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Movement Patterns of Stream-Resident Cutthroat Trout in Beaver Creek, Idaho–Utah

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Abstract.—We used mark–recapture, radiotelemetry, and two-way traps to determine daily, seasonal, and annual movements of cutthroat trout *Oncorhynchus clarki* in Beaver Creek, Idaho–Utah. We recaptured 26 of 167 (16%) passive integrated transponder (PIT)-tagged cutthroat trout; 16 of the fish were recaptured less than 300 m from the point of capture 1 year earlier, whereas 10 fish were recaptured a median of 1,407 m (range 331–3,292 m) from their captured point of the previous year. Radio-tagged individuals moved less frequently and shorter distances (median = 0 m) during autumn and winter, more frequently and farther during spring in association with spawning (median = 576 m), and variably and sporadically during summer (median = 55 m). We found substantial local movements during a diel period that would not have been found using a once weekly observation period. Frequency of cutthroat trout movement through two-way traps was greatest in July and early August and had stopped almost entirely by early September. Movement timing and frequency were similar between the traps and the radio-tagged fish. Our results demonstrate the mobility potential of cutthroat trout and the importance of selecting appropriate spatial and temporal scales of observation when studying their ecology.

Until recently, many scientists regarded trout as sedentary following Gerking's (1959) idea of restricted movement in stream fishes, termed the restricted movement paradigm (RMP) by Gowan et al. (1994). Heggenes et al. (1991) reported almost 50% of cutthroat trout *Oncorhynchus clarki* in their study reach moved less than 3 m from the original point of capture between spring and fall, and only about 18% moved more than 50 m. Similar results have been reported for brook trout *Salvelinus fontinalis* (Shetter 1968), brown trout *Salmo trutta* (Stefanich 1952; Shetter 1968 Bachman 1984; Heggenes 1988), and cutthroat trout (Fleener 1951; Miller 1957).

However, evidence also exists for wide-ranging movements by trout. A large percentage of marked cutthroat and rainbow trout *Oncorhynchus mykiss* and bull trout *Salvelinus confluentus* in the Salmon River, Idaho, moved more than 8 km over several months (Bjornn and Mallet 1964); many moved 40 km or more. Similar results have also been reported for cutthroat (Bernard and Israelsen 1982; Young 1996; Harvey 1998), brook (Riley et al. 1992; Gowan and Fausch 1996a, 1996b), brown (Clapp et al. 1990; Meyers et al. 1992; Young 1994), and rainbow trout (Young et al. 1997a), indicating a widespread pattern across stream-dwelling salmonids.

Accumulating evidence on trout mobility prompted a reexamination and challenge of the RMP by Gowan et al. (1994), who called for a revision of current views. Data in the studies used to support or refute RMP are often similar but are interpreted in different ways. Concluding that salmonids are either mobile or sedentary is misleading because populations may be composed of both mobile and sedentary individuals. Most individual trout in mark–recapture experiments typically remain near the point of capture, but examination of several published papers (Heggenes 1988; Heggenes et al. 1991; Gowan and Fausch 1996a) revealed that a variable percentage (>20%) disperses. Individual fish may also switch between behaviors, exhibiting discrete seasonal or annual periods of site fidelity and punctuated by bouts of movement (Harcup et al. 1984; Brown and Mackay 1995). Identifying and describing the scales and magnitudes of fish movements may be important in the management and ecology of stream-dwelling salmonids.

We monitored cutthroat trout movements, because although information has been accumulating in the last decade on salmonid movements with the advent of radiotelemetry, relatively little exists for cutthroat trout (Brown and Mackay 1995; Young 1996; Jakober et al. 1998). The difficulty and expense of acquiring information on cutthroat trout movements throughout winter has resulted in small sample sizes and little information: infor-

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mation that may be important for developing conservation and recovery plans for the various subspecies. Therefore, our first objective was to determine movements of cutthroat trout on annual, seasonal, and diel scales. Our second and final objective was to compare the timing, frequency, and directions of fish movements determined by radiotelemetry and with two-way traps sampling the general population.

