Changes in Habitat Availability and Habitat Use and Movements by Two Trout Species in Response to Declining Discharge in a Regulated River during Winter

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Abstract.—We assessed habitat availability and habitat use by subadult cutthroat trout *Oncorhynchus clarki* and brown trout *Salmo trutta* during a four-stage flow manipulation in the Shoshone River, Wyoming, to determine how the physical characteristics of a medium-size river and the habitat use and movement patterns of subadult trout change in response to declining discharge. Discharge was reduced from 20.9 to 5.7 m³/s between December 1998 and February 1999. Changes in riverine physical characteristics included decreased water depths and velocities, increased pool area, and dewatering of riffles. Changes in habitat use differed between cutthroat and brown trout; however, both species were typically observed at locations with greater-than-average water depths and slower-than-average water velocities, especially pools with abundant cover. The observed patterns of habitat use by subadult cutthroat trout and brown trout were similar to those found for salmonids in other variable environments during winter. Selection of stable pool habitat and a tendency by both species to move relatively short distances during winter indicate that short-term (14–21-d) reductions in discharge may have little effect on subadult trout.

Though hypolimnetic water releases from upstream reservoirs often dampen fluctuations in water temperature and prevent ice formation in regulated rivers (Ward and Stanford 1979), winter can be a difficult time for salmonids in these systems. Discharge is often reduced to the lowest levels of the year during winter, and decreases in discharge may limit habitat availability and reduce food supplies (Cushman 1985; Baran et al. 1995), with consequences for salmonids that feed throughout winter (Hebdon 1999; Simpkins et al. 2000a)

Research on variable discharge has described the effects of increased discharge (Fjellheim et al. 1993; Gido et al. 2000; McKinney et al. 2001) or hydropower-peaking operations (Fraley et al. 1986; Valentin et al. 1996) or has modeled changes in habitat within the context of the instream flow incremental methodology (Baran et al. 1995; Heggenes et al. 1996). Field studies of the effects of decreasing discharge on habitat availability and use by salmonids is lacking.

We examined the effects of declining discharge on habitat availability, habitat use, and movements of subadult cutthroat trout *Oncorhynchus clarki* and brown trout *Salmo trutta* in the winter of 1998–1999, based on a controlled flow manipulation in which discharge was reduced by approximately 400% over 3 months. We are unaware of any published research that has directly examined changes in habitat availability and fish habitat use during a controlled decrease in discharge for a system as large as the Shoshone River. Logistical constraints have precluded such research in the past, but we were given the unique opportunity to explore questions pertaining to decreased discharge during winter because of the importance of the Shoshone River fishery in Wyoming.

We addressed two questions. First, as the physical characteristics of a river change in response to decreased discharge, how does habitat use by cutthroat trout and brown trout change? Second, do movement patterns change in response to declining discharge?

Based on these questions, we formulated three a priori hypotheses: (1) use of pools by both species would increase as discharge decreased; (2) spatial segregation between the two species would
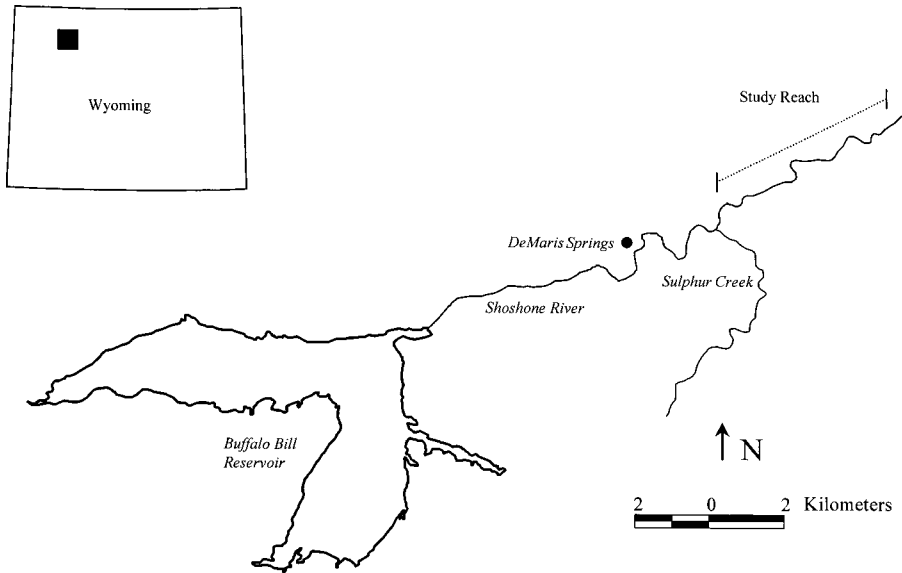
FIGURE 1.—The Shoshone River downstream from Buffalo Bill Dam, Wyoming, showing the location of DeMaris Springs and the study reach where habitat availability and habitat use were studied during 1998–1999.

decline as discharge decreased; and (3) because cutthroat trout tend to be more mobile (Brown and Mackay 1995; Young 1996; Hilderbrand and Kershner 2000) than brown trout, cutthroat trout would move more frequently and for longer distances than brown trout as discharge decreased.

