Autumn and winter movement and habitat use of resident bull trout and westslope cutthroat trout in Montana
by Michael Joel Jakober

A thesis submitted in partial fulfillment of the requirements for the degree Of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
Autumn and winter movements and habitat use of resident bull trout and westslope cutthroat trout were investigated using radiotelemetry and snorkeling. Movement occurred in two distinct stages and was closely tuned to unique stream icing conditions. As autumn water temperatures declined, bull trout moved downstream into beaver ponds and pools containing complex large woody debris (LWD). Bull trout remained in these habitats throughout winter in streams lacking anchor ice. With extensive anchor ice formation, however, bull trout abandoned autumn pool habitats and moved further downstream in search of favorable overwintering habitats. Westslope cutthroat trout moved little (< 100 m) , preferring to overwinter in LWD-dominated pools near summer habitats. Beaver ponds and deep pools offering combinations of LWD and large substrate were critical overwintering habitats for both species. Trout exhibited different diel behavioral strategies during winter. During the day, small trout concealed in LWD and substrate interstices. Trout too large to find suitable hiding cover aggregated in deep pools. At night, fish of all sizes moved into the water column away from cover. Both species selected nighttime focal points closer to the substrate, further from cover, in shallower water, and in slower velocities than daytime positions. Although cutthroat trout preferred winter focal positions higher in the water column than bull trout, microhabitat use was similar for both species. As water temperature declined below 7 C, daytime trout densities declined in all habitats except beaver ponds. Pond densities dramatically increased as large aggregations (> 100 cutthroat and bull trout) formed prior to winter ice cover. Winter night densities were 5-6 times greater than winter day densities. Preferred winter habitats possessed extensive cover, low velocity flow (< 10 cm/s), and depth (> 50 cm) . Complex LWD accumulations were an important winter hiding cover for both species regardless of stream size.

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 1995

APPROVAL

of a thesis submitted by

Michael Joel Jakober

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENTS

I would like to extend my sincere thanks to all those who assisted in this research effort. I would especially like to thank Dr. Thomas McMahon, who selflessly offered direction, support, and encouragement from start to finish. Drs. Robert White, Jay Rotella, and Calvin Kaya reviewed the manuscript. Jack McIntyre, Bruce Rieman, and Russ Thurow of the Forest Service Intermountain Research Station provided funding and helpful advice. Rich Torquemada and Rick Swanson of the Bitterroot National Forest got the project started and provided equipment, funding, and support. Chris Clancy of Montana Fish, Wildlife, and Parks provided his usual expertise on many occasions. Trout Unlimited helped fund my tuition by awarding me the 1994 Lee Wulff Memorial Scholarship. Dee Topp of the Biology Department was extremely helpful with the details needed to complete graduate school. Special thanks to Marty Beck, Dale Hoth, Larry Javorsky, Mike Weldon, Jerry O'Hara, Dave Lockman, and my father for assisting me on those cold, winter nights. Finally, I would like to express my love and gratitude to my wife, Laurie. Her love, support, and encouragement were the most important contributions of all.

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ABSTRACT

Autumn and winter movements and habitat use of resident bull trout and westslope cutthroat trout were investigated using radiotelemetry and snorkeling. Movement occurred in two distinct stages and was closely tuned to unique stream icing conditions. As autumn water temperatures declined, bull trout moved downstream into beaver ponds and pools containing complex large woody debris (LWD). Bull trout remained in these habitats throughout winter in streams lacking anchor ice. With extensive anchor ice formation, however, bull trout abandoned autumn pool habitats and moved further downstream in search of favorable overwintering habitats. Westslope cutthroat trout moved little (< 100 m), preferring to overwinter in LWD-dominated pools near summer habitats. Beaver ponds and deep pools offering combinations of LWD and large substrate were critical overwintering habitats for both species. Trout exhibited different diel behavioral strategies during winter. During the day, small trout concealed in LWD and substrate interstices. Trout too large to find suitable hiding cover aggregated in deep pools. At night, fish of all sizes moved into the water column away from cover. Both species selected nighttime focal points closer to the substrate, further from cover, in shallower water, and in slower velocities than daytime positions. Although cutthroat trout preferred winter focal positions higher in the water column than bull trout, microhabitat use was similar for both species. As water temperature declined below 7 C, daytime trout densities declined in all habitats except beaver ponds. Pond densities dramatically increased as large aggregations (> 100 cutthroat and bull trout) formed prior to winter ice cover. Winter night densities were 5-6 times greater than winter day densities. Preferred winter habitats possessed extensive cover, low velocity flow (< 10 cm/s), and depth (> 50 cm). Complex LWD accumulations were an important winter hiding cover for both species regardless of stream size.

CHAPTER 1

GENERAL INTRODUCTION

Bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarki lewisi*), two native salmonids of the interior Pacific northwest, have declined substantially throughout their native ranges due to a variety of factors, including the degradation and loss of spawning and rearing habitat, competition and hybridization with introduced salmonids, habitat fragmentation, and overexploitation (Liknes and Graham 1988; Fraley et al. 1989). In order to effectively manage both species and prevent further declines, more specific habitat information is needed over different stages of life history and different seasons, especially information pertaining to movements, behavior, and habitat requirements during winter.

Although once abundantly distributed throughout all major watersheds west of the Continental Divide, bull trout in Montana have suffered severe reductions in abundance and distribution in the last century and are currently only found in limited numbers and habitat (Thomas 1992). The bull trout is presently listed as a Category I species by the United States Fish and Wildlife Service (USFWS), meaning that listing under the federal Endangered Species Act is warranted.

Westslope cutthroat trout were once abundantly distributed throughout western Montana (east and west of the Continental Divide), central and northern Idaho, a small section of Wyoming, and southern portions of three Canadian provinces (Liknes and Graham 1988). Within the last century, the westslope cutthroat has declined throughout its historic range due to competition from introduced salmonids, habitat degradation, introgression, and overexploitation, and is presently only found in 27% of its historic range in Montana (Liknes 1984; Liknes and Graham 1988). The westslope cutthroat trout is listed as a Class B Species of Special Concern by the Montana Department of Fish, Wildlife, and Parks (MDFWP), and special harvest restrictions have been widely implemented to preserve and perpetuate the remaining wild stocks.

Both species exhibit three similar life history patterns: (1) fish reside in large rivers or streams and migrate up smaller tributaries to spawn (fluvial); (2) fish reside in lakes or reservoirs and migrate up smaller tributaries to spawn (adfluvial); and (3) fish do not migrate and spend their entire lives in small headwater streams (resident) (Liknes and Graham 1988; Goetz 1989). Small tributaries act as rearing areas for juveniles of migratory fish, and juveniles live in these tributaries for

1 to 4 years before migrating downstream to rivers, lakes, or reservoirs (Liknes and Graham 1988; Fraley and Shepard 1989). Resident fish of both species are greatly reduced in size compared to their migratory counterparts, and have low fecundity (Goetz 1989). Most of the literature available on bull trout is based on studies of migratory populations (Fraley and Shepard 1989; Goetz 1989), whereas almost no information is available on small, resident populations.

Although movement is a fundamental characteristic that differentiates bull trout life history forms, it is not known whether resident populations have always been distinct from migratory forms, or if resident fish are the remnants of formerly fluvial populations. Knowledge of the spawning movements of all three life history forms can help answer this question. Adfluvial bull trout typically commence spawning migrations in late spring, arriving at the mouths of spawning tributaries by mid-summer (Shepard et al. 1984). Both adfluvial and fluvial bull trout ascend spawning tributaries in late summer (late July - September), staging in deep pools offering extensive cover (complex woody debris jams, undercut banks, etc.) near spawning beds of unembedded, loosely compacted gravel and cobble substrate (McPhail and Murray 1979; Shepard et al. 1984). Sites offering groundwater infiltration appear to be highly important bull trout spawning areas (Shepard et al. 1984). Although the timing and magnitude of adfluvial and fluvial bull trout spawning movements have been well documented (Shepard et al. 1984; Fraley and Shepard 1989), the extent of spawning migrations conducted by resident bull trout inhabiting small headwater streams is unknown.

Resident (fluvial) westslope cutthroat, conversely, are thought to be relatively sedentary throughout their lives (Leathe and Enk 1985). Recent evidence, however, suggests that westslope cutthroat trout in headwater streams may move often, sometimes over relatively long distances, to find suitable overwintering habitat (Bernard and Israelsen 1982; Brown, in press).

The quantity and quality of available overwintering habitat in small streams strongly affects movement patterns and may be the limiting factor for stream salmonid populations (Hunt 1974; Mason 1976). As water temperatures decrease rapidly in late autumn, fish metabolic rates decline, and suitable cover areas become more critical. Although salmonids continue to feed throughout the winter, activity and aggression are greatly reduced and survival depends more on finding suitable shelter and minimizing energetic costs than on capturing food (Mason 1976; Cunjak and Power 1987a).

Winter cover requirements differ from, and are more restrictive than those of summer. Structurally complex accumulations of large woody debris (LWD) are an important component of winter habitat (Bustard and Narver 1975;

Tschaplinski and Hartman 1983). Large woody debris increases pool frequency, depth, and volume, retains sediment, protects fish from the scouring effects of ice, and creates low velocity pockets of shelter offering shade and complex 3-dimensional hiding structure (Bustard and Narver 1975; Bilby and Likens 1980; Lisle 1986; McMahon and Hartman 1989).

In larger streams where LWD is less common, the amount of unembedded substrate or undercut banks probably controls the availability of quality overwintering habitat (Hillman et al. 1987; Smith and Griffith 1994). Clean substrate interstices provide critical overwintering habitat for many species of juvenile salmonids (Rimmer et al. 1984; Heifetz et al. 1986; Heggenes et al. 1993; Bonneau 1994), and the deposition of fine sediments can fill interstitial spaces and substantially decrease winter survival rate (Smith and Griffith 1994).

Resource partitioning is an important mechanism controlling seasonal interactions between juvenile bull trout and westslope cutthroat trout (Nakano et al. 1992). The summer habitat preferences of both species reflect differences in foraging tactics and microhabitats. Cutthroat trout prefer deep-water pool habitats offering mid-water column feeding stations beneath overhead cover, whereas bull trout prefer more diverse habitats containing complex substrate cover (Nakano et al. 1992). In winter, the need to minimize energetic costs and obtain shelter from predators dominates the behavior of both species; therefore, winter habitat requirements are much more similar (Bonneau 1994).

This study examines the autumn and winter movement patterns of resident bull trout and westslope cutthroat (Chapter 2), and compares differences in autumn and winter habitat use at the microhabitat and channel unit scales (Chapter 3) in two headwater tributaries of the Bitterroot River in western Montana.

Historic bull trout populations in the Bitterroot River drainage were probably dominated by fluvial fish in the mainstem Bitterroot River (Chris Clancy, MDFWP, personal communication). However, the historic presence of resident bull trout in headwater tributaries has not been established. Today, fluvial bull trout in the mainstem are rare, and most of the remaining bull trout populations consist of small, resident fish sympatric with westslope cutthroat in small headwater streams. Current management goals seek to preserve remaining bull trout populations, while attempting to describe critical habitat needs and define core areas containing the strongest populations with the highest potential for future recolonization.

Suitable winter habitat in Bitterroot River tributaries may depend on channel morphology and stream size. Streams within the drainage can be roughly classified into two morphological types: (1) small (mean wetted width < 7 m) LWD-dominated streams lacking boulders; and (2) larger (mean wetted width > 7 m) boulder-dominated streams lacking LWD. The quantity of instream LWD is probably the most important feature limiting the availability of quality overwintering habitat in smaller streams, while the amount of unembedded substrate probably controls the availability of quality overwintering habitat in larger streams.

Specific objectives of this study were to (1) compare the autumn and winter microhabitat preferences of both species, (2) document autumn and winter movement patterns, (3) compare differences in winter habitat use, and (4) define critical overwintering habitats which may be limiting the abundance and distribution of resident bull trout and westslope cutthroat trout populations in the Bitterroot drainage.

CHAPTER 2

ROLE OF STREAM ICING CONDITIONS ON WINTER MOVEMENTS AND HABITAT USE BY BULL TROUT AND WESTSLOPE CUTTHROAT TROUT

Introduction

The movement patterns and habitat preferences of headwater populations of resident bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarki lewisi*) are not well understood. Until recently, most researchers have concluded that movement is not a critical component in the life histories of resident salmonids (Miller 1957; Leathe and Enk 1985). Adult resident trout are assumed to establish feeding territories or dominance hierarchies and remain within a restricted home range for most or all of their lives (Riley et al. 1992). However, because seasonal habitat, spawning areas, and food resources are patchily distributed in streams, movement is possibly more common in stream salmonids than previously thought. This is particularly true during autumn, as fish seek out suitable overwintering habitats in response to declining water temperatures and photoperiod (Rimmer and Paim 1990; Meyers et al. 1992; Fraser et al. 1993).

