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Role of Stream Ice on Fall and Winter Movements and Habitat Use by Bull Trout and Cutthroat Trout in Montana Headwater Streams

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Abstract.—We used radiotelemetry and underwater observation to assess fall and winter movements and habitat use by bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarki lewisi* in two headwater streams in the Bitterroot River drainage, Montana, that varied markedly in habitat availability and stream ice conditions. Bull trout and cutthroat trout made extensive (>1 km) downstream overwintering movements with declining temperature in the fall. Most fish remained stationary for the remainder of the study (until late February), but some fish made additional downstream movements (1.1–1.7 km) in winter during a low-temperature (≤1°C) period marked by anchor ice formation. Winter movement was more extensive in the mid-elevation stream where frequent freezing and thawing led to variable surface ice cover and frequent supercooling (<0°C). Habitat use of both species varied with availability; beaver ponds and pools with large woody debris were preferred in one stream, and pools with boulders were preferred in the other. Trout overwintered in beaver ponds in large (N = 80–120), mixed aggregations. In both streams, both species decreased use of submerged cover following the formation of surface ice. Our results indicate that (1) continued activity by trout during winter is common in streams with dynamic ice conditions and (2) complex mixes of habitat are needed to provide suitable fall and winter habitat for these species.

Populations of bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarki lewisi* have declined substantially throughout their native ranges (Liknes and Graham 1988; Rieman and McIntyre 1993). Though migratory (fluvial and adfluvial) life history forms were formerly common, as a result of fragmentation and loss of habitat and of competition and hybridization with nonnative salmonids, many remaining populations persist as nonmigratory ''resident'' forms confined to headwaters (Ziller 1992; Rieman and McIntyre 1993). Little is known about movement patterns and habitat preferences of these headwater populations.

We focused on defining the fall and winter movement and habitat use in headwater populations of bull trout and cutthroat trout because this period is considered limiting to salmonids (Cunjak 1996). Movement of stream-resident salmonids is especially common in the fall as fish seek suitable overwintering sites in response to declining water temperatures (Bjornn 1971; Cunjak 1996) and suitable spawning sites in the case of fall-spawning salmonids like bull trout (Elle 1995). Extent of movements may vary widely, from 0 to more than 100 km, depending on life history form and habitat availability (Bjornn and Mallet 1964; West et al. 1992; Brown and Mackay 1995).

Several investigators have hypothesized that subsurface ice formation and groundwater influx are major factors determining habitat suitability and carrying capacity for salmonids in many ice-covered streams (Maciolek and Needham 1952; West et al. 1992; Brown and Mackay 1995; Cunjak 1996). However, this hypothesis remains largely untested since most winter studies have focused on streams that remain relatively ice-free. In the ice-covered Ram River, Alberta, Brown and Mack-

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ay (1995) reported that some cutthroat trout underwent complex, two-stage movements during fall and winter. During ‘‘first-stage’’ movements in mid-September, fish moved in response to declining temperature up to 3 km to overwinter habitats of deep pools with cover of woody debris or undercut banks. Later in the fall, subsurface (frazil and anchor) ice formed in these sites, adhering to cover and filling pools, which triggered ‘‘second-stage’’ movement by trout for several kilometers to groundwater-fed sites and other areas lacking subsurface ice. Winter severity for salmonids may be determined more by degree of subsurface ice formation rather than by temperature (Chisholm et al. 1987; Berg 1994; Brown et al. 1994). Thus, the harshest winter conditions may occur where incomplete surface ice cover results in extensive anchor and frazil ice formation (Maciolek and Needham 1952; Chisholm et al. 1987).

In the Bitterroot River drainage, Montana, bull trout and cutthroat trout persist in two types of low-order streams that differ markedly in habitat availability and winter ice conditions. Small, high-elevation streams are characterized by abundant large woody debris (LWD) and extensive surface ice in winter; moderate-sized, mid-elevation streams are characterized by fluctuating surface and subsurface ice and boulder–cobble substrate. To better define critical habitat needs to aid protection and recovery of these species, we examined seasonal habitat use and movement, particularly the timing and magnitude of movements in response to differing stream ice conditions.

Study Area

We examined two streams that typify sites where both species persist in headwater populations. Meadow Creek was a high elevation, third-order tributary to the East Fork of the Bitterroot River near Sula, Montana. Wetted width in the study area averaged 2–3 m at base flow, mean elevation was 1,818 m, and average gradient was 2.1%. Large woody debris ($>$10 cm in diameter and $>$2 m in length) was abundant (116 pieces/100 m) and substrate was primarily gravel and cobble with few boulders (23/100 m; Jakober 1995). Pools and beaver ponds were the most common habitat types (36% and 40%, respectively, of the total surface area). The stream was almost entirely covered with surface ice from early November through late March.

Daly Creek, located about 33 km north of Meadow Creek, was a moderate-sized (5–7 m wide), mid-elevation, fourth-order tributary to Skalkaho Creek, a major tributary to the Bitterroot River near Hamilton, Montana. The average gradient in the study area was 4.1% and mean elevation was 1,424 m. Riffles and glides were the predominant habitat type (77% of surface area), and LWD was about 50% less abundant than in Meadow Creek (67 pieces/100 m). No beaver ponds were present, and substrate was primarily boulders (250/100 m) and cobble. Surface ice fluctuated markedly during the winter in response to frequent freezing and thawing events, and anchor and frazil ice were common.

In each stream we established a 2-km study section located near the lower limit of bull trout distribution. Cutthroat trout and brown trout *Salmo trutta* were the predominant salmonids downstream. There were no barriers to movement for at least 6 km upstream from study reaches. In Meadow Creek, fish had unimpeded access to the mainstem Bitterroot River 16 km downstream; in Daly Creek, a low-head irrigation dam and dewatering 15 km downstream created a seasonal barrier to migration.