Methods

Flow manipulation.—Discharge from Buffalo Bill Dam was reduced in four stages over a 3-month period from 1 December 1998 to 21 February 1999. Planned discharge was 20.9 m³/s at stage 1, 13.9 m³/s at stage 2, 8.2 m³/s at stage 3, and 5.7 m³/s at stage 4. Discharge was reduced during a 2–5 d period between stages. Stages 1 and 4 lasted for approximately 21 d, and stages 2 and 3 lasted for approximately 14 d. The experimental flow regime was developed in terms of two main considerations. First, a sufficiently high initial discharge was needed to allow for appreciable decreases during successive stages of the flow manipulation. Second, we set a minimum discharge of 5.7 m³/s to avoid long-term negative impacts on the fish community downstream from Buffalo Bill Dam.

Temperature.—Five continuously recording thermographs were spaced at 2-km intervals downstream from DeMaris Springs and at the base of Buffalo Bill Dam. Thermographs were set to record at 60-min intervals, and data were downloaded every 2–3 weeks from 1 December 1998 through 29 February 1999. Daily mean air temperature data were obtained from a National Weather Service historical database (Weather Underground, Inc. 1999).

Habitat availability.—Habitat availability data were collected during each stage of discharge in a 5-km study reach downstream from Buffalo Bill Dam (Figure 1). The study reach was divided into 50 segments of 100 m each, and a transect was randomly placed 0, 25, 50, or 75 m downstream from the upper end of each segment. Habitat data were collected with the area-based sampling protocol described by Dare and Hubert (2000). Habitat measurements were made within a series of 4-m-diameter circles evenly spaced along each transect. Spacing of sampling areas was determined by dividing wetted width of the transect by the number of sampling areas that could be placed along the transect. Wetted widths and transect spacing determined at the highest flow were used at each successive stage, resulting in identical sampling areas throughout the experiment. Within each sampling area, the maximum and minimum water depths (cm) and the maximum and minimum water velocities (m/s) were measured. The presence of boulder, deep-water, and vegetation cover was noted. Deep-water cover was defined as any area of cover that was at least 0.4 m in water depth and that was not formed by an object within or adjacent to the sampling area boundaries (Wesche et al. 1987). From the water depth and water ve-
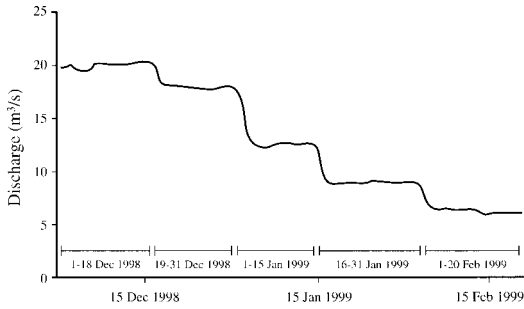
FIGURE 2.—Hydrograph for the Shoshone River during the 1998–1999 flow manipulation. Mean daily discharge data were collected at U.S. Geological Survey gaging station 06282000, located between DeMaris Springs and the study reach.

locity measurements, we estimated vertical relief (cm) and water velocity gradient (m/s) within each sampling area.

Each sampling area was classified as being in one of three mesohabitat types (pool, run, or riffle) in a manner similar to Rimmer et al. (1983). Pools either had maximum depths of at least 1.50 m or had depths greater than 0.75 m plus maximum water velocities less than 0.30 m/s. Riffles either had maximum depths less than 0.30 m or had depths less than 0.75 m plus minimum water velocities greater than 0.65 m/s. Runs had maximum depths of 0.30–1.50 m, intermediate water velocities, and no surface turbulence.

Habitat use.—We collected 24 cutthroat trout and 24 brown trout (20–30 cm total length) by electro-
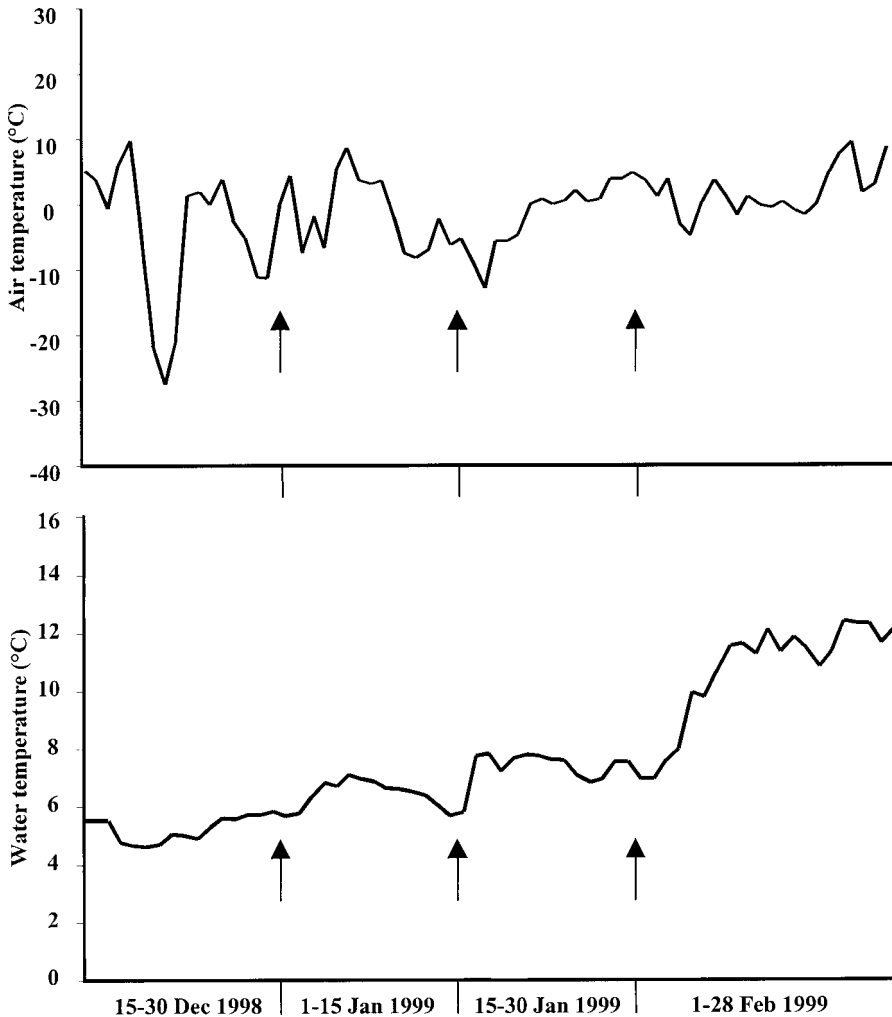