Methods

Study area.—Beaver Creek is a first-order stream in the Bear River Drainage, southeast Idaho, that originates at 2,400 m elevation. It flows south for approximately 10 km before crossing into Utah and continues another 9 km before entering the Logan River. No migration barriers are present in Beaver Creek, and the first migration barrier a fish would encounter is a dam (Third Dam) located approximately 20 km down the Logan River from the mouth of Beaver Creek. Consequently, about 60 km of connected stream are available to fish. Beaver Creek contains self-sustaining populations of stream-resident Bonneville cutthroat trout *O. c. utah* and brook trout, the only species present. Densities are relatively high, averaging more than 0.1 trout/m^2. The study location resides in the uppermost 6 km of stream occupied by trout (Figure 1). This area is entirely national forest with minor recreational and cattle-grazing impacts. Climatic conditions at this altitude can be harsh, with anchor ice and over 2 m of snow cover in winter, overbank flows during the annual spring runoff, and low summer flow from droughts, but the stream remains perennial with stable groundwater-driven base flows. Habitat conditions include high gradient reaches (>3%) with step pools under a forest canopy of lodgepole pine *Pinus contorta* and Douglas fir *Pseudotsuga menziesii*, low gradient reaches (<1.5%) that meander through grassy meadows, and beaver ponds with dams constructed primarily of willow *Salix* spp.

Fish capture and marking.—We captured cutthroat trout by electrofishing and surgically implanted 25 fish (>200 mm total length) over three seasons with 2.3-g (wet weight), 40-MHz radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) with internal antennas using methods following Young (1995). Fish were held overnight so their condition could be checked after surgery, then released at or near their point of capture into one of three different habitat types: (1) high gradient (>3% slope), (2) low-gradient meadow (<1.5% slope), or (3) beaver pond. However, three individuals each during summer and autumn escaped from the holding area and were not returned to their area of capture. Because these stream-resident fish were relatively small (<200 g), we used small transmitters that had a relatively short battery life (≈90 d). Because we were interested in annual movements, we implanted fish during different seasons: eight trout released July 12, 1995 (summer); eight released August 31, 1995 (autumn); and nine released December 1, 1995 (winter and spring; Table 1). For fish released in the winter, we used transmitters with pulse rates lowered from 45 to 30 pulses/min. This reduction extended the battery life from about 90 d to more than 190 d and allowed us to follow the same fish through winter and spring 1996; one individual could not be located after April 1995. Fish were located weekly except when harsh weather and logistical complications allowed only monthly tracking during winter and early spring and prohibited travel to the site during May. Fish were located to within 2 m by triangulation with a directional loop antenna, and we recorded location and habitat type for each fish. The universal transverse meridian (UTM) coordinates of each fish were determined by using a 10-min averaging session with a global positioning system (GPS; Garmin GPS 100 SRVY, field-determined accuracy <75 m), and distances moved were later calculated using a 1:100,000-scale digital stream layer in ARC/INFO, a geographic information system software program. On September 7, 1995, we located 11 fish (six summer-released fish and five autumn fish) hourly for 24 h to determine daily activity patterns. This date was chosen to include the 2-week overlap between summer and autumn radio-tagged fish. Distances moved during this period were determined with a measuring tape. For both the seasonal and diel samples, we defined home range following Young (1998) as the distance between the most upstream and most downstream positions, whereas the total distance moved was calculated by summing all distances moved by an individual.

In 1995, we used two-way traps to monitor the magnitude, timing, and direction of trout movements and to corroborate and validate the radiotelemetry data. In early July we installed three traps at roughly 2.5-km intervals in the stream (Figure 1). Trap construction was based on Riley et al. (1992) with a mesh diameter of 13 mm. These traps effectively captured and retained individuals greater than 120 mm, although a few smaller individuals were observed escaping. Traps were

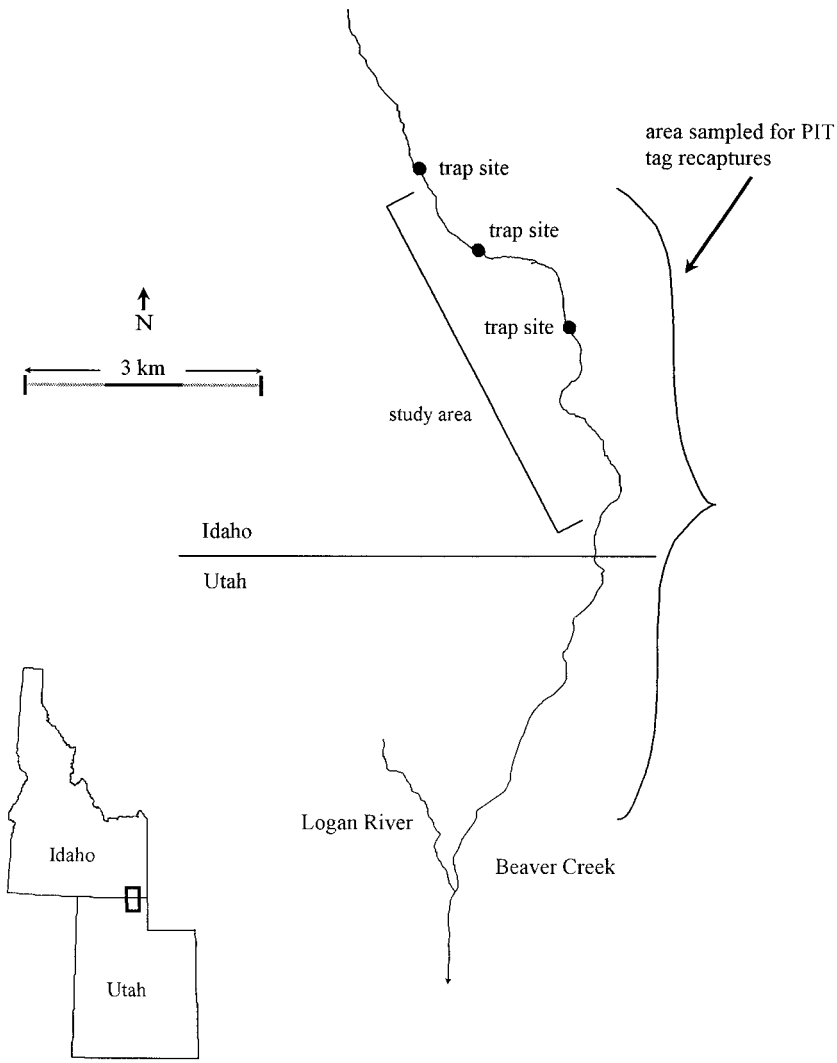

FIGURE 1.—Location of the study area, the area sampled for PIT tag recaptures, and two-way traps on Beaver Creek, Idaho–Utah.

checked daily from early July through mid-November until maximum daily water temperatures fell below 2°C and ice formation limited trap function. All captured fish were implanted with 11-mm passive integrated transponder (PIT) tags, each with a unique identity code, and released at or near their point of capture in the direction they were traveling. Additional fish from the general population were captured by electrofishing and by hook and line throughout a 5-km reach to provide a sample of tagged fish for all three major habitat types. Locations of tagged fish and the traps (UTM

TABLE 1.—Characteristics of cutthroat trout implanted with radio transmitters in Beaver Creek in 1995 and 1996.

		Length (mm)		Weight (g)		Transmitter : fish weight ratio	
Season	*N*	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Summer	8	236 (12)	218–256	127 (28)	109–152	0.018 (0.004)	0.013–0.024
Autumn	8	242 (14)	222–261	135 (17)	93–181	0.017 (0.002)	0.015–0.021
Winter–spring	9	254 (16)	225–281	164 (34)	123–238	0.014 (0.003)	0.010–0.019

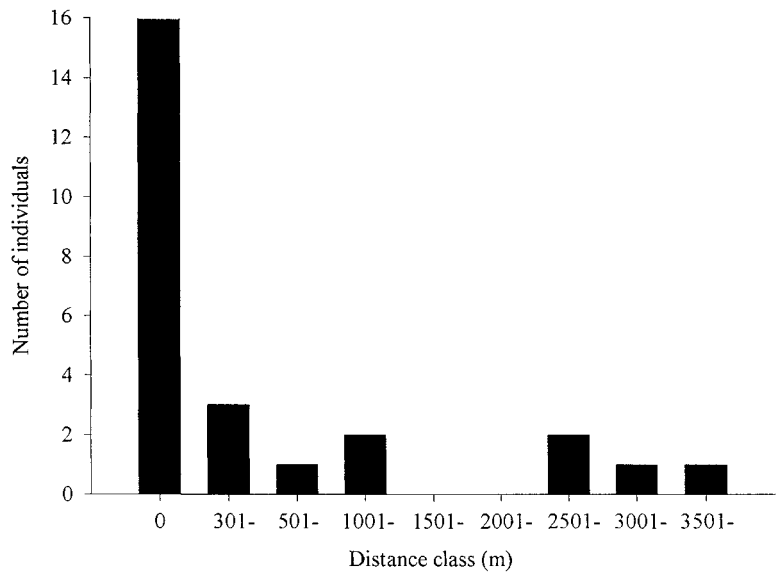

FIGURE 2.—Distribution of distances moved by PIT-tagged cutthroat trout captured over 12 km of stream 1 year after marking and release.

coordinates) were determined using a GPS. We PIT-tagged and released 200 trout (167 cutthroat and 32 brook) during the summer of 1995. During summer 1996, we intensively electrofished a 7-km reach encompassing the area of all PIT tag releases and less intensively sampled an additional 6 km adjacent to the study area to recapture tagged fish. Recaptured fish locations were determined with a GPS, and distances from original capture location were calculated using ARC/INFO. Fish recaptured more than 300 m from their release point were considered mobile, whereas those within 300 m were considered sedentary.

Data analysis.—We examined seasonal differences in movements of radio-tagged cutthroat trout using the Kruskal–Wallis test, but because of a perceived capture effect on movements for fish implanted with radio transmitters during summer, we excluded the first 10 d of movements from the analysis. This test was used instead of its parametric counterpart because of low sample sizes and nonormal distributions of distances moved and was done by performing a one-way analysis of variance (ANOVA) on ranked data with Tukey's multiple contrast test for post hoc comparisons between seasons. We used Spearman rank correlation to examine the relationship between diel movement distances and total distances moved during a season. To determine whether fish movements were different from random dispersal, we compared the distances moved by PIT-tagged fish against a Poisson distribution for random dispersion using the chi-square goodness-of-fit test. Movement of PIT-tagged fish in relation to habitat was tested using the chi-square test. We determined the effect of fish length on tendency to move using logistic regression, the relationship between fish length and distance moved using Spearman rank correlation, and the relationship between fish length and timing of movement using Spearman rank correlation. Finally, the directions of fish movements through traps were examined using the chi-square test. All analyses were conducted using the Statistical Analysis System (SAS 1988) and were considered significant at P less than 0.05.

Results

Annual Movements—PIT Tag Recaptures

We recaptured 26 of 167 (15.5%) PIT-tagged cutthroat trout 1 year after their release and compared movements. Ten of the 26 recaptures were more than 300 m away from their release point (Figure 2). Distances moved by these 10 mobile fish ranged from 331 to 3292 m (median = 1,407 m). The distribution of distances moved was significantly different from a Poisson distribution (chi-square: $\chi^2 = 89.7$, $n = 26$, df, $P < 0.001$), indicating a highly nonrandom dispersion pattern. More individuals than expected occurred on both tails of the distribution, either remaining sedentary or moving long distances. In addition, no reach

TABLE 2.—Seasonal distances moved and home ranges for radio-tagged cutthroat trout. Note that movements during the first 10 d of the summer group were excluded because of a perceived capture effect, and we had one less fish in spring than winter because of our inability to locate one individual during spring.[a]

	Summer	Autumn	Winter	Spring
Sample size	8	8	9	8
Number of fish moving (%)	4 (50)	2 (25)	3 (33)	7 (88)
Median distance moved (range) (m)	55 (0–708) ab	0 (0–715) a	0 (0–188) a	577 (0–5,149) b
Median home range size (range) (m)	55 (0–708) ab	0 (0–715) a	0 (0–188) a	274 (0–5,149) b

[a] For comparisons between seasons for total distances moved and for home ranges, values followed by the same letter were not significantly different based on Tukey's multiple comparison test after performing a Kruskal–Wallis test.

type appeared more preferable to fish over the others; the proportions of each mobility component were similar among habitats (chi-square exact test; $\chi^2 = 2.14$, $n = 26$, 2 = df, $P = 0.40$). Length of fish prior to movement was associated with neither the tendency to move (logistic regression; Wald $\chi^2 = 0.36$, $n = 26$, 1 = df, $P = 0.55$) nor the distance moved (Spearman rank correlation: $r_s = 0.25$, $n = 26$, $P = 0.20$). None of the results changed when the criterion for movement was reduced from 300 to 100 m from the initial point of capture.

Seasonal Movements—Radiotelemetry

Substantial differences in movements existed among seasons for radio-tagged cutthroat trout (Kruskal–Wallis: $F = 4.95$, 3, 29 = df; $P = 0.007$; Table 2). Tukey's multiple comparisons identified significantly greater total distances moved during spring than during either autumn or winter. In contrast, distances moved were not significantly different between summer- and spring-tagged fish, or between radio-tagged fish in summer, autumn, or winter. Seasonal home ranges followed a pattern identical to total distances moved (Kruskal–Wallis; $F = 3.90$; 3,29 = df; $P = 0.018$), owing largely to individuals moving in either upstream or downstream directions and not changing course during a season. The multiple comparisons test for home range sizes were significantly larger during spring than during autumn or winter but did not differ in other comparisons between seasons.

Only two of the eight individuals tagged and tracked during autumn moved (Table 2; median = 0 m, range 0–715 m), whereas the remaining six cutthroat were stationary during the entire period. Each of these mobile fish moved during a different 1–2 d period in early September, after which they too remained stationary. No movements were observed as water temperatures decreased from a maximum daily average of 11°C in September to 6°C in October and to 1°C by early November. Similarly, no movements occurred after minimum daily water temperatures fell below 7°C.

Radio-tagged individuals released in winter moved little between December and April (Table 2; median = 0 m, range 0–188 m). Three individuals each made one-time, downstream movements of less than 200 m, whereas the remaining six individuals did not move (Figure 3).

In contrast to the site fidelity exhibited in winter, movements of the same individuals increased substantially during spring (Figure 3). Seven of eight fish (one fish could not be found after April) moved between April and June: three individuals moved downstream, three upstream, and a single individual moved almost 300 m downstream only to return to its original location 2 weeks later in late June (Figure 3). Median distance moved during spring was 577 m (Table 2; range 0–5149 m), and median home range size was 274 m (Table 2; range 0–5149 m). We attribute the increase in movements to spawning, as many cutthroat trout (including two radio-tagged individuals) were observed performing behaviors related to spawning throughout June.

During summer, seven of eight fish moved immediately after release but established a stationary pattern until the end of the monitoring period in mid-September. Median distance moved was 425 m (range 0–2188 m), but only four fish moved after the first week (Figure 3). If we assume these initial movements were probably due to a capture effect (Figure 3) and ignore the first week, median distance decreased to 55 m (Table 2; range 0–708 m), and home ranges were the same as total distances move (Table 2).

The area where radio-tagged fish were released did not appear to influence movement. Three individuals escaped from our postsurgery holding cage during both the summer and autumn radio-tagging periods. Movements of these individuals, introduced into foreign areas, did not appear different from those fish released at or near their point of capture. Similarly, beaver dams did not appear to limit fish movement, as individuals appeared to traverse them both upstream and downstream.

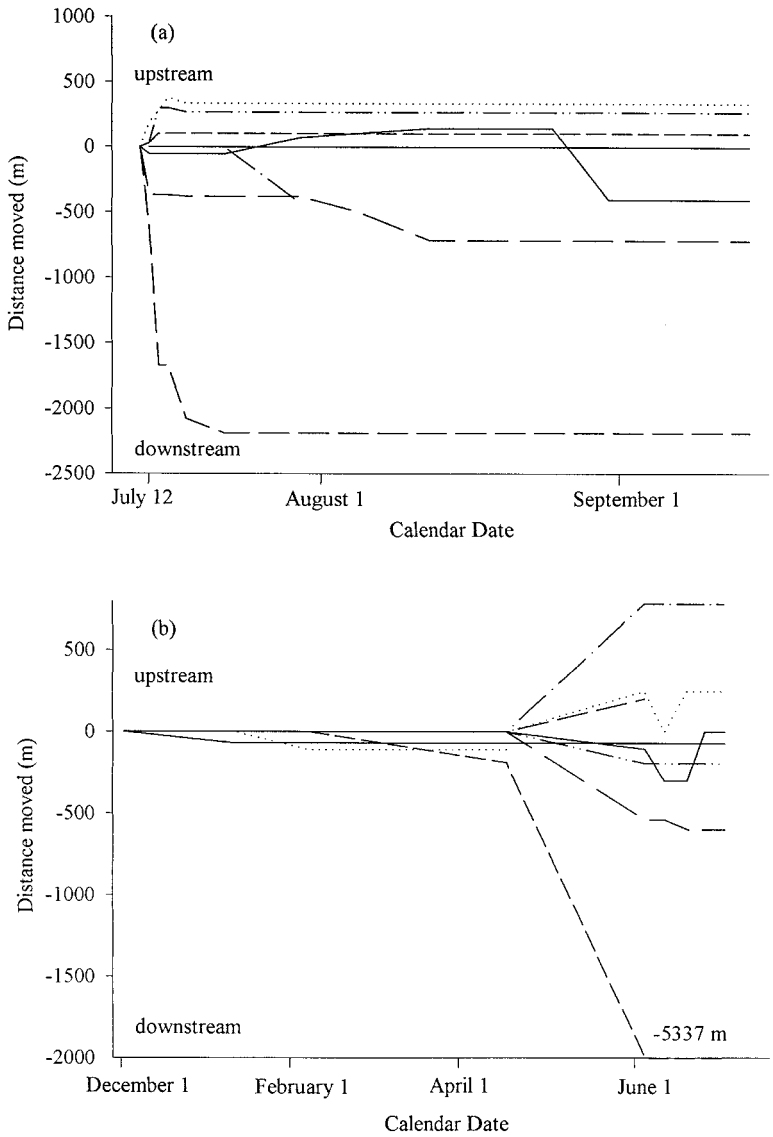

FIGURE 3.—Distances moved by calendar date for radio-tagged cutthroat trout followed from **(a)** July 1995 to early September 1995 and **(b)** December 1995 to June 1996. Values on the *y*-axis indicate distances moved upstream (positive values) and downstream (negative values). Note that the first 10 d of movements for summer 1995 were due to a capture effect.

Diel Movements—Radiotelemetry

Although summer fish appeared mostly stationary after week 1, diel observations on September 7, 1995, showed that substantial movements occurred locally during a 24-h period. All six of the summer-tagged fish and one of the five autumn-tagged fish monitored during the diel sample moved at least twice (range 2–13 movements; mean = 6 movements per fish) and movements ranged from 6 to 121 m (median = 36 m). In contrast, none of these same individuals would have been found to move if only the weekly observation for seasonal movements for that week was used (Figure 4). Total distances moved during the diel period ranged from 0 to 259 m (median = 39 m) with home ranges between 0 and 60 m (median = 13 m; Figure 4). Most of the mobile fish appeared to use separate areas between daylight and dark, with individuals moving into areas of low current velocity at night and moving into

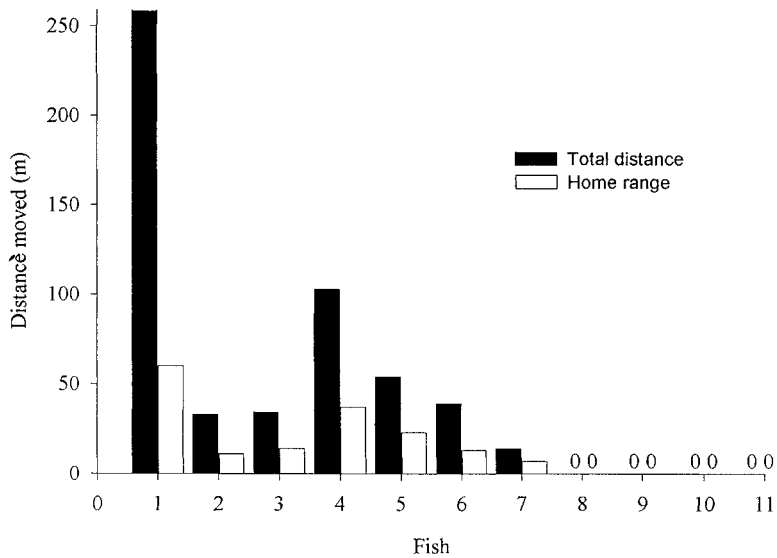

FIGURE 4.—Total distances moved and home ranges for 11 radio-tagged cutthroat trout located hourly during diel observations on September 7, 1995.

higher velocity areas during daylight to feed. Movement frequency was highest near dawn (0500 hours) and dusk (2100 hours), slightly lower during daylight and lowest during darkness. There was a positive relationship between total distances moved during a season (adjusting for the capture effect in summer) and distances moved during the diel period (Spearman rank correlation; $r_s = 0.86$, $n = 11$, $P < 0.001$). This relationship remained significant when only mobile fish were examined (Spearman rank correlation; $r_s = 0.90$, $n = 5$, $P = 0.037$).

Comparison of Trap Captures with Radiotelemetry

Movement patterns of fish radio-tagged in summer and autumn were generally comparable with those observed from two-way traps. We captured 45 cutthroat trout and 27 brook trout in the lower two traps between July 9 and November 7. No fish were captured in the most upstream trap, sited approximately 200 m above the uppermost limits of fish distribution to detect upstream movements beyond the present distribution limits. Most cutthroat trout moved through traps during mid-July, and fewer moved after mid-August (Figure 5), similar to the pattern observed for radio-tagged trout. Four times as many cutthroat trout were trapped moving upstream as downstream during July and August (chi-square; $\chi^2 = 18.7$, $n = 45$, 1 = df, $P < 0.001$). This upstream trend held for both small (<150 mm total length [TL], $n = 17$) and large (>150 mm TL, $n = 28$) cutthroat trout, and no relationship existed between size of individual and date of movement (Spearman rank correlation; $r_s = -0.04$, $n = 45$, $P = 0.77$). There were no apparent directional trends in movements of radio-tagged fish (Figure 3).

Brook trout captured in weirs exhibited a summer movement pattern similar to cutthroat trout (Figure 5). Three times as many brook trout were captured moving upstream than downstream (chi-square; $\chi^2 = 4.0$, $n = 16$, 1 = df, $P = 0.046$) during July and early August. Movements ceased between mid-August and late September but resumed during autumn with the onset of spawning. Movement direction reversed in autumn compared to summer with six times as many brook trout moving downstream as upstream (chi-square; $\chi^2 = 7.1$, $n = 13$, 1 = df, $P = 0.008$).

Discussion

Recaptures of PIT-tagged cutthroat trout in Beaver Creek indicated that most (61%) individuals exhibited site fidelity, whereas fewer (39%) were mobile, similar to patterns exhibited by brook (Gowan and Fausch 1996a), brown (Heggenes 1988), and coastal cutthroat trout *O.c. clarki* (Heggenes et al. 1991). Although most fish were sedentary, movements made by ''mobile'' fish were for relatively long distances. Mobility could enable organisms to track changes in environmental

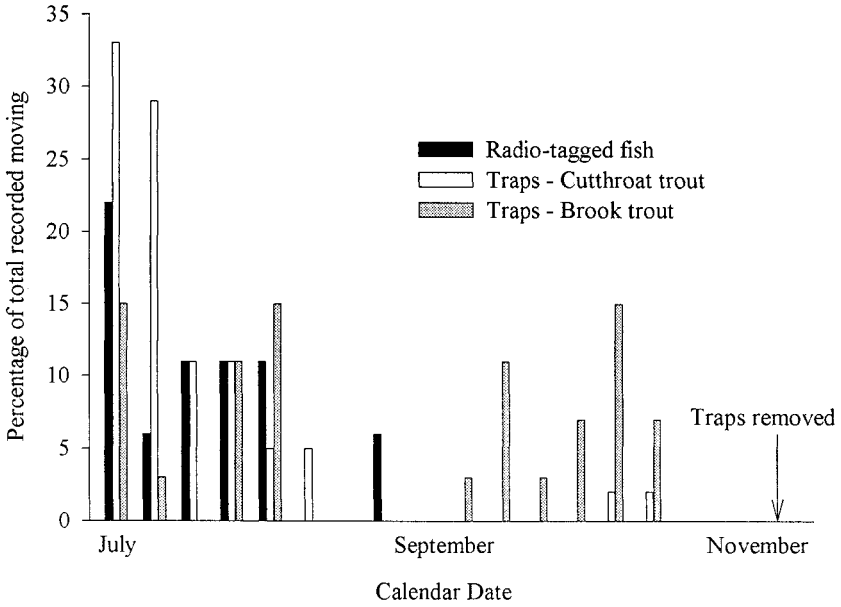

FIGURE 5.—Comparison of the timing and frequency of fish movements by week during the period July–November 1995. The percentage of radio-tagged fish moving during a week relative to the total number of recorded movements are represented by dark bars. The open (cutthroat trout) and grey (brook trout) bars represent the percentage of fish captured each week relative to the total captured for each species in the two-way traps. Values are based on 65 radiotelemetry observations and 45 cutthroat trout and 27 brook trout captured in the two-way traps.

conditions and take advantage of resources that are patchily distributed in space or time, but both behaviors (mobility and site fidelity) may be expressed because of environmental fluctuations and changing local conditions. Mobility would be favored during periods of uncertainty or predictable events, such as anchor ice formation (Brown and Mackay 1995) or seasonal dewatering (Erman and Leidy 1975; Bernard and Israelsen 1982), whereas site fidelity may be advantageous under more stable conditions (Jenkins 1969). Additionally, mobility results in a source of individuals to disperse into habitats that are created or become vacant (Heggenes et al. 1991).

