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[Article]

Seasonal Movement and Habitat Use by Subadult Bull Trout in the Upper Flathead River System, Montana

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Abstract.—Despite the importance of large-scale habitat connectivity to the threatened bull trout *Salvelinus confluentus*, little is known about the life history characteristics and processes influencing natural dispersal of migratory populations. We used radiotelemetry to investigate the seasonal movements and habitat use by subadult bull trout (i.e., fish that emigrated from natal streams to the river system) tracked for varying durations from 1999 to 2002 in the upper Flathead River system in northwestern Montana. Telemetry data revealed migratory (N = 32 fish) and nonmigratory (N = 35 fish) behavior, indicating variable movement patterns in the subadult phase of bull trout life history. Most migrating subadults (84%) made rapid or incremental downriver movements (mean distance, 33 km; range, 6–129 km) to lower portions of the river system and to Flathead Lake during high spring flows and as temperatures declined in the fall and winter. Bull trout subadults used complex daytime habitat throughout the upper river system, including deep runs that contained unembedded boulder and cobble substrates, pools with large woody debris, and deep lake-influenced areas of the lower river system. Our results elucidate the importance of maintaining natural connections and a diversity of complex habitats over a large spatial scale to conserve the full expression of life history traits and processes influencing the natural dispersal of bull trout populations. Managers should seek to restore and enhance critical river corridor habitat and remove migration barriers, where possible, for recovery and management programs.

Potadromous salmonids exhibit a wide variety of migration strategies that occur from spatial, seasonal, and ontogenetic shifts in habitat use for growth, survival, and reproduction (Northcote 1997). Several studies have examined the migration behavior of salmonid species, although results are variable and sometimes contradictory between and within a particular species (Fausch and Young 1995). Several telemetry studies have shown that salmonid populations may make long movements between trophic, refuge, and reproductive habitats (Bjornn and Mallet 1964; Cunjak and Power 1986; Brown and Mackay 1995; Swanberg 1997; Schmetterling 2001; Meka et al. 2003), whereas relatively sedentary behavior has been observed for the same species where optimal habitat is locally available (Chisholm et al. 1987; Young 1996; Jakober et al. 1998; Young 1998; Muhlfeld et al. 2001). Despite the high variation in movement patterns of salmonid populations, however, no studies have described seasonal movements of bull trout *Salvelinus confluentus* rearing in large, interconnected river–lake systems.

Populations of bull trout have declined throughout much of their native range (Rieman et al. 1997) and the species is currently listed as threatened under the U.S. Endangered Species Act of 1970. Declines are largely attributed to habitat degradation and fragmentation (Fraley and Shepard 1989; Rieman and McIntyre 1995; Schmetterling 2003) and interactions with nonnative salmonids (Kitano et al. 1994; Deleray et al. 1999; Rich et al. 2003). Loss of connectivity can be especially detrimental to migratory (fluvial and adfluvial) populations that require a large spatial scale and diverse, connected habitats for spawning and rearing (Fraley and Shepard 1989; Rieman and McIntyre 1995; Swanberg 1997; Schmetterling 2003). Maintaining suitable habitat connectivity between habitats that provide for the full expression of life history variation is critical to maintaining genetic diversity and dispersal among populations, which, in turn, are critical to the persistence of bull trout populations (Rieman and Allendorf 2001). Therefore, understanding movement patterns and habitat requirements is key to species recovery and management of all life stages and to predicting how resource management decisions influence populations.

Several studies have shown that large-scale movements and suitable habitat availability are major factors determining the persistence of mi-

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gratory bull trout populations throughout their range (Fraley and Shepard 1989; Rieman and McIntyre 1995; Swanberg 1997; Dunham and Rieman 1999; Spruell et al. 2001; Schmetterling 2003). Seasonal movement patterns and habitat requirements, however, are not well documented for the subadult phase of bull trout life history (i.e., once fish emigrate from natal streams and enter the river–lake system), although Fraley and Shepard (1989) speculated that subadult bull trout move rapidly downriver during spring, summer, and fall. Therefore, during the fall and winter of 1999 to 2002 we assessed the spatial and temporal distribution of bull trout subadults after they entered the river system during spring high flows in the North Fork Flathead River in Montana and once fish arrived in the main stem. We were primarily interested in testing whether fish were using the river as a migration corridor or actually using it as rearing habitat. Our objectives were to describe the seasonal movements and habitat use and to identify factors influencing movement.

Study Area

The Flathead River drainage, in northwestern Montana, is an 18,400-km^2 headwater drainage of the Columbia River basin (Figure 1); it includes Flathead Lake and the river system upstream (the main-stem, North Fork, Middle Fork, and South Fork Flathead rivers). Our study was conducted in the North Fork and the main-stem Flathead River from the U.S.–Canadian border downstream to Flathead Lake (Figure 1). The North Fork Flathead River originates in the Rocky Mountains of British Columbia, Canada, and flows approximately 160 km south to its confluence with the Middle Fork Flathead River near West Glacier, Montana. The North Fork has a drainage area of 4,009 km^2 and a mean annual discharge of 83.5 m^3/s, accounts for approximately 32% of the discharge in the Flathead River, and is a classified as a Wild and Scenic River under the National Wild and Scenic River Act of 1976. The main-stem Flathead River is a partially regulated river that begins at the confluence of the South Fork, controlled by Hungry Horse Dam, and the unregulated Middle Fork and flows 69 km south to Flathead Lake through agricultural, residential, and forested areas of the Flathead Valley (Figure 1). The mean annual discharge is 271 m^3/s, and the drainage area is 11,562 km^2. Hungry Horse Dam, located 8.5 km upriver of the South Fork, regulates river discharge, precludes upstream fish migration, and isolates fish populations upstream. The main stem contains two distinct river reaches: a free-flowing section that extends 38 km from the South Fork downriver to the Stillwater River confluence (herein referred to as the upper main stem) and a lake-influenced section that extends an additional 31 km downriver to Flathead Lake (herein referred to as the lower main stem).

Bull trout exhibit a migratory life history strategy (i.e., fluvial and adfluvial) in the upper Flathead River and lake system (Fraley and Shepard 1989), although a resident form may exist. Bull trout grow to maturity in the lake or river system and then begin spawning migrations from May through July, traveling 88–250 km upriver to natal tributaries in the north, middle, and south forks of the Flathead River. Spawning occurs from late August through early October, when water temperatures fall below 9°C in low-gradient reaches that contain clean gravel, groundwater influence, and cover. Juveniles rear in natal spawning and rearing streams for 1–4 years and then emigrate (primarily during high spring flows) to the river or lake (i.e., subadult phase).

Methods

We used radiotelemetry to investigate the seasonal movements and habitat use by subadult bull trout tracked for varying durations from 1999 to 2002 in the upper Flathead River system. Fish were captured by means of boat electrofishing, surgically implanted with radio transmitters (Muhlfeld et al. 2003), and released near their capture locations. In the North Fork, we implanted radio tags in subadult bull trout downstream of the U.S.–Canadian border (Figure 1) during spring high flows, May–July, and in the main stem we implanted fish near Columbia Falls and Kalispell (Figure 1; Table 1) as part of a larger effort to investigate impacts of dam operations on the fishery (Muhlfeld et al. 2003).

Fish were implanted with transmitters that weighed 2.0–8.9 g in air (Models MCFT-3HM, MCFT-3D, MCFT-3EM, Lotek Wireless Inc., Newmarket, Ontario), depending on the size and weight of the fish (Table 1). Transmitter life ranged from 40 to 399 d, and each tag emitted a signal every 5 s at 148.730 MHz. In the North Fork, large subadult bull trout (>100 g) were not readily available during electrofishing surveys. Consequently, 21 fish received radio transmitters that exceeded 2% of the fish's weight (mean, 2.8%; range, 1.0–5.9%), which is the maximum suggested by Winter (1983). Therefore, we compared total distance moved for fish with transmitter weights above and

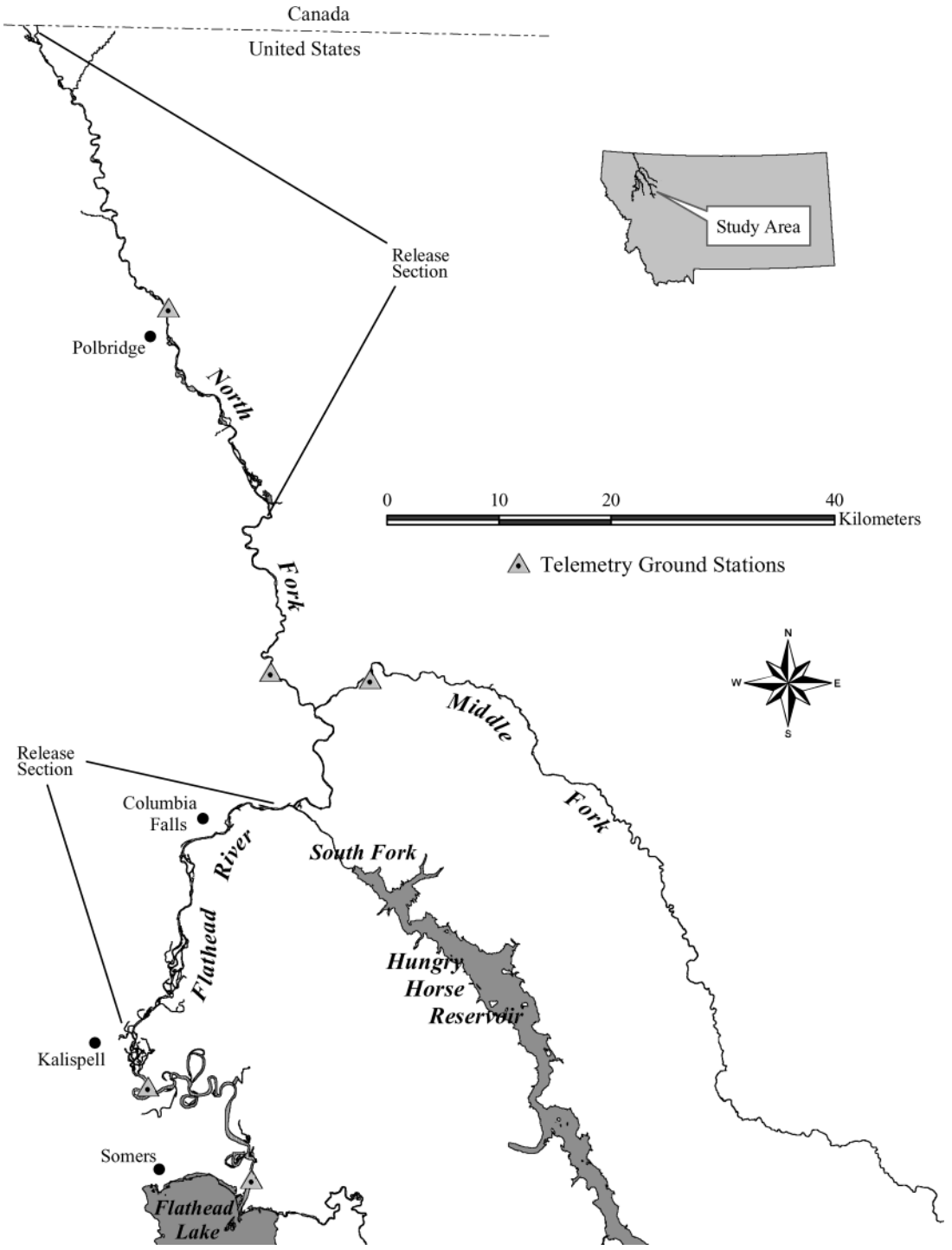

FIGURE 1.—Map showing the study area in the upper Flathead River drainage, Montana.

TABLE 1.—Sample locations, collection dates, sample sizes, mean total lengths (TL), and tracking information for radio-tagged subadult bull trout in the main-stem and North Fork Flathead River. Numbers in parentheses are SDs.

Release location	Date collected	*N*	Mean TL (mm)	Transmitter weight (g)	Average number of relocations	Average number of days tracked
Main stem	Oct 29, 1999	3	280 (24)	3.7	15 (4)	106 (8)
	Feb 16–Mar 3, 2000	3	265 (6)	3.7	15 (6)	86 (30)
	Oct 24–31, 2000	10	292 (34)	3.7	15 (6)	97 (27)
	Oct 17–31, 2000	5	371 (19)	8.9	32 (5)	247 (68)
	Jun 14–29, 2001	4	281 (26)	3.7	5 (4)	57 (31)
	Mar 2, 2001	1	389	8.9	22	199
	Mar 2–7, 2001	4	311 (32)	3.7	9 (2)	96 (24)
	Oct 24–26, 2001	9	310 (40)	3.7	16 (5)	105 (20)
North Fork	Jun 13–19, 2000	2	208 (11)	2.0	8 (5)	36 (20)
	Jun 14–19, 2000	7	247 (47)	3.7	14 (4)	78 (31)
	May 9–Jun 13, 2001	9	283 (37)	3.7	12 (4)	83 (28)
	Jul 3–12, 2002	7	215 (7)	2.0	7 (3)	30 (14)
	Jul 9–12, 2002	3	260 (8)	3.7	12 (2)	69 (23)

below 2% body weight by means of a Mann–Whitney *U*-test to assess whether the transmitter to body weight ratio influenced survival. We compared total distance moved by individual fish using a Spearman's rank of correlation analysis (Statistica 1995) to assess if the tag life influenced the timing and magnitude of movement.

In the North Fork, field crews located each fish once a week from an inflatable raft equipped with a three-element directional Yagi antenna and a portable scanning receiver (Lotek Model SRX-400). In the main stem, individual fish were tracked at least once a week (up to four times per week) from a jet boat equipped with a portable scanning receiver and a whip antenna (Muhlfeld et al. 2003). Fish were also located on several occasions with a fixed-wing aircraft and a three-element directional Yagi antenna (mounted on the wing strut) to survey remote and inaccessible areas throughout the river system and to determine whether missing fish migrated from the study area. Additionally, we installed remote detection ground stations throughout the river system (upper North Fork at Polebridge, North Fork mouth, Middle Fork mouth, main-stem Flathead River, and Flathead River mouth; Figure 1) that continuously monitored (24 h–7 d per week) fish movements. Each ground station had a range of 250 m and consisted of a Lotek data-logging receiver equipped with a three-element directional Yagi antenna powered by a 12-V deep-cycle marine battery.

Georeferenced locations (±1 m) were obtained at each fish location using a global positioning system unit (TSC1 Asset Surveyor, Trimble Navigation Limited, Sunnyvale, California). In a geographic information system, we overlayed the point locations on a hydrography layer for analysis of distance moved. Individual fish movements were calculated by measuring the distance between each consecutive location in Arc View (Environmental Systems Research Institute 1999) and computed as (1) the distance a fish traveled between consecutive locations (total distance) and (2) the distance moved between the release and final location of a given fish (net distance). We delineated seasons based on historic temperature and flow data in the Flathead River valley (U.S. Geological Survey, unpublished data) and made classifications as follows: winter (1 December–31 March); spring (1 April–30 June); summer (1 July–15 September); and fall (15 September–30 November). Fall and winter data were pooled because some fish were implanted in late October (Table 1) in the main stem. Movements were compared among seasons and years using a Kruskal–Wallis analysis of variance (ANOVA); post hoc comparisons were conducted using Mann–Whitney *U*-tests (Statistica 1995). Using simple linear correlation, we compared total distances moved with the number of relocations and individual fish total length (TL) (Statistica 1995).

Habitat use information was recorded each time a fish was located. We did not, however, measure habitat availability throughout the upper Flathead River system. Mesohabitat use data were modified from Bisson et al. (1982), Jakober et al. (1998), and Muhlfeld et al. (2003): riffle, run with boulders, run with large woody debris (LWD), run lacking boulders and LWD, pool with LWD, pool with boulders, pool lacking boulders and LWD, pocket water (small pools formed by boulders within a riffle or run), shoals (shallow, low-velocity areas along the channel margins), and lake-influenced (backwater areas upstream of Flat-

head Lake). In the main stem, substrate composition (within a 1-m radius) was visually ranked as sand–silt (<0.2 cm; rank = 1), small gravel (0.2–0.6 cm; rank = 2), large gravel (0.6–7.5 cm; rank = 3), cobble (7.5–30.0 cm; rank = 4), boulder (30.0–60.0 cm; rank = 5), and bedrock (rank = 6) and weighted by the proportional area to obtain a single value representative of each location (Baltz et al. 1991). In the North Fork, dominant and subdominant substrate particle sizes were recorded at each location based on the above categories. Mean daily water temperature and discharge data were obtained from the U.S. Geological Survey stations on the North Fork (Glacier Rim) and main stem Flathead River (Columbia Falls), Montana.

Results

From 1999 to 2002, we monitored 39 subadult bull trout implanted in late fall and winter in the main-stem Flathead River for an average of 116 ± 63 d and 28 fish implanted in the North Fork during spring 2000–2002 for an average of 64 ± 33 d. Telemetry showed that movement patterns were complex and diverse (Figures 2, 3); some subadult bull trout (N = 32; 48%) made extensive (>5 km) movements, whereas others (N = 35; 52%) remained relatively sedentary (mean distance, 0.1 km; SD, 1.7). Most migrating bull trout subadults (84%) made rapid and lengthy downriver movements (mean distance, 32.7 km; range, 6.2–129.4 km) to lower portions of the river system and to Flathead Lake during high spring flows and as temperatures declined (to below 5°C) in the fall and winter. In contrast, some migrants (16%) moved upriver (mean distance, 21.8 km; range, 5.9–45.6 km) as flows subsided following spring runoff and as mean daily temperatures gradually rose above 7°C.

Movement, Main-Stem Flathead River

We implanted radio transmitters in 44 subadult bull trout (mean TL, 309 mm; SD, 45; range, 247–399 mm) in the main-stem Flathead River (Table 1). Of the 44 implanted transmitters, 3 transmitters were recovered from the streambed and along the bank shortly after release and 2 were lost because they were not detected during ground, aerial, or fixed-station surveys. We maintained a mean transmitter to body weight ratio of 2.0% (SD, 0.5; range, 1.0–3.0%).

We obtained 616 relocations from the 39 bull trout (mean TL, 306 mm; SD, 43) tagged in the main stem. Surveyors tracked fish an average of 116 d (SD, 63; range, 24–335 d) and relocated each fish an average of 16 times (SD, 9; range, 2–39). Total distance moved was not significantly correlated to the number of relocations (P = 0.396) or fish TL (P = 0.103) and was not different among seasons (P = 0.236). Relocations of migrating bull trout revealed a general pattern of downriver movement during late fall and winter as temperatures declined to below 5°C (2–5°C) and additional downriver movement occurred in the spring as flows increased (Figure 2).

Fall–winter movement.—In winter, most bull trout (70%) moved little, whereas others (30%) moved to overwintering areas in the lower river and Flathead Lake. The three radio-tagged bull trout tracked during winter 1999–2000 displayed variable movements in the upper river system: one moved 14 km downriver in mid-December; one remained near the release location (±0.5 km); and one moved 32 km upriver and overwintered in a deep canyon in the lower portion of the North Fork. Of the 15 fish monitored during winter 2000–2001, 7 (47%) made downriver overwintering movements (mean distance, 21.3 km; SD, 21.5), whereas 8 (53%) remained an average of 1.8 km (SD, 1.9 km) from their release locations. Five fish moved rapidly downriver 4–10 d after release in late-October, and three of them moved to sloughs in the lower river (i.e., lake-influenced section). Two subadult bull trout entered Flathead Lake on 8 December 2000 and 29 February 2001, indicating an adfluvial life history; migrations to the lake lasted 7 and 23 d, respectively. Larger-sized bull trout moved greater distances during winter 2000–2001; fish TL was positively correlated with total distance moved (r_s = 0.68, P = 0.0054). In contrast, the nine bull trout tracked during late fall and winter 2001–2002 displayed little movement, moving a mean net distance of 0.2 km (SD, 0.7) from their release locations; they moved a mean total distance of 2.3 km (SD, 2.1).

Spring.—Five of 10 bull trout (50%) tagged in the Flathead River (near Kalispell) moved downriver as river discharge increased with the onset of spring runoff. Four of the downriver migrants moved an average net distance of 38.1 km (SD, 2.1) to Flathead Lake in 2–13 d, and one fish moved 7.6 km downriver in the main stem. In contrast, one fish moved 11.3 km upriver in the main stem on the rising limb of the hydrograph in 2001. The four remaining subadult bull trout remained near the site of original capture and release (mean distance, 0.3 km; SD, 1.6). Additionally, three fish

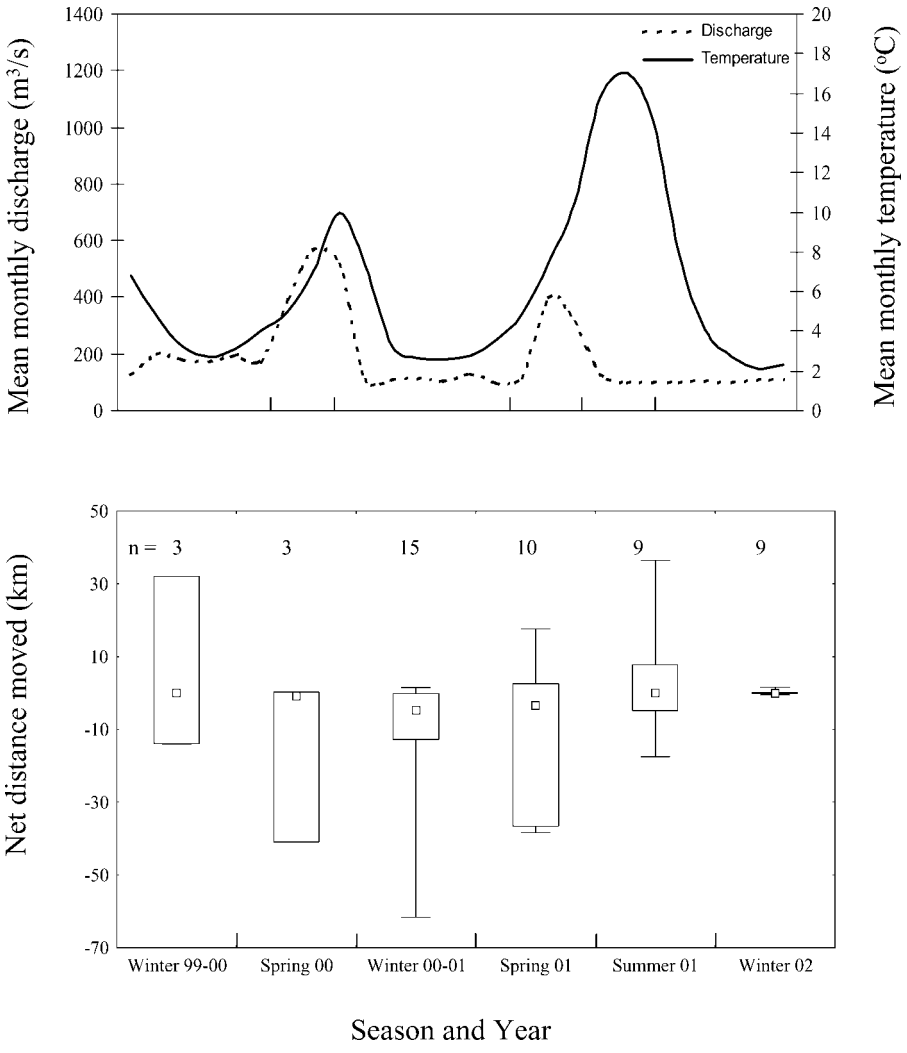

FIGURE 2.—Net distance moved (distance between the point of release and final location of a given fish) by radio-tagged subadult bull trout (bottom panel) in relation to mean monthly water temperature and mean monthly discharge (top panel) in the main-stem Flathead River. Negative values represent downstream movements. Small boxes represent median values, large boxes the 25th and 75th percentiles, and whiskers the minimum and maximum values. Sample size is given above each season. The tick marks along the *x*-axis in the top panel correspond to the time periods indicated in the bottom panel.

that had previously moved to the lower river and the mouth at Flathead Lake during winter 2000 remained in these areas (mean distance, 8.4 km; SD, 7.7) during the spring of 2001.

Summer.—Subadult bull trout made variable movements in the Flathead River during the summer of 2001. Total distances moved averaged 21.6 km (SD, 29.3) and net distances averaged 3.5 km (SD, 16.2). Two fish moved downriver to the lower river (lake-influenced area) as river discharge approached base flow conditions, and the fish remained there throughout the summer. Similarly, three bull trout remained in deep areas of the lower river and one in Flathead Lake after previously moving there in the winter and spring. In contrast, three fish made upriver movements (mean distance, 21.4 km; SD, 14.4) as flows stabilized after spring runoff, and two of these fish moved back downriver in late summer. One 312 mm fish moved 19.9 km upriver past the Middle Fork ground station and was not relocated in subsequent tracking surveys. This fish likely moved to Lake McDonald

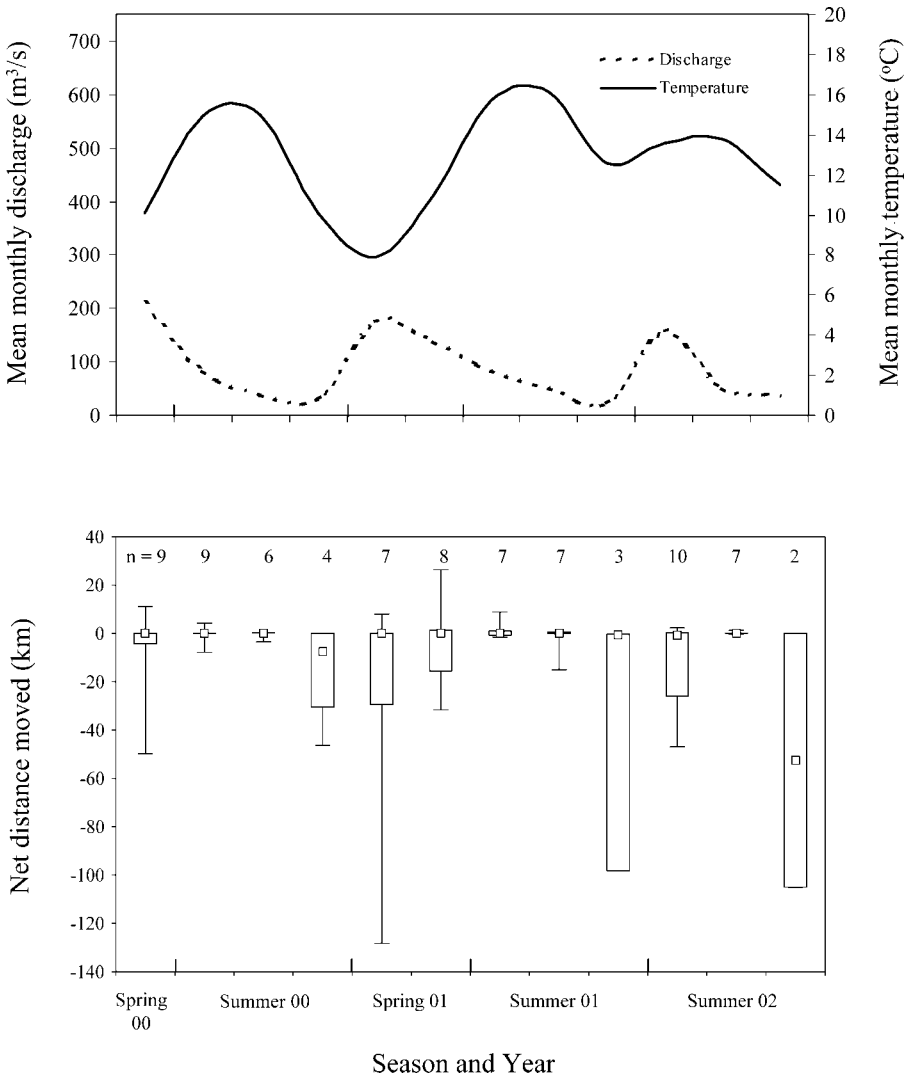

FIGURE 3.—Net distance moved by radio-tagged subadult bull trout (bottom panel) in relation to mean monthly water temperature and mean monthly discharge (top panel) in the North Fork Flathead River. See Figure 2 for additional details.

(Glacier National Park) where deep water precluded signal detection.

Movement, North Fork Flathead River

Forty-two bull trout subadults (mean length, 238 mm; SD, 40) were implanted during spring in the North Fork from 2000 to 2002 (Table 1), and 28 of these fish (mean length, 249 mm; SD, 42) were successfully tracked until battery expiration. Of the 14 lost tags, 12 were found within the streambed and along the bank 6–54 d after implantation; the other two were not relocated during subsequent aerial surveys. The recovered transmitters were presumed to be from fish that died or expelled their tag during high spring flows. Interestingly, recovered transmitters came from fish that were significantly smaller ($U = 92$; $P = 0.025$) and had higher transmitter to body weight ratios ($U = 69$; $P = 0.004$) than those fish that were tracked; indeed, all lost fish carried transmitters that were greater than 2% body weight. However, for those fish that survived, we found no effect of transmitter weight on total distance moved by fish with transmitter weights greater ($N = 20$) or less ($N = 8$) than 2% of body weight ($U = 61$; $P = 0.333$).

The 28 subadult bull trout tagged in the North

Fork were radio-tracked an average of 64 d (SD, 33; range, 23–114 d) and relocated a total of 311 times (mean per fish, 11; SD, 4). Total distances moved were not significantly related to the number of relocations ($P = 0.396$) or with fish TL ($P = 0.103$). Net distances moved were significantly different among seasons (Kruskal–Wallis ANOVA; $P = 0.047$) and were not different among years (Kruskal–Wallis ANOVA; $P = 0.529$). Movement was significantly greater during high spring flows (May–July) and in early fall (September) and significantly lower in August (Figure 3).

In the North Fork, radio-tagged subadult bull trout moved a mean total distance of 28.8 km from the point of release (Figure 3; SD, 36.4; range, 0–129.4 km). Net direction moved was predominately downstream; 13 fish (46%) moved downstream from the point of release (range, 6.2–129.4 km), 10 fish (36%) remained within 1 km (range, 0–0.8 km), and 5 fish (18%) moved more than 1 km upstream of their release location (range, 1.6–10.6 km).

Ten subadult bull trout made pronounced downstream movements during spring as flows subsided following peak runoff. Of the nine radio-tagged bull trout released in June 2000, two (22%) moved downstream to lower portions of the North Fork. One fish moved 51 km downstream to a debris jam in a braided section of the North Fork 5 d after release, and the other moved 16.5 km downstream in late June and early July. In 2001, four of the nine (44%) bull trout tagged in May moved downriver an average of 71.0 km (range, 6.2–129.4 km) to areas lower in the Flathead River drainage; two fish moved (6.2 and 44.8 km) to the lower North Fork, one bull trout moved to the main stem Flathead River (103.5 km), and the remaining migrant moved 129.4 km to Flathead Lake 20 d after release (including one movement of 71.8 km in 8 d). Downriver migrations averaged 31 d (range, 20–42 d), and these fish began their migrations 5 d (range, 3–7 d) following release in 2001. In 2002, 4 of the 10 (40%) bull trout tagged in early July moved downstream an average of 16.0 km (range, 8.4–26.1 km) to lower portions of the North Fork. These fish began migrations an average of 6 d (range, 2–10 d) after release, and the migrations lasted an average of 9 d (range, 5–12 d).

Two radio-tagged bull trout moved upstream (10.6 and 59.3 km) in the North Fork (British Columbia, Canada) on the falling limb of the hydrograph as turbidity decreased. Interestingly, these fish were two of the largest tagged fish (307 and 353 mm, respectively), suggesting a possible fluvial life history in the North Fork.

Of the nine subadults monitored during September in the North Fork, three (33%) moved downriver (mean total distance, 52.3 km; range, 17.0–93.8 km). Two bull trout moved to lower portions of the North Fork, and one fish moved to a slough in the main-stem Flathead River near Flathead Lake. These fish began migrating in early September as river discharge approached base flow conditions and as water temperatures declined to below 12°C.

Some bull trout ($N = 10$) displayed sedentary behavior in the North Fork, moving an average net distance of 0.03 km (range, 0–0.8 km) from their release locations. Sedentary fish, however, made short upstream and downstream movements (mean total distance moved, 4.8 km; range, 0–10.5 km) within short sections of the river. Sedentary fish commonly occupied deep runs and pools with complex cover in the form of unembedded substrate and LWD.

Factors Affecting Movements

Water temperature and river discharge appeared to influence the timing and extent of movement by subadult bull trout migrants in the North Fork and main-stem Flathead River (Figures 2, 3). In the North Fork, fish began moving immediately following release on the descending limb of the hydrograph and during peak river discharge as water temperature rose above 7°C. Additional downstream movements were observed in early September as mean daily water temperatures declined to below 12°C. Movements were significantly lower during August in the North Fork when the highest summer maximum temperatures were recorded (mean daily water temperature, 15.0°C; range, 12.0–17.5°C). In the main stem, bull trout made extensive downriver movements with declining water temperature (6.5–1.5°C) in the fall and winter and during high spring flows (increasing, peak, and declining portions of the hydrograph) and as mean daily water temperatures rose above 6.5°C.

Habitat Use

Bull trout subadults used the entire extent of the river system for extended periods of time, including all portions of the river corridors (free-flowing, partially regulated, and lake-influenced areas) and Flathead Lake. Subadult bull trout tended to occupy daytime locations in deep runs and complex pools in the main-stem Flathead River (Table 2). During all seasons, deep runs were the primary

TABLE 2.—Mean proportional use of habitat by subadult bull trout in the main-stem Flathead River during fall–winter, spring, and summer 1999–2002 and in the North Fork Flathead River in 2000 (June–September), 2001 (May–September), and 2002 (July–September). The abbreviation LWD stands for large woody debris.

Location	Number of fish	Number of observations	Mean number of observations per fish (SD)	Habitat type									
				Run	Run with substrate	Run with LWD	Pool	Pool with LWD	Pool with substrate	Back-water	Shoal	Riffle	Pocket water
Fall–winter													
Main stem	33	317	10 (6)	49	19	1	14	13	3	0	0	0	0
Spring													
Main stem	13	68	5 (4)	52	5	0	14	8	8	1	11	0	0
North Fork	15	45	3 (1)	9	41	5	13	22	8	0	0	1	0
Summer													
Main stem	4	23	6 (1)	54	25	10	0	4	6	0	0	0	0
North Fork	28	160	6 (4)	8	28	1	7	30	11	0	0	6	10

habitats used in the main stem, followed by runs and pools with cobble and boulder substrates and LWD. Subadult bull trout exhibited minor shifts in seasonal habitat use that reflected changes in river discharge and water temperature. For example, use of runs and cobble and boulder substrates intensified in the summer months when water temperatures were highest (Figure 4). During peak spring flows, some bull trout avoided faster-water areas of the channel and moved to the channel margins (i.e., shoals). Further, lake-influenced areas of the Flathead River and Flathead Lake were important rearing areas during all seasons. Fish commonly moved to and remained in deep areas of the main channel of the lower river and in oxbow and slough habitats or moved into Flathead Lake. In the North Fork, bull trout used runs that contained unembedded boulder and cobble substrates and pools with extensive amounts of LWD during spring and summer days (Table 2). Unembedded boulder and cobbles were the dominant substrate particle sizes used by subadult bull trout in the North Fork (Figure 4).

Discussion

Understanding the dispersal behavior of subadult bull trout is key to developing effective recovery and management programs for all life history stages of bull trout populations throughout their range. Prior to our work, however, seasonal movement patterns and habitat use of subadult bull trout rearing in large river systems was largely unknown. Telemetry data revealed variable life history patterns in the subadult phase of their life history. Complex daytime habitat was used by migrating and nonmigrating fish during the day. Furthermore, most migrating subadults made rapid or incremental downriver movements to lower portions of the river system and to Flathead Lake during high spring flows and as temperatures declined in the fall and winter. Results elucidate the importance of maintaining natural connections and a diversity of complex habitats over a large spatial scale to conserve the full expression of life history traits and processes influencing natural dispersal of bull trout populations.

Seasonal Movement

Our results indicate that subadult bull trout exhibit migratory and nonmigratory movement behavior in the upper Flathead River system. About half of the radio-tagged fish remained within 1 km of their release location in the North Fork and main stem, while others made extensive downriver migrations (up to 129 km). Further, the duration of migration varied as some fish moved rapidly, whereas others moved incrementally, downriver. These results differ from Shepard et al. (1984) and Fraley and Shepard (1989) who speculated that subadult bull trout moved rapidly downstream after emigrating from their natal tributaries during spring, summer, and fall. Migratory behavior is usually triggered by unfavorable environmental conditions, limited food and space resources, and intra- or interspecific competition and predation (Bell 1991). Thus, our data suggest that river corridors are important rearing areas for bull trout during the subadult phase in their life history and that fish may rear for extended periods along their migration pathway once they encounter suitable habitat.

To the best of our knowledge, no studies have quantified distances moved by subadult bull trout in the upper Columbia River basin, which makes

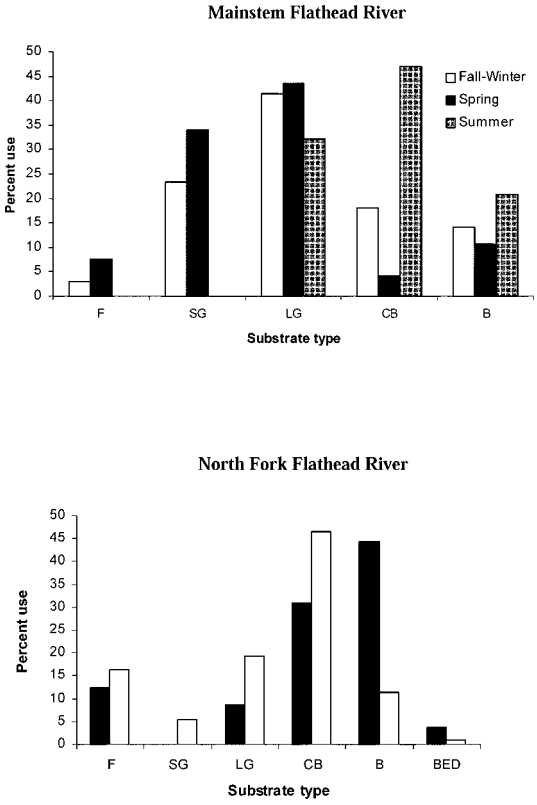

FIGURE 4.—Mean proportional use of substrate types by subadult bull trout (N = 39 fish) in the main-stem Flathead River during fall–winter, spring, and summer 1999–2002 (top panel) and use of dominant (black bars) and subdominant (white bars) substrate by type by subadult bull trout (N = 28 fish) in the North Fork Flathead River during 2000 (June–September), 2001 (May–September), and 2002 (July–September) combined (lower panel). Substrate type designations are as follows: fines (F; <0.2 cm), small gravel (SG; 0.2–0.6 cm), large gravel (LG; 0.6–7.5 cm), cobble (CB; 7.5–30.0 cm), boulder (B; 30.0–60.0 cm), and bedrock (BED).

comparisons with our work difficult. Nonetheless, we can draw inferences to movements of adult migratory bull trout (fluvial and adfluvial) populations that are relatively well documented (Bjornn and Mallet 1964; Shepard et al. 1984; Fraley and Shepard 1989; Theisfeld et al. 1996; Swanberg 1997; Brenkman et al. 2001). Bull trout migrate distances greater than 200 km between spawning streams and rearing and overwintering habitats in rivers and lakes. Fraley and Shepard (1989) found that adult migratory bull trout moved 88–250 km to spawning tributaries in the North Fork and Middle Fork Flathead rivers. Thus, we would expect that subadult migrants would have to move similar distances to rearing and overwintering areas. In our study, however, subadult bull trout moved downstream an average net distance of 33 km and a maximum total distance of 129 km. The distances moved do not represent the potential distribution and range of bull trout populations inhabiting the drainage and are likely a function of capture location because juveniles had previously moved an unknown distance from their natal tributaries before capture. Also, because tagged fish primarily moved downstream, once they entered the lake they were undetectable due to poor signal transmission caused by deep water, so the full extent of their movements could not be measured. Regardless, our results revealed greater movements than reported for stream-resident bull trout (Jakober et al. 1998) and fall in the range of migration distances reported for migratory adult bull trout populations in Montana (Swanberg 1997; Schmetterling 2003) and elsewhere throughout their range (Brenkman et al. 2001).

Our movement results are also related to life history. The upper Flathead River system harbors migratory bull trout populations that move between spawning streams and rearing and overwintering habitats in the river and lake. Migratory life history forms were formerly widespread throughout the bull trout's native range, but, unlike the Flathead River drainage, many of the remaining populations persist fragmented in headwater stream systems (Rieman et al. 1997) that limit bull trout movement. For example, Jakober et al. (1998) studied movement patterns of bull trout in two headwater streams in the Bitterroot River drainage, Montana, and found that radio-tagged bull trout moved an average net distance of about 500 m and a mean total distance of 1,375 m, which are distances far less than shown by migratory forms. Our work provides insight on life history patterns of a migratory life form that uses the entire extent of the watershed, including headwater streams, rivers, and lakes.

Our results are similar to other radio-telemetry studies that identified water temperature and stream discharge as key factors influencing bull trout migrations (Swanberg 1997; Jakober et al. 1998). We were unable to distinguish which of these variables was the primary factor related to movements because they covaried on a seasonal basis (Swanberg 1997). Nonetheless, fish began migrations in response to increased flows in the spring and as water temperatures declined in the fall and winter. Similarly, Downs and Jakubowski (2003) found that out-migration of juvenile bull

trout from Trestle Creek, a tributary to Lake Pend Oreille, Idaho, occurred primarily during high spring flows and in the fall. Temperature declines in the fall and winter can induce stream-dwelling salmonids to make extensive movements from headwater streams to larger river systems where conditions are more hospitable for overwintering (Bjornn and Mallet 1964; Bjornn 1971; Brown and Mackay 1995); water temperatures below 4–6°C stimulate winter concealment by bull trout (Goetz 1997; Thurow 1997; Bonneau and Scarnecchia 1998; Jakober et al. 1998). Migrations may also be related to photoperiod; Theisfeld et al. (1996) found that bull trout migration appeared to be related to photoperiod in the Metolius River, Oregon, as temperature and discharge were stable during the study period.

Habitat Use

Our data showed that bull trout subadults used complex daytime habitat throughout the upper river system, including deep runs that contained unembedded boulder and cobble substrates, pools with LWD, and deep lake-influenced areas of the lower river and lake. Results are consistent with previous studies that reported that juvenile bull trout are closely associated with stream substrate and cover (e.g., LWD, unembedded cobble and boulders, and undercut banks) in tributary streams (Fraley and Graham 1982; Pratt 1984; Shepard et al. 1984; Fraley and Shepard 1989; Goetz 1994; Sexauer and James 1997; Thurow 1997; Bonneau and Scarnecchia 1998; Jakober et al. 1998; Rich et al. 2003). Subadult bull trout may occupy deep complex areas of the channel during the day to maximize energy conservation (Fausch 1984), evade predation (Harvey 1991), and avoid high light intensities (Goetz 1997; Swanberg 1997; Muhlfeld et al. 2003) but are known to move to shallow shoreline areas of the river channel at night to feed (Muhlfeld et al. 2003), demonstrating the importance of habitat complexity in their early life history.

Overwintering conditions are harsh in the upper Flathead River system due to anchor and frazil ice formation. Deep, slow habitats used by subadult bull trout likely provide areas of protection from unfavorable conditions such as anchor and frazil ice formation (Chisholm et al. 1987; Brown and Mackay 1995; Jakober et al. 1998) and from potential predators and competitors (Chapman and Bjornn 1969; Harvey 1991).

Limitations of the Study

Our results suggest that subadult bull trout tagged in the North Fork that either expelled their transmitter during high spring flows or died shortly following implantation were significantly smaller and carried transmitters that constituted greater than 2% of the fish's weight. However, we did not detect high mortality and tag loss in the main stem when fish were implanted during fall and winter, indicating that high spring flow conditions and increasing water temperature may be responsible for the higher mortality observed or that smaller-sized bull trout may be especially sensitive to transmitter implantation. Recent information suggests that the ''2% rule'' should be replaced by an index with a more scientific basis for each species of interest (Brown et al. 1999). Brown et al. (1999) found that the swimming performance of interperitoneally implanted juvenile rainbow trout *Oncorhynchus mykiss* was not significantly altered by the presence of the tag or the effects of the operation even though the transmitter constituted 6–12% of the fish's weight. Additional research is needed to determine the effect of surgical implantations for various sizes of subadult bull trout under a variety of environmental conditions.

Our results are limited to larger-sized subadult bull trout. Fraley and Shepard (1989) reported that juvenile bull trout emigrated from natal tributaries to the river system from June through August at age-1 (18%), age-2 (49%), age-3 (32%), and age-4 (1%). Based on length, most of the fish that we implanted in the North Fork and main stem were likely age-3 and age-4 fish (Shepard et al. 1984; Fraley and Shepard 1989), respectively, although smaller-sized subadults (age-1 and age-2) were prevalent during electrofishing surveys (C. Muhlfeld, unpublished data). However, we were unable to implant smaller-sized fish due to body size and weight limitations. Consequently, our results may pertain to older subadult bull trout that may have recently entered the river system or that moved there previously. Additional research is needed to assess movements of age-1 and age-2 bull trout emigrants to understand fully the life history dynamics of migratory populations.

We were unable to track fish in the lake and deep portions of the lower river because deep water precluded transmitter signal detection. Our results indicate that lake environments are critical rearing and overwintering areas for migratory bull trout populations. Thus, additional telemetry stud-

ies are needed to address this unknown life history characteristic.

While we report habitat use information, habitat availability was not measured in this study. Therefore, we could not determine if habitat variables were used in proportion to resource availability to show resource selection or lack thereof (Jacobs 1974). We recommend that future research is needed to develop selectivity indices or suitability curves for subadult bull trout.

Conclusions

Habitat degradation and fragmentation are leading causes of the decline and extirpation of migratory bull trout populations throughout their range (Fraley and Shepard 1989; Rieman and McIntyre 1995; Rieman et al. 1997; Baxter et al. 1999). Maintenance of complex river habitats with abundant cover appears to be critical for the conservation of the remaining populations of migratory bull trout in Montana and elsewhere in the Columbia River basin. Land development activities that alter substrate composition and reduce the frequency and abundance of complex habitats, such as logging, road construction, fire prevention activities, grazing, mining, and construction and operation of dams, could have deleterious effects on the abundance and distribution of bull trout. Further, maintaining natural connections of suitable spawning and rearing habitat is critical to maintaining the full expression of life history forms. Barriers to fish migration such as dams, irrigation diversions, and road culverts appear to be especially detrimental to migratory bull trout. Our results elucidate the importance of maintaining natural connections and a diversity of habitats over a large spatial scale to conserve the full expression of life history and processes influencing natural dispersal of bull trout populations. Managers should seek to restore and enhance suitable habitat in river corridors and remove barriers to migration for recovery and management programs.

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