FIGURE 3.—Mean daily water and air temperatures recorded at the Shoshone River study area during 1998–1999. Arrows denote changes in discharge during the flow manipulation.

fishing on 2 December 1998. We surgically implanted a radio transmitter (Advanced Telemetry Systems, model 357; 48.200–48.980 MHz; mean weight 3.0 g; whip antenna length = 10 cm) into the abdomen of each fish with the technique described by Bidgood (1980). Twelve additional cutthroat trout were captured and radio-tagged during the last week of December. Fish were located and their microhabitat characteristics were measured every 2–4 d. Habitat use data were collected with the area-based protocol, and the measured variables were identical to those collected during habitat availability sampling. Sampling areas were centered on each triangulated fish location. The selection of 4-m-diameter circles was based on the work of Simpkins and Hubert (1998). Because we used the same gear and sampled in similar conditions as Simpkins and Hubert (1998), we were 95% confident that the actual fish location was within the 4-m-diameter sampling area, when locations were triangulated at distances of 10–15 m.

The distance of a fish position from the bank was determined by measuring the straight-line distance (m) from the center point of a triangulated fish location to a point on the nearest stream bank. Fish movement distance (straight-line distance within the stream channel) between consecutive locations was measured with a tape if less than 100 m, or estimated from 1:24,000-scale topographic maps if greater than 100 m. Movements greater than 5 m were defined as changes in position. Individuals that moved more than 300 m from their initial location during the experiment were considered mobile (Hilderbrand and Kershner 2000).

Data analysis.—We analyzed habitat availability data at three spatial scales: whole system, mesohabitat, and local microhabitat. At the whole-system scale, we examined changes in the mean microhabitat characteristics of the entire study reach, without regard to mesohabitat type. At the mesohabitat scale, we analyzed the proportional composition of pools, runs, and riffles within the study reach. At the local microhabitat scale, we examined the microhabitat characteristics within each mesohabitat type as discharge decreased. We lacked sufficient sample sizes to analyze trout habitat use at the local microhabitat scale; therefore, habitat use data were analyzed only at the whole-system and mesohabitat scales.

The relations between decreasing discharge and changes in microhabitat characteristics at the whole-system and local microhabitat scales were assessed by linear regression. Chi-square tests of

independence were used to assess changes in mesohabitat and cover availability with decreasing discharge. Adjusted residuals were calculated to evaluate specific changes in habitat features with decreasing discharge. Adjusted residual values greater than 3.0 or lower than −3.0 indicated significant changes in the proportional availability of a mesohabitat or cover type (Agresti and Finlay 1997).

We used linear regression to determine whether the whole-system-scale microhabitat use by each species changed with decreased discharge. An individual fish was included in the analysis if we observed that individual at all stages of the flow manipulation. Regressions were based on means of each microhabitat variable for an individual fish during each stage of the flow manipulation. The suite of individual means for each species was regressed against discharge, and 95% confidence bands were fitted to each line. We used a two-sample *t*-test to compare interspecific microhabitat use when neither species of trout showed a significant trend with discharge. A chi-square test of independence and adjusted residuals were used to identify changes in the proportional use of mesohabitats and cover by each species as discharge decreased.

We assessed movement frequencies by comparing the proportion of observations of each species made at new versus previously held locations at each discharge. Interspecies comparisons were made with two-sample *t*-tests.

Natural-log transformations were applied as needed to meet the assumptions of normality, linearity, and homogeneity of variance. These assumptions were tested with the default procedures in Minitab (Minitab 2000) and by inspection of graphs. In comparisons of two samples with heteroscedastic data, a two-sample *t*-test that did not assume equal variances was used. When multiple tests of the same hypothesis were conducted, we applied a Bonferroni correction to the decision rule of each test to maintain an overall error rate of 0.05. When conventional transformations (e.g., natural logarithm) did not result in homoscedasticity of samples to be analyzed with linear regression, the Box–Cox procedure (Box and Cox 1964) was used to determine the appropriate transformation. Linearity of data was verified by pure error lack-of-fit tests on regression models. The lack-of-fit test is appropriate when there are multiple values of the response variable at each value of the predictor (Neter et al. 1996). All statistical tests were conducted with SPSS (SPSS 1998) or Minitab (Minitab 2000) and were considered significant at α values of 0.05.

TABLE 1.—Whole-system means (SE) of microhabitat characteristics measured in the Shoshone River at three stages of a flow manipulation.