Spawning movements of fall-spawning salmonids may also be triggered by declining water temperatures in autumn. Bull trout spawning primarily occurs in September and October and is thought to be triggered by declines in water temperature below 9 C (McPhail and Murray 1979; Fraley and Shepard 1989). Despite considerable knowledge of the spawning behavior of adfluvial and fluvial bull trout, little is known of the spawning movements of resident bull trout. Adfluvial bull trout commence long (e.g. 50-200 km) upstream spawning migrations in late spring, arriving in staging areas by late summer (Fraley and Shepard 1989). Fluvial bull trout also display extensive spawning migrations (Goetz 1989). Resident fish, in contrast, are believed to move relatively short distances within their natal streams to spawn, although I could find no previous studies documenting the spawning behavior of resident bull trout.

Winter ice formation and flow reduction can reduce the amount of available overwintering habitat for salmonids in mountain streams and influence the distance required to obtain suitable winter habitat (Hunt 1974; Chisholm et al. 1987). Bjornn and Mallet (1964) recorded autumn downstream movements of up to 100 km for cutthroat trout in an Idaho river, while Miller (1957) and Leathe and Enk (1985) observed cutthroat overwintering within 50 m of their summer habitats in small streams. Bull trout winter movements are largely unknown, and I could find no previous studies documenting the winter movements of resident bull trout.

In winter, stream salmonids seek habitats which offer a combination of dense cover, low water velocities, and depth (Hartman 1965; Cunjak and Power 1986; Chisholm et al. 1987). Effective winter habitat can take the form of complex large woody debris (LWD) jams (Heifetz et al. 1986), substrate interstices (Smith and Griffith 1994), undercut banks (Hillman et al. 1987), surface ice (Maciolek and Needham 1951), beaver ponds (Chisholm et al. 1987), off-channel alcoves (Swales et al. 1986), and perennial springs (Craig 1978).

Stream ice conditions may affect cover availability, predation risk, and the timing and magnitude of winter movements (Chisholm et al. 1987; Heggenes and Borgstrom 1988; Brown, in press). Ice formation in streams is influenced by interactions between stream elevation, stream size, climate, and snowfall depth (Chisholm et al. 1987; Berg 1994). High elevation streams are characterized by snow-bridging, no surface ice, and little-to-no habitat exclusion, whereas low elevation streams are characterized by extensive surface ice cover, little snowfall, and moderate habitat exclusion (Chisholm et al. 1987). The harshest winter conditions are typically observed in mid elevation streams where incomplete surface ice cover is coupled with extensive anchor ice formation.

The type of ice may influence winter habitat conditions in fluvial environments (Maciolek and Needham 1951). Surface ice initially forms on low velocity pools when sub-surface waters are well above freezing. Without an insulating layer of snow (> 30 cm), surface ice can continue to thicken in a downward direction until the water column is completely frozen (Berg 1994). Surface ice in conjunction with an insulating layer of snow can be beneficial to overwintering trout by preventing excessive radiant heat loss from the streambed, maintaining water temperatures slightly above freezing, and providing overhead cover (Power et al. 1993). Sub-surface ice formation (i.e. frazil and anchor ice), in contrast, is detrimental to stream fishes (Power et al. 1993). On sub-freezing clear winter nights, radiant heat loss from the streambed is sufficient to supercool the temperature of the water slightly below 0.0 C (Benson 1955). When turbulent water is supercooled, small (0.1-5.0 mm) ice crystals nucleate in the water column, forming frazil ice (Benson 1955). Frazil ice crystals are adhesive and stick to each other, underwater objects, and the substrate to form anchor ice (Needham and Jones 1959). Anchor ice forms primarily in riffles and may dam and flood large sections of stream, dramatically altering winter habitat composition (Maciolek and Needham 1951; Needham and Jones 1959). Extensive anchor ice accumulation can exclude large areas of stream, forcing trout to aggregate in the few remaining pockets of open water (Cunjak and Power 1986).

This study was designed to examine the autumn and winter movements and habitat preferences of resident bull trout and westslope cutthroat in two streams which typify those commonly occurring in the Bitterroot drainage of western Montana: a small (mean wetted width < 7 m), high elevation (1818 m), LWD-dominated stream lacking boulder substrate and sub-surface ice; and a larger (mean wetted width > 7 m), mid elevation (1424 m), boulder-dominated stream lacking LWD with large accumulations of sub-surface ice. These two streams were specifically chosen to compare the relative importance of LWD and large substrate to overwintering bull trout and westslope cutthroat trout and to examine the effects of different ice conditions on winter movements and habitat preferences. Additional sampling in nearby streams having similar morphologies was not possible because of a lack of strong bull trout populations in the drainage.

Study Area

Meadow Creek (UTM 280982 5080827) is a fourth-order, LWD-dominated tributary to the East Fork of the Bitterroot River in the Bitterroot National Forest, Ravalli County, Montana. Meadow Creek originates at an elevation of 2317 m, and flows north for 16 km (mean gradient 5.5%) before emptying into the East Fork of the Bitterroot River at an elevation of 1515 m (Figure 2.1). It drains an area of 85.5 km^2 and the geology is comprised of hard and weathered granitics. Meadow Creek ranges in wetted width from 2.0 m to 5.0 m at base flow. Gravel and cobble dominate the substrate, with very few boulders and substantial amounts of LWD. Beaver (*Castor canadensis*) dams are common in the middle section and near the mouth of Meadow Creek, but do not appear to impede fish passage. Riparian areas are primarily forested with mixed stands of lodgepole pine (*Pinus contorta*) and Englemann spruce (*Picea engelmannii*). The watershed is used for timber harvest, livestock grazing, and recreation. Angling use is light (C. Clancy, MDFWP, personal communication). Mean annual precipitation in the vicinity of the study area is about 75 cm, 80% of which falls as snow between October and May. Meadow Creek has a discharge pattern typical of those in the central Rocky Mountains - low flows from late summer until spring, after which snowmelt causes peak runoff (May and June). During

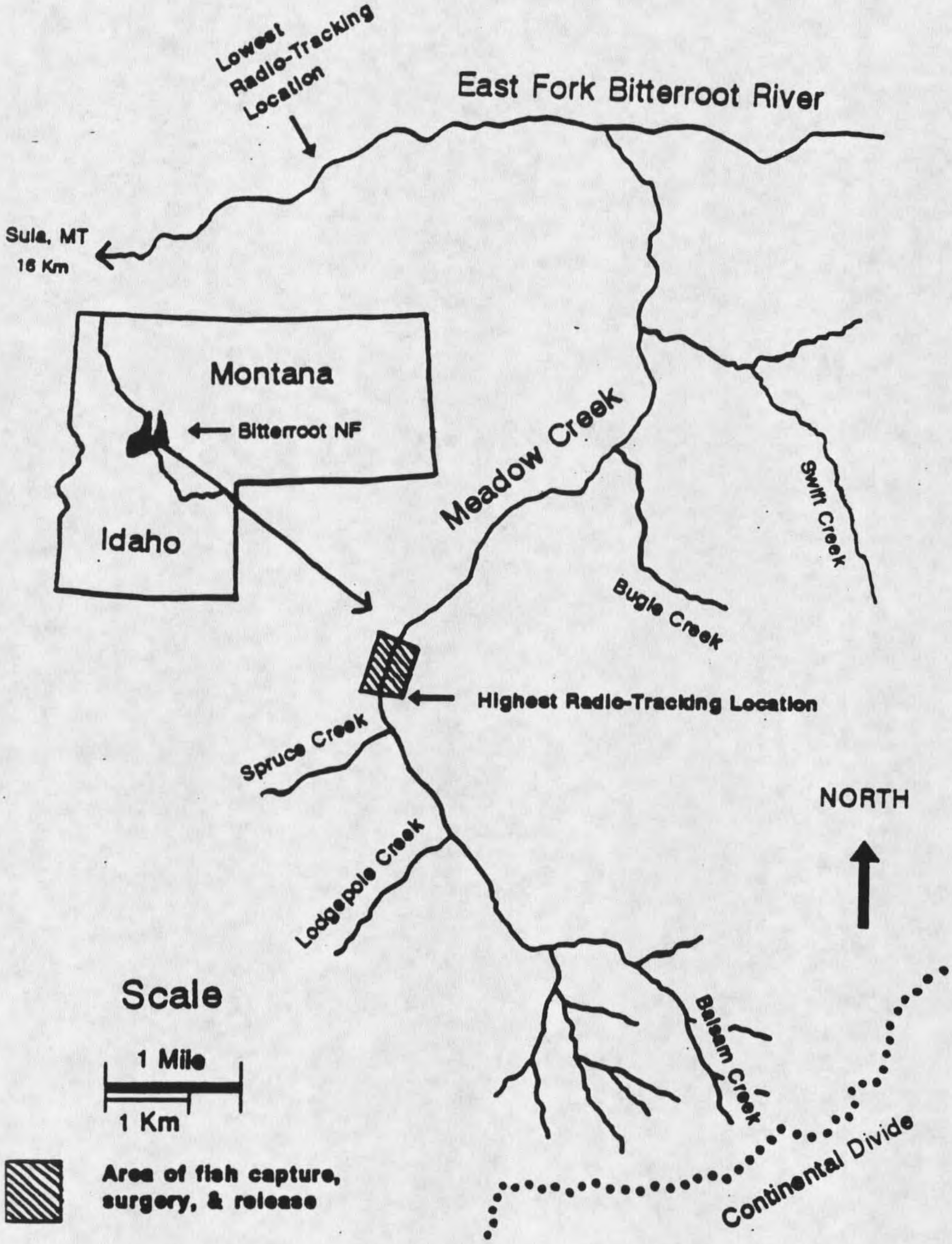


Figure 2.1. Map of the Meadow Creek drainage and radiotracking section, Bitterroot National Forest, Ravalli County, Montana.

autumn and winter study periods, flows were below 0.25 m^3/s. Peak summer water temperatures rarely exceed 13.0 C, while winter water temperatures range between 0.0-0.5 C. Meadow Creek is almost entirely covered (> 95%) with surface ice (10-30 mm thickness) from early November through late March, and this ice cover is typically insulated with > 50 cm of snow. Sub-surface ice (anchor and frazil ice) is present only in riffles in limited amounts (late October) prior to surface ice formation, and anchor ice dams are rare. The fish fauna in Meadow Creek consists entirely of endemic species: bull trout, westslope cutthroat trout, and slimy sculpin (*Cottus cognatus*). Small numbers of exotic brook trout (*Salvelinus fontinalis*) are present in lower Meadow Creek but are probably restricted to that section at present time.

Daly Creek (UTM 276191 5117775) is a fourth-order, boulder-dominated tributary to the Bitterroot River in the Bitterroot National Forest. Daly Creek originates at an elevation of 2268 m, and flows southwest for 18 km with a mean gradient of 4.85% before joining Skalkaho Creek at an elevation of 1408 m (Figure 2.2). It drains an area of 98.4 km^2 and the geology is comprised of mixed quartzite and granitic formations. Wetted width ranges from 0.7 m to 8.0 m at base flow. Boulders and large cobbles dominate the substrate and LWD is uncommon. No barriers to fish movement exist in the lower 12 km of Daly Creek where the study was