The degree of mobility in individuals appears flexible within stream-resident salmonids. Several radio-tagged individuals exhibited both mobile and sedentary behaviors within and between seasons, a behavior Harcup et al. (1984) termed ''switching'' when encountering similar behavioral patterns in brown trout. This pattern was also found in cutthroat trout in the Ram River, Alberta, where individuals were sedentary most of the time but would move fairly long distances over short time periods before settling once more into a stationary pattern (Brown and Mackay 1995). Our results demonstrate that descriptions based solely on the autumn observations would incorrectly classify the Beaver Creek population as sedentary, whereas observations during spring would overemphasize mobility due to movements associated with spawning. Although both of these descriptions are correct within short time spans, neither is complete. Just as the dichotomy of mobile versus sedentary is a misleading descriptor of a population, the temporal scale of observation must be of sufficient length to determine movements throughout the year. Frequency of observations also appears to be important, as we found a large amount of movement during diel observations despite fish exhibiting sedentary patterns based on weekly observations. This alteration is exemplified by several cutthroat trout that were recorded during the diel observations to spend the night in low-velocity areas of beaver ponds, move into areas of the faster water of riffles to feed during daylight, and return back to beaver ponds again at night, similar to behaviors exhibited by California golden trout *O. m. aquabonita* (Matthews 1996). Similarly, Young et al. (1997a) reported a brown trout to remain in the same daytime position for 8 months based on weekly observations, but during three diel sampling periods, it had a home of more than 30 m. Although several individuals switched be-

tween sedentary and mobile behaviors, the positive relationship we found between total seasonal distances moved and distances moved during diel observations suggests a linkage in an individual's movement behaviors. Even during sedentary periods, diel home ranges of the more mobile individuals were greater than those of the more sedentary individuals. Although our data are limited, this may be a profitable area for future research, as the correlation was strong.

Despite directional temperature-related autumn movements in Yellowstone cutthroat trout *O. c. bouvieri* (Griffith and Smith 1993) and westslope cutthroat trout *O. c. lewisi* (Brown and Mackay 1995; Jakober et al. 1998), we found no late-season movements of either radio-tagged individuals or of brook or cutthroat trout through traps, even as maximum daily water temperatures declined from 14°C to less than 1°C (minimum water temperatures from 9°C down to 0°C) when traps were pulled in November, similar to patterns found for Colorado River cutthroat trout *O. c. pleuriticus* (Young 1998). Westslope cutthroat trout exhibited a two-stage migration for cutthroat trout during which individuals first moved to pools with submersed cover and later into areas with groundwater inputs or pools without anchor ice (Brown and Mackay 1995), whereas Chisholm et al. (1987) found that brook trout in high-elevation streams moved to deep, low-velocity areas in low-gradient reaches. It is possible that the low-gradient reaches near beaver ponds where our traps were located, and where the autumn radio-tagged individuals were released, contained sufficient habitat to eliminate the need for fish to migrate.

The similarity in frequency and timing of movements between movement data that we obtained through radiotelemetry and two-way traps suggests that the radio-tagged fish provided a representative sample despite the relatively small sample size. Cutthroat trout movements were most frequent during July, when flows were still elevated from spring runoff, and gradually tapered off until movement virtually ceased by early September. Colorado River cutthroat trout exhibited a similar pattern (Young 1996) and also demonstrated no discernible directional trends for radio-tagged fish (Young 1996; Young et al. 1997b). However, we did find an upstream trend for both brook and cutthroat trout caught in the two-way traps that was similar to movement patterns of brook trout in two Colorado streams, as well as similarity in movement peaks during runoff and again in mid-September when brook trout began spawning (Gowan and Fausch 1996a).

Our determination of mobility using PIT tags was based on just one sample with no additional information about individual movements during that period. Although a potential problem, numerous studies have shown that individuals exhibiting site fidelity can be found repeatedly in proximity to the same location for one or more years (Miller 1957; Bachman 1984; Heggenes 1988). However, we cannot distinguish between stationary and truly mobile individuals who left and later returned to their point of initial capture during the year. One solution would be repeated sampling over the 12 km of stream, but repeated sampling could bias results because of increased mortality and injury associated with repeated electrofishing (Habera et al. 1996; Kocovsky et al. 1997). Another concern is whether some sedentary individuals were in fact sedentary or had ejected their radio transmitters. We cannot answer definitively for every fish, but several individuals exhibiting no movements were captured by electrofishing prior to battery failure and these individuals still retained their transmitters. However, we were unable to assess transmitter loss for individuals followed during autumn because the onset of winter made electrofishing impractical. We have assumed throughout that all fish retained their transmitters and believe that this probably correct.

Although trout are often classified as mobile or sedentary, our results demonstrate the incompleteness of this descriptor because individual trout may switch seasonally between behaviors. Also, apparently sedentary individuals may exhibit frequent diel movements. Because of this variability, we should consider all population behaviors when addressing issues concerning the ecology of stream-resident cutthroat trout.

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