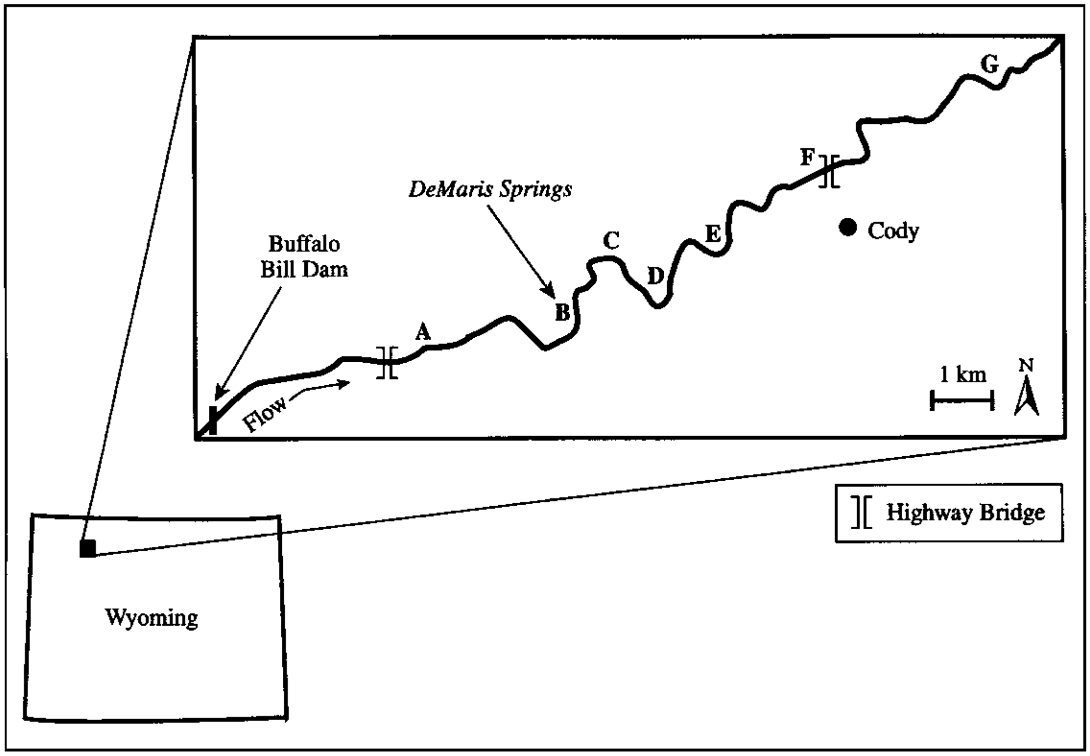

Figure 1. The study reach and water temperature sampling sites in the Shoshone River. Letters indicate water quality monitoring sites. Habitat availability and use were monitored between sites E and G.

The fine-spotted form of Yellowstone cutthroat trout (*O. clarki bouvieri*) that is native to the Snake River watershed is stocked annually downstream from Buffalo Bill Dam during the early summer. By October cutthroat trout reach 20-30 cm total length (TL). Brown trout were introduced in the 1930s and have been self-sustaining downstream from Buffalo Bill Dam since the 1960s. The density of each species has been estimated to be about 500 fish/km (Steven Yekel, Wyoming Game and Fish Department, personal communication).

Methods

Seven recording thermographs were placed at approximate 2-km intervals downstream from Buffalo Bill Dam from DeMaris Springs to the downstream end of the study reach (Figure 1). The most downstream sampling site was 27 km downstream from Buffalo Bill Dam. Thermographs were set to record at 30-min intervals from 15 November 1997 through 31 March 1998.

The 5-km study reach was divided into 50 segments each 100-m in length and a transect was randomly placed at 0, 25, 50, or 75 m down from the upstream end of each segment. Habitat availability was measured within a series of 4-m-diameter circles evenly spaced along each transect. Spacing of sampling areas was determined by dividing the transect wetted width by the number of sampling areas that could be placed along the transect. For example, a transect with a wetted width of 36 m would have nine sampling areas with 4 m between adjacent centerpoints. Both microhabitat and mesohabitat features were described and assessed. Microhabitat features were specific to the 4-m-diameter sampling in which the fish occurred. Mesohabitat features were measures of larger-scale habitat features within the study reach.