Microhabitat variable	Discharge (m^3/s)		
	13.9	8.2	5.7
Maximum depth (cm)	74.0 (1.9)	69.0 (1.8)	67.0 (1.9)
Minimum depth (cm)	38.0 (1.9)	31.0 (1.8)	26.0 (1.6)
Vertical relief (cm)	37.0 (1.1)	38.0 (0.9)	41.0 (1.1)
Maximum velocity (m/s)	0.77 (0.13)	0.59 (0.02)	0.49 (0.02)
Minimum velocity (m/s)	0.29 (0.05)	0.19 (0.01)	0.12 (0.01)
Velocity gradient (m/s)	0.49 (0.13)	0.40 (0.01)	0.37 (0.01)

Results

Flow Manipulation and Temperature

The flow manipulation proceeded entirely as planned (Figure 2) except for an unscheduled 2.8-m^3/s decrease in discharge (from 20.9 to 18.1 m^3/s) on 18 December 1998. Water temperatures steadily rose from about 5°C in December to about 12°C in February (Figure 3). Increases in mean daily water temperature coincided with declines in discharge. Air temperature was highly variable during the experiment (Figure 3). The maximum daily mean air temperature was 9.8°C on 17 December 1998, and the minimum was −27.4°C on 20 December.

Habitat Availability

Habitat availability sampling during stage 1 was initiated on 8 December; however, sampling was not completed prior to the unscheduled 2.8-m^3/s decrease in discharge on 18 December. At the time of the decrease, the upper 2.1 km of the study reach had been sampled. An analysis comparing habitat measurements made in this upstream reach with those made in the entire 5-km reach revealed differences in estimates between the first stage and subsequent stages. Differences primarily stemmed from the number and size of pools present in the upstream and downstream portions of the study reach, with more pools present downstream. Therefore, data from the upper 2.1 km of the study reach were not considered representative of the entire study reach, and the data collected during stage 1 were not included in the analysis of habitat availability.

There were several significant changes in habitat availability at the whole-system scale as discharge declined from 13.9 to 5.7 m^3/s (Table 1). Maximum depth (one-tailed $t = 2.9$; df = 1, 162; $P = 0.004$), minimum depth (one-tailed $t = 4.3$; df = 1, 161; $P < 0.001$), and vertical relief (one-tailed $t = 2.9$; df = 1, 162; $P = 0.004$) all decreased as discharge declined. Maximum water velocity (one-tailed $t = 5.4$; df = 1, 161; $P < 0.001$) and minimum water velocity (one-tailed $t = 4.9$; df = 1, 161; $P < 0.001$) also decreased with decreasing discharge.

There were significant differences in proportions of pool, run, and riffle habitat as discharge decreased (Table 2; $\chi^2 = 13.693$, df = 4, $P = 0.008$). The adjusted residuals showed an increase in the frequency of pools and a decrease in the frequency of riffles as discharge decreased. Sixty-eight of 421 sampling areas were dewatered at discharges between 13.9 and 5.7 m^3/s, representing a 16% loss of stream area. The majority of dewatering occurred in riffles, 57% of which were dewatered between stages 2 and 4.

Microhabitat characteristics of pools and runs changed as discharge decreased (Table 3). In pools, maximum depth (one-tailed $t = 3.0$, df = 102, $P = 0.004$), minimum depth (one-tailed $t = 2.2$, df = 102, $P = 0.034$), maximum water velocity (one-tailed $t = 2.3$, df = 102, $P = 0.023$), and water velocity gradient (one-tailed $t = 3.3$, df = 102, $P = 0.001$) all decreased as discharge decreased. Similarly, maximum depth (one-tailed $t = 5.5$, df = 853, $P < 0.001$), minimum depth (one-tailed $t = 1.9$, df = 853, $P < 0.001$), maximum water velocity (one-tailed $t = 2.2$, df = 853, $P =$

TABLE 2.—Frequency (percentage of totals in parentheses) and adjusted residuals of sampling areas classified as mesohabitats that were observed along transects at three stages of a flow manipulation in the Shoshone River.

Discharge (m^3/s)	Pool		Run		Riffle	
	Frequency	Adj. residual	Frequency	Adj. residual	Frequency	Adj. residual
13.9	32 (7.6)	−1.2	336 (79.8)	−1.1	53 (12.6)	2.6
8.2	29 (7.5)	−1.3	324 (83.3)	1.2	36 (9.2)	−0.3
5.7	43 (12.2)	2.6	287 (81.3)	0.1	23 (6.5)	−2.4

TABLE 3.—Microhabitat characteristics (SE) measured along transects at three stages of a flow manipulation in the Shoshone River.

Microhabitat Variable	Discharge (m^3/s)		
	13.9	8.2	5.7
Pool			
N	32	29	43
Maximum depth (cm)	155.6 (8.2)	139.3 (9.0)	122.9 (6.9)
Minimum depth (cm)	99.3 (10.5)	96.9 (11.0)	69.9 (6.8)
Vertical relief (cm)	56.3 (7.5)	42.4 (5.2)	52.9 (5.2)
Maximum velocity (m/s)	0.34 (0.04)	0.25 (0.25)	0.18 (0.01)
Minimum velocity (m/s)	0.14 (0.03)	0.14 (0.03)	0.08 (0.09)
Velocity gradient (m/s)	0.19 (0.03)	0.11 (0.01)	0.10 (0.01)
Run			
N	336	324	287
Maximum depth (cm)	73.7 (1.5)	67.5 (1.5)	61.6 (1.5)
Minimum depth (cm)	36.2 (1.7)	28.0 (1.5)	20.7 (1.4)
Vertical relief (cm)	37.6 (1.0)	39.5 (1.0)	40.9 (1.0)
Maximum velocity (m/s)	0.84 (0.16)	0.62 (0.02)	0.53 (0.02)
Minimum velocity (m/s)	0.31 (0.06)	0.19 (0.02)	0.12 (0.09)
Velocity gradient (m/s)	0.53 (0.17)	0.43 (0.15)	0.41 (0.02)
Riffle			
N	53	36	23
Maximum depth (cm)	31.7 (3.0)	34.2 (3.0)	32.4 (3.0)
Minimum depth (cm)	12.0 (2.7)	10.1 (2.9)	8.2 (3.5)
Vertical relief (cm)	19.7 (0.8)	24.1 (1.6)	24.2 (1.2)
Maximum velocity (m/s)	0.57 (0.06)	0.65 (0.06)	0.53 (0.07)
Minimum velocity (m/s)	0.24 (0.05)	0.28 (0.06)	0.15 (0.06)
Velocity gradient (m/s)	0.33 (0.04)	0.37 (0.13)	0.38 (0.04)

0.025), and minimum water velocity ($t = 3.2$, df $= 853$, $P = 0.001$) in runs decreased as discharge decreased. The only significant change in riffles was a decrease in minimum water velocity ($t = 3.0$, df $= 110$, $P = 0.003$).

Cover availability changed with decreasing discharge (Table 4). In pools, the amount of deep-water cover increased and the amount of vegeta-

tion cover decreased ($\chi^2 = 34.359$, df $= 4$, $P < 0.001$). The only significant change in cover availability in runs was a decrease in vegetation cover ($\chi^2 = 15.65$, df $= 4$, $P = 0.004$).

Habitat Use

Habitat use sampling began on 12 December, and we obtained habitat use data for 11 cutthroat

TABLE 4.—Frequency (percentages of totals in parentheses) of three types of cover observed in sampling areas along transects during three stages of a flow manipulation in the Shoshone River. Proportions do not sum to 100% because cover was not observed at all sampling areas or multiple cover types were observed in a single sampling area. Riffles were not included in the analysis.

Discharge (m^3/s)	Boulders		Deep water		Vegetation	
	Frequency	Adj. residual	Frequency	Adj. residual	Frequency	Adj. residual
Pool						
13.9	6 (0.19)	−0.2	22 (0.69)	−2.5	27 (0.84)	2.7
8.2	5 (0.17)	−0.9	25 (0.86)	−2.2	29 (1.00)	2.9
5.7	8 (0.19)	1.2	41 (0.95)	4.8	1 (0.02)	−5.8
Run						
13.9	143 (0.43)	−0.6	53 (0.16)	−1.8	43 (0.13)	3.4
8.2	136 (0.42)	0.2	58 (0.18)	−0.1	25 (0.08)	−0.5
5.7	121 (0.42)	0.4	60 (0.21)	1.8	12 (0.04)	−3.1
Riffle						
13.9	4 (0.08)		0		0	
8.2	1 (0.03)		0		1 (0.03)	
5.7	2 (0.09)		0		0	

trout and 16 brown trout at all four stages, with 3–7 observations on each individual during each stage. The 12 additional cutthroat trout we implanted with radio tags during the last week of December were observed only during stages 3 and 4. A number of trends were evident in microhabitat use by each species as discharge declined (Figure 4). Cutthroat trout locations had greater minimum depths ($t = -3.74$, df = 41, $P < 0.001$), less vertical relief ($t = 2.61$, df = 41, $P = 0.012$), and higher minimum water velocities ($t = -3.05$, df = 41, $P = 0.005$) as discharge declined, whereas brown trout locations had no discharge-related trends for the three variables. Brown trout locations had lower maximum water velocities ($t = 2.09$, df = 75, $P = 0.04$) and lower water velocity gradients ($t = 2.31$, df = 75, $P = 0.023$) as discharge declined.

Proportional use of pools and runs by cutthroat and brown trout remained similar as discharge declined (Table 5). Chi-square tests revealed no significant differences in the frequencies of pool and run use by either species.

Deep water was the most common cover type at locations of both species (Table 6). Deep-water cover was more common than boulder cover at cutthroat trout locations during all stages of the flow manipulation ($\chi^2 = 7.484$, df = 3, $P = 0.058$). Boulders were found less often, and deep water more often, at brown trout locations as discharge declined ($\chi^2 = 11.434$, df = 3, $P = 0.01$). Vegetation cover was not included in the analysis because both species used this type of cover only rarely.

When cover-use data were analyzed at the mesohabitat scale, we found that both cutthroat trout and brown trout used cover differently in different mesohabitats (Figure 5). When the frequencies of boulder and deep-water cover at locations in pools were compared with those at locations in runs, significant differences were found for both cutthroat trout ($\chi^2 = 101.7$, df = 2, $P < 0.001$) and brown trout ($\chi^2 = 109.1$, df = 2, $P < 0.001$). Both species were more likely to be associated with deep-water cover in pools and with boulder cover in runs.

There were no significant differences between cutthroat trout and brown trout with respect to mean distance from the bank at any discharge. On average, individuals of both species were observed 8 m from the bank throughout the flow manipulation.

Movement

Analysis of movement compared 8 cutthroat trout with 15 brown trout observed during the en- tire flow manipulation. Both species moved frequently throughout the experiment, and both were observed at new locations 60–70% of the time at discharges of 18.1–20.9 m³/s. However, as discharge decreased, so did the fish movement frequency. Less than 50% of observations of both species were made at new locations during the last stage. The trend was significant for cutthroat trout ($F_{1,2} = 35.2$, $P = 0.027$), but not for brown trout. There were no significant differences between the two species with respect to movement frequencies at any stage.

We found no significant difference in mean movement distances of cutthroat trout and brown trout among stages. However, there was substantial variation in distances moved (Table 7). The majority of movements by individuals of both species were less than 50 m in length, but movements greater than 250 m were substantially more common for cutthroat trout than for brown trout (Figure 6). No brown trout movements were greater than 500 m. Aggregate distances moved by individuals appeared to be greater for cutthroat trout than for brown trout. Seven of eight cutthroat trout included in the movement analysis moved more than 300 m from their initial location, whereas only 4 of 15 brown trout did so.

A storm on 18–21 December, when when air temperatures fell to $-27.4°C$, prevented us from monitoring habitat use and movement. The storm coincided with the unscheduled 2.8 m³/s decrease in discharge and a 1.5°C decline in water temperature. Prior to the storm, 19 cutthroat trout were present in the study reach, but only 9 remained following the storm. Of the 10 missing cutthroat trout, seven were found 7–10 km downstream from their initial location. After making the long-distance movements, the seven individuals remained near the same locations for the duration of the study. The other four missing cutthroat trout were not relocated. We observed no downstream movements of brown trout associated with the storm event.

Discussion

The changes in habitat that we observed following decreased discharge, namely, decreased water depths and velocities and the dewatering of riffles, were expected based on previous research (Kraft 1972). The increase in availability of pool habitat and deep-water cover as discharge declined can be explained by the concurrent decreases in water velocities within the study reach, as well as by the methods used to classify habitat features. At high
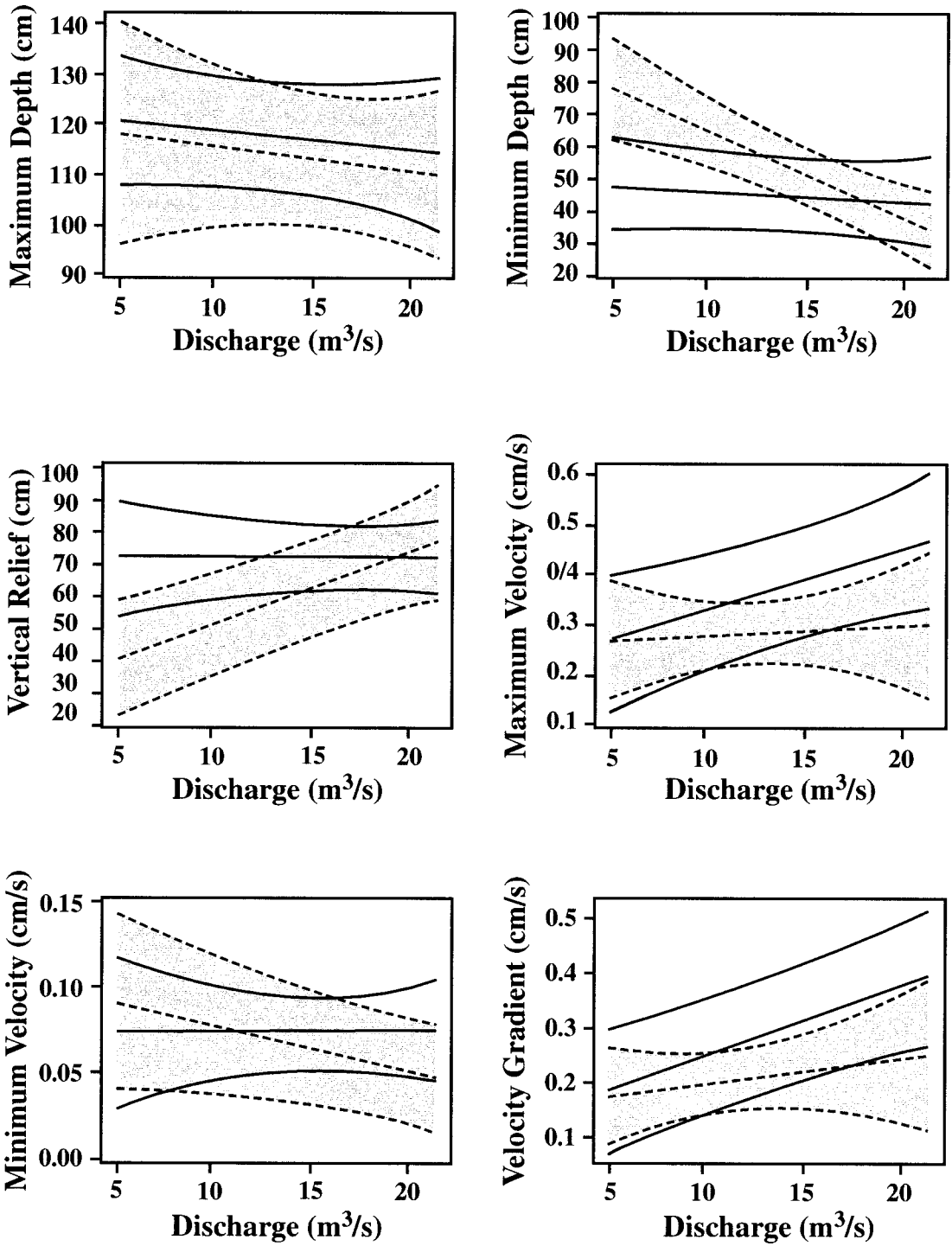
FIGURE 4.—Linear regression lines of Shoshone River cutthroat trout (dashed lines) and brown trout (solid lines) microhabitat use variables versus discharge, with 95% confidence bands.

TABLE 5.—Frequency of observation of cutthroat trout and brown trout in two mesohabitats during four stages of a flow manipulation in the Shoshone River. Neither species was observed in riffle habitat.

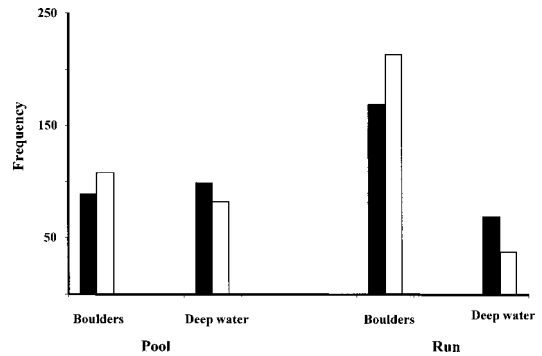| Mesohabitat	Discharge (m^3/s)			
	18.1–20.9	13.9	8.2	5.7
Cutthroat trout				
Pool	24	14	31	32
Run	18	12	26	18
Total	42	26	57	50
Brown trout				
Pool	29	38	35	25
Run	34	22	21	26
Total	63	60	56	51

FIGURE 5.—Frequency of observations (pooled among sites) of deep-water and boulder cover types at cutthroat trout (solid bars) and brown trout (open bars) locations in Shoshone River pool and run habitats.

discharges, deep runs typically had water velocities too high to allow classification of the runs as cover. As discharge declined, water depths in these areas remained greater than 0.75 m and maximum water velocities decreased to less than 0.3 m/s, resulting in an increase in the area classified as deep-water cover.

Our hypothesis that there would be proportionally greater use of pools by both cutthroat trout and brown trout with declining discharge was supported. The hypothesis was based on observations that pools provide a more stable environment for fish during variable discharge conditions (Aadland 1993; Heggenes et al. 1993; Jakober et al. 1998; Simpkins et al. 2000b) and that such stability would attract and concentrate salmonids during winter (Brown and Mackay 1995). All cutthroat trout, and 14 of 16 brown trout, were observed in both pool and run mesohabitats at some time during flow manipulation. However, movements from runs to pools were much more common than movements from pools to runs, indicating that once an individual moved into a pool, it rarely moved out. Although we cannot separate the effects of vari-

able and low discharge onthe use of pools, our results emphasize the importance of pools as winter habitat for salmonids in regulated rivers.

We observed no spatial segregation between cutthroat trout and brown trout. During a preliminary study in 1997–1998, when discharge was relatively high and stable (14.1–14.9 m^3/s), cutthroat trout were consistently found further from structures (e.g., boulders) and the bank than were brown trout, and neither species was concentrated in pools (Dare 2001). Because both species congregated in pools during this study, it appears that when the environment is variable the preference for pools outweighs differences in habitat preference that are evident in a more stable environment.

Both cutthroat and brown trout moved frequently throughout the experiment. The preponderance of short-distance movements by both species indicated that individuals often "cruised" around a pool. Both species were observed at new locations 30–40% of the time during a preliminary study in 1997–1998, when discharge was stable (Dare 2001);

TABLE 6.—Frequency of observation of three types of cover at cutthroat trout and brown trout locations during four stages of a flow manipulation in the Shoshone River. Adjusted residuals are shown in parentheses. Vegetation cover was not included in the analysis.

Cover type	Discharge (m^3/s)			
	18.1–20.9	13.9	8.2	5.7
Cutthroat trout				
Boulders	15 (1.2)	2 (−2.6)	17 (0.0)	18 (0.9)
Deep water	27 (−1.2)	25 (2.6)	43 (0.0)	37 (−0.9)
Vegetation	14	5	5	2
Brown trout				
Boulders	37 (3.3)	21 (−1.4)	18 (−1.4)	20 (−0.6)
Deep water	27 (−3.3)	43 (1.4)	38 (1.4)	34 (0.6)
Vegetation	11	2	0	1

TABLE 7.—Sample size, mean movement distance (m), and range of individual mean movements (m) for cutthroat trout and brown trout at four stages of a flow manipulation in the Shoshone River during winter 1998–1999.

| | | Cutthroat trout | | | Brown trout | |
| | | Grand | Range of | | Grand | Range of |
Stage	N	mean	means	N	mean	means
1	7	369.0	12.3–1,105.0	15	52.3	10.0–251.2
2	5	12.6	6.3–200.0	14	13.1	5.7–32.3
3	7	64.0	5.0–341.7	12	13.8	7.5–20.0
4	5	204.0	5.0–700.0	11	15.5	7.5–36.7

therefore, movement frequency appeared to have been elevated during the flow manipulation. Other researchers have found that salmonids move more frequently when the environment is variable (Erman and Leidy 1975; Brown and Mackay 1995; Simpkins et al. 2000b). However, relatively warm water temperatures stemming from hypolimnetic water releases from Buffalo Bill Dam and inputs from a geothermal spring located upstream of the study reach may have contributed to the increased movement frequency that we observed (Dare et al. 2001).

Our hypothesis that movement distances of cutthroat trout would be greater than that of brown trout was partially supported. The disparity in movement distances was due primarily to long-distance movements by several cutthroat trout, which were associated with a storm event on 18–21 December 1998. During this storm, air temperatures decreased to −27.4°C, water temperatures declined by about 1.5°C, and 7 of 19 cutthroat trout made downstream movements greater than 7 km. Of the 7 individuals, all were located in run habitat prior to movement. No such movements by brown trout were observed. Although the movement distances of cutthroat trout during stages 2 through 4 were not significantly greater than those of brown trout, a greater proportion of cutthroat trout than brown trout was classified as mobile. Moreover, the proportion of mobile cutthroat trout was even higher than the data suggest, because individuals that left the study area before the completion of the flow manipulation were not included in the movement analysis. Cutthroat trout have been characterized as a mobile species (Bernard and Israelsen 1982; Hilderbrand and Kershner 2000); however, movements during winter tend to be restricted (Heggenes et al.
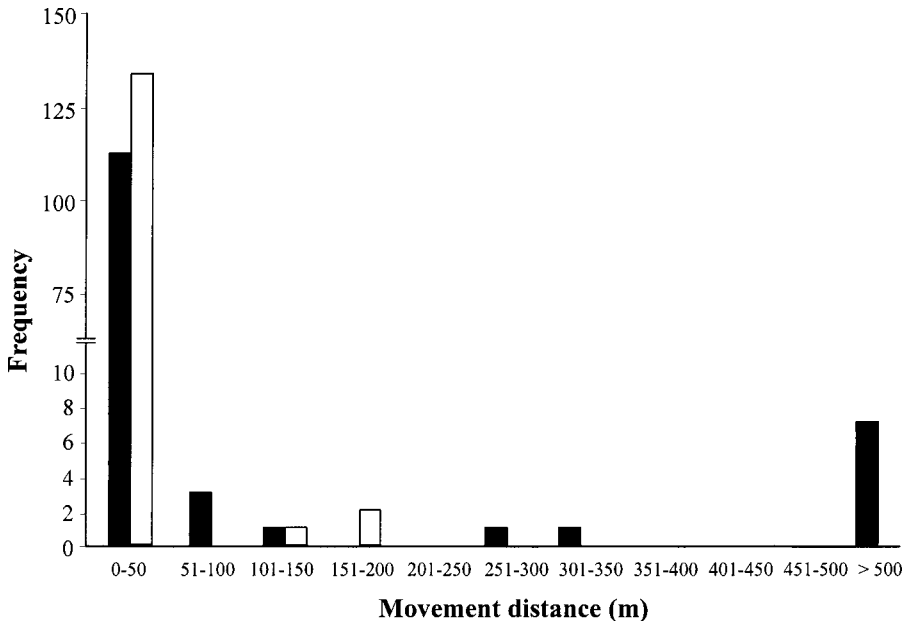

FIGURE 6.—Frequency histogram of distances moved by cutthroat trout (solid bars) and brown trout (open bars) during a four-stage flow manipulation in the Shoshone River.

1991) unless ice-motivated (e.g. Brown and Mackay 1995; Jakober et al. 1998). In fact, Hilderbrand and Kershner (2000) found that although about 30% of the cutthroat trout population in a small stream was mobile during spring, summer, and fall, none of the population was mobile during winter. The greater mobility we observed may be a consequence of the difference between hatchery-reared cutthroat trout and naturalized brown trout (Bachman 1984; Mesa 1991) or of the warmer winter water temperatures in the Shoshone River than in those of other tailwaters in Wyoming (Hebdon 1999) and unregulated rivers.

Although water temperature generally increased as discharge decreased, we do not believe that temperature was a substantial confounding factor in trout habitat use or movement. Cutthroat trout can be more active than brown trout at near-freezing water temperatures (Dwyer and Kramer 1975; Elliot 1976); however, water temperatures were well above freezing throughout the winter. Individuals of both species were observed feeding and there was considerable movement throughout the winter. Given that movement frequency decreased as water temperatures increased, decreased discharge apparently outweighed water temperature as a causal mechanism of the variation in habitat use and movement.

Our study has shown that subadult cutthroat trout and brown trout respond to declining discharge in a similar manner. When discharge was decreasing, both species inhabited deep, slow-flowing water, predominantly in pools. Pool mesohabitat was the type least affected by decreasing discharge, and the use of pools by trout corroborates previous findings that trout select stable habitats during inclement conditions (Heggenes et al. 1991; Brown and Mackay 1995; Simpkins et al. 2000b). Though individuals of both species moved frequently during the experiment, we could not isolate discharge as a cause of downstream movements, which suggests that trout populations in winter may be resilient to short-term decreases in discharge, provided ample pool habitat is available.

The long-distance downstream movements by some cutthroat trout suggest that the cutthroat trout population may be more greatly affected by winter conditions than the brown trout population. Because only one major winter storm occurred during this study, we were unable to determine whether weather was the major cause of the downstream movements that we observed in December. If a substantial proportion of the cutthroat trout population make long-distance downstream movements during storms, this could confound man-agers' efforts to maintain high numbers of cutthroat trout in the section of the Shoshone River that receives the majority of angling pressure throughout the year.

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