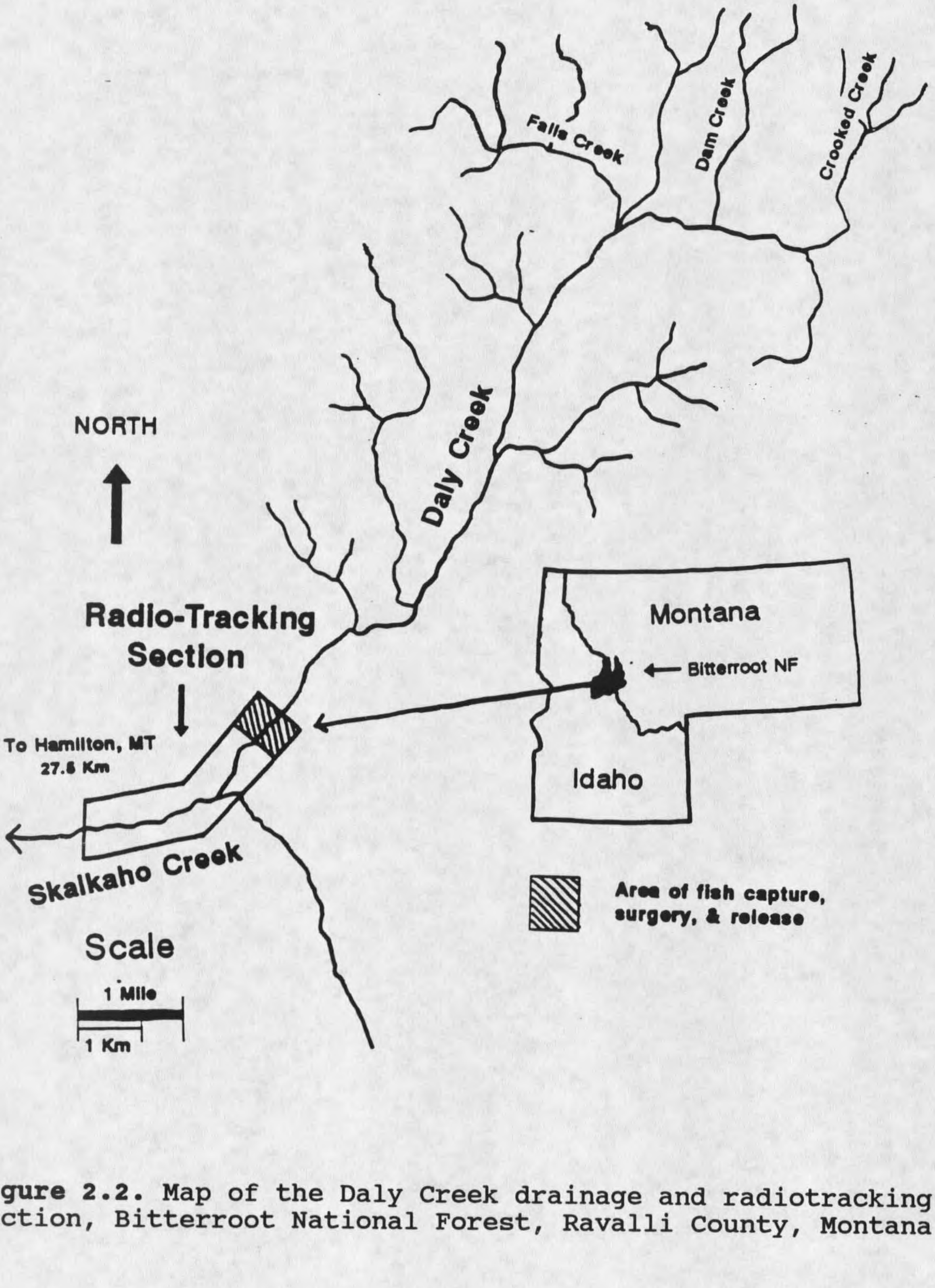


Figure 2.2. Map of the Daly Creek drainage and radiotracking section, Bitterroot National Forest, Ravalli County, Montana.

conducted. Mixed stands of Engelmann spruce and Douglas fir (*Pseudotsuga menziesii*) heavily shade riparian areas. The Daly Creek watershed is used for limited timber harvest and recreation, with moderate angler use (C. Clancy, MDFWP, personal communication). Mean annual precipitation in lower Daly Creek is about 50 cm, 70% of which falls as snow between October and May, and the discharge pattern is similar to Meadow Creek. During autumn and winter study periods, flows ranged from 0.40-0.90 m^3/s. Peak summer water temperatures rarely exceed 13.0 C and winter water temperatures range between 0.0-1.0 C. Surface ice cover in Daly Creek is highly dynamic, ranging from 60-90% depending on air temperature. Ice thickness commonly exceeds 40 cm and is generally insulated with 20-50 cm of snow. Subsurface ice formation is extensive throughout winter in open water leads, and anchor ice dams are common. The Daly Creek fish fauna is identical to that of Meadow Creek: bull trout, westslope cutthroat trout, and slimy sculpin. Brook trout are not present in Daly Creek, but are present in low numbers in Skalkaho Creek several kilometers downstream.

Methods

Radiotelemetry was used to measure the autumn and winter movements and habitat use of 18 bull trout and six westslope cutthroat trout from late August 1992 through February 1993. Due to the small size of fish (range 231-434 mm total length/TL), I was limited to using small transmitters with short (90 d) battery lives. Thus, movements were monitored during two different time periods (autumn phase & winter phase) using different sets of radiotagged fish. During the autumn phase, only bull trout were radiotagged in order to assess spawning movements whereas both species were monitored during winter.

Radiotagging

Four bull trout > 231 mm TL were radiotagged in both streams in late August 1992. Fish were captured with a Coffelt Mark-10 backpack electrofishing unit or a boat-mounted Coffelt Mark-22M electrofishing unit. In late October 1992, additional bull trout (Daly Creek N=6; Meadow Creek N=4) and westslope cutthroat trout (Daly Creek N=2; Meadow Creek N=4) were radiotagged in each stream to assess winter movements.

Following capture, fish were anesthetized with a 200 mg/L solution of MS-222, weighed (g), and measured (mm). Radio transmitters were surgically implanted using standard procedures reported for fish of similar size (Schrader 1989). The surgical procedure involved placing the fish ventral side up in a V-shaped PVC trough padded with wet sponges with the head and gills submerged in anesthetic. A 1.5-2.0 cm incision was made through the ventral abdominal wall immediately anterior and slightly dorsal to the pelvic girdle. Incisions were made only large enough to gently slip the transmitter into the peritoneal cavity. After inserting the transmitter, the incision was closed with a single row of three to four sutures through the peritoneum and dermis using a curved cutting needle (FS-1; 1/2 in) with absorbable Ethicon 2-0 chromic gut suture material. Sutures were firmly cinched using two double surgical knots separated by a single knot. Fish were tagged with different colored Floy tags to facilitate visual identification of radiotagged individuals. Fish were released approximately one hour later in the exact location where they were captured. All fish were active when released and surgery and anesthesia did not have any obvious negative effects.

Capsule-shaped, beeswax-coated transmitters (Custom Telemetry and Consulting, Athens, Georgia) with internal loop antennas were used in this study. Transmitters were approximately 30 mm long by 14 mm in diameter, and operated on unique, individual frequencies ranging between 40.4112 MHz to 40.5612 MHz. Guidelines suggest that the transmitter weight in water should make up no more than 2% of the fish's body weight (Brown, in press). Transmitter weights in my study ranged between 3.6 to 4.0 g or 0.7 to 3.5% of the fish's body weight.

Radiotracking Protocol

A 40-MHz receiver with 16 operational channels (Advanced Telemetry Systems Inc., Isanti, Minnesota) and a hand-held bi-directional loop antenna (60 cm by 65 cm) mounted on a 3-m pole were used to triangulate fish locations to within 1.0 m^2. Headphones were used with the receiver when locating fish. On approximately 25% of the locations, I was able to visually observe the radiotagged fish using the fish's uniquely colored Floy tag.

Radiotracking equipment was extensively checked prior to data collection. Transmitter strength and performance were tested in air, stream water, and under ice in a cooler. All transmitters were operated for 24 h in ice water prior to implantation. Receiver accuracy was calibrated by tracking the location of a hidden transmitter located on the ground. Transmitter signals were initially detected at a distance of approximately 100-150 m and signal strength was not attenuated by the presence of snow or ice.

Fish were located twice weekly during autumn and once weekly during winter. A minimum of 48 h elapsed between locations to meet the assumption of independence for radiotracking studies (Alldredge and Ratti 1986). Most locations were made during the day (0900-1600 h); however, each fish was also located at night (1900-0400 h) on at least two occasions. Transmitter duration averaged 67 d in autumn (range 53-82 d) and 112 d (range 56-119 d) in winter.

Movement and Habitat Use

For each relocation, the distance (m) and direction (up or downstream) moved from the original point-of-release and last location, the habitat type occupied (Table 2.1), and the cover type used (Table 2.2) within a 1 m radius were recorded. Thermographs were used to record temperature. Percent ice cover was visually estimated during each sampling period to assess possible effects of ice on timing and magnitude of movements.

To compare habitat use with availability, I classified all habitat units positioned between the uppermost and lowermost fish locations and calculated the percent composition of each habitat unit type. All units between those two points were assumed to be available to radiotagged fish (White and Garrott 1990).

Autumn habitat availability was measured at base flow in both streams during late September-early October 1993. Although flows were higher (0.28 m^3/s in Daly Creek; 0.17 m^3/s in Meadow Creek) in autumn 1993 than in 1992,

Table 2.1. Habitat types designated in Daly Creek (D) and Meadow Creek (M) as modified from Bisson et al. (1981).

Riffle (D & M) - Stream unit with moderate current velocity (20-50 cm/s) and moderate turbulence.

Glide (D & M) - Stream unit lacking pronounced turbulence characterized by moderately shallow water with an even flow.

LWD-formed pool (D & M) - Stream unit in which LWD has caused scouring water to carve out a hole in the channel bed and provides the dominant cover type (contains > 20 cm of submerged LWD/m^2 pool area).

Boulder-formed pool (D) - Stream unit in which boulders have caused scouring water to carve out a hole in the channel bed and boulder crevices and ledges provide the dominant cover.

Pocket water (D) - Stream unit with moderate-to-fast current velocity (20-100 cm/s) and moderate turbulence interspersed with numerous boulder-formed pocket pools.

Beaver pond (M) - Stream unit formed by the damming activities of beaver characterized by deep water (> 50 cm), low velocity (< 5 cm/s), and fine sediment (< 8 cm).

Pool lacking LWD (M) - Stream unit formed by scouring flow impinging against one streambank due to a meander bend in the channel (contains < 20 cm of submerged LWD/m^2 of pool area).

Table 2.2. Cover type classification as modified from Dolloff and Reeves (1990).

Cover type	**Description**
No Cover	No cover within a 30 cm radius
Cobble	Rock crevices (diameter 64-256 mm)
Boulder	Rock crevices (diameter > 256 mm)
Large woody debris	> 1 woody piece (diameter > 10 cm)
Fine woody debris	> 1 woody piece (diameter < 10 cm)
Undercut bank	Earth bank (< 45 cm from water)
Aquatic vegetation	Submerged aquatic macrophyte capable of hiding > 75% of a fish's body
Surface ice	Ice used as overhead cover

there were no noticeable changes in habitat composition between years in either stream.

Winter habitat unit availability could not be measured with the same procedure in each stream. Sub-surface ice was uncommon in Meadow Creek due to the rapid formation of surface ice. This prevented the formation of anchor ice dams necessary for altering habitat composition; therefore, autumn and winter habitat composition were assumed to be similar. In Daly Creek, winter habitat composition differed depending on dynamic surface and sub-surface ice conditions. I classified winter habitat conditions into two categories:

(1) Moderate ice cover - Surface ice covers < 75% of the wetted stream area and sub-surface ice and anchor ice dams are not present.

(2) Extensive ice cover - Surface ice covers > 75% of the wetted stream area and sub-surface ice and anchor ice dams are common.

I then measured habitat availability at each condition during December 1993 and averaged the two measurements to calculate a baseline winter habitat composition. I also measured the amount of pool habitat at three different winter ice conditions (none, moderate, extensive).

Data Analysis

A chi-square goodness-of-fit test (Zar 1984) was used to test the null hypothesis that habitat unit use occurred in proportion to availability (Alldredge and Ratti 1986). If the null hypothesis was rejected, simultaneous Bonferroni confidence intervals (Byers et al. 1984) were calculated to determine whether a habitat type was preferred, avoided, or used in proportion to availability. Fish preferred or avoided habitat types when percent availability did not overlap the confidence interval (Byers et al. 1984).

Winter survivorship of radiotagged fish in Daly Creek in relation to water temperature and percent ice cover was estimated with the Kaplan-Meier procedure (Cox and Oates 1984). This procedure computes the percentage of radiotagged fish dying on each day of the study from all radiotagged fish at risk at the beginning of that day. The STATGRAPHICS statistical program (1991) was used to perform all statistical computations. Significance was defined as $P < 0.05$.

Results

Autumn Movement

Meadow Creek bull trout conducted relatively long distance movements downstream during autumn. Three fish exhibited the resident life history form, whereas one fish displayed movements typical of a fluvial bull trout. I defined a fluvial bull trout as one which moved out of Meadow Creek and into the East Fork during the tracking phase. Consult Appendix Table 1 for specific data on the net movements of individual fish in both streams.

Resident bull trout in Meadow Creek moved downstream (range 731-1,478 m) into a large beaver pond complex (9 contiguous ponds) between mid September and early October 1992 (Figure 2.3). On several occasions, more than one radiotagged fish was located within the same pond.

One Meadow Creek bull trout was observed spawning. On September 2, a radiotagged male (434 mm TL) spawned with a much smaller female (250 mm TL) in the tailout of a lateral scour pool. Appendix Table 2 presents habitat parameters measured at bull trout redds in Daly and Meadow Creeks. The fluvial bull trout (242 mm TL) moved 337 m upstream following capture, possibly spawned on September 17 (not observed) and then rapidly moved 11.9 km downstream, including a movement of 4.9 km in < 3 d (Figure 2.3).