Microhabitat features measured within each sampling area included minimum and maximum water depth, minimum and maximum water velocity, substrate composition, and presence of cover. Substrate composition was estimated by determining the area of each of six substrate size classes present within each sampling area. Size classes ranged from silt/sand (size 1) to bedrock (size 6) and the area of each size class was estimated to the nearest 10%. We used a weighted average to calculate the mean substrate size within each sampling area. Cover was classified based on the physical features associated with its formation—boulders, aquatic vegetation, or deep-water cover. Deep-water cover was identified as any area where the water velocities were near zero that lacked an associated structural feature, such as a boulder (Wesche et al. 1987). To be considered cover, any area or structural feature had to have a maximum water depth of at least 0.4 m to provide an overhead cover component. Vertical relief and water velocity gradients were estimated by subtracting a minimum depth or velocity value from the corresponding maximum. A detailed description of our habitat sampling methodology can be found in Dare and Hubert (2000).

Each sampling area was classified as one of three mesohabitat types: pool, run, or riffle in a manner similar to Rimmer et al. (1983) with the quantitative characteristics of each mesohabitat type modified to characterize the Shoshone River more accurately. Pools were areas having 1.50-m maximum depth, or >0.75-m maximum depth and <0.30-m/s maximum water velocity. Runs were intermediate areas having 0.30-1.50 m maximum depth, intermediate water velocities, and no surface turbulence. Riffles were stream areas having <0.30-m maximum depth, or <0.75-m maximum depth and >0.65-m/s minimum water velocity.

Twenty cutthroat trout and 20 brown trout (23-30 cm TL) were collected by angling and electrofishing on 13-17 November 1997. A radio transmitter (Advanced Telemetry Systems Model 357; 48.200-48.980 Mhz, mean weight 3.0 g; whip antenna length: 10 cm) was surgically implanted into the abdomen following the technique of Bidgood (1980). After a period of recovery (30-120 min) each fish was released near its point of capture.

Fish were located every 2-4 d using a receiver and handheld loop antenna from 22 November 1997 through 28 February 1998. Fish were tracked from a boat or from the bank, and fish locations were determined using two-point triangulation (Simpkins and Hubert 1998). Upon locating a fish we described microhabitat and mesohabitat features at the location within a few minutes of finding the fish. Microhabitat and mesohabitat features were measured or described within an area having a 2-m radius to collect data that were consistent with the habitat availability measurements. Microhabitat at an individual location was the depth, velocity, substrate, and cover present with the 2-m diameter sampling area. Based on the depth and velocity characteristics we characterized each location as one of the three mesohabitats. Sampling methodologies for habitat availability and habitat use data were identical. The distance of a fish position from the bank was determined by measuring the straight-line distance (m) from the triangulated fish location to the nearest stream bank. Fish movement distance (straight-line distance within the stream channel) between consecutive locations was measured (m) with a tape if less than 100 m, or estimated from 1:24,000 scale topographic maps if greater than 100 m. The resolution of the maps was sufficient to identify the fish location to within 5 m, therefore only movements greater than 5 m were recorded.

We assessed the effect of fish length (within each species) on microhabitat use and movement using simple-linear regression. No significant relationships were found between fish length and water depth and water velocity use or movement, so we discounted fish length as a source of variability in microhabitat use and movement patterns. Additionally, neither species was observed in riffle habitat, therefore, this habitat type was excluded from the analysis of mesohabitat use.

We made separate comparisons of microhabitat use by cutthroat trout and brown trout in pools and runs using individual fish as the sampling unit. Fish were included in an analysis if they were observed at least five times within a mesohabitat type. To discern differences in mesohabitat use, we calculated the proportion of observations of individual fish of each species recorded in pools and runs and compared the proportions using a two-sample t-test. For each test a one-sided alternative hypothesis was used. We analyzed microhabitat use within each mesohabitat type to remove variation associated with the differences in the physical characteristics of pools and runs. For each individual we calculated a mean for each continuous microhabitat variable and then used a two-sample t-test to compare the suite of cutthroat trout individual means to the suite of brown trout individual means. To test for differences in cover types used by cutthroat trout and brown trout within each mesohabitat type, we also used a two-sample t-test. We calculated the proportion of locations of each individual having boulder cover or deep-water cover present. Given the expected differences between the two species, we used a one-sided alternative hypothesis that cutthroat trout used boulder cover less frequently and deep-water cover more frequently than brown trout.

The mean distance from the bank at locations of each species was calculated using data from dates when we observed at least 10 individuals of each species. We used time-series plots to determine if there was a trend through the winter in mean distance from the bank for each species.

To test if the frequency of movements differed between cutthroat trout and brown trout, we calculated the proportion of observations of individuals of each species made at new versus previously held locations. Proportions for each species were compared using a two-sample t-test. We compared movement distances by calculating the mean movement distance during each month of the study for individuals of each species and assessing differences using a two-sample t-test for each month.

We insured the data met the assumptions of parametric statistical tests (Sokal and Rohlf 1995). Transformations were applied to data as necessary. In all cases where a transformation was required, natural log transformations were used. In cases where two samples were compared, if the assumption of homoscedasticity was violated, a t-test that did not assume equal variances was used. When multiple tests of the same hypothesis were conducted (e.g. microhabitat use comparisons), a Bonferroni correction was applied to the decision rule of each test (Sokal and Rohlf 1995). The significance level was set at 5%.

Results

Water temperatures declined from fall to winter but remained several degrees above freezing throughout the winter (Figure 2). Additionally, water temperatures were quite stable throughout the winter. The lowest mean daily water temperature in the middle of the study reach was 2.8°C on 12 January 1998, and water temperature rose to 6°C by 15 February 1998.

Runs were the most common mesohabitat type in the study area, whereas pools and riffles were relatively rare (Table 1). Water depths and water velocities reflected the characteristics of each mesohabitat type. Pools had the greatest water depth and vertical relief, whereas runs had the greatest maximum and minimum water velocities. Riffles had the greatest variation in water velocity. The substrate size in pool habitat was

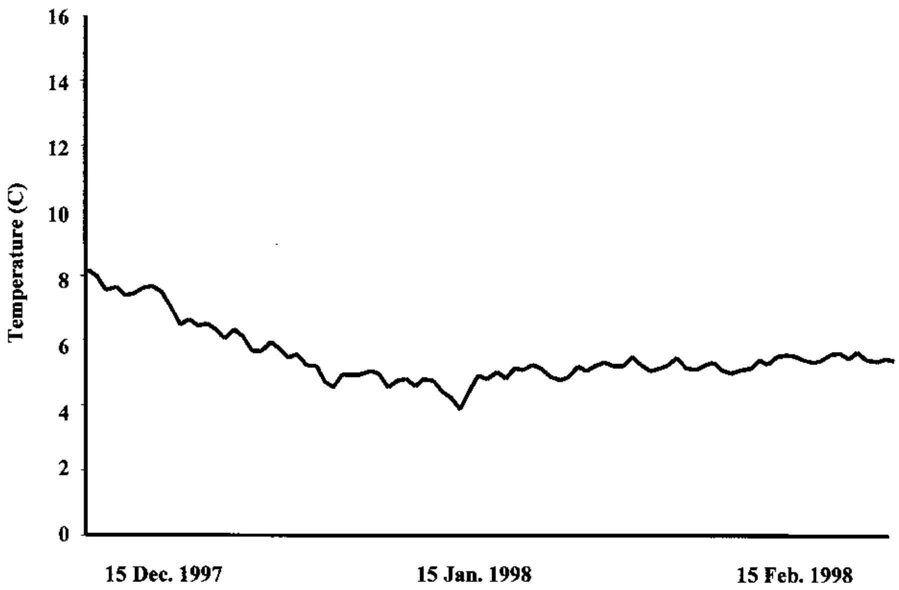

Figure 2. Mean daily water temperatures recorded in the Shoshone River during winter 1997-1998.

TABLE 1. Area of mesohabitats and average microhabitat characteristics within mesohabitats measured at 400 sampling areas along transects. Percentile values for cover refer to the percentage of sampling areas having that cover type present.

	Mesohabitat		
Habitat feature	Pool	Run	Riffle
Area (%)	7.5	83.5	9.0
Maximum depth (cm)	161.7	76.5	23.1
Minimum depth (cm)	112.3	43.0	1.0
Vertical relief (cm)	49.7	33.5	22.4
Maximum water velocity (m/s)	0.48	0.82	0.48
Minimum water velocity (m/s)	0.27	0.46	0.10
Water velocity gradient (m/s)	0.22	0.36	0.39
Mean substrate size class	4.2	5.3	5.0
Boulder cover (%)	65.5	62.9	5.6
Vegetation cover (%)	0.0	2.1	2.8
Deep water (%)	26.7	2.4	0.0

on average only one size class smaller than in runs and riffles reflecting the large substrate sizes throughout the study reach.

The preponderance of large substrate was also reflected in the abundance of boulder cover (Table 1). Boulder cover was observed in over half of the sampling areas in both pools and runs and was substantially more common than aquatic vegetation or deep-water cover. Cover was infrequently observed in riffles.

Eighteen individuals from each species were tracked throughout the study. Two individuals of each species were not relocated after surgery. Fourteen cutthroat trout and 11 brown trout in pools and 14 individuals of each species in runs were observed at least five times and were included in the analysis.

Pool habitat was used by both species five to six times more frequently than would be expected if pool habitat were used in proportion to its availability. Pool habitat constituted 7.5% of the available habitat within the study area, however, 43% (SE = 10%) of cutthroat trout observations and 38% (SE = 10%) of brown trout observations were made in pools.

Both cutthroat trout and brown trout were found more frequently in runs than in pools and neither species used riffle habitat during the study. On average, 57% of cutthroat trout locations and 62% of brown trout locations were in runs, however, there was substantial variation among individuals of both species. Four cutthroat trout were found exclusively in pools, four were exclusively in runs, and 10 used both pools and runs. Similarly, four brown trout were found exclusively in pools, seven were only found in runs, and seven were observed in both pools and runs.

TABLE 2. Grand mean and range of means for microhabitat parameters measured at and estimated for fish locations in two mesohabitats in the Shoshone River.

Habitat feature	Pool		Run	
	Grand mean	Range of means	Grand mean	Range of means
Cutthroat trout				
Maximum depth (cm)	190.6	119.1-405.0	102.9	56.2-136.3
Minimum depth (cm)	88.3	30.4-140.2	52.5	17.1-81.4
Vertical relief (cm)	102.2	51.2-295.0	50.2	43.1-66.5
Maximum velocity (m/s)	0.37	0.25-0.57	0.57	0.38-0.79
Minimum velocity (m/s)	0.13	0.06-0.30	0.16	0.01-0.39
Velocity gradient (m/s)	0.25	0.14-0.37	0.41	0.23-0.69
Brown trout				
Maximum depth (cm)	206.7	82.4-400.4	103.0	65.8-127.5
Minimum depth (cm)	74.9	19.1-151.9	38.3	0.0-67.3
Vertical relief (cm)	125.3	40.8-292.4	64.2	41.2-128.5
Maximum velocity (m/s)	0.42	0.20-0.81	0.68	0.48-0.86
Minimum velocity (m/s)	0.17	0.03-0.35	0.18	0.01-0.37
Velocity gradient (m/s)	0.29	0.14-0.60	0.50	0.30-0.38

Cutthroat trout and brown trout in both pools and runs used locations having similar microhabitat characteristics (Table 2). There were no significant differences between the two species with respect to microhabitat features used when in either pools or runs. Both species were consistently observed at locations that averaged 5-6 m from the stream bank.

Cover was always present at locations of both cutthroat trout and brown trout, however, there were some differences between the two species. When in pools, deep-water cover was observed at 61% of cutthroat trout locations, which was approximately double the frequency with which this cover type was observed at brown trout locations ($P = 0.02$). However, when in runs, both species used boulder cover more frequently than deep-water cover, with boulder cover present at 75% of cutthroat trout locations and 89% of brown trout locations. Boulder cover was significantly more common at brown trout locations than at cutthroat trout locations in runs ($P = 0.02$)

The movement frequencies of cutthroat trout and brown trout did not differ significantly. Thirty-seven percent of cutthroat trout observations were made at new locations (range: 10-60%), whereas 31% of brown trout observations were made at new locations (range: 12-54%). Similarly, distances moved by the two species did not differ significantly (Table 3) with the exception of January ($P = 0.001$) when the mean movement distance of cutthroat trout was greater than brown trout. Mean monthly movement distances varied considerably among individuals, particularly cutthroat trout. A greater number of cutthroat trout moved long distances. Seventeen of 18 brown trout remained within 300 m of their initial location, while five of 18 cutthroat trout moved to locations that were farther than 300 m from their initial location at some time during winter.

TABLE 3. Sample size, mean movement distance (m), and range of individual means (m) for three months for cutthroat trout and brown trout in the Shoshone River during the winter of 1997-1998.

Month	Cutthroat trout			Brown trout		
	N	Grand mean	Range of means	N	Grand mean	Range of means
December	15	6.7	1.0-187.3	14	3.5	0.6-9.7
January	17	14.4	2.0-59.8	18	4.1	0.9-82.8
February	12	5.5	0.7-185.0	14	3.3	0.8-19.2

Discussion

Few differences in habitat use were observed between cutthroat trout and brown trout during winter in the Shoshone River. Despite substantial differences in habitat use described through previous research on the two species, cutthroat trout and brown trout used similar habitat during winter low-flow periods in a regulated river system where both species have been introduced.

Both cutthroat trout and brown trout selected pool habitat. While only 7.5% of the study area was classified as pool habitat (Table 1), 38-43% of observations of both species were made in pools. This was five to six times greater than would be expected if both species were using pool habitat in proportion to its availability. Cunjak and Power (1986) stated that pools provide low water velocities and overhead cover in the form of deep water. This was true in the Shoshone River, where pools provided greater water depths and slower water velocities compared to runs. Brown and Mackay (1995) found that pools were the predominant habitat used by cutthroat trout during winter because water temperatures were slightly higher in pools providing protection from river ice. Water temperatures in the Shoshone River prevent river ice formation, so that avoidance of ice was not a factor in our study.

While there was selection for pools, both cutthroat trout and brown trout used runs most frequently. Within runs, we observed a wide array of stream microhabitats at individual locations. The variation in mean microhabitat characteristics and mesohabitat use among individuals of both species (Table 2) suggests that under these conditions both species are somewhat plastic in their selection of over-wintering habitat.

Both cutthroat trout and brown trout used similar microhabitats (Table 2). Both species were consistently found at locations having deeper than average water depths and slower than average water velocities. These findings are similar to those reported for other salmonid species in unnatural sympatry (Fausch and White 1981, Lohr and West 1992). Additionally, cutthroat trout and brown trout selected areas having greater than average vertical relief and water velocity gradients. However, since both species were able to use suitable over-wintering habitats that provided slow water velocities and overhead cover, habitat was likely not limiting at the discharges and water temperatures we observed during 1997-1998.

The patterns of cover use we observed suggest that while both species selected areas having slower than average water velocities brown trout were more commonly associated with instream structure than cutthroat trout. Additionally, cover use by cutthroat trout appeared to vary between mesohabitats. While in pools cutthroat trout were not associated with cover structures, but structures such as boulders were frequently observed at cutthroat trout locations when they were in runs. Brown trout did not display this variation in cover use between mesohabitats, consistently displaying the high degree of affinity for cover structures as observed during other studies (Bachman 1984; Cunjak and Power 1986; Greenberg et al. 1996). While we cannot rule out interspecies interactions as a mechanism behind the contrasting cover use patterns we observed, the wealth of supporting research regarding cutthroat trout habitat preferences in allopatry (Brown and Mackay 1995) and sympatry (Nakano et al. 1992) suggests that innate differences in cover preference and the ubiquity of deep-water cover in pools allowed for a small degree of spatial segregation to occur in pool habitat.

Both cutthroat trout and brown trout remained active during the day even when water temperatures were below 5°C. We noted fluctuations in the radio transmitter signals during nearly all observations of both species that suggested that fish were active and making short-distance movements (Clapp et al. 1990; Young et al. 1997).

Given the water temperatures in the Shoshone River during winter, the habitat use patterns we observed likely indicated that fish were feeding throughout the winter. Hebdon (1999) found that cutthroat trout feed throughout the winter in the Shoshone River and we observed individuals of both species feeding during our study. Therefore, the nature of the environment in which we observed these fish resulted in a contrast with winter habitat use patterns by salmonids that have been recorded in natural-flowing streams (Heggenes et al. 1991). Chapman (1966) described food acquisition as the major factor in habitat use throughout most of the year, however, sheltering from predation and the environment takes precedence during winter. Because of the stability of the regulated river environment, cutthroat trout and brown trout in the Shoshone River continually employed a feeding strategy even at low water temperatures.

Cutthroat trout and brown trout were found at similar distances from the bank through with winter with the exception of late February when cutthroat trout were farther from shore (Figure 3). Cutthroat trout movement away from the bank as water temperatures declined during winter has been observed in another river system (Brown and Mackay 1995), but those movements were believed to be in response to river ice formation. We did not detect variation in water temperature (Figure 2), occurrence of river ice, or changes in other habitat features that would account for this difference in late February in the Shoshone River. Additionally, we were not able to isolate these observations as statistical artifacts, therefore, the movement by cutthroat trout toward mid-channel remains unexplained.

A study that examined cutthroat trout movement in Utah classified individuals as mobile if they moved more than 300 m from their initial point of capture during a season (Hilderbrand and Kershner 2000). While the 300-m criterion was somewhat arbitrary, according to it, five of the 18 cutthroat trout we monitored would be considered mobile. Using this criterion, no brown trout were mobile. Our observation of mobile cutthroat trout during winter contrasts with the observations of Hilderbrand and Kershner (2000), who observed that ~25% of the cutthroat trout

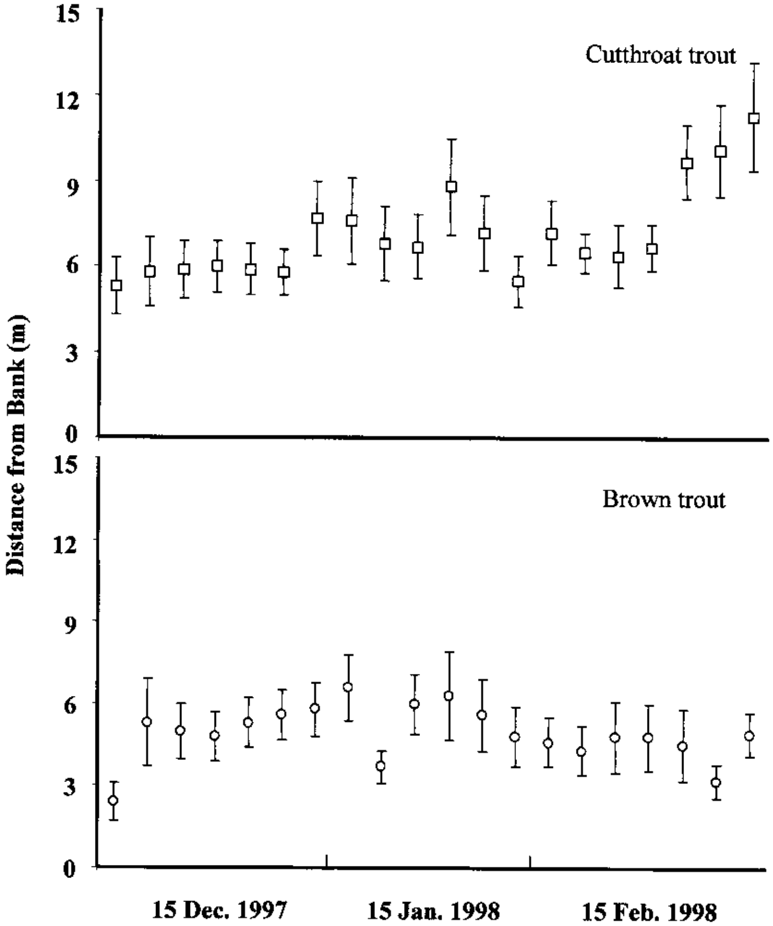

Figure 3. Average distance from the bank, ± 1 SE, for cutthroat trout and brown trout in the Shoshone River on 20 dates during the 1997-1998 winter.

population were mobile during other times of the year, but not during winter. Other studies have reported restricted cutthroat trout movement during winter (Heggenes et al. 1991). Our contrasting observations are most likely a manifestation of the differences in water temperature and environmental stochasticity between regulated and unregulated rivers during winter.

This study suggests that cutthroat trout and brown trout use a variety of similar habitats during winter when in unnatural sympatry in a regulated river system. However, winter water temperatures in the Shoshone River are substantially higher than other regulated river systems in Wyoming (Hebdon 1999) and discharge was stable during this study. The relatively benign environmental conditions that characterized the 1997-1998 winter likely contributed to a high degree of plasticity in habitat use among individuals of both species. Because of the inter-individual variation in habitat use, we observed few statistically significant differences in habitat use. Habitat segregation may be more pronounced in other regulated rivers with colder winter conditions and with less stable discharges.

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