Methods

Movements and habitat use were assessed by a combination of radiotelemetry and underwater observation to balance the advantages and limitations of each sampling approach (Alldredge and Ratti 1986).

Radiotelemetry.—We used radio transmitters to monitor movements of 18 bull trout and 6 cutthroat trout from late August 1992 through February 1993. Because fish from these headwater populations typically were less than 300 mm in total length, we were limited to small transmitters with 90-d battery lives. We therefore monitored movements of two sets of radio-tagged fish during two different time periods. To assess spawning movement of bull trout, only this species was radio-tracked during the fall phase (28 August–13 November), whereas both species were tracked during the winter phase (31 October–24 February).

We captured fish by electrofishing within the 2-km study reaches. Four bull trout (mean total length, 282 mm; range, 242–434 mm) were radio-tagged in each stream in late August 1992 to assess fall movements. In late October 1992, ten more bull trout (four in Meadow Creek and six in Daly Creek; mean length, 281 mm; range, 231–317 mm) and six cutthroat trout (four in Meadow Creek and two in Daly Creek; mean length, 273; range, 234–330 mm) were radio-tagged to assess winter movements.

Fish were anesthetized with tricaine methanesulfonate (MS-222), weighed, and measured, and radio transmitters were surgically implanted via a 1–2-cm incision in the peritoneal cavity immediately anterior to the pelvic girdle. Fish were also tagged with colored Floy tags. Surgery lasted about 10 min, and no mortalities occurred during surgery or the 1-h recovery period prior to release near the capture site.

Transmitters (dimensions, 40 × 13 mm; Custom Telemetry, Athens, Georgia) had an internal loop antenna and emitted a unique frequency from 40.4 to 40.5 mHz. Transmitter weight (5 g in air) ranged from 0.9 to 4.9% (mean, 2.9%) of body weight. Moser et al. (1990) found that small radio-tagged coho salmon *O. kisutch* (150–211 mm, total length) exhibited normal behavior and swimming performance when transmitter weights were less than 5% of body weight. However, we violated the ''2% rule'' (Winter 1983) of transmitter weight to body weight for 18 of 24 radio-tagged fish; therefore, using simple linear correlation, we compared total distance moved by individual fish with percent transmitter weight, and we compared movement distance of fish with transmitter weights above and below 2% of body weight with a *t*-test (Zar 1984).

A receiver and hand-held bidirectional loop antenna were used to locate radio-tagged fish. Signal range was about 500 m, and signals were first located by driving along roads located within 200 m of the streams. Fish location was then triangulated from along the streambank. Location accuracy, tested by triangulating the location of a hidden transmitter, was about 1 m^2 within 10 m, and all fish locations were made within this distance. Signal strength was not attenuated by snow or ice. When transmitters could not be found within 1 km of last location, we tracked 3–16 km upstream and downstream from the last known position to relocate fish that had moved or to verify that batteries had expired.

Radio-tagged fish were located at least twice per week during fall and once per week during winter for a total of 327 observations in 180 d. To meet the assumption of independence for radio-tracking studies, a minimum of 48 h elapsed between relocations (Alldredge and Ratti 1986). For each relocation, we recorded the distance and direction moved from the original point-of-release and last location and also the habitat type used. Movement was computed as (1) the sum of the distances a fish traveled between consecutive locations (total distance) and (2) the distance between point of release and final location (net distance). Movement data were grouped as the mean total movement of all relocations per week. We compared total and net distances moved among seasons by using a *t*-test and determined the proportion of fish that moved more than 100 m with a χ^2 test (Zar 1984). Bull trout were recorded as having spawned if they were observed spawning or near a known redd site.

Habitat was classified according to type, as modified from Bisson et al. (1988): riffle, glide, pool with LWD, pool with boulders, pool lacking LWD or boulders, pocket water (small pools formed by boulders within riffle or glide), and beaver pond. Habitat availability was determined by measuring the lengths of all habitat units between the uppermost and lowermost fish locations within each stream and then calculating the percent composition of each habitat type. Habitat availability during fall was measured at base flow from late September to early October 1993. In Meadow Creek, fall and winter habitat availabilities were assumed to be similar because flows were stable and anchor ice dams were uncommon. In Daly Creek, winter habitat availability varied with streamflow and frequently changing ice conditions. Therefore, we measured winter habitat for three different ice conditions during December: low, less than 5% surface ice and no formation of anchor ice dams; moderate, 5–75% surface ice with anchor ice damming uncommon; and extensive, more than 75% surface ice and anchor ice dams common. We used the average of the three values as our estimate of availability. Surface ice was estimated visually during radio-tracking. We compared habitat use with availability according to the protocol of Byers et al. (1984). Bonferroni confidence intervals were calculated for habitat use data, and preference or avoidance was judged to occur if the confidence interval did not overlap the proportion of each habitat type available. We measured water temperature with electronic thermographs (measured every 4.8 h; accuracy, 0.7°C; range, −20°C to 70°C) or with maximum–minimum thermometers (fall 1992 in Meadow Creek only).

Underwater observation.—To further assess seasonal habitat shifts and preferences, we made repeated underwater fish counts by using a dry suit, mask, and snorkel during September–December 1993. Fish were counted by entering the downstream end of a habitat unit and slowly moving upstream in a zigzag fashion. We classified fish by size categories of 50–100 mm, 101–200 mm, and greater than 200 mm. Because we observed few fish longer than 200 mm, we could not directly compare habitat use with our larger, radio-tagged fish. Bull trout and cutthroat trout exhibit concealment behavior in winter (Griffith and Smith 1993; Thurow 1997), thus we overturned stones and used a dive light to illuminate areas beneath LWD, streambanks, and ice ledges. Fish exhibited low fright response to the light.

We sampled 41 habitats in Meadow Creek and 29 habitats in Daly Creek. Sampled habitats were chosen randomly, and a minimum of five replicates of each habitat type were surveyed. Nine counts (5 day, 0930–1600 hours, and 4 night, 1930–0400 hours) were made in Meadow Creek from 1 September to 28 October; extensive surface ice prevented further surveys. Ten counts (5 day, 5 night) were made in Daly Creek from 7 September to 15 December. In all habitat types except beaver ponds, we confined our analyses to night counts. Fish were concealed during the day, and day counts underestimated electrofishing removal estimates by 70–95% ($N = 10$), whereas night counts were within 35% of removal estimates (Jakober 1995). Beaver ponds lacked submerged cover, and day and night counts were similar.

We observed 192 bull trout and 1,935 cutthroat trout in Meadow Creek, and 254 bull trout and 608 cutthroat trout in Daly Creek during night counts. We determined habitat use with the equation of Bisson et al. (1988):

$$\text{habitat use index} = (D_h - D_t)/D_t,$$

where D_h is the mean density of fish in a habitat type, and D_t is the mean density of fish in all habitat types combined. Positive scores indicated selection and negative values indicated avoidance. We compared fall (>4°C) with winter (≤4°C) habitat use; 4°C was the division between seasons because most overwinter movement occurred when mean temperatures dropped below this level. This temperature drop occurred on 27 September for Meadow Creek and 1 November for Daly Creek.

Results

Movement

Fish were radio-tracked an average of 67 d in fall (range, 53–82 d) and 100 d (range, 28–119 d) in winter. Nearly all radio-tagged fish were observed at least once from the streambank or during underwater censuses. Surgery scars healed quickly, and fish were behaving normally when observed. Each fish was located an average of 13 times (range, 5–18), and 21 of the 24 radio-tagged fish were successfully tracked until battery expiration. The three lost transmitters were found in mink dens along streambanks 28–53 d after implantation.

The 18 bull trout monitored from 31 August 1992 to 24 February 1993 moved a mean total distance of 1,375 m from the point of release (range 6–11,968 m). Mean net movement distance was not significantly different between the two streams (Meadow Creek mean, 588 m; Daly Creek mean, 980 m; $t = 0.9$, $P = 0.4$). Unlike bull trout, only two cutthroat trout (33%) moved more than 75 m (mean 81 m, range 1–332 m). Net movement was predominantly downstream (72% of bull trout, 83% of cutthroat trout).

We found no effect of transmitter weight on total distance moved by season ($r < 0.7$, $P > 0.4$) or by species with transmitter weights greater or less than 2% of body weight ($t = 0.6$, $P = 0.5$). Fish longer than 285 mm ($N = 10$) also showed no significant tendency to move greater distances than fish less than 285 mm ($N = 12$; $U = -1.9$, $P = 0.06$); indeed, one of the smaller tagged fish (242 mm) moved the longest distance (12,890 m).

Spawning and fall phase movement.—Three of eight bull trout tagged in the fall moved upstream (mean, 211 m; range, 62–337 m) and spawned in pool tailouts in early to late September (Figures 1, 2). After spawning, bull trout in Meadow Creek (Figure 1) moved a mean distance of 1,179 m (range, 467–12,890 m; $N = 4$) downstream to overwinter areas, whereas bull trout in Daly Creek moved relatively little (mean distance, 96 m; range 10–319 m; Figure 2). One bull trout in Meadow Creek exhibited a fluvial life history, moving 12,890 m downstream after spawning to the East Fork of the Bitterroot River (including movements of 4.9 km in 3 d), where it remained for 10 d prior to loss of signal. Even excluding movement by this fluvial fish, bull trout in Meadow Creek averaged 10× greater net distance (916 versus 96 m, $t = 3.1$, $P = 0.03$) and 3× greater total distance (1,363 versus 328 m, $t = 2.8$, $P = 0.04$) than bull trout averaged in Daly Creek. Bull trout in Meadow Creek also showed significantly more long-distance (>100 m) movement than bull trout showed in Daly Creek (28% versus 5%; $\chi^2 = 16.7$, $P < 0.001$). Peak movement in Meadow Creek (Figure 1) occurred from 21 September to 10 October, when mean weekly movement was greater than 200 m. During this period, bull trout moved downstream an average of 486 m (range, 290–706 m) to a series of beaver ponds. These fish then remained in the ponds to the end of fall tracking in early November.

Weekly underwater counts in Meadow Creek

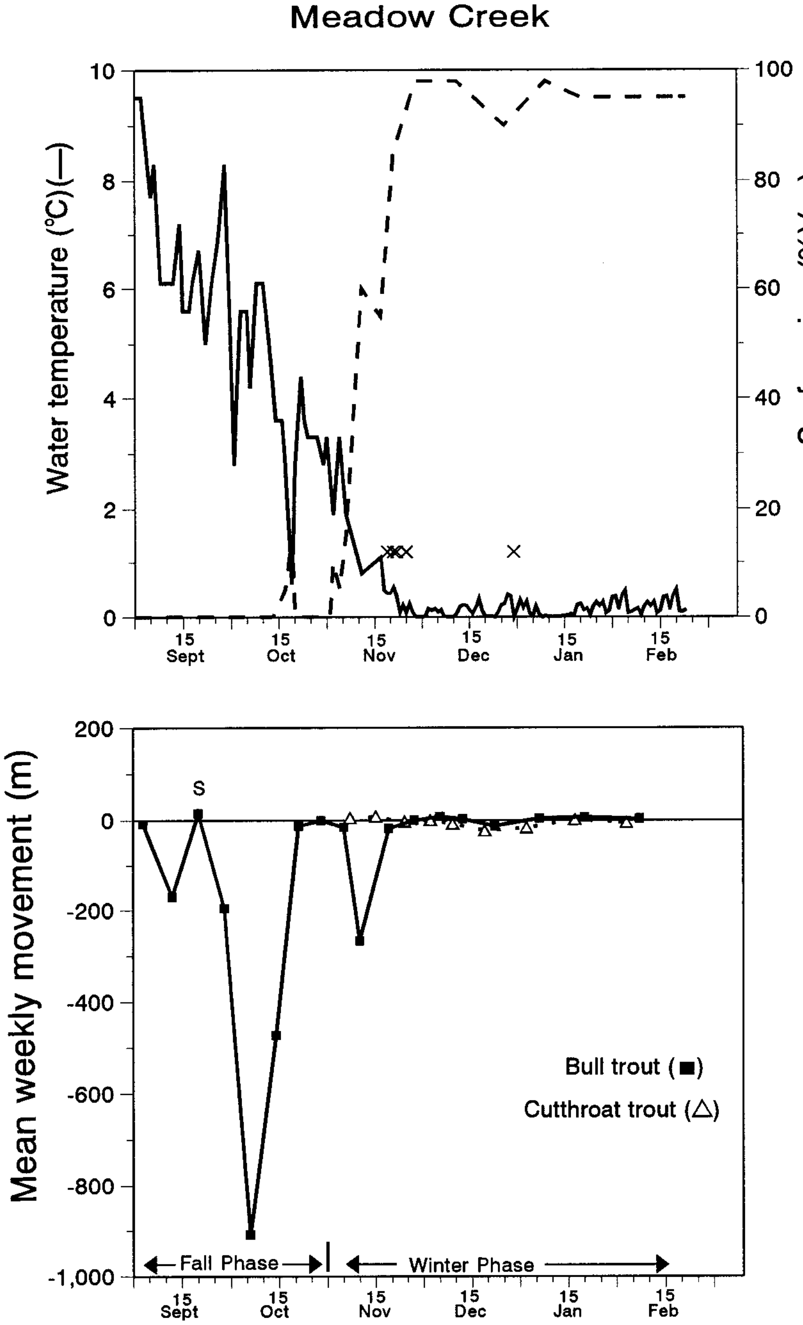

FIGURE 1.—Mean weekly distance moved by bull trout and cutthroat trout during fall and winter radio-tracking phases in relation to mean daily water temperature and surface ice cover in Meadow Creek, Montana; S indicates spawning; ×s indicate days with supercooled water temperatures (<0°C).

beaver ponds during fall 1993 (1 September–28 October) showed a similar pattern of downstream movement with declining temperature. Cutthroat trout numbers increased more than fourfold (*N* = 93–416) and bull trout numbers doubled (*N* = 12–25) in Meadow Creek beaver ponds, with the greatest increase (65–140%) observed in late September when mean daily temperature declined to be-

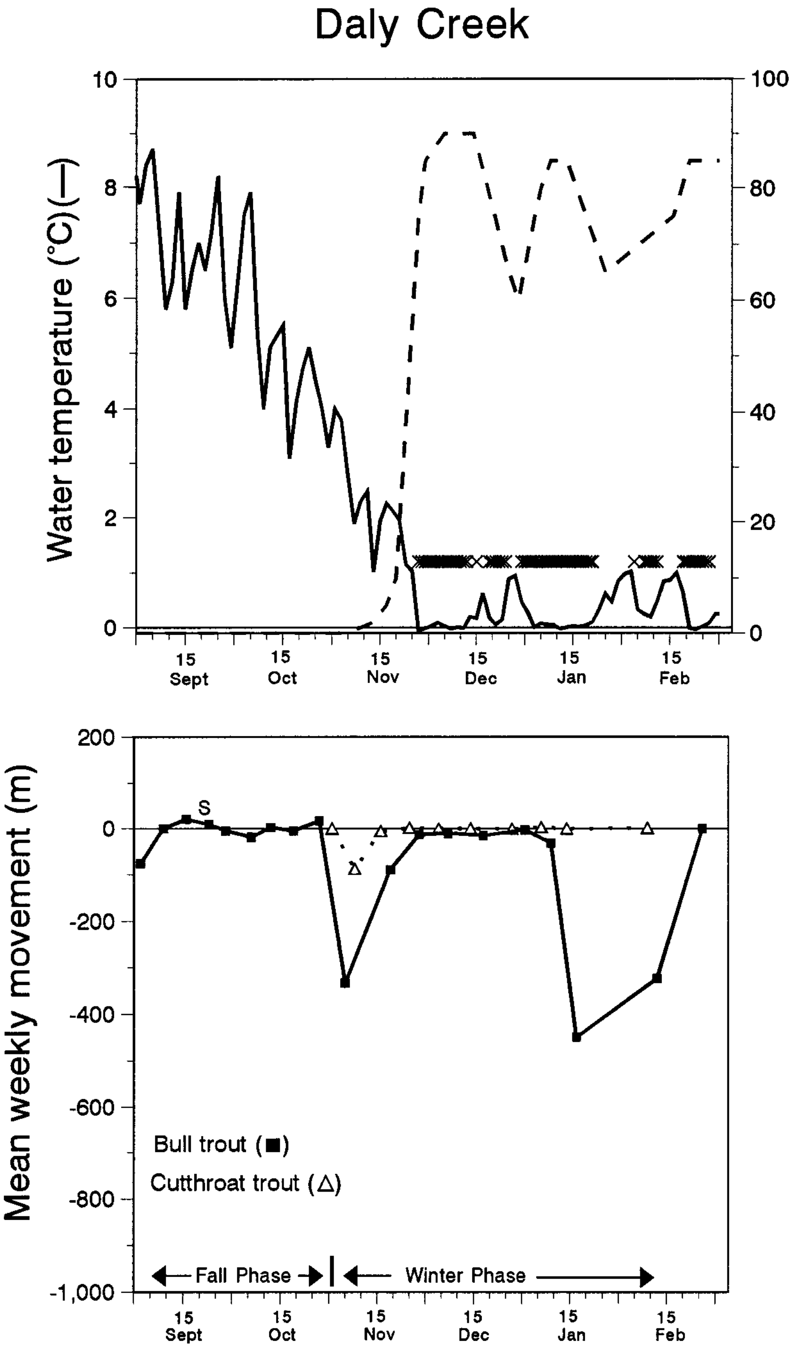

FIGURE 2.—Mean weekly distance moved by bull trout and cutthroat trout during fall and winter radio-tracking phases in relation to mean daily water temperature and surface ice cover in Daly Creek, Montana; S indicates spawning; ×s indicate days with supercooled water temperatures (<0°C).

low 4°C and minimum temperature was below 1°C. Both species overwintered at these sites in large ($N = 80–120$) aggregations made up of about 90% cutthroat trout and 10% bull trout.

Winter phase movement.—In winter, bull trout movement exhibited an opposite pattern from the fall. Bull trout in Meadow Creek (Figure 1) moved little, whereas those in Daly Creek (Figure 2) moved to overwintering sites at distances similar in magnitude to those displayed by Meadow Creek fish in September. Bull trout in Daly Creek moved an average of 4.5× greater net (1,506 versus 341 m, $t = 2.4$, $P = 0.05$) and 4.5× greater total (1,773 versus 388 m, $t = 2.7$, $P = 0.04$) distance than bull trout moved in Meadow Creek, and they displayed a significantly greater proportion of long-distance (>100 m) movement (26% versus 7%; $\chi^2 = 17.7$, $P < 0.001$). Fish moved to overwinter sites in early November and then moved little for the next 2 months. In mid-January, two of four radio-tagged bull trout then moved more than 1 km (range, 1.1–1.7 km). Such mid-winter movements did not occur in Meadow Creek; the only significant movement occurred in mid-November during rapid cooling and surface ice formation, when two of four radio-tagged fish moved 180–1,024 m downstream (Figure 1).

Cutthroat trout overwintered within 30 m (range, 1–84 m) downstream from their point of release in Meadow Creek (Figure 1) and within 185 m (range, 34–332 m) in Daly Creek (Figure 2). In Daly Creek, downstream movement by cutthroat trout coincided with initial overwintering movement by bull trout in November.

Factors affecting movements.—Changes in temperature and surface ice cover appeared to influence timing and magnitude of movement in both streams. Movement to overwintering sites in Meadow Creek commenced in mid-September as daily average and daily minimum temperatures declined to below 6°C and 3°C, respectively (Figure 1). Additional movement occurred in early November as minimum water temperatures declined to 0°C and surface ice formed. Water temperature remained stable and fish moved little for the remainder of the winter tracking period. Surface ice formed rapidly in Meadow Creek and remained near 100% throughout winter. Snow 10–70 cm deep insulated the surface ice, and only 5 nights with supercooled water temperatures (<0°C) were recorded during winter tracking despite air temperatures of −20°C to −35°C.

Water temperatures were generally warmer but more variable in Daly Creek (Figure 2). Initial overwinter movement began in early November, about 6 weeks later than in Meadow Creek. Fish moved when daily average and daily minimum temperatures declined to below 4°C and 2°C, respectively. In winter, surface ice fluctuated between 60–90%, periods of supercooling (<0°C) were frequent (52 d), and frazil and anchor ice were common. Mid-winter movement greater than 1 km by bull trout occurred during an extended period of supercooling, when temperatures were 1°C or lower and extensive subsurface ice formation caused habitat exclusion and formation of large anchor ice dams.

Habitat Use

In both streams, radio-tagged bull trout strongly selected pools and avoided fast-water habitats in fall and winter (Figure 3). Seasonal habitat selection reflected differences in habitat availability between study streams. In the fall, bull trout in Meadow Creek selected primarily beaver ponds and pools with LWD, but primary habitat shifted to beaver ponds and pools lacking LWD or boulders after surface ice formed. Daly Creek lacked beaver ponds and extensive surface ice, and bull trout selected pools with LWD and boulders during fall and winter. Radio-tagged cutthroat trout also avoided fast-water habitats in winter, selecting pools with LWD in Meadow Creek, and pocket water in Daly Creek.

Bull trout and cutthroat trout that were observed underwater at night (Figure 4) generally showed less selection for habitats with submerged cover than did radio-tagged fish located during the day (Figure 3). Both species were often observed aggregated at night more than 1 m from cover. In Meadow Creek, bull trout and cutthroat trout were most abundant in beaver ponds and in pools lacking LWD or boulders during both fall and winter, whereas radio-tagged fish used beaver ponds and pools with LWD extensively. In Daly Creek, both species strongly selected glides and pools with LWD and showed little selection of pocketwater or pools with boulders, unlike the radio-tagged fish. Bull trout showed no strong seasonal shifts from fall to winter in either creek. Cutthroat trout used beaver ponds more (Meadow Creek) and glides less (Daly Creek) as temperature declined.

Discussion

Seasonal Movement

In Meadow and Daly creeks, radio-tagged bull trout moved an average net distance of more than 500 m and peak weekly movement exceeded 200

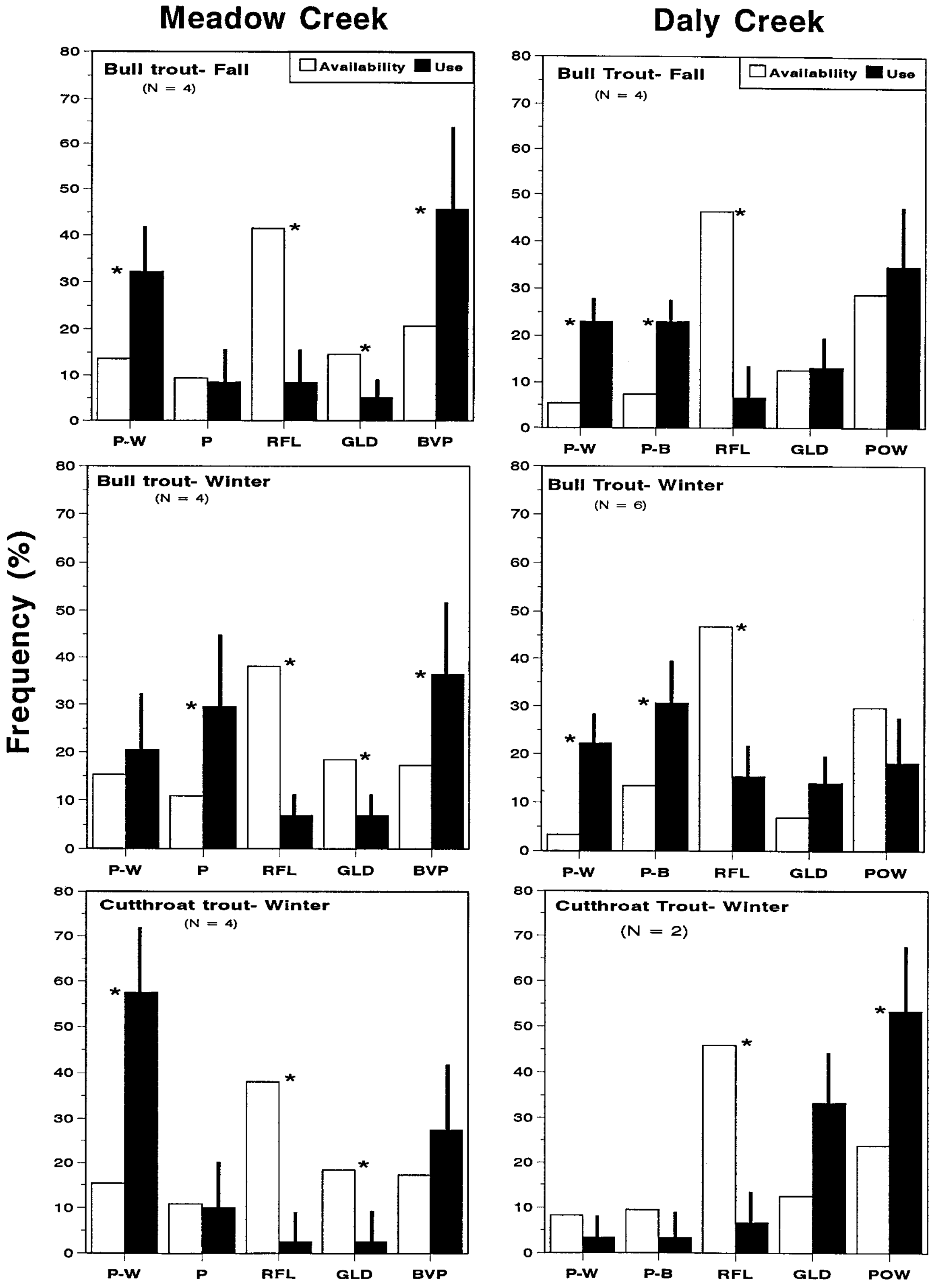

FIGURE 3.—Percent use by bull trout and cutthroat trout of available habitats during fall (1 September–31 October 1992) and winter (1 November 1992–24 February 1993) radio-tracking phases in Meadow and Daly creeks, Montana.

m. Movement followed a general pattern of upstream spawning movement in September, downstream movement to overwintering sites in late September–early November, and for some fish, additional movement downstream in mid-winter in response to changing stream ice conditions. Though radio-tagged cutthroat trout generally moved much less than bull trout during winter (mean 30–185 m), some Floy-tagged fish in Meadow Creek moved 1–2 km to overwinter sites in early October (Jakober 1995).

Distances moved by bull trout and cutthroat trout in our study were much greater than reported in most previous studies of stream resident (nonfluvial) salmonids (see Gowan et al. 1994). Based on recapture of marked fish, Miller (1957) and Heggenes et al. (1991) reported home ranges or average net movements of less than 20 m in cutthroat trout. Using radio-tracking, Young (1996) found that cutthroat trout occupying small streams in Wyoming had median home ranges of 223 m and a peak weekly movement of 50 m, less than half of the movement recorded in our study. Contrasting results from salmonid movement studies have largely been attributed to differences in methods used to measure movement; radio-tracking studies, for example, tend to show much greater movement than do traditional mark–recapture designs (Gowan et al. 1994; Young 1994). However, differences in timing of sampling probably also account for contrasting results on the extent of movement among stream-resident salmonids. Bjornn (1971) provided early evidence that declining temperatures in the fall trigger significant habitat shifts and movement in stream salmonids. However, the majority of salmonid movement studies have sampled during the spring–summer period (e.g., Miller 1957; Heggenes et al. 1991; Young 1996) when conditions are generally more stable and favorable. Our results and those of Brown and Mackay (1995) indicate that extensive movement (>500–1,000 m) may be common among stream-resident salmonids during dynamic conditions encountered during fall and winter periods.

Though fall and winter movement of 1 km was common in our study, these movements are far less than that shown by migratory life history forms. Fluvial and adfluvial bull trout and cutthroat trout may move more than 100 km between spawning tributaries and large rivers or lakes used for rearing and overwintering (Bjornn and Mallet 1964; Fraley and Shepard 1989; Elle 1995; Swanberg 1997; Thiesfeld et al. 1996). Migratory bull trout commonly begin spawning migrations in June, entering spawning tributaries about 2 months prior to spawning in September, and returning to downstream overwintering sites soon after spawning (e.g., Fraley and Shepard 1989; Swanberg 1997). Bull trout in our study spawned at a similar time, but spawning movements were much reduced (62–337 m) compared with migratory fish. Though some spawning movement may have occurred prior to late August, we believe spawning migrations were less than 1 km for most Daly Creek and Meadow Creek bull trout because they were rarely observed downstream from where we initially radio-tagged fish. Historically, fluvial bull trout were much more prevalent in the Bitterroot drainage and probably conducted much more extensive spawning migrations. Downstream movement of 12–30 km by one radio-tagged and one Floy-tagged bull trout (Jakober 1995) suggests a small remnant population of fluvial bull trout in Meadow Creek. We found no evidence for fluvial fish in Daly Creek, where extensive dewatering and diversion dams in lower Skalkaho Creek disrupt migration routes and minimize the chance of survival of fluvial fish.

Fall and winter movement of bull trout generally conformed to the two-stage pattern first described by Brown and Mackay (1995) for cutthroat trout in ice-covered Alberta streams. First-stage movements in fall coincided with declining water temperatures and were probably the result of a shift to concealment behavior by stream salmonids at the onset of winter temperatures (Griffith and Smith 1993; Thurow 1997). The 6-week divergence in timing of first-stage movement of bull trout in our two study streams appeared to reflect different temperature regimes associated with elevational differences. Initial overwinter movements commenced at mean temperatures of 4–6°C and minimum temperatures less than 2°C just prior to surface and subsurface ice formation.

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Vertical bars indicate a 95% confidence interval above means. Significant difference ($P < 0.05$) between percent use and availability is shown by an asterisk (*). Habitat type designations: P–W = pool with woody debris; P = pool without cover; RFL = riffle; GLD = glide; BVP = beaver pond; P–B = pool with boulders; and POW = pocket water. Note that availability of habitat types varied by stream.

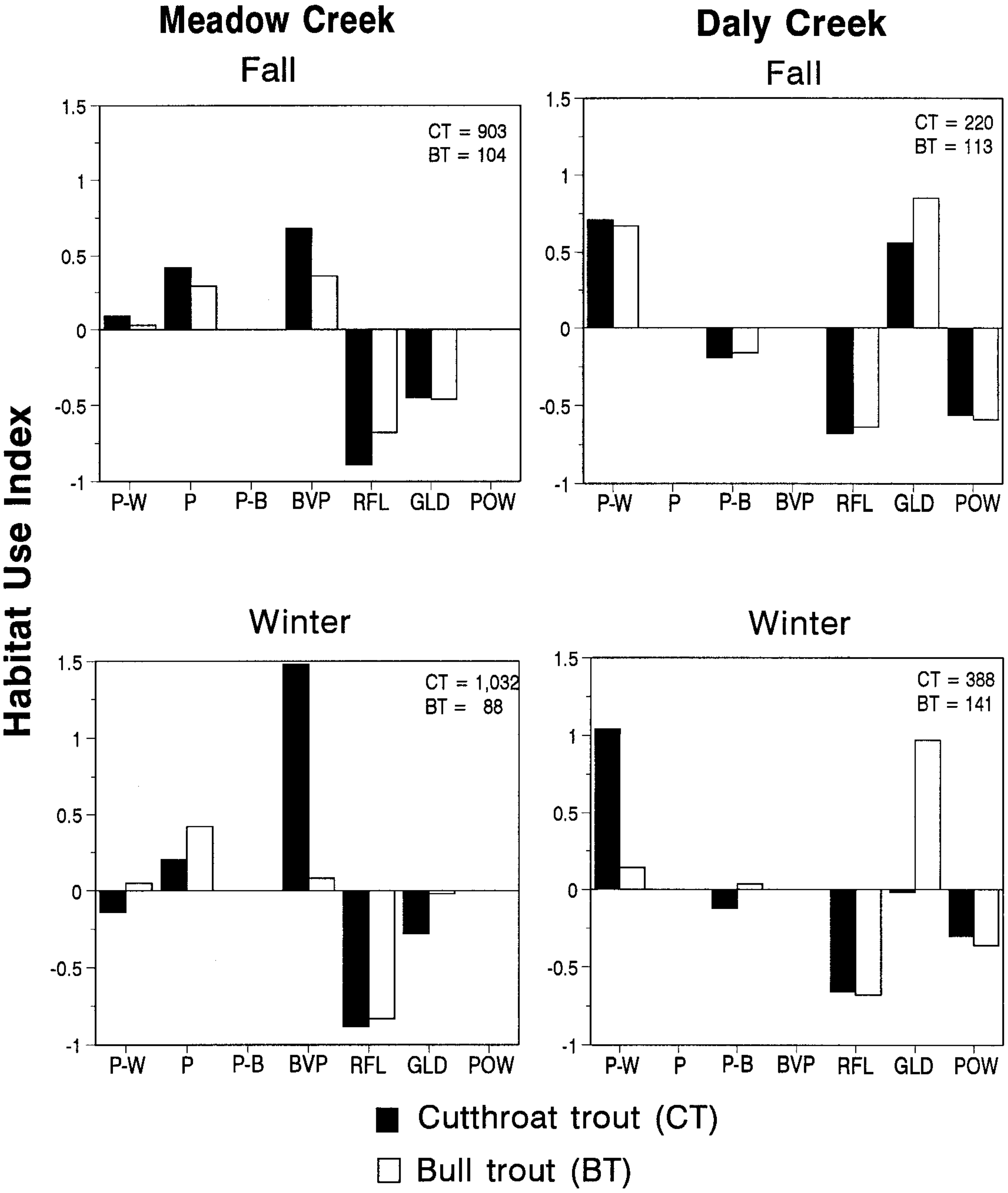

FIGURE 4.—Influence of habitat type on the index of habitat use by bull trout and cutthroat trout observed during underwater counts at night during fall and winter 1993. Habitat type abbreviations are defined in Figure 3.

After first-stage movements most fish moved little, but about one-third of bull trout underwent another significant shift, including mid-winter movement in Daly Creek of more than 1 km at temperatures of 1°C or lower. As did Brown and Mackay (1995), we found that habitat exclusion of preferred cover habitats triggered second-stage movement. At the mid-elevation (Daly Creek) site, frequent supercooling caused ice filling of pools and undercut banks and formation of anchor ice dams, which led to large fluctuations in water depth and pool area. In contrast, second-stage movement was less common in Meadow Creek, despite colder temperatures, because more complete ice cover moderated temperature fluctuations and limited supercooling and anchor ice formation. Thus, in streams lacking anchor ice, stream salmonids move little following the initial overwinter habitat shift, but continued activity appears common in streams with dynamic ice conditions (Chisholm et al. 1987; Berg 1994; Brown et al. 1994).

Our results support the hypothesis that streams with more variable temperatures and ice cover provide more adverse overwintering conditions than sites that are completely ice covered throughout the winter (Chisholm et al. 1987; Brown and Mackay 1995). Though overwinter mortality of salmonids typically increases at colder temperatures (Hunt 1969; Smith and Griffith 1994), high winter temperature flux may be more physiologically stressful (Cunjak 1988). High mortality of trout has been observed during the formation and breakup of anchor ice dams due to stranding, ice collapse, and physical abrasion from suspended ice particles (Maciolek and Needham 1952; Brown et al. 1994). In streams subject to frequent freezing and thawing, supercooling promotes formation of frazil and anchor ice in large areas (Maciolek and Needham 1952; Chisholm et al. 1987; Brown et al. 1994; Cunjak and Caissie 1994). Movement to areas with low temperature flux (e.g., ice-covered beaver ponds, groundwater-fed sites; Chisholm et al. 1987; Brown and Mackay 1995; Cunjak 1996; this study) probably enhances overwinter survival.

Habitat Use

Habitat use by bull trout and cutthroat trout varied with type of habitat available in each stream. In Meadow Creek, beaver ponds and pools with LWD were the preferred habitats of radio-tagged fish, whereas bull trout selected pools with boulders and LWD in Daly Creek. These observations concur with the strong preference by salmonids for winter habitats offering depth, low velocity, overhead shading, and lateral concealment (McMahon and Hartman 1989; Griffith and Smith 1993). Both species showed an increased preference for sites with less submerged cover (beaver ponds and pools lacking LWD) following the formation of surface ice. Brown and Mackay (1995) observed a similar decrease in submerged cover use by cutthroat trout from fall to winter and attributed this change to habitat exclusion due to anchor ice formation. They concluded that LWD and boulders were preferred, but sites containing abundant submerged cover were later abandoned because of the tendency for these sites to accumulate frazil and anchor ice during supercooling periods. Reduced use of submerged cover in ice-covered streams also may be related to a lowering of predation risk from aerial predators with increased ice cover (Gregory and Griffith 1996).

Though differences in sample size and fish size could have played a role, we believe diel habitat shifts more likely accounted for the differences in seasonal habitat use found between day radio-tracking and night underwater observations. At night, bull trout and cutthroat trout showed a higher selection for glides and a lower selection for pools with boulders or for pocket water (Daly Creek) than during the day. During winter, salmonids exhibit a diel shift from concealment in cover during the day to night feeding positions in areas of reduced cover (Griffith and Smith 1993; Thurow 1997).

Beaver ponds were important winter habitat for both bull trout and cutthroat trout in Meadow Creek. Favorable winter habitat characteristics of beaver ponds include overhead ice cover, deep and slow water, a lack of anchor ice, and stable water temperatures (Chisholm et al. 1987). Beaver ponds are preferred overwintering sites for salmonids in diverse habitats, including brook trout *Salvelinus fontinalis* occupying high-elevation, snow-dominated streams (Chisholm et al. 1987) and coho salmon and Dolly Varden *Salvelinus malma* occupying coastal, rain-dominated streams (Dolloff 1987). Previous studies also have found that sites of groundwater upwelling are important overwintering habitats, especially where anchor ice is common (Brown and Mackay 1995; Cunjak 1996), but we did not detect this habitat feature in our study streams.

Conclusions

Our results complement recent radio-tracking studies, demonstrating that stream-resident salmonids may undergo complex and lengthy seasonal movements (Brown and Mackay 1995; Young 1996). During fall and winter, periods of little movement are interspersed with short periods of extensive movement in response to declining temperatures and increasing ice formation. Greater knowledge of factors affecting frazil and anchor ice formation appears key to understanding the dynamics of winter habitat use, movements, and survival of fishes in ice-covered streams (Brown et al. 1994; Brown and Mackay 1995; Cunjak 1996). Even at temperatures near freezing, movement and habitat shifts may be a common occurrence in stream salmonids. These findings have important implications for defining suitable habitat and for assessing response to management actions, including placement of barriers for protecting native salmonids from invasion by nonnative species (Young 1994; Brown and Mackay 1995; Cunjak 1996).

Complex mixes of habitat are needed to maintain suitable fall and winter habitat for stream-resident bull trout and westslope cutthroat trout populations. Beaver ponds, deep pools, and submerged cover of LWD, boulders, and undercut banks are important components of this mix. Bull trout appear particularly susceptible to loss of habitat complexity. In the Bitterroot River drainage, bull trout are rare in watersheds with a high degree of disturbance (Clancy 1993) and without LWD or pools (Rich 1996). Shallow, wide streams not only lack suitable winter cover, but also promote subsurface ice formation (Chisholm et al. 1987; Brown et al. 1994). In degraded areas, activities that moderate fluctuations in winter stream temperature (i.e., riparian vegetation restoration) and that create deep water habitats (i.e., beaver reintroduction) may help alleviate poor winter habitat conditions.

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