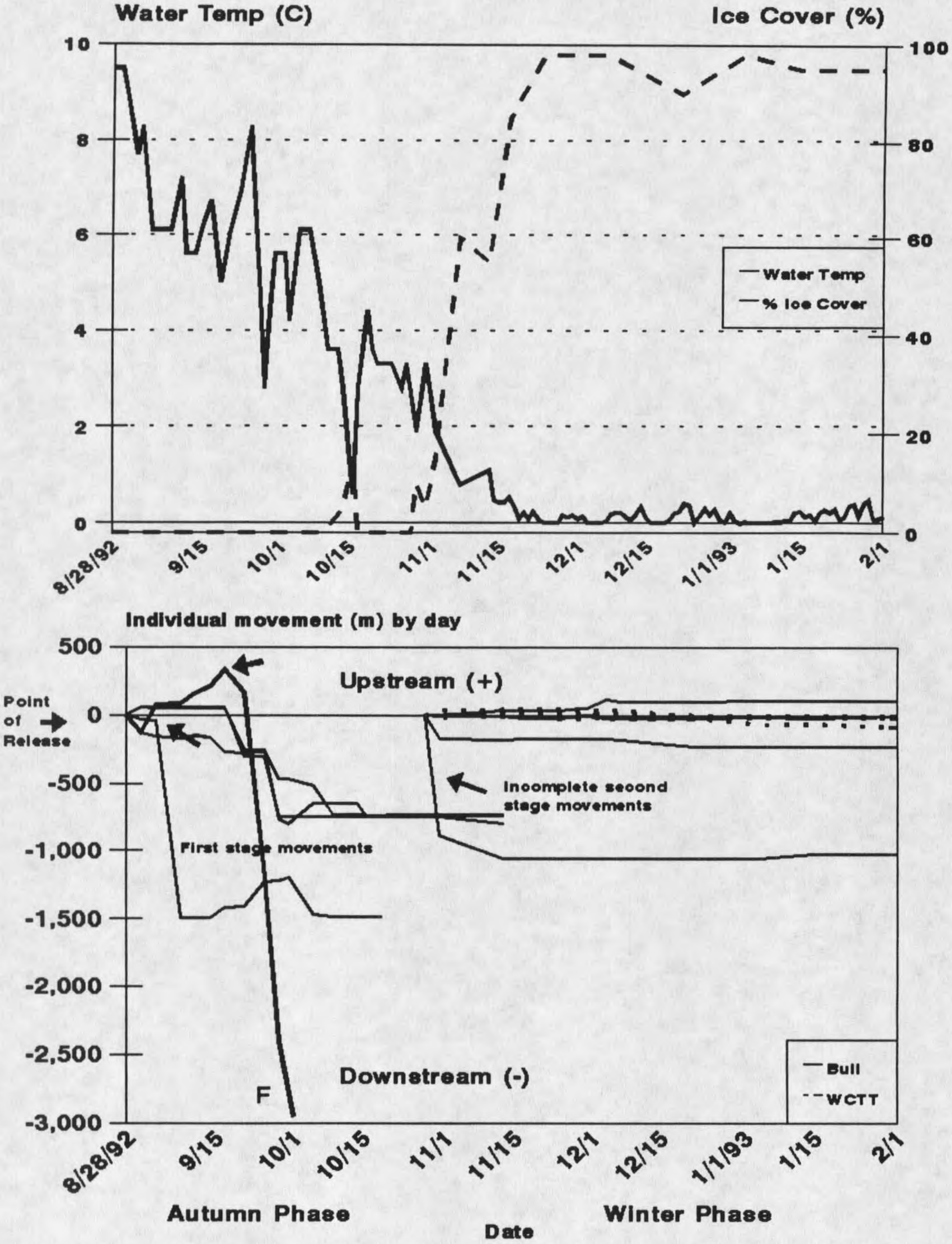


Figure 2.3. Distance, direction, and timing of movements displayed by 9 bull trout (8 radiotagged; 1 control) and 4 radiotagged westslope cutthroat trout in response to water temperature and ice cover in Meadow Creek. Arrows = spawning; F = fluvial bull trout movement (11,918 m downstream).

Monitoring of the fluvial bull trout indicated that long, post-spawning downstream movements were primarily conducted at night. Bull trout spawning activity in Meadow Creek occurred between early and mid September in water temperatures ranging between 6.0-9.4 C.

Far less movement was observed in Daly Creek during autumn. The direction and magnitude of net movements were small and variable, and only one radiotagged bull trout moved > 50 m (Figure 2.4). Two bull trout moved slightly upstream (10-35 m), while two moved downstream (2-316 m). One radiotagged fish was observed spawning. A 269 mm TL male moved 235 m upstream, spawned on September 24, and then moved back downstream 220 m to the vicinity of his point-of-capture in early October. Bull trout spawning in Daly Creek occurred during mid-to-late September in water temperatures ranging from 5.6-6.7 C.

Winter Movement

Meadow Creek bull trout were relatively sedentary throughout winter. With the exception of one long downstream movement (887 m) immediately following implantation (307 mm TL male; October 28-31), bull trout exhibited only limited movement following winter ice formation in early November (Figure 2.3). Net movements were both up (107 m) and downstream (6-1024 m), and usually occurred under surface ice cover. Meadow Creek westslope

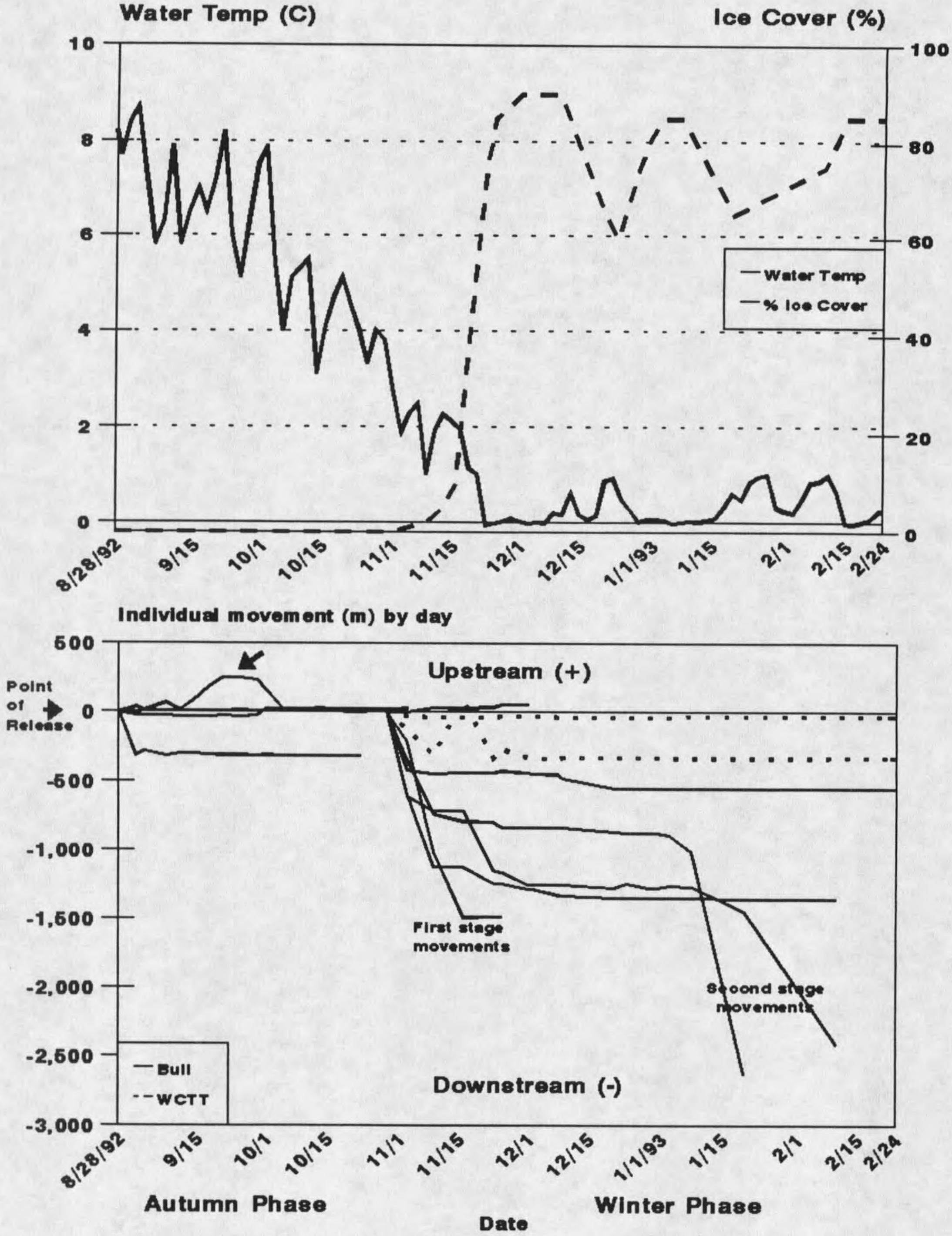


Figure 2.4. Distance, direction, and timing of movements displayed by 10 radiotagged bull trout and 2 radiotagged westslope cutthroat trout in response to water temperature and ice cover in Daly Creek. Arrow = spawning.

cutthroat trout were also relatively sedentary throughout winter. All cutthroat trout overwintered within 85 m of their point-of-release (Figure 2.3). Net movements were of a small magnitude (< 85 m) and in a downstream direction.

In contrast, bull trout in Daly Creek exhibited large downstream movements during early winter. Downstream movements in early November were similar in magnitude to those displayed by Meadow Creek bull trout in September (Figure 2.4). During mid winter, two bull trout also moved downstream again over 1 km into Skalkaho Creek. Cutthroat trout in Daly Creek exhibited more variable winter movement than Meadow Creek cutthroat (Figure 2.4). Net movement was 34 and 332 m downstream; however, one fish (330 mm TL male) moved distances > 300 m both up and downstream throughout winter between two pools.

Triggers to Movement

Bull trout spawning commenced in both streams as water temperatures declined below 9 C. Following spawning, bull trout in Meadow Creek initiated long distance downstream movement as mean water temperatures declined below 5.5-6.0 C in mid September (Figure 2.3). Arrival of the radiotagged bull trout into beaver ponds coincided with the formation of surface ice on the ponds during cold, clear nights in early October. Extensive surface ice (> 95% coverage; 10-30 cm thickness) formed rapidly in Meadow Creek during late autumn with little anchor ice formation. Snow 30-100 mm deep insulated the surface ice throughout winter and prevented its downward growth, thus minimizing winter habitat exclusion even in severe sub-zero temperatures (-20 to -35 C). Ice conditions and water temperatures in Meadow Creek remained stable throughout winter and little movement (< 50 m) was observed (Figure 2.3). Minor mid winter thaws did not trigger movement.

By contrast, bull trout in Daly Creek moved little during autumn in response to similar temperature declines (Figure 2.4). Initial downstream movements in Daly Creek commenced later in autumn (early November) than in Meadow Creek, as mean water temperatures dropped below 4 C. Almost all winter movements occurred either prior to ice formation or during mid winter thaws when anchor ice melted. Almost no movement occurred during periods of anchor ice formation and supercooled (range -0.01 to -0.10 C) water temperatures (Figure 2.4). Pool habitat composition was dramatically altered during supercooled periods (Figure 2.5), as fish were likely confined to temporary pools formed by large downstream anchor ice dams. The mid winter downstream movements (968 m and 1613 m) of bull trout in Daly Creek coincided with rising water temperatures, erosion of anchor ice dams, and decreases in surface ice cover from about 90% to 60% (Figure 2.4).

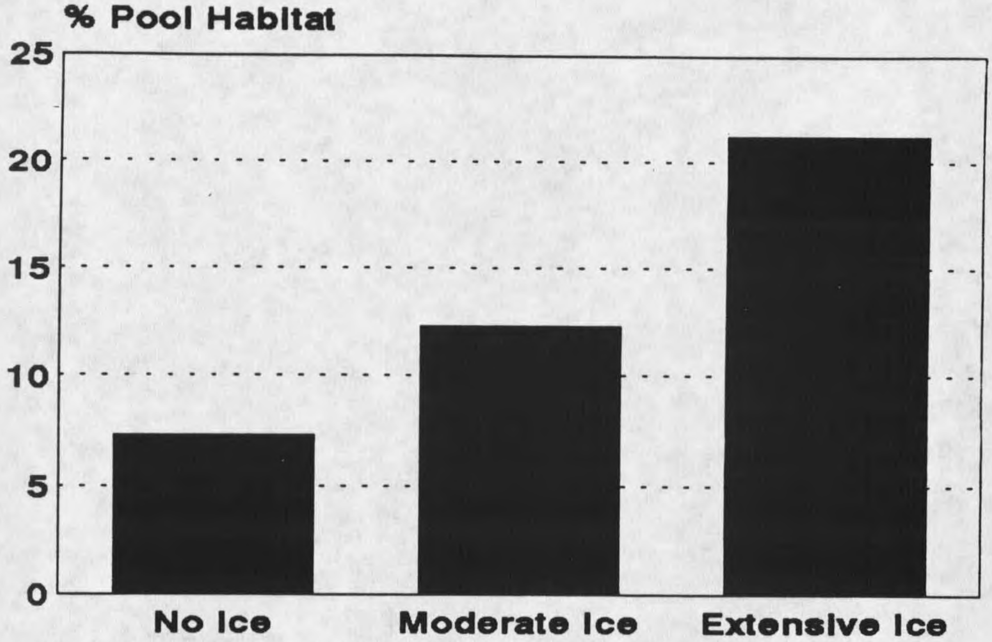


Figure 2.5. Percent pool habitat observed in the Daly Creek radiotracking section at three different conditions. No Ice = late autumn base flow prior to ice formation; Moderate Ice = 1-75% surface ice cover; Extensive Ice = > 75% surface ice cover.

