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[Article]

Population-Scale Movement of Coastal Cutthroat Trout in a Naturally Isolated Stream Network

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Abstract.—To identify population-scale patterns of movement, coastal cutthroat trout *Oncorhynchus clarkii clarkii* tagged and marked (35 radio-tagged, 749 passive integrated transponder [PIT]-tagged, and 3,025 fin-clipped) were monitored from June 1999 to August 2000. The study watershed, located in western Oregon, was above a natural barrier to upstream movement. Emigration out of the watershed was estimated with a rotating fish trap. Approximately 70% of recaptured coastal cutthroat trout with PIT tags and 86% of those with radio tags moved predominantly at the channel-unit scale (2–95 m); fewer tagged fish moved at the reach scale (66–734 m) and segment scale (229–3,479 m). In general, movement was greatest in April as spawning peaked and lowest in October, when discharge was at its lowest. Only 63 (<1% of tagged and marked fish) coastal cutthroat trout were captured in the fish trap. Trap efficiency was about 33%, and the expanded estimate of emigrants between February and June was 173 fish. These results suggest that unit-scale movement is common throughout the year and that reach- and segment-scale movements are important during the winter and spring. Although movement in headwater streams is most common at the channel-unit scale, restoration of individual channel units of stream may not benefit the population at the watershed scale unless these activities are undertaken in the context of the greater whole. Individual coastal cutthroat trout move great distances, even within the small watersheds in the Oregon Coast Range, and although these movements may be infrequent, they may contribute substantially to recolonization after stochastic extirpation events (e.g., landslides and debris flows). Management strategies that focus on maintaining and restoring connectivity in a watershed represent an important step toward protecting the evolutionary capacity of stream salmonids.

Most animals have the ability to move when local environmental conditions are not compatible with their requirements for survival, growth, and reproduction (Warren and Liss 1980). This behavioral adaptation is expressed in most fish species, and salmonids, in particular, display movements that range from the local scale (e.g., microhabitats in streams and lakes) to the landscape scale (e.g., reproductive migrations that extend thousands of kilometers; Northcote 1992). Information on the migratory behavior of diadromous (movement between freshwater and marine systems; Myers 1949; McDowall 1987; Northcote 1992) and potamodromous fishes (movements exclusively in freshwater; Varley and Gresswell 1988; Gresswell 1997; Northcote 1997) is abundant. In headwater streams and some lakes, however, salmonids may not exhibit true migrations, and the extent of movement is less well documented in these areas (Northcote 1992, 1997).

Migratory behavior and the environmental factors that influence this behavior are discussed in many papers concerning the movement of salmonid fishes (e.g., Northcote 1992; Gresswell et al. 1997; Schmetterling 2001). Migration is movement that alternates between two (or more) usually well-separated habitats, occurs with regular periodicity (often seasonal), includes a large proportion of the population, and is directed rather than random wandering or passive drift (Northcote 1978). In contrast, nonmigratory movement occurs at frequent intervals (hours–days), and although it may also be directed, it generally encompasses smaller spatial scales (10–100 m). Indeed, Northcote (1978) referred to movement at frequent intervals and at small spatial scales as "micromigrations." This type of movement generally occurs in relation to food and shelter. At any point in time, a substantial number of fish may be involved in nonmigratory movements, but synchrony among individuals is not required.

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Research examining the relationship between nonmigratory movement and habitat use has not received much emphasis, and information on the extent and frequency of movement in headwater stream networks is especially limited. Studies have generally been conducted on individual sections of stream. Even when the scale of a study is extended to a watershed, the number of study sections is low (usually less than five), and maximum lengths of sample sections rarely exceed 500 m (Gowan et al. 1994). Inference is limited by the duration of the study (generally less than 6 months) and the number of fish sampled (generally less than 100 individuals). Furthermore, infrequent sampling may fail to detect substantial changes in location (Gowan et al. 1994).

A thorough understanding of movement in a stream network is crucial for the management of salmonids and the watersheds in which they exist. Efforts to understand relationships between fish abundance and habitat variables can be significantly compromised if movement patterns are not evaluated and incorporated into study designs (Kocik and Ferreri 1998). Furthermore, habitat fragmentation and the loss of connectivity among habitat patches are major issues in the conservation of native fishes (Rieman et al. 1997). Although the negative effects of large dams on the anadromous migrations of salmon and trout *Oncorhynchus* spp. have been documented, the influence of natural and artificial barriers to movement on salmonid persistence in headwater streams has not been assessed directly. Furthermore, little is known about the influence of land management activities (e.g., timber harvest, livestock grazing, mining, and associated road construction and maintenance) on movement and distribution patterns of salmonids in headwater systems.

These issues are especially relevant for salmonids that live in headwater streams above barriers to upstream migration. In such systems, fishes are directly linked to the freshwater habitat and surrounding catchment throughout their lives. This relationship is affected by the extent and frequency of movement in the watershed and the interactions among movement, physical habitat, and life stage of an individual fish. Sometimes downstream migration of individuals from these isolated watersheds may contribute demographically and genetically to below-barrier populations; however, the magnitude of this movement is poorly documented (Johnson et al. 1999).

The purpose of this study is to examine the seasonal distribution patterns of coastal cutthroat trout *O. clarkii clarkii* throughout an isolated headwater stream of the Oregon Coast Range. By examining movement at the population scale, we sought to (1) contrast movement of coastal cutthroat trout at four spatial scales (channel unit, reach, segment, and watershed) and at four temporal scales (day, week, month, and study period); (2) evaluate seasonal influences of water temperature and discharge on distribution; and (3) determine the effect of fish size and channel-unit characteristics on movement. To address these objectives, the distribution of more than 6,000 coastal cutthroat trout was assessed in a small watershed isolated above a barrier to anadromous salmonids, and the locations of tagged and marked fish were monitored throughout the watershed for 14 months.

Methods

Study area.—The study was conducted in Camp Creek, a stream that flows west through the Oregon Coast Range for 20 km before joining Mill Creek, a tributary to the Umpqua River. Sampling occurred above a 4-m-high waterfall that is approximately 13 km upstream from the confluence of Camp and Mill creeks. The main stem of Camp Creek extends 7 km above the barrier, and there are four fish-bearing perennial tributaries with a cumulative length of approximately 3 km (Figure 1). In addition, several small ephemeral tributaries flow during periods of high discharge in winter months. The drainage area is approximately 1,500 ha.

The study area is characterized by steep canyons of sedimentary rock (Bateman Formation) and a bedrock-dominated stream channel (BLM 1995). Elevation ranges from approximately 170 m (above mean sea level [AMSL]) at the barrier waterfall to 370 m AMSL at the upper end of the main stem of Camp Creek. Culverts that completely block upstream fish movement (Wofford et al. 2005) are located on two perennial tributaries (tributaries 1 and 4; Figure 1). An examination of historical aerial photographs indicated that the culverts were installed in the mid to late 1950s. A 2-m-high waterfall in tributary 4 is also a complete barrier to upstream movement, but a 30-m-long bedrock cascade with a 15% slope on the main stem (boundary between segment 2 and segment 3) apparently only inhibits movement intermittently (Wofford et al. 2005).

Precipitation is primarily rainfall from November through March and averages 100–160 cm annually (BLM 1995). Higher stream discharge (>1 m^3/s) is associated with storms from November through March, and discharge (to 0.05 m^3/s) is lower from June through October. Fifty-year average (1951–2001) maximum and minimum air temperatures are 9.4°C and 2.2°C, respectively, for January and 28.8°C and 10.7°C, respectively, for July (Western Regional Climate Center 2001).

Vegetation in the watershed consists primarily of red

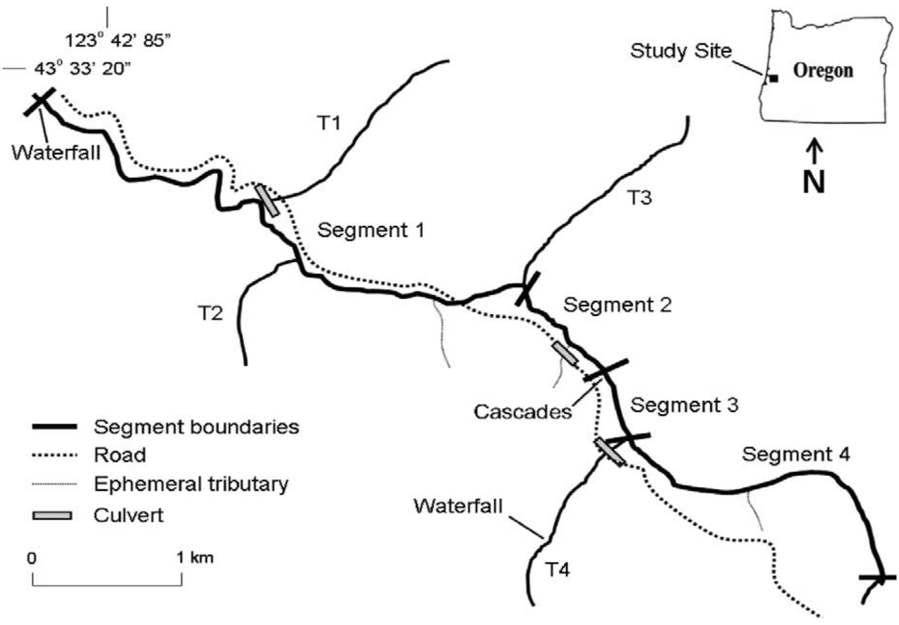

FIGURE 1.—Camp Creek study area. The streams labeled T1–T4 are perennial tributaries; all other landscape features are indicated in the caption.

alder *Alnus rubra*, vine maple *Acer circinatum*, bigleaf maple *A. macrophyllum*, and salmonberry *Rubus spectabilis* in the riparian zone (BLM 1995). The dominant overstory species is Douglas-fir *Pseudotsuga menziesii*, but western red cedar *Thuja plicata* and western hemlock *Tsuga heterophylla* also occur (BLM 1995). Coastal cutthroat trout is the only salmonid species present in the study area. Other aquatic vertebrates include reticulate sculpin *Cottus perplexus*, longnose dace *Rhinichthys cataractae*, and Pacific giant salamander *Dicamphadon tenebrosus*.

The U.S. Bureau of Land Management (BLM) manages the watershed above the migration barrier. There was no commercial timber harvest in the study area until the 1940s. Approximately 51% of the watershed in the study area has been harvested in the past 60 years, primarily in the upper portions of tributaries and ridge tops (BLM 1995). Large late-successional Douglas-fir and western red cedar are present throughout the riparian corridor (BLM 1995). A paved road follows Camp Creek through the lower 5 km of the study area.

Nonmigratory coastal cutthroat trout in small headwater streams (summer discharge < 0.1 m^3/s) are small and short lived (generally less than 5 years; Trotter 1989). Movement appears to be limited (Wyatt 1959), but individuals may drift downstream for winter refuge (Trotter 1989). Although spawning migrations have not been documented, mature coastal cutthroat trout begin to move to areas with concentrated spawning gravel in late winter and early spring as water temperatures rise (5–6°C; Trotter 1989).

Habitat inventory.—A nested hierarchical system of stream classification (Frissell et al. 1986) was used to characterize the stream at the segment, geomorphic-reach, and channel-unit scales. During June 1999, segment boundaries were delineated in the field at (1) junctions with tributaries that were contributing more than 15% of main-stem discharge and (2) natural barriers to fish migration (waterfalls $>$ 4 m). Each segment was divided into geomorphic-reach types (cascade, step-pool, plane-bed, pool–riffle, dune–ripple, colluvial, or bedrock channels) that were based on major changes in gradient, substrate, bed morphology, and pool spacing (Montgomery and Buffington 1997). Minimum length for a geomorphic reach was 10 channel widths. Channel units were categorized as pool, riffle, cascade, or step (Bisson et al. 1982). During field surveys, gradient, wetted width, channel-unit length, maximum pool depth, dominant and subdominant substrate type, large-wood abundance ($>$30 cm diameter and $>$3 m length), riparian vegetation, and valley form were measured for each channel unit (Bisson et al. 1982; Platts et al. 1983). Each pool and cascade unit was marked for subsequent identification.

Water temperature and stream discharge data were collected throughout the study period. Ten temperature data loggers (Onset Computer Corp., Pocasset, Massachusetts; Optic StowAway) were placed in the watershed, including six in the main stem (one each at the lower and upper ends of the study area [$n = 2$]; one above each tributary junction [$n = 4$]) and one in each tributary ($n = 4$). In June 1999, a staff gauge was installed at the lower end of the study site (25 m upstream of the barrier), and the stage was measured on each subsequent visit. Discharge was measured at the staff gauge 12 times to establish a stage–discharge relationship (Buchanan and Somers 1969).

Fish sampling.—Two basic methods, mark–recapture and radiotelemetry, were used to assess movement in Camp Creek at a variety of spatial and temporal scales. From June 1999 to July 2000, 3,025 coastal cutthroat trout were marked by removing a combination of fins (pelvic, caudal, and anal fins) so that recaptured fish could be identified by capture location at the stream-segment scale. Passive integrated transponder (PIT) tags were implanted in 749 individuals (>70 mm fork length) to enable identification of individual fish in specific habitat units. The PIT tags were used only in the lower 5 km of the main stem and in tributaries 3 and 4 because movement from the main stem into tributary 1 was blocked by a barrier to fish passage (culvert) and very few fish were collected in tributary 2.

Movement of marked fish was assessed during 11 multiple-day sampling periods (Table 1). For 9 of these periods (June–October 1999 and March–August 2000), coastal cutthroat trout were captured primarily by single-pass electrofishing (Bateman et al. 2005) with a pulsed-DC backpack electrofisher (40 Hz, 200–300 V, 4- to 6-ms fixed pulse width). Because high discharge, decreased water clarity, and low water temperatures (<8°C) reduced electrofishing efficiency in December–February, angling was the primary means of capturing fish during two sampling periods. Fish collection for nine sample periods (including angling samples) was spatially continuous in the main stem from the waterfall at the downstream terminus of the study area to a point in segment 4 upstream of tributary 4. Both the main stem and all tributaries were sampled in June 1999 and August 2000 (sampling in the main stem and tributaries occurred simultaneously). Tributaries 3 and 4 were sampled five additional times, including two periods (May and July 2000) when only these two tributaries were sampled (Table 1).

During all sample periods, each coastal cutthroat trout was measured (fork length to the nearest millimeter) and weighed (to the nearest 0.1 g), and channel-unit number and type were recorded at the site of capture. Captured trout were inspected for missing fins or scanned for PIT tags. Unmarked individuals received the appropriate segment-scale fin clips.

To provide a more temporally continuous and spatially explicit assessment of movement within reaches, 40 adult coastal cutthroat trout (>150 mm) in the lower 5 km of the main stem of Camp Creek were surgically implanted with radio transmitters. Initially, radio transmitters were placed in 20 individuals captured between 19 and 22 January 2000, and an additional 15 tags were implanted from 9 to 11 February 2000. Subsequently, five transmitters were recovered from the stream bottom and streambank; these were implanted in additional fish on 7 March ($n = 3$) and 4 April ($n = 2$) 2000. Transmitters and coiled antennae formed a single unit sealed in epoxy, and total weight was either 1.9 g or 2.4 g (Advanced Telemetry Systems, Inc. [ATS], Isanti, Minnesota; Models 384 and 393, respectively). Coastal cutthroat trout that received a transmitter weighed from 38.1 to 123.6 g, and the transmitter-to-body weight ratio of tagged fish ranged from 1.8% to 4.9%. Surgical techniques were similar to those described by Young (1995), but clove oil was used as the anesthetic. Fish were released at their capture site upon recovery from the surgery process. The sex of each fish was determined during surgery.

An ATS scanning receiver with a handheld loop antenna was used to locate radio-tagged coastal cutthroat trout. Between 22 January and 19 June 2000, searches (tracking events) were conducted during the day, 3–6 times each week (depending on water and weather conditions). Nighttime searches were conducted on eight occasions between 24 February and 19 April 2000. During each tracking event, fish were initially detected from the road paralleling the stream. Precise locations were estimated by triangulation while walking the streambank and wading. Prestudy trials revealed that location of individuals could be determined accurately within 1 m of the transmitter. Information recorded for each relocation included segment, reach, and channel-unit number; channel-unit type; presence and type of cover being used by the fish; and time of observation.

To estimate the number of coastal cutthroat trout emigrating from the Camp Creek study area, a rotating fish trap (1.5-m orifice) was operated below the waterfall at the lower study boundary from 25 February to 19 June 2000. Fish were collected from the trap 5 d each week. Captured coastal cutthroat trout were counted, measured, weighed, inspected for missing fins or PIT tags, and given a fin clip that was unique to fish captured in the trap. Because these fish were assumed to be migrating downstream, trap efficiency was estimated by releasing captured fish approximately

TABLE 1.—Releases and recaptures of coastal cutthroat trout in the Camp Creek main stem (MS) and tributaries (T) that were implanted with PIT tags or marked by fin clips, June 1999–August 2000. Some fish were recaptured more than once. See Figure 1 for the locations of the segments and tributaries.

	Sampling period (area)					
Variable	Jun 20–Jul 5, 1999 (MS, T1–4)	Aug 12–17, 1999 (MS)	Oct 2–17, 1999 (MS, T1–4)	Nov 30–Dec 19, 1999 (MS, T4)	Jan 19–Feb 11, 2000 (MS, T3)	Mar 6–Apr 4, 2000 (MS, T4)
Sampling days	10	6	6	20	13	8
PIT tags						
Number released	462	99	188			
Number recaptured						
Electrofishing		99	143	2	24	18
Hook and line		0	0	50	36	4
Total		99	143	52	60	22
Number released by segment and tributary						
Segment 1	232	99	118			
Segment 2	68	0	8			
Segment 3	32	0	14			
Segment 4–8	30	0	0			
T1	0					
T2	7					
T3	42		23			
T4	51		25			
Total	462	99	188	0	0	0
Number recaptured by segment and tributary						
Segment 1	0	56	73	37	36	3
Segment 2	0	22	16	0	3	5
Segment 3	0	9	11	0	8	0
Segment 4	0	12	9	13	10	4
T1	0					
T2	0					
T3	0		15		3	
T4	0		19	2		10
Total		99	143	52	60	22
Percent		11	10	21	14	14
Fin clips						
Number released	259	661	939	117	211	68
Number recaptured						
Electrofishing		15	198	7	79	64
Hook and line		0	0	76	85	7
Total		15	198	83	164	71
Number released by segment and tributary						
Segment 1	6	364	416	72	113	7
Segment 2	9	176	153	0	6	12
Segment 3	0	47	58	0	6	
Segment 4	128	74	83	26	19	21
T1	81					
T2	4					
T3	30		122		67	
T4	1		107	19		28
Total	259	661	939	117	211	68
Number recaptured by segment and tributary						
Segment 1	0	6	103	53	89	6
Segment 2	0	7	55		9	22
Segment 3	0	1	14		18	0
Segment 4	0	1	26	23	28	23
T1	0					
T2	0					
T3	0		0		20	
T4	0		0	7		20
Total	0	15	198	83	164	71
Percent		2	13	33	38	44
Summary statistics						
Mortalities	16	18	3	1	2	3
Mean length (range [mm])	129 (27–259)	112 (40–259)	97 (32–241)	143 (48–258)	118 (50–259)	114 (59–234)
Number <70 mm	55	262	403	9	32	7
Number <80 mm	55	336	591	16	73	27
Percent <80 mm	8	38	40	6	17	17
Percent <80 mm and <70 mm	100	78	68	56	44	26

[a] Total number of fish used for this estimate includes 2,256 unmarked coastal cutthroat trout that were released following capture.

TABLE 1.—Extended.

Variable	Sampling period (area)					
	Apr 24–27, 2000 (MS)	May 4–16, 2000 (T3–4)	Jun 5–8, 2000 (MS)	Jul 5–6, 2000 (T3–4)	Aug 16–21, 2000 (MS, T1–4)	Total
Sampling days	4	2	4	2	6	81
PIT tags						
Number released						749
Number recaptured						
Electrofishing	48	16	67	11	72	500
Hook and line	0	0	0	0	0	90
Total	48	16	67	11	72	590
Number released by segment and tributary						
Segment 1						449
Segment 2						76
Segment 3						46
Segment 4–8						30
T1						0
T2						7
T3						65
T4						76
Total	0	0	0	0	0	749
Number recaptured by segment and tributary						
Segment 1	24		49		46	324
Segment 2	10				8	64
Segment 3	8				6	42
Segment 4	6		18		1	73
T1						0
T2					0	0
T3		6		5	2	31
T4		10		6	9	56
Total	48	16	67	11	72	590
Percent	12	6	10	4	2[a]	
Fin clips						
Number released	164	147	288	171		5,281
Number recaptured						
Electrofishing	201	87	322	83	592	1,648
Hook and line	0	0	0	0	0	168
Total	201	87	322	83	592	1,816
Number released by segment and tributary						
Segment 1	111		208			1,297
Segment 2	34					390
Segment 3	8					119
Segment 4	11		80			442
T1						81
T2						4
T3		93		95		407
T4		54		76		285
Total	164	147	288	171		3,025
Number recaptured by segment and tributary						
Segment 1	103		215		320	895
Segment 2	53				82	228
Segment 3	13				31	77
Segment 4	32		107		45	285
T1					4	4
T2					1	1
T3		45		46	51	162
T4		42		37	58	164
Total	201	87	322	83	592	1,816
Percent	49	35	48	31	20[a]	
Summary statistics						
Mortalities	1	0	3	0	0	47
Mean length (range [mm])	124 (74–224)	102 (22–135)	127 (33–263)	85 (30–177)	92 31–254)	(27–259)
Number <70 mm	0	3	49	114	1,317	2,251
Number <80 mm	1	21	49	114	1,597	2,880
Percent <80 mm	0	8	7	43	55	
Percent <80 mm and <70 mm	0	14	100	100	82	

250 m upstream of the trapping site and by dividing the number of recaptured fish by the total number of fish released above the trap.

Data summary and analysis.—Relocation data were used to evaluate the scales of movement, movement patterns, and direction of movement. Total movement was the sum of all movements (upstream and downstream) for the duration of the study (estimated for radio-tagged and PIT-tagged fish that were recaptured more that once). Dispersal distance (Turchin 1998) was defined as the maximum distance moved (difference between the most upstream and downstream locations) by an individual (also defined as "home range"; Young 1996).

Movement distance for radio-tagged and PIT-tagged fish was measured by the number of channel units between relocations; however, fin clips were unique only at the segment scale, and movement of fin-clipped fish was only detectable at the segment and watershed scales. Distance was also measured in meters for comparison with previous studies, but interpretation was confounded because of the wide range of channel-unit lengths (range = 2–95 m) observed in the watershed. For example, an individual moving 50 m in one part of the study area may never have reached a channel-unit boundary, but an individual in another part of the watershed moving the same distance may have moved 3–4 channel units. Assessing the number of channel units that an individual moved between relocations was assumed to be more ecologically meaningful because it was directly related to the type of habitat occupied.

Relocations of radio-tagged coastal cutthroat trout were summarized at four spatial scales (channel unit, reach, segment, and watershed) and at four temporal scales (day, week, month, and 5 months), and seasonal habitat use and dispersal distance were analyzed by month. Directional movement was assessed for all relocated individuals by calculating the percentage of coastal cutthroat trout moving upstream, downstream, or both upstream and downstream. The percentage of movements between channel units (e.g., pool–pool, pool–riffle, pool–cascade, and cascade–cascade) was estimated for radio- and PIT-tagged fish. Mean monthly activity (proportion of observations indicating change in location) of all radio-tagged coastal cutthroat trout and activity of individual radio-tagged fish were also estimated.

Number Cruncher Statistical System (Hintze 1999) was used for all statistical analyses. In cases where data were not normally distributed, nonparametric tests were used to evaluate differences among groups. The relationship between length of radio-tagged and PIT-tagged coastal cutthroat trout and dispersal distance was evaluated initially with Spearman's rank correlation coefficient and, subsequently, with linear regression; total movement was the response variable and fish length was the predictor variable. This analytical approach was repeated to examine the relationship between movement frequency and length of radio-tagged coastal cutthroat trout. Differences in the median dispersal distance by male and female radio-tagged fish were tested for statistical significance with a Mann–Whitney test. Pool metrics (median length, depth, and volume) for PIT-tagged coastal cutthroat trout that remained in a single channel unit or moved among channel units were also compared with the Mann–Whitney test. A chi-square test was used to detect differences in frequency distribution of locations of fin-clipped coastal cutthroat trout and observed and expected monthly activity of radio-tagged coastal cutthroat trout.

Results

Spatial Patterns of Movement

From June 1999 through August 2000, 3,774 coastal cutthroat trout were marked (with a fin clip or PIT tag) in Camp Creek (Table 1). Of the total, 3,025 individuals were fin-clipped (2,248 in the main stem and 777 in all four tributaries), and 1,816 (60%) fin-clipped fish were recaptured (1,485 in the main stem and 331 in the tributaries). During the study, 749 fish were implanted with PIT tags (601 in the main stem and 148 in tributaries 3 and 4), and 352 (47%) individual PIT-tagged fish were recaptured (287 in the main stem and 65 in tributaries). Because some individuals were recaptured more than once (range = 1–6 recaptures; mean = 1.7), 590 relocations were recorded for PIT-tagged fish.

Because fin clips were unique at the segment scale, recaptured fish could be identified by capture location at the that scale. Only 40 (3%) fin-clipped coastal cutthroat trout recaptured in the main stem moved among stream segments ($\geq$1 segment) during the 14-month study period; 4 of these individuals were originally marked in tributaries. Most fish (29 or 82%) had moved upstream. Mean dispersal distance of fin-clipped coastal cutthroat trout in the main stem was 1.8 segments, or approximately 2,017 m (calculated with the midpoint of each segment to estimate distance traveled). Upstream and downstream movement distances were approximately equal (1.8 and 1.5 segments for upstream and downstream, respectively). Differences in proportion of coastal cutthroat trout captured upstream, downstream, and unchanged in relation to initial capture sites were statistically significant (P = 0.00); 29 individuals were located upstream (range = 1–3 segments), 11 had moved downstream (range =

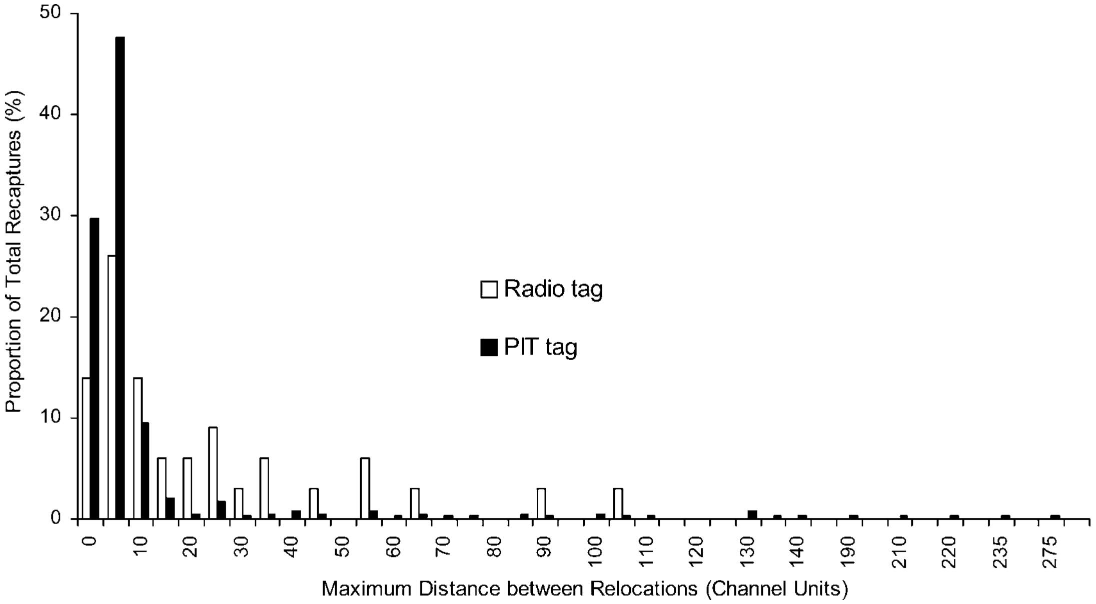

FIGURE 2.—Dispersal distance of radio-tagged ($n = 35$) and PIT-tagged ($n = 6$) coastal cutthroat trout in Camp Creek from June 1999 to August 2000. Dispersal distance is defined as the number of channel units moved between the most upstream and most downstream locations for individual fish. Intervals are five channel units (except for zero).

1–2 segments), and 1,770 were located in the same segment as they were originally marked. Four fin-clipped fish moved out of the tributaries and into the main stem and 13 moved downstream into the fish trap. Mean dispersal distance for coastal cutthroat trout that left the tributaries was 1.0 segment (approximately 2,081 m).

About 1.8% (six) of coastal cutthroat trout that were recaptured in tributaries moved beyond the segment of initial capture, and five of these fish moved into tributaries from the main stem. The mean dispersal distance for coastal cutthroat trout recaptured in tributaries was 1.0 segments, or approximately 2,435 m. Only one fish originally marked in the tributaries was recaptured later in a tributary; it had moved from tributary 3 upstream to tributary 4 (three segments).

Approximately 70% of 287 PIT-tagged coastal cutthroat trout that were recaptured in the main stem had moved among channel units (>1 channel unit), but there was no statistically significant difference in the proportions of fish moving upstream and downstream ($P = 0.12$). The median dispersal distance of PIT-tagged coastal cutthroat trout in the main stem was 2 channel units or 28 m (range = 0–2,519 m), and the distribution was highly skewed (Figure 2). The difference in the distance moved upstream and downstream (median = 2 and 2 channel units for upstream and downstream movements, respectively) was not statistically significant ($P = 0.87$). Comparisons of initial and final locations (proportion upstream, downstream, and unchanged) yielded no statistically significant differences ($P = 0.12$); 112 individuals were located upstream (range = 1–113 channel units), 90 had moved downstream (range = 1–108 channel units), and 85 were located in the same unit in which they were originally marked.

About 62% of recaptured coastal cutthroat trout that were originally PIT-tagged in tributaries 3 and 4 had moved more than 1 channel unit. The median dispersal distance for coastal cutthroat trout in these tributaries was 2 channel units, or 22 m (range = 0–3,993 m). Eleven fish moved out of the tributaries and into the main stem, and three left the study area and were captured in the fish trap. Median dispersal distance for coastal cutthroat trout that left the tributaries was 133 channel units (range = 21–274 channel units). Only three fish originally tagged in the tributaries were recaptured more than once in the main stem, and those individuals remained near the site of the original recapture in the main stem (range = 2–11 channel units).

The PIT-tagged coastal cutthroat trout that changed locations generally occupied smaller channel units than those that did not move. For example, pools (units most frequently used by coastal cutthroat trout) were shallower (median maximum depth = 0.6 and 0.7 m,

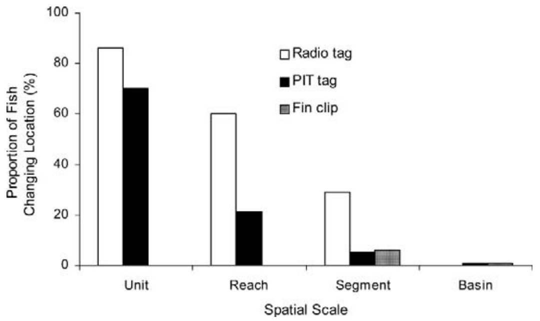

FIGURE 3.—Spatial movement patterns exhibited by radio-tagged (n = 35), PIT-tagged (n = 12), and fin-clipped (n = 1,092) coastal cutthroat trout in Camp Creek from June 1999 to August 2000. The percentages of fish moving between channel units, reaches, segments, and out of the basin are shown. The movement of fin-clipped fish was only detectable at the segment and basin scales.

respectively, for pools from where individuals moved [n = 157] and did not move [n = 73]) and had less volume (median = 45 m^3 and 98 m^3, respectively). When all unit types (i.e., pools, riffles, and cascades) were analyzed together, units from which fish moved (n = 202) were shorter than those in which fish did not move (n = 85; median = 17 m and 22 m, respectively). Differences in dimensions (medians) of channel units occupied by fish that moved and those that did not move were all statistically significant (Mann–Whitney test: $P < 0.01$).

Radio tags were surgically implanted in 40 coastal cutthroat trout (>150 mm) between 19 January and 4 April 2000. Data from 5 radio-tagged fish that had fewer than nine relocations were not included in the analysis. The remaining 35 coastal cutthroat trout were relocated 14–77 times (mean = 59) during the 145-d tracking period (27 January–19 June 2000), and there were 2,053 relocations. The large number of relocations provided a more comprehensive assessment of movement, but inferences were specific to fish larger than 150 mm.

Approximately 86% (n = 30) of radio-tagged coastal cutthroat trout moved 1 or more channel units. The median dispersal distance was 9 channel units per relocation (107 m; range = 0–1,526 m), and the distribution was highly skewed (Figure 2). The median number of channel units moved by individual radio-tagged coastal cutthroat trout (summed over the entire study period) was 48 channel units (range = 0–567 channel units) or 868 m (range = 0–7,913 m). When radio-tagged coastal cutthroat trout were located for the final time, 15 (43%) were found in the channel unit in which they were originally tagged. Of those found in new locations, 13 were found in downstream locations (median = 3 channel units; range = 1–87 channel units) and 7 were located upstream (median = 3 channel units; range = 1–12 channel units).

As expected, there was a strong positive relationship between dispersal distance and the number of movements by individual radio-tagged coastal cutthroat trout (r = 0.89; P = 0.00; n = 35). Five individuals (14%) never left the original tagging location. Of the radio-tagged coastal cutthroat trout that moved 1–20 times (n = 16), all but two individuals moved less than 60 channel units and none moved more than 120 channel units. When the number of moves exceeded 20, two different patterns of dispersal emerged: seven individuals moved less than 130 channel units (only three moved more than 100 channel units) and seven moved 260–567 channel units. Of 21 coastal cutthroat trout that dispersed 6 channel units or more, 18 returned to their original capture location (nonreproductive homing; Gerking 1959) at least once during the study period. Five radio-tagged fish entered four different tributaries in the watershed, three of which were ephemeral.

Although direct comparison of PIT tag and radio tag data are confounded by differences in sampling frequency and extent of sampling period, the pattern of movement was similar for both groups (i.e., the proportion of fish moving declined as spatial scale increased [channel unit, reach, segment, and basin]; Figure 3). A total of 625 movements were recorded for radio-tagged fish; 34% (n = 201) crossed reach boundaries and 4% (n = 25) crossed segment boundaries. Of the 342 movements recorded for PIT-tagged fish, 23% (n = 78) crossed reach boundaries and 6% (n = 22) crossed segment boundaries. Median movement of male coastal cutthroat trout with radio tags (21 channel units; n = 13) did not differ statistically from that of female fish (7 channel units; n = 11; Mann–Whitney: P = 0.10).

There was a weak positive correlation (r = 0.45) between length of radio-tagged coastal cutthroat trout and dispersal distance, and the relationship was statistically significant ($P < 0.05$). Although this relationship suggests that larger fish moved longer distances than smaller fish, only 19% of the variation was explained by a linear regression model of fish length and dispersal distance. In the main stem, dispersal distance was also positively correlated with the length of PIT-tagged coastal cutthroat trout (r = 0.13; $P < 0.05$; n = 287), but a negative relationship between fish length and total dispersal distance was observed for PIT-tagged fish in the tributaries (r = −0.31; $P < 0.05$; n = 67). There was no significant relationship between fish length and size of the channel unit occupied (r = 0.07; $P < 0.21$). Variation explained

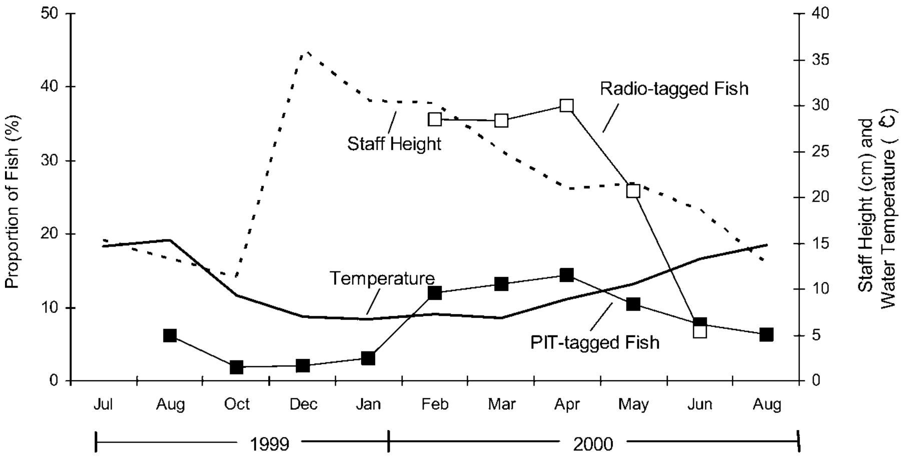

FIGURE 4.—Seasonal movement patterns of radio- and PIT-tagged coastal cutthroat trout in Camp Creek, August 1999–August 2000. The trend for radio-tagged coastal cutthroat trout ($n = 155$ relocations) is the proportion moving more than 5 channel units each month. The trend for PIT-tagged coastal cutthroat trout ($n = 485$ relocations) is the proportion moving more than 5 channel units per month for each recapture period. Staff height and water temperature are monthly averages measured above the waterfall at the lower end of the study site.

by a simple linear regression model of fish length and total dispersal distance was extremely low for both the main stem and tributaries ($r^2 = 0.02$ for the main stem; $r^2 = 0.11$ for the tributaries). In spite of inherent differences in the two sampling techniques, neither suggested a strong relationship between fish length and distance moved.

During the period in which the fish trap was operated (25 February–19 June 2000), 63 coastal cutthroat trout were captured after moving downstream and over the barrier. Peak emigration occurred in mid-April after water temperatures exceeded 8°C. The length of adult coastal cutthroat trout captured in the trap ranged from 94 mm to 242 mm (mean = 141 mm). Coastal cutthroat trout fry (26–55 mm; $n = 10$) were first captured on 24 April 2000. No radio-tagged fish moved out of the study area, but 7 PIT-tagged and 19 fin-clipped fish were captured in the trap. Many of these marked coastal cutthroat trout had moved long distances to leave the watershed, and a few had moved more than 4 km. Three fish were originally marked in tributaries.

Only 30% ($n = 19$) of fish released above the trap were later recaptured, and some coastal cutthroat trout captured and released above the trap did not continue their downstream migration. Six of the 63 fish released upstream were recaptured during subsequent electrofishing surveys above the barrier, including 1 individual with a PIT tag that moved upstream 86 channel units (1,646 m) to its original capture location. Assuming that the remaining 57 coastal cutthroat trout all moved back downstream, the adjusted trap efficiency was estimated to be 33%. The expanded estimate yielded 173 coastal cutthroat trout emigrating downstream out of the study area (below the barrier waterfall). Angling in the pools near the trap yielded only 14 coastal cutthroat trout during the period of trap operation. One of these fish was fin-clipped (main-stem segment 1), and 8 were originally captured in the trap, released upstream, and missed the trap the second time.

Temporal Patterns of Movement

Diel movement patterns appeared to be influenced by seasonal changes in water temperature. When water temperatures were below 8°C in January, February, and March 2000, nine (26%) radio-tagged coastal cutthroat trout did not move from the initial site of release; however, during the eight nocturnal samples, these same individuals were active. On each occasion, coastal cutthroat trout emerged from cover at dusk and were usually active in the channel unit of origin, but some moved 1–2 channel units upstream or downstream before returning to their initial location. After water temperatures exceeded 8°C in April 2000, all radio-tagged fish were active during the day.

Seasonal factors also influenced the extent of coastal cutthroat trout movements. In the main stem, the proportion of PIT-tagged trout that moved more than 5 channel units per month was low between August 1999 and January 2000, increased February through April, and subsequently declined June–August (Figure 4). During April, 15% of recaptured fish moved more than 5 channel units. Movement patterns of radio-tagged trout were similar to PIT-tagged trout during periods

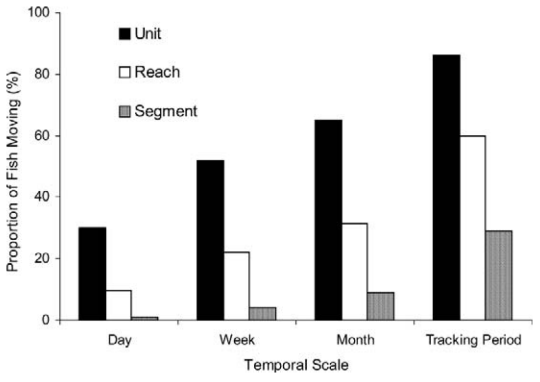

FIGURE 5.—Percentages of radio-tagged coastal cutthroat trout moving at each spatial (unit, reach, and segment) and temporal (day, week, month, and 5-month tracking period) scale in Camp Creek, January–June 2000. The values shown for the day scale include all radio-tagged relocations (n = 2,060). The values shown for the week scale include all observations summarized by week (n = 502), those for the month scale all observations summarized by month (n = 155), and those for the tracking period all observations per individual summarized for the study period (n = 35).

when they were monitored simultaneously (February–June). The proportion of radio-tagged fish moving more than 5 channel units was high from February through April, but by May the proportion decreased and reached a low in June (Figure 4). Dispersal distance for radio-tagged trout also peaked in April, when 40% of fish moved more than 5 channel units.

The number of radio-tagged coastal cutthroat trout that changed location increased with the temporal scale of observation (day, week, month, and tracking period; Figure 5), but there was no distinct pattern in the direction of movement (Table 2). At shorter time periods (day to day), few fish moved; however, when movement occurred, it was usually in both directions. Similar trends in directional movement were also detected for PIT-tagged fish, but the greater length of time between recaptures made it difficult to discern a trend.

Monthly activity of radio-tagged coastal cutthroat trout (percent of observations when fish moved at least 1 channel unit from the previous observation) remained relatively constant from February through June (mean = 30%), ranging from a high of 34% in April to a low of 27% in May and June. There was no significant difference among months in the proportion of coastal cutthroat trout moving ($\chi^2 = 7.8$; $P = 0.10$). Individual relocations suggested that an average of approximately 31% of radio-tagged coastal cutthroat trout changed location between observations (range = 0–72%).

Discussion

The spatial and temporal extent and sampling intensity of this study contributed to new insights concerning the movement of salmonid fishes in headwater streams. By sampling in a spatially continuous manner across all portions of the watershed inhabited by coastal cutthroat trout and by resampling frequently during the 14-month study period, we could examine movement at a variety of spatial scales among seasons. This strategy also reduced the influence of distance weighting (i.e., bias toward detection of short movement distances when sample sections are small relative to movements by animals being studied) on observed movements (Gowan and Fausch 1996; Albanese et al. 2003). Furthermore, by marking a large proportion of coastal cutthroat trout in the watershed, we were able to develop a reasonable perception of trout movement at the population scale. The use of multiple marking techniques provided the means to study movement at a variety of spatial and temporal scales and thereby obtain a more complete understanding of movement in the watershed.

Spatial Patterns of Movement

The dispersal of radio- and PIT-tagged coastal cutthroat trout in Camp Creek was complex. Some fish did not move during the entire study period, but local movement (1–5 channel units) was common. Dispersal distance increased with the number of

TABLE 2.—Summary of directional movements of radio-tagged coastal cutthroat trout (n = 35) at four temporal scales (day, week, month, and 5-month tracking period) in Camp Creek, January–June 2000.

Variable	Day	Week	Month	Tracking period
Number of observations	2,060	502	155	35
Number of observations per fish	2	3–6	9–27	14–77
Movements (% of fish)				
Downstream	15	9	5	0
Upstream	15	10	4	3
Upstream and downstream	[a]	32	56	83
No movement	70	49	35	14

[a] No data.

observations, but only a few of the coastal cutthroat trout in this study moved extensively. In the past, researchers have described two patterns of movement for stream salmonids: sedentary and mobile. Often, most of the fish were assumed to be sedentary (e.g., Solomon and Templeton 1976; Hesthagen 1988; Heggenes et al. 1991). Movement of most (79%) PIT-tagged coastal cutthroat trout in this study was limited (0–5 channel units), and distances that these fish moved were similar to previous mark–recapture studies that reported limited movement of salmonids (e.g., Miller 1957; Shetter 1968; Rinne 1982) and other fishes (Hill and Grossman 1987; Smithson and Johnston 1999). In an attempt to correct the bias toward restricted movement associated with mark–recapture techniques, we tagged and marked a large number of fish, sampled more than 8 km of the stream network repeatedly during the 14-month sampling period, and attempted to monitor fish leaving the study area. Despite these efforts, less than 50% of PIT-tagged fish were recaptured and, consequently, we assume that estimates based on PIT-tagged recaptures represent the minimum level of movement in the study area. This finding provides additional evidence that mark–recapture techniques, even in temporally and spatially extensive studies, may be limited by low recapture rates.

In contrast, estimates of movement based on radiotelemetry may be inflated in this study because only fish larger than 38 g (>150 mm) were implanted with transmitters and there was some evidence that larger radio-tagged fish move further. In addition, the telemetry study took place from January through June, a period when increased movement was expected, especially for larger fish, because of spawning. Frequent observations of radio-tagged fish provided finer-resolution estimates of the timing and distance of movements than PIT tagging, but repeated samples of PIT-tagged fish movements over a 14-month period increased the probability of detecting what appear to be infrequent movements of greater magnitude. Together, the two monitoring methods probably provide a more complete understanding of coastal cutthroat trout dispersal in Camp Creek.

During the study, radio- and PIT-tagged coastal cutthroat trout commonly moved at the channel-unit scale (Figure 3). Many fish also traveled among reaches and segments, but few left the watershed. Based upon the number of radio- and PIT-tagged fish that crossed reach and segment boundaries, it appeared that reach boundaries did not inhibit movement; however, segment boundaries, especially the 4-m waterfall at the lower end of the study site, did appear to reduce relocations (filter movement) at the larger spatial scale. Data from fin-clipped fish also suggest that movement at the segment scale is not frequent. In a watershed-scale examination of genetic variation in Camp Creek, Wofford et al. (2005) found that dispersal barriers strongly influenced coastal cutthroat trout genetic structure by reducing genetic diversity and increasing genetic differentiation.

There is some evidence that habitat characteristics affected the relocation patterns of PIT-tagged coastal cutthroat trout in this study. Trout that did not move among channel units were generally found in deeper and larger pools and in longer channel units overall. Other researchers have observed similar patterns at the channel-unit scale (Heggenes et al. 1991; Kahler et al. 2001), and in an artificial stream experiment, Lonzarich and Quinn (1995) found that yearling coastal cutthroat trout never occupied shallow pool habitat, even when cover was present.

Homing.—Observations of radio-tagged fish in this study suggested a pattern of nonreproductive homing. Gerking (1959) defined nonreproductive homing as the choice to return to a place formerly occupied instead of going to other equally probable places. In this study, most radio-tagged coastal cutthroat trout (18 of 21) that moved more than 5 channel units subsequently returned to a formerly occupied channel unit at least once and often repeatedly. In addition, two radio-tagged fish that did not appear to exhibit homing also had been implanted with PIT tags earlier in the study, and these individuals had returned to the site where they were initially PIT-tagged.

Researchers have documented that salmonids will return to the original site of capture when artificially displaced (Miller 1954; Harcup et al. 1984; Halvorsen and Stabell 1990), and this phenomenon also appears to occur naturally. Burrell et al. (2000) reported that brown trout *Salmo trutta* often returned to their original capture location shortly after spawning, and Brown and Mackay (1995) observed cutthroat trout returning to the same winter refuge areas in consecutive years. Brown trout have also been observed returning to the same feeding areas during three successive years (Bachman 1984). Similarly, coastal cutthroat trout in Camp Creek may move to new areas for feeding or temporary refuge, but often return to a formerly occupied area.

The nonreproductive homing behavior exhibited by radio-tagged fish may partially explain the lower movement rates observed for PIT-tagged fish. Furthermore, it is possible that the length of time between samples confounded the ability to distinguish between PIT-tagged fish that did not move and those that moved and later returned to their original point of capture (Hilderbrand and Kershner 2000). In Camp Creek, a minimum of 30 d elapsed between recaptures of PIT-tagged fish, and the average time between recaptures exceeded 100 d. In contrast, by monitoring radio-tagged fish several times a week, it was possible to observe frequent, and often extensive, upstream and downstream movements.

Emigration.—Information collected at the fish trap suggests that few coastal cutthroat trout emigrated from the watershed during trap operation (February–June); however, some of those fish leaving the watershed traveled long distances before capture. Because the downstream trap was only operational during periods of higher discharge, estimates of movement out of the watershed are probably low. On the other hand, the trap was functional during the period when coastal cutthroat trout were actively moving (sometimes extensive distances), and there was no evidence that downstream movement was more common or extended farther.

Temporal Patterns of Movement

The seasonal movement patterns exhibited by coastal cutthroat trout in Camp Creek appear to reflect concordant responses of fish to changes in discharge and water temperature and life history requirements (e.g., feeding, refuge, and spawning; Figure 4). Coastal cutthroat trout movements generally decreased from August through October during a period of low discharge, increased moderately from October through February as discharge increased, peaked in April when water temperatures were increasing, and declined June through August as discharge decreased and water temperatures rose to annual maxima. Seasonal shifts in movement patterns have also been documented for cutthroat trout in Utah, but movement was lowest during the winter (Hilderbrand and Kershner 2000). Although less frequent sampling during winter (once per month) may have led to underestimates (Hilderbrand and Kershner 2000), lower seasonal water temperatures, such as those observed in northeastern Utah, are often associated with a reduced level of daytime movements (Cunjak 1988; Grunbaum 1996; Harvey 1998). In the warmer climate conditions of coastal Oregon, coastal cutthroat trout might be expected to move frequently during the winter (except during the coldest weather).

The movement recorded in February and March may be related to spawning activity, which often begins in January for coastal cutthroat trout (Trotter 1989). Furthermore, the greatest number of spawning redds in Camp Creek was observed in April, when distances traveled by radio- and PIT-tagged coastal cutthroat trout were greatest and those individuals with radio tags were most active. Decreased discharge, increased water clarity, and increased water temperatures (>8°C) may also account for the increased movement observed in April and May. Fish may have been moving from winter habitats to spring feeding areas as productivity increased in headwater streams before development of the deciduous canopy (Connolly 1996).

The limited movement observed in Camp Creek from August through October may be related to a low level of discharge (0.02 m^3/s) that impeded travel among pools. Apparently, fish were not meeting food requirements for growth because most PIT-tagged fish lost weight during this period (S. R. Hendricks, unpublished data). Increased movement recorded from October through December is believed to be related to rising water levels that allowed coastal cutthroat trout to move out of low-water refuge areas.

Radiotelemetry provided the means to observe the diel patterns of coastal cutthroat trout movement during this study. When water temperatures were less than 8°C in Camp Creek, some radio-tagged fish were inactive during the daylight hours and only moved locally at night. Diurnal concealment has been observed in other salmonids during both the winter (Cunjak 1988; Contor and Griffith 1995; Harvey et al. 1999) and summer (Fraser et al. 1995; Gries and Juanes 1998), when water temperatures were less than 8°C. Furthermore, Grunbaum (1996) reported that the length of time rainbow trout *O. mykiss* remained concealed during the winter days differed between the Oregon Coast Range and Oregon Cascades, and more frequent daytime movement was related to higher water temperatures associated with warmer climatic patterns of the coastal region.

The detection of movement by coastal cutthroat trout in Camp Creek was heavily influenced by the temporal scale of observations. At different scales, the probability of fish movement changed and so did the ability to detect movement. Most radio-tagged coastal cutthroat trout (70%) did not change channel units on a daily basis (Table 2); however, when movement occurred, the distances moved upstream and downstream were similar. At coarser time scales (week and month), more fish moved in both directions, and the probability of exclusively upstream or downstream movement was equivalent. Movement was frequent when summarized for the entire telemetry period (5 months), and 83% of the coastal cutthroat trout moved both upstream and downstream. Although movement was not as common at the finest temporal scale, if tracking had not occurred 3–6 d/week, the frequency of movement may have been underestimated. Behaviors such as homing, nocturnal activity, intermittent movement, and the frequent occurrences of fish moving both upstream and downstream would have been hard to detect. Awareness of these temporal complexities can improve detection of movement and movement patterns and are, therefore, important considerations for decisions concerning the appropriate temporal resolution and scope of future research projects.

Synthesis

The movements of radio- and PIT-tagged coastal cutthroat trout in Camp Creek underscore the complexity of habitat use by coastal cutthroat trout in small streams. Our results suggest that movement patterns are linked to physical changes in the stream (e.g., discharge and temperature); however, ontological factors (size-class) and life history requirements (reproduction, refuge, and feeding) may also influence how far and how often fish move and where fish occur during particular portions of their life and at particular seasons of the year. In addition, there were pronounced seasonal patterns to movement, but the greatest proportion of movement in this isolated headwater stream was within and among pool habitats.

Data from this study suggest that coastal cutthroat trout commonly move at the channel-unit scale. The perception of extent, frequency, and duration of movement at various spatial and temporal scales was influenced substantially by the methods used to monitor fish location. Although each marking, monitoring, and capture technique has limitations, when used concurrently, these tools provided a more comprehensive view of movement and habitat use. The complexities of movement and habitat use suggest that future research would benefit from the use of multiple capture, marking, and monitoring techniques for large spatial and temporal scales.

Finally, our observation that movement in headwater streams is most common at the channel-unit scale suggests that site-based habitat restoration projects primarily have local effects on fish populations. Restoration of individual channel units of stream may not benefit the population at the watershed scale unless these activities are undertaken in the context of the greater whole. Individual coastal cutthroat trout move great distances, even within the small watersheds in the Oregon Coast Range, and although these movements may be infrequent, they may contribute substantially to recolonization after stochastic extirpation events (e.g., landslides and debris flows). Management strategies that focus on maintaining connectivity in a watershed represent an important step toward protecting the evolutionary capacity of stream salmonids.

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