Habitat Use

Pools were the preferred habitats of bull trout in both streams throughout autumn and winter. In autumn, bull trout in Meadow Creek significantly preferred beaver ponds and pools with abundant LWD (Figure 2.6). Beaver ponds and pools lacking LWD were preferred bull trout habitats in Meadow Creek during winter. In Daly Creek, bull trout preferred LWD-dominated pools and boulder-dominated pools during both autumn and winter (Figure 2.6).

Westslope cutthroat trout in both streams also preferred pools with abundant hiding cover during winter. In Meadow Creek, cutthroat trout preferred pools containing

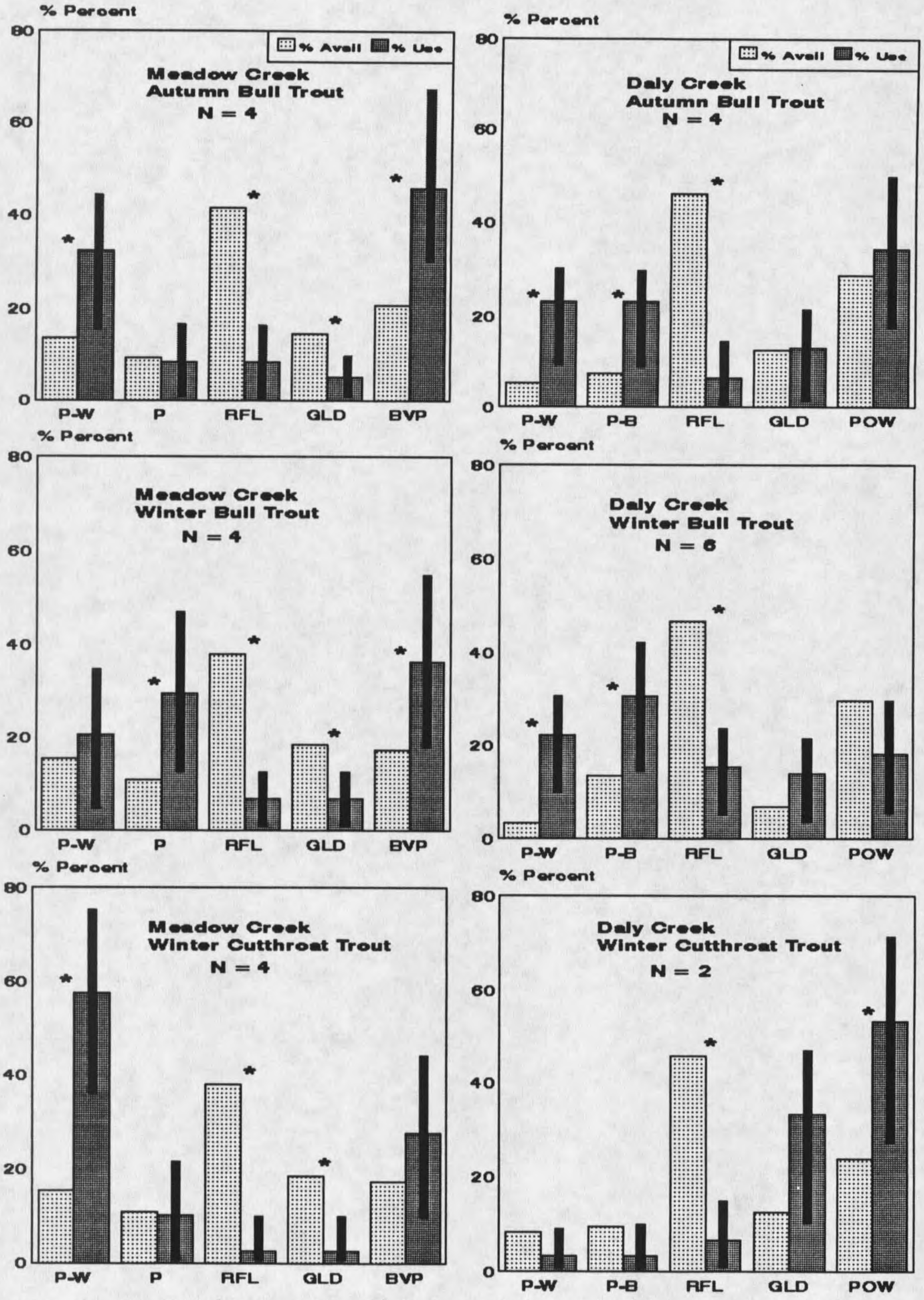


Figure 2.6. Habitat use displayed by radiotagged bull trout and cutthroat trout in Meadow Creek and Daly Creek. * = prefer/avoid ($P < 0.05$); Bar = 95% use interval; P = pool lacking LWD; P-W = LWD pool; P-B = boulder pool; BVP = beaver pond; GLD = glide; RFL = riffle; POW = pocket water.

abundant LWD (Figure 2.6). Daly Creek cutthroat trout preferred pocket water habitats which essentially functioned as pools due to the effects of downstream anchor ice dams (Figure 2.6).

Although cover use varied between seasons, important between-stream differences were apparent. Bull trout in Meadow Creek primarily used undercut banks and LWD during autumn and surface ice, LWD, and undercut banks in winter (Figure 2.7). By contrast, bull trout in Daly Creek used large substrate cover much more than undercut banks (Figure 2.7). LWD and surface ice use were similar in both streams during autumn and winter.

Westslope cutthroat trout exhibited similar differences in cover use. In Meadow Creek, radiotagged cutthroat trout most often used LWD, surface ice, and undercut bank cover (Figure 2.7). In Daly Creek, surface ice and large substrate dominated cover use and undercut banks and LWD were used to a lesser degree (Figure 2.7).

Survival

In Daly Creek, two radiotagged bull trout were killed by mink (*Mustela vison*) immediately following the onset of extensive ice formation in late November 1992 (Figure 2.8). No further losses occurred following initial ice formation. In Meadow Creek, one radiotagged bull trout was killed by a mink while migrating downstream after spawning; however, no

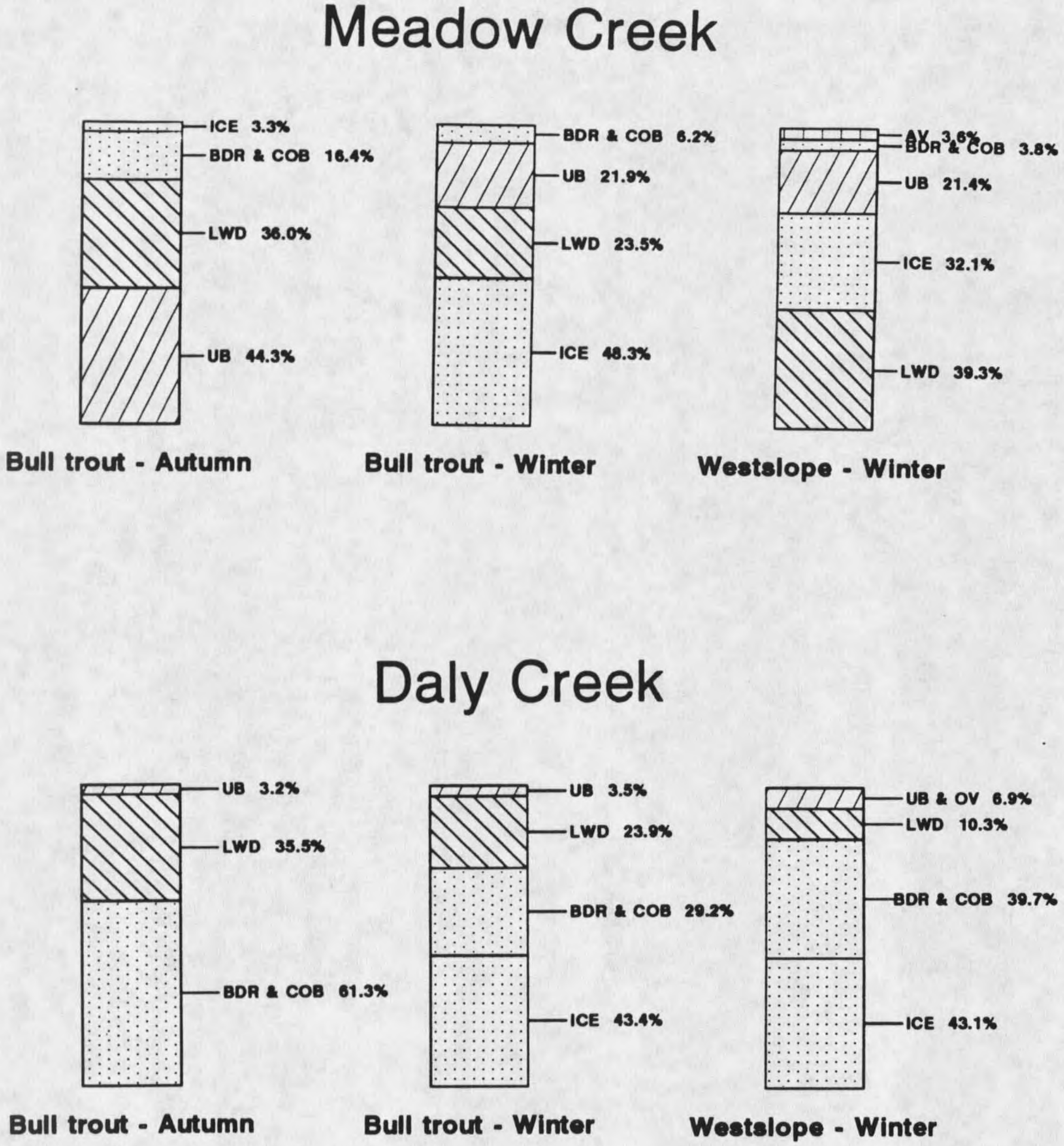


Figure 2.7. Cover use exhibited by radiotagged bull trout and westslope cutthroat trout in Meadow Creek and Daly Creek during autumn and winter, 1992-93. UB = undercut bank; LWD = large woody debris; BDR & COB = boulder and cobble; ICE = surface ice; AV = submerged aquatic vegetation; OV = overhead vegetation.

radiotagged fish were lost to predators following winter ice formation.

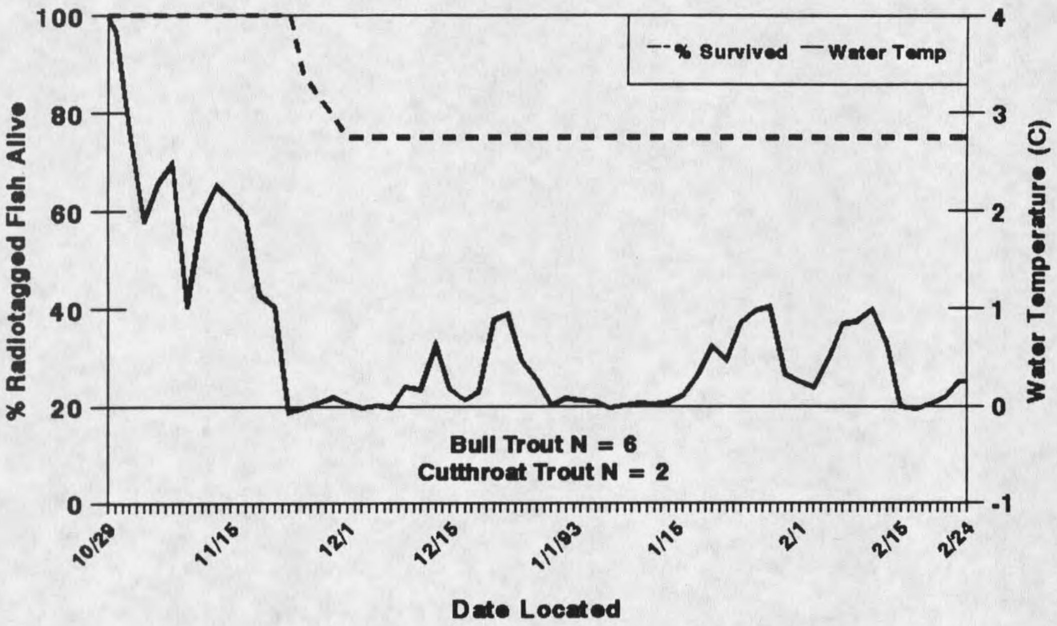


Figure 2.8. Kaplan-Meier survivorship curve for radiotagged fish in Daly Creek during winter, 1992-93. The curve measures the percent of radiotagged fish alive on any given day.

Discussion

Brown (in press) reports that winter movements of cutthroat trout occur in two distinct stages in streams subjected to harsh winter conditions. First stage movements occur in response to the changing physiological needs of the fish brought about by declining autumn water temperatures. Because of high winter metabolic maintenance costs and reduced swimming performance (Hartman 1963; Cunjak 1988a), stream salmonids seek out habitats offering a combination of complex cover, low velocity water, and depth (Chisholm et al. 1987; McMahon and Hartman 1989; Meyers et al. 1992). Second stage movements occur when first stage habitats (coined "staging pools") are eliminated by anchor and frazil ice formation and fish are forced to seek out other suitable habitats free of sub-surface ice.

The autumn and winter movements of bull trout and westslope cutthroat trout appeared to follow a modification of the two-stage movement pattern. Declining autumn water temperatures triggered substantial first stage downstream movements in both streams; however, water temperatures required to initiate movement varied between streams. In Meadow Creek, downstream movement of bull trout occurred during the last half of September as mean water temperatures declined below 6 C. Bull trout spawning in early September also conducted this first stage movement by moving downstream into winter habitat immediately following the completion of upstream spawning activity. Although first stage movement can occur in either the upstream or downstream direction (Bjornn and Mallet 1964; Bernard and Israelsen 1982; Brown, in press), all bull trout moved downstream in Meadow Creek during the first stage. Mean movement distances were similar to the limited (< 500 m) overwintering movements observed by Chisholm et al. (1987) for radiotagged brook trout.

Although movement distances were similar, the timing of first stage movements differed in each stream. First stage movements in Daly Creek did not occur until early November when water temperatures declined below 4 C. In contrast, first stage movements in Meadow Creek commenced in mid September as temperatures declined below 6 C. Differences in the timing of first stage movements between the two streams were probably caused by differences in water temperature declines and icing conditions. Due to its higher elevation and reduced canopy cover, Meadow Creek water temperatures were colder and more variable during ice-free periods. Late summer water temperatures were similar in the two streams; however, autumn water temperatures declined faster in Meadow Creek and were consistently 1-2 C colder throughout September and October. Daly Creek water temperatures lagged behind Meadow Creek temperatures by about 15 days throughout autumn, and winter ice formed about

3 weeks later. Meadow Creek responded to cold fronts quickly, exhibiting substantial (2-4 C) water temperature drops, moderate anchor ice formation in riffles, and complete surface ice formation on beaver ponds and most pools. Temperature declines in Daly Creek were more gradual, and ice formation did not occur during this period.

First stage movements were generally completed prior to the initial formation of sub-surface ice. Although rare in winter, anchor and frazil ice formed in Meadow Creek riffles in mid October as nighttime water temperatures fell to 0 C. Anchor ice accumulations in Meadow Creek were not extensive enough to persist to the following afternoon; however, bull trout had already moved to staging pools free of anchor ice such as beaver ponds (resident bull trout) or East Fork pools (fluvial bull trout) prior to its formation. In Daly Creek, anchor ice was absent during autumn, but formed extensive accumulations in late November that persisted through March. Daly Creek bull trout and westslope cutthroat trout also completed first stage movements into staging pools 1-2 weeks prior to the appearance of anchor ice.

The magnitude and direction of second stage movements were variable and appeared dependent on stream ice conditions. In Meadow Creek, winter movements of westslope cutthroat trout were short (< 85 m) downstream movements between pools. Fish typically moved until encountering the closest favorable pool. Most Meadow Creek bull trout also displayed relatively short, second stage movements during a brief period near the time of surface ice formation in early November. Only limited movement occurred during the remainder of winter. Second stage movements of bull trout in Daly Creek appeared closely timed to thaw periods when mean water temperatures approached 1 C, anchor ice dams eroded, and surface ice cover declined. Mid winter thaws eroded downstream anchor ice dams and provided access to downstream habitats.

The incomplete nature or lack of second stage movements observed in Meadow Creek can be attributed to the severity of winter ice conditions. In streams characterized by mild winter ice conditions (lack of sub-surface ice), first stage movements alone may be adequate for winter survival, and second stage movements probably do not occur (Cunjak and Power 1986; Chisholm et al. 1987; Meyers et al. 1992). In Meadow Creek, relatively mild winter conditions typified by a lack of anchor ice, thick (> 50 cm) insulating snow cover, and little habitat exclusion were probably the main factors responsible for the lack of distinct second stage movements. Without exclusion from sub-surface ice, cutthroat trout in Meadow Creek maintained year-round access to complex LWD cover, thus precluding the need for large second stage movements. Miller (1957), Leathe and Enk (1985), and Brown (in press) all observed cutthroat trout overwintering in close proximity (< 100 m) to their summer habitats in streams subjected to mild winter ice conditions. Fish that abandoned staging pools in Meadow Creek possibly moved for reasons other than ice exclusion, such as insufficient cover, water velocities, or prey availability within a pool. Daly Creek, similar to middle elevation streams described by Chisholm et al. (1987), suffered harsh winter conditions. Periods of supercooled water (-0.10-0.0 C) and extensive anchor ice accumulation alternated with thaw periods characterized by the erosion of anchor ice dams. The sporadic occurrence of second stage movements in Daly Creek reflected this variability. Fish in staging habitats that did not accumulate anchor ice did not move, whereas those in less suitable staging habitats conducted additional movements in mid winter. Skalkaho Creek, the low elevation overwintering destination for Daly Creek bull trout, exhibited intermediate winter conditions characterized by extensive surface ice, little snowfall, and moderate habitat exclusion (Chisholm et al. 1987). Sub-surface ice in riffles washed downstream into ice-covered pools and glides and possibly formed hanging dams (Tsang 1982), thereby increasing pool velocities, decreasing depths, and reducing the overall suitability of winter staging habitat (Brown, in press). As a result, bull trout abandoned seemingly favorable first stage pool habitats during mid winter and conducted relatively long downstream movements in search of suitable habitat.

Cover was a major factor determining the autumn and winter occupancy of pools by bull trout. Spawning bull trout staged in pools containing complex LWD jams in both streams. Fraley and Shepard (1989) reported use of complex LWD cover by adfluvial bull trout during migration upstream. Within LWD-dominated pools, bull trout usually concealed themselves within complex LWD jams during daylight hours; however, hiding beneath undercut banks (Meadow Creek) or boulder ledges (Daly Creek) was also common. Goetz (1991) observed similar daytime preferences for undercut banks during autumn. The abundant cover available in LWD-dominated pools is likely important for predator avoidance as fish are highly vulnerable to predation in small streams during upstream spawning migrations, spawning activity, and downstream first stage movements (Heggenes and Borgstrom 1988, Meyers et al. 1992, Brown, in press). While conducting downstream first stage movements, bull trout in Daly Creek exhibited a "pool-hopping" pattern, often moving distances > 300 m in one day, then stopping in deep pools with abundant cover for several days prior to moving to the next large pool downstream. Several resting pools used by migrating bull trout in November 1992 were also used by downstream migrants in early winter 1991 (C. Clancy, MDFWP, personal communication).

Beaver ponds were favored overwintering habitat for bull trout and westslope cutthroat trout in Meadow Creek. Ponds also functioned as stopover areas for migrating fluvial bull trout. Both species overwintered in beaver ponds in large, mixed species aggregations (80-120 fish; 90% cutthroat trout and 10% bull trout) under the ice. Favorable winter habitat characteristics of beaver ponds include excellent overhead cover (100% surface ice), deep water (> 80 cm), low velocity flows (< 5 cm/s), a lack of anchor ice, and stable water temperatures slightly above freezing from late autumn to early spring (Chisholm et al. 1987). Large aggregations (50-120 fish) of westslope cutthroat trout commonly formed in ponds during late autumn (Chapter 3), and may have provided the prey base for overwintering bull trout. Pools resembling small beaver ponds (large meander pools lacking LWD) also exhibited similar favorable winter habitat characteristics and were preferred by overwintering bull trout. Beaver ponds have been shown to be preferred overwintering sites for salmonids occupying diverse habitats, such as brook trout in snow-dominated, high elevation (> 3000 m) streams (Chisholm et al. 1987) and juvenile coho salmon (*Oncorhynchus kisutch*) in rain-dominated, coastal streams (Nickelson et al. 1992).

How habitats responded to dynamic ice conditions likely determined their suitability as overwintering sites. Large, deep pools with abundant cover were unaffected by anchor ice dams and offered adequate protection from accumulations of frazil ice. Anchor ice dams, however, radically changed the structure of shallow pools, glide, pocket water, and riffle habitats by damming large volumes of water and creating temporary "pools" which quickly filled with drifting frazil ice.

Stream ice characteristics also appeared to influence predation risk in winter. Erlinge (1972) reported that fish are a much more important component of mink diets during winter, and Heggenes and Borgstrom (1988) documented significant declines in winter smolt densities in stream reaches artificially subjected to mink predation.. In Daly Creek, two bull trout were killed by mink following the rapid formation of early winter mid channel ice shelves. Mink also used ice shelves to access open water leads throughout winter. In Meadow Creek, by contrast, the extensive overhead ice cover and lack of open water leads appeared to protect fish from mammalian predators.

Conclusions and Management Implications

This study represents our best understanding to date of the autumn and winter movement patterns and habitat preferences of resident bull trout and westslope cutthroat trout. The movement patterns and habitat preferences of both species appear to be quite flexible, and are closely tuned to the unique and often dynamic ice regimes of their particular stream. The variability in movement patterns displayed by bull trout and westslope cutthroat trout in this study will make trout winter habitat management more difficult. Specific winter habitat needs appear to vary from stream-to-stream and a thorough understanding of stream-specific ice conditions is required to accurately predict winter habitat preferences. Our current understanding of the effects of various ice conditions on overwintering salmonids is quite rudimentary and will have to improve considerably before we can effectively manage for trout winter habitat on a large scale.

The major conclusion of this study is that beaver ponds and deep pools offering complex LWD in conjunction with large substrate both function as critical overwintering habitats for salmonids in small Rocky Mountain streams. Winter occupancy of these habitats usually involves more complex movements than previously thought for small resident trout. In addition, movements into overwintering habitats may occur in two distinct stages, with the occurrence and magnitude of second stage movements determined by the severity of ice conditions particular to a specific stream. First stage movements appear to be triggered by declining water temperatures and are usually completed by the time of sub-surface ice formation. Generally, bull trout and westslope cutthroat in both streams are in their staging or overwintering areas 1-4 weeks prior to anchor ice formation.

Whether fish remain in these habitats throughout winter is determined by the severity of sub-surface ice. In streams lacking anchor ice, distinct second stage movements are likely to be absent. In streams containing substantial amounts of anchor ice, however, second stage movements will probably occur by those fish occupying pool habitats that become subject to severe icing conditions.

Beaver are recolonizing much of their historic range in western North America (Naiman et al. 1988). Winter habitat use of ponds by salmonids needs further investigation. If overwintering habitat is the limiting factor for bull trout and westslope cutthroat trout in Rocky Mountain streams, could diminished fish populations be strengthened through beaver recolonization? In the future, overwintering habitat may be constructed to aid in the recovery of bull trout and westslope cutthroat, and we will have to better understand the function of beaver ponds to effectively manage winter habitat.

This study also confirms the existence of a remnant fluvial bull trout population in the East Fork drainage. Fluvial fish are likely critical to the future viability of bull trout since a migratory population component will be needed to recolonize former habitat and restore historic metapopulation links fragmented by habitat degradation (Rieman and McIntyre 1993). The viability of resident bull trout populations has been questioned since they may face a higher probability of extinction from deterministic, stochastic, and genetic risks (Rieman and McIntyre 1993). Immediate threats to the connectivity of isolated bull trout populations in the East Fork drainage include introgression by brook trout and habitat loss. Bull trout recovery strategies must ensure that fluvial bull trout are protected from these threats.

CHAPTER 3

DIEL HABITAT USE OF BULL TROUT AND WESTSLOPE CUTTHROAT TROUT DURING AUTUMN AND WINTER IN STREAMS OF DIFFERENT MORPHOLOGY

Introduction

Most winter habitat studies have been conducted in coastal streams with little or no ice formation (Bustard and Narver 1975; Campbell and Neuner 1985; McMahon and Hartman 1989) or have made deductions about winter behavior based on autumnal observations taken prior to ice-over (Rimmer et al. 1983, 1984). Furthermore, the habitat preferences of stream salmonids have often been studied in summer, and summer habitat use has then been assumed to be representative of winter behavior. Accumulating evidence, however, has suggested that suitable overwintering habitat is more restrictive than summer habitat, and may be a critical limiting factor to the distribution and abundance of stream salmonid populations (Cunjak and Power 1986; Ireland 1993). Due to harsh winter conditions typical of Rocky Mountain headwater streams, the winter habitat requirements of resident bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarki lewisi*) are largely unknown, and knowledge of their summer habitat preferences probably fails to reveal limitations resulting from insufficient winter habitat.

Stream morphology affects the type of habitat and cover available. Boulder-strewn riffles (Rimmer et al. 1983), beaver ponds (Chisholm et al. 1987), deep pools (Cunjak and Power 1986), groundwater seeps (Brown, in press), surface ice (Maciolek and Needham 1951), and woody debris jams (McMahon and Hartman 1989) are important habitats for stream fishes during winter. However, the availability and accessibility of suitable habitat varies with stream size, elevation, and the dynamic nature of winter ice conditions (Bernard and Israelsen 1982; Chisholm et al. 1987; Power et al. 1993). In larger streams, woody debris-dominated habitats are less common and ice conditions often more severe (Chisholm et al. 1987; Bilby and Ward 1989). Thus, bull trout and westslope cutthroat trout overwintering in larger streams may prefer winter habitats and cover types markedly different from those in smaller streams containing abundant woody debris.

During periods of low water temperature, stream salmonids have lower metabolism, decreased food requirements, and reduced swimming ability (Hartman 1963). Winter survival depends more on finding areas of shelter than obtaining food (Mason 1976). As a result, fish must select microhabitats offering a combination of low velocity water to minimize energy expenditures (Cunjak 1988a), and cover to protect against a high risk of predation (Cunjak and Power 1987b).

In addition to changing habitat requirements, stream salmonids also respond to declining water temperature by largely restricting their foraging activities to night (Campbell and Neuner 1985; Fraser et al. 1993). During autumn and winter daylight hours, smaller trout (< 20 cm) extensively hide in substrate interstices, complex LWD jams, or submerged vegetation, and are usually not visible in the water column (Contor 1989; Fraser et al. 1993; Bonneau 1994). Larger trout (> 20 cm) tend to aggregate in deep, low velocity habitats with abundant cover (Cunjak and Power 1986; Heggenes et al. 1993). On winter nights, trout of all sizes become active and move away from cover, maintaining feeding or resting positions on or above the substrate (Campbell and Neuner 1985; Heggenes et al. 1993; Vore 1993; Bonneau 1994). The switch from diurnal (summer) to nocturnal (autumn & winter) activity occurs primarily in response to declines in autumn water temperature below some threshold level, although photoperiod also appears to play a role (Rimmer and Paim 1990; Fraser et al. 1993). Daytime concealment has generally been observed in water temperatures < 8 C and is thought to reduce energy expenditure and predation risk (Bustard and Narver 1975; Cunjak 1988b; Contor 1989; Hillman et al. 1992; Riehle and Griffith 1993). Nocturnal foraging is believed to lessen the risk of microhabitat exclusion or entrapment by anchor ice (Heggenes et al. 1993).

Although the daytime behavior of westslope cutthroat trout and bull trout appears consistent with this concealment strategy during winter (Goetz 1991; Schill 1991; Vore 1993; Bonneau 1994), nighttime behavior is not well understood. In water temperatures < 8 C, juveniles of both species extensively conceal themselves in complex forms of cover during daylight hours (Shepard et al. 1984; Goetz 1991; Vore 1993; Bonneau 1994). Adult westslope cutthroat trout tend to aggregate in deep pools offering low velocity (0-5 cm/s) focal points and hiding cover (Vore 1993). Little is known about the winter hiding behavior and habitat preferences of adult bull trout.

Differences in choice of winter habitat may be a function of winter competition for similar shelters (Cunjak and Power 1986). Heggenes et al. (1993) suggested that interspecific interactions among stream salmonids may be severe because of more restricted habitat requirements during winter. In summer, bull trout and westslope cutthroat trout appear to avoid direct competition for food or habitat by selecting different microhabitats and foraging sites (Nakano et al. 1992). Juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*), a comparable species assemblage, also exhibit similar summer microhabitat differences (Dolloff and Reeves 1990).

Although differential microhabitat use between bull trout and westslope cutthroat trout during winter was recently documented by Bonneau (1994), competition for limited winter space has not been examined as the cause of these differences.

Autumn and winter daytime snorkeling surveys may be inadequate for defining winter habitat requirements of stream salmonids due to daytime concealment. Several studies suggest that night snorkeling may be a more effective method for observing stream salmonids during winter (Campbell and Neuner 1985; Heggenes et al. 1993). Goetz (1991) observed 2.5 times more juvenile bull trout at night in water temperatures < 6.5 C and Vore (1993) observed twice as many westslope cutthroat and bull trout on winter nights than on winter days.

My study was designed to compare diel differences in density and habitat use of resident bull trout and westslope cutthroat trout during autumn and winter in streams of different morphology. Study sites included a small, LWD-dominated stream lacking boulder substrate and a larger, boulder-dominated stream lacking LWD. Specific questions addressed were (1) how does stream morphology influence the diel habitat use of resident bull trout and westslope cutthroat trout during autumn and winter?; and (2) do the species exhibit similar winter habitat preferences both day and night?

Study Area

Diel behavior and habitat use of westslope cutthroat trout and bull trout was compared in Meadow Creek, a woody debris-dominated stream lacking boulder substrate (Figure 3.1), and Daly Creek, a boulder-dominated stream lacking woody debris (Figure 3.2). Meadow Creek, a fourth-order stream that originates at an elevation of 2317 m, flows north for 16 km before joining the East Fork of the Bitterroot River. It drains an area of 85.5 km^2, and ranges in width from 2.0 to 5.0 m. A 1 km-long study section was established 8 km above the mouth (Figure 3.1). Gradient averages 2.1%, and substrate is dominated by gravel and fine sediments with few boulders but substantial amounts of LWD. Several beaver (*Castor canadensis*) dams are located in the lower sections of the reach. The stream is bordered by mixed stands of lodgepole pine (*Pinus contorta*), Englemann spruce (*Picea engelmannii*), and willow (*Salix* spp.). The watershed is used for timber harvest, livestock grazing, and recreation. Angling use is low (Chris Clancy, MDFWP fisheries biologist, personal communication). Meadow Creek has a snow-dominated hydrograph typical of streams in the central Rocky Mountains; low flow from late summer until early spring, and peak runoff in May and June following snowmelt. During autumn and winter, flow was less than 0.25 m^3/s. Autumn (September - late October) water temperatures

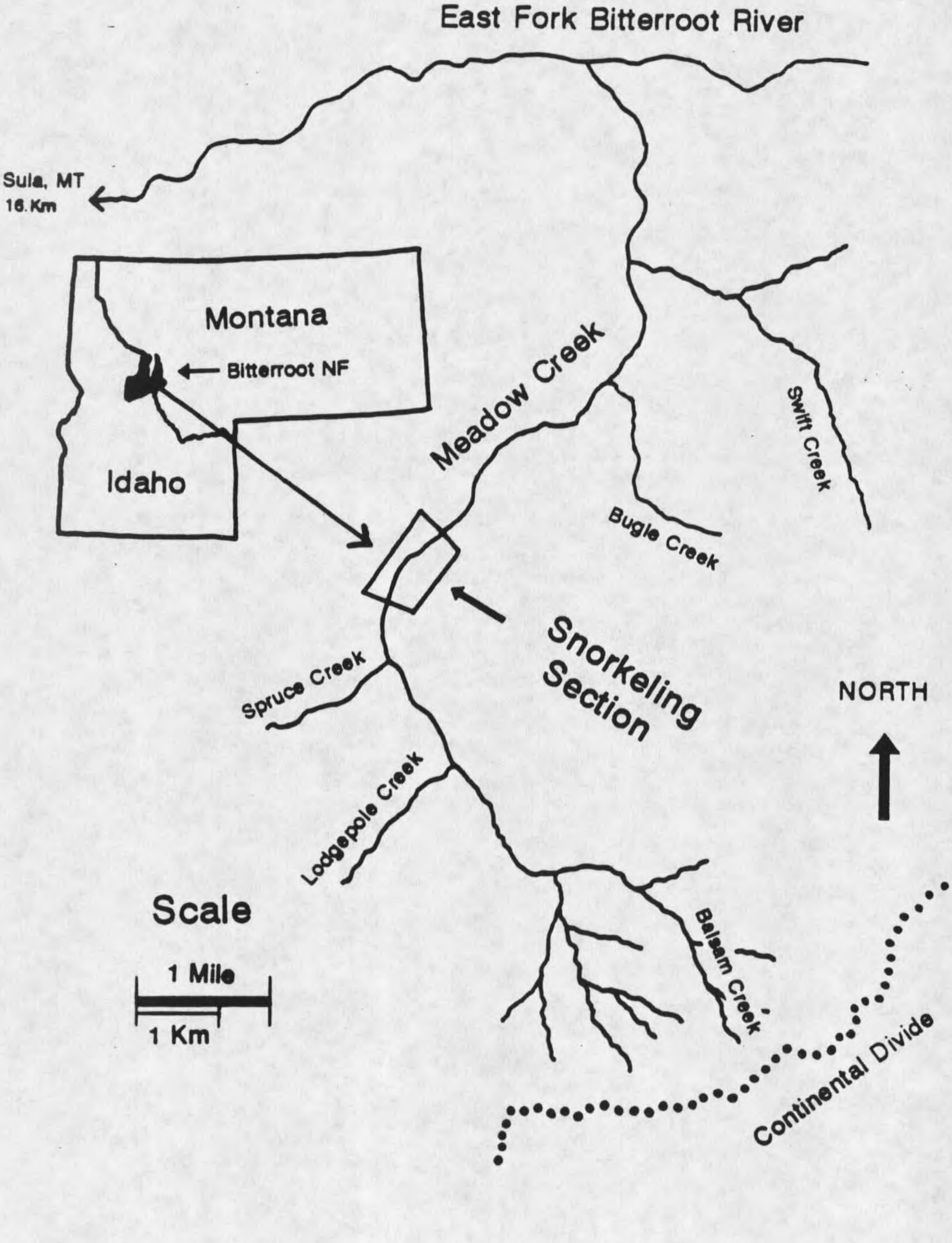


Figure 3.1. Map of the Meadow Creek drainage and snorkeling section, Bitterroot National Forest, Ravalli County, Montana.

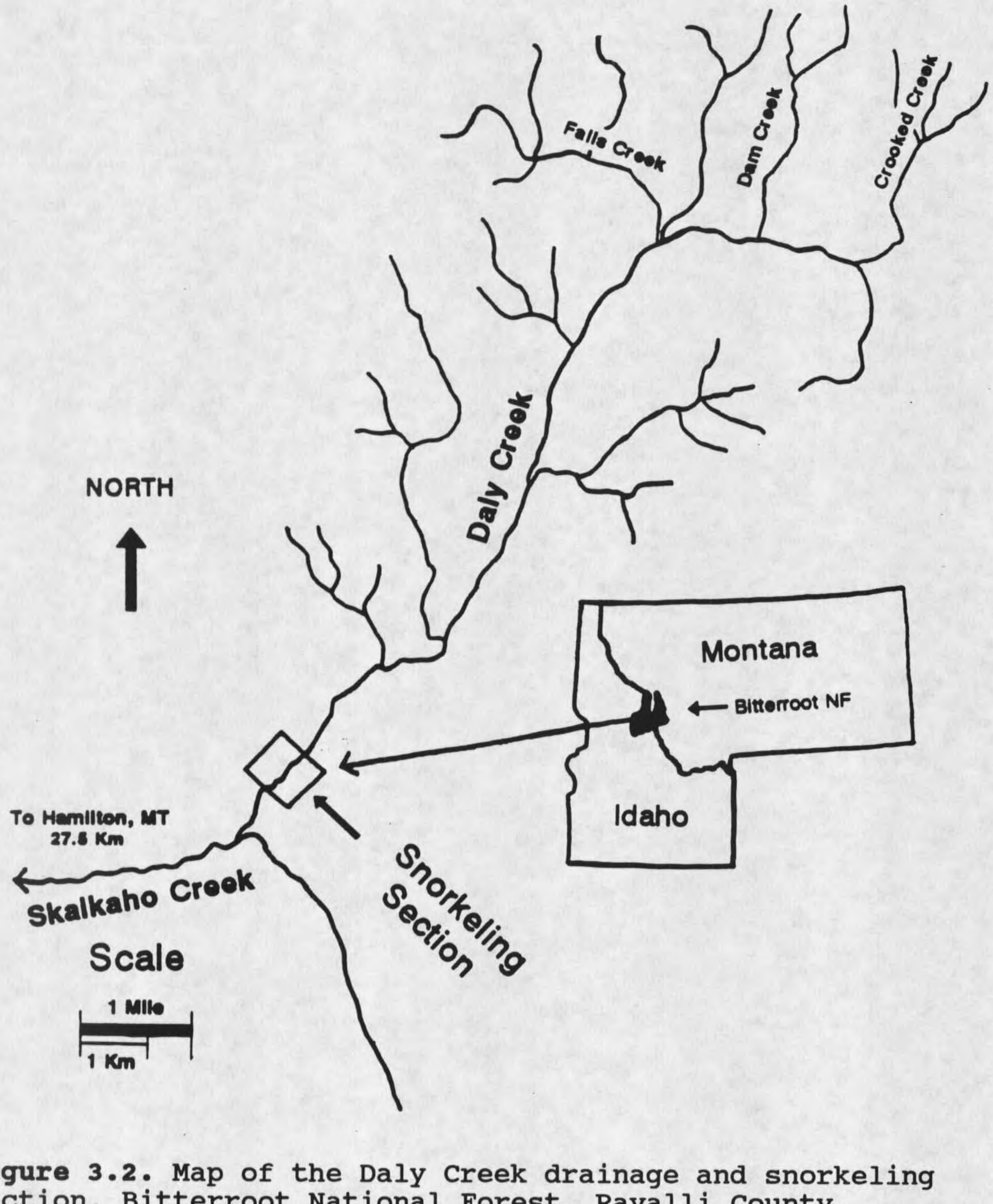


Figure 3.2. Map of the Daly Creek drainage and snorkeling section, Bitterroot National Forest, Ravalli County, Montana.

were < 9.5 C, while winter (late October - early March) water temperatures ranged between 0.0-0.5 C. The stream is mostly ice-covered (> 95% wetted surface area) from early November through late March. Sub-surface ice (anchor and frazil ice) is rare, present only in riffles prior to surface ice formation. Slimy sculpin (*Cottus cognatus*) is the only other fish species that occurs besides bull trout and westslope cutthroat trout.

Daly Creek, a fourth-order stream that originates at an elevation of 2268 m, flows southwest for 18 km before joining Skalkaho Creek at an elevation of 1408 m. It drains an area of 98.4 km^2, and ranges in wetted width from 0.7 m to 8.0 m. A 1 km-long study section was established approximately 0.6 km above Skalkaho Creek (Figure 3.2). Gradient averages 4.1%, and substrate is comprised mostly of cobble and gravel, with boulders common but LWD scarce. Beaver ponds are not present in Daly Creek. The watershed is used for limited timber harvest and recreation, and angler use is moderate (C. Clancy, MDFWP, personal communication). During autumn and winter, discharge declined from 0.90-0.40 m^3/s. Autumn water temperatures were < 9.5 C, and winter water temperatures ranged between 0.0-1.0 C (early November - early March). Surface ice formation varies widely depending on air temperature, and sub-surface ice is common. The fish community is the same as that in Meadow Creek.

Methods

Habitat Classification

Habitat units within each study section were classified according to Bisson et al. (1981) (Table 3.1). Specific habitat units for snorkeling observations were then chosen randomly with most selected habitats separated by unsampled sections of stream. Approximately equal areas (Meadow Creek=2621.0 m^2; Daly Creek=2975.5 m^2) within each stream were snorkeled with at least five habitat units of each type sampled. Meadow Creek contained 41 snorkeling units (total length=474 m) stratified into six habitat types: (1) beaver pond; (2) riffle; (3) glide; (4) pools with abundant LWD; (5) pools with moderate LWD; (6) and pools lacking LWD. Daly Creek contained 29 snorkeling units (total length=367 m) stratified into five habitat types: (1) LWD pool; (2) boulder pool; (3) riffle; (4) glide; and (5) pocket water.

Microhabitat Use

Microhabitat observations of bull trout and westslope cutthroat trout were conducted by underwater observation using a dry suit, mask, snorkel, and underwater flashlight. Snorkel surveys occurred over two autumn and winter periods (Sep 1992-Mar 1993 and Sep-Dec 1993). A total of 12 dives (9 day, 3 night, 60 h total observations) in Meadow Creek, and 21 dives (10 day, 11 night, 85 h total observations) in

Table 3.1. Habitat unit types designated in the Daly Creek (D) and Meadow Creek (M) snorkeling sections as modified from Bisson et al. (1981).

Riffle (D & M) - Stream unit with moderate current velocity (20-50 cm/s) and moderate turbulence. Substrate composed of large gravel and cobble (8-256 mm).

Glide (D & M) - Stream unit lacking pronounced turbulence characterized by moderately shallow water with an even flow. Substrate composed of fines and large gravel (0-64 mm).

LWD-formed pool (D) - Stream unit in which LWD has caused scouring water to carve out a non-uniform hole in the channel bed and provides the dominant cover type (contains > 20 cm of submerged LWD/m^2 pool area).

Boulder-formed pool (D) - Stream unit in which boulders have caused scouring water to carve out a non-uniform hole in the channel bed and interstitial crevices and ledges provide the dominant cover.

Pocket water (D) - Stream unit with moderate-to-fast current velocity (20-100 cm/s) and moderate turbulence interspersed with numerous boulder-formed pocket pools. Substrate composed of cobble and boulder (> 256 mm).

Beaver pond (M) - Stream unit formed by the damming activities of beaver characterized by deep water (> 50 cm), low velocity (< 5 cm/s), and fine sediment (< 8 cm).

Pool with abundant LWD (M) - Pool whose dominant formative feature and cover type is LWD (contains > 50 cm of submerged LWD/m^2 pool area). Scour hole position is variable.

Pool with moderate LWD (M) - Pool whose dominant formative feature may be LWD, but LWD is less abundant (contains 20-50 cm of submerged LWD/m^2 pool area). Scour hole position is variable.

Pool lacking LWD (M) - Stream unit formed by scouring flow impinging against one streambank due to a meander bend in the channel (contains < 20 cm of submerged LWD/m^2 of pool area).

Daly Creek were made over the course of the study. Consult Appendix Table 3 for specific snorkeling dates, times, and water temperatures. Each stream was generally snorkeled twice a month. A minimum of 7 d separated consecutive observations to reduce potential disturbance. Daytime observations were conducted between 0930-1600 and nighttime observations between 1930-0400. "Nighttime" commenced one hour after sunset and continued until one hour before sunrise. Meadow Creek could not be snorkeled after early November due to extensive surface ice cover. Surface ice cover in Daly Creek was less extensive and snorkel observations were made throughout the winter.

I entered the stream at the downstream end of a habitat unit and searched methodically for trout by slowly crawling upstream in a zigzag pattern across the stream. The majority of fish could be approached quite closely without disturbance (usually within 1 m) and were readily counted and observed. I inspected all sites with sufficient water depth (> 15 cm) and overturned cobbles to search for trout hiding in substrate interstices. Shallow areas (< 15 cm) were searched in daylight and at night by flashlight. Due to the cryptic behavior and coloration of bull trout, an underwater flashlight was necessary during both day and night dives to efficiently search substrate interstices, LWD jams, undercut banks, and ice ledges. The flashlight beam did not appear to frighten fish provided that I moved slowly and deliberately. Underwater visibility was excellent (> 5 m) in both streams during the study.

When a trout was encountered, it was observed for a few moments to determine its focal point. Microhabitat data was not recorded for disturbed fish that fled their focal stations or rapidly approached the diver. A numbered, painted stone was placed on the stream bottom directly below the focal point. Trout species, size, elevation above the streambed, dominant cover, and the number of other fish present within a 30-cm radius of the focal point were recorded. Each species was readily identified underwater due to unique physical characteristics. Size was estimated according to categories which generally correspond to YOY (< 50 mm TL), juvenile (50-200 mm TL), and adult (> 200 mm TL) bull trout and westslope cutthroat trout. Trout < 50 mm TL (YOY) were uncommon and I did not collect microhabitat data on these small fish. I practiced estimating sizes of fish by classifying wooden dowels of unknown length into proper size categories from an underwater distance of 2-3 m, and correctly categorized dowels > 95% of the time following 30 minutes of practice. I defined dominant cover as the nearest cover (Table 2.2) to the focal point capable of hiding at least 75% of the fish's body. Aggregations of fish were common in this study, so I treated these groups as discrete entities and analyzed microhabitat use separately. Aggregations were defined as a group of at least five fish of one or more species, in close association (approximately one body length of each other), and displaying a common behavioral pattern (Cunjak and Power 1986). Microhabitat use was quantified by taking the mean of measurements at the anterior, posterior, and center of the group; cover use was based on the position of the majority of the fish within the aggregation (Cunjak and Power 1986).

Several additional variables were measured at focal points following snorkel surveys (Table 3.2). Total depth

Table 3.2. Focal point characteristics measured in microhabitat analysis.

Characteristic	Description
Total depth	Distance (cm) from the substrate to the water surface
Distance to cover	Minimum distance (cm) to the nearest cover object capable of hiding at least 75% of the fish's body
Focal point velocity	Velocity (cm/s) measured at the snout of the fish
Mean column velocity	Velocity (cm/s) measured at 0.6 of the total depth in water < 75 cm deep; measured as the mean of velocity readings at 0.2 and 0.8 of the total depth in water > 75 cm deep
Substrate composition	Dominant and subdominant particle size within a 30 cm radius of the fish's snout (fines < 8 mm diameter; large gravel 8-64 mm; cobble 64-256 mm; boulder > 256 mm)

and distance to the nearest cover were measured using a meter stick and water velocities with a Marsh-McBirney model 201 electronic flowmeter mounted on a top-setting wading rod. For focal points located under winter ice shelves, I used a small folding ruler to reach under the ice while lying in an open water section of stream. I also measured velocities under ice cover in a similar fashion by holding the wading rod horizontally above the focal point. Water temperatures were recorded throughout the study period using continuously recording electronic thermographs, and point measurements of air and water temperatures were taken with a hand-held thermometer at regular intervals while snorkeling.

Habitat Availability

Transects were established in both streams during late September 1993 to quantify microhabitat availability at base flow conditions without ice cover. Autumn base flow was similar over both seasons, so I assumed that microhabitat characteristics did not change between autumn 1992 and 1993. Transects were placed systematically at 2.4 m intervals in all sampled habitat units, yielding 200 total transects in Meadow Creek and 150 total transects in Daly Creek. At each transect, ten points were measured at equally-spaced intervals (Baltz 1990). At each point, I measured total depth, dominant and subdominant substrate particle size, bottom velocity (cm/s), mean column velocity, and dominant cover. The number of microhabitat availability observations (2000 points in the Meadow Creek, 1500 points in Daly Creek) exceeded the number of microhabitat use observations, a requirement for valid comparisons between habitat use and availability (Baltz 1990).

In Daly Creek, the same transects were remeasured in late December 1993 to quantify winter cover availability at base flow conditions with moderate (50-75% wetted width covered) ice cover. I designated cover as "surface ice" only if water depth under the ice was > 10 cm and mean water column velocity was < 15 cm/s. Velocities were measured under ice-covered points to determine the suitability of surface ice as overhead cover, but were not measured in open water sections. Meadow Creek was not remeasured, since extensive ice cover prevented sampling. Ice conditions in Daly Creek were similar between winters. Winter cover availability was quantified by determining the dominant cover at each point along transects.

Density Observations

Day and night habitat unit densities of westslope cutthroat trout and bull trout were determined by counting the number of fish in each habitat unit. Density was expressed as the number of fish per 100 m^2 by habitat unit type.

Calibration of Snorkeling Observations

I tested the efficiency of day and night snorkeling by comparing snorkel estimates with electrofishing removal estimates. Ten habitat units were randomly selected in each stream (two of each habitat type excluding beaver ponds). In October 1993, daytime snorkeling estimates in each unit were followed by a 2-pass removal technique using either a Coffelt Mark-10 backpack electroshocking unit (Meadow Creek; pulse DC; 60 Hz; 250 volts) or a Coffelt Mark-22M streambank electroshocking unit (Daly Creek; straight DC; 250 volts). Block nets were used to enclose habitat units in Meadow Creek, but could not be deployed effectively in Daly Creek due to its larger size. Therefore, block nets were spread along the bottom of Daly Creek habitat units and an observer counted all fish moving over the top of the net. Nighttime efficiency was determined by snorkeling the same habitat units at night within 5 days of the electroshocking removal estimates.

Data Analysis

Snorkeling the same habitats with multiple surveys over a span of several months technically violates the statistical assumption of independence because fish may be observed more than once (Baltz 1990). However, observations of 24 floy-tagged fish in the study area indicated that repeat observations comprised a small percentage (< 5%) of the total number of observations. Also, the long time intervals between surveys (14-21 d) allowed for considerable movement between observations, and large sample sizes minimized the possible bias associated with repeat observations.

I used nonparametric tests in statistical comparisons because microhabitat variables often violated the assumption of normality required for parametric tests. Microhabitat use was analyzed using both univariate and multivariate approaches. SAS (Release 6.03 Edition for the personal computer, 1988) and STATGRAPHICS (Version 5, 1991) statistical programs were used to perform all statistical computations and significance was defined as $P < 0.05$ unless otherwise stated.

Continuous microhabitat variables (focal point elevation, depth, distance to the nearest cover, and focal point velocity) were compared among species in each stream using a Mann-Whitney U-test (Zar 1984). A chi-square goodness-of-fit test (Zar 1984) was used to compare cover use (categorical variable) versus availability. Simultaneous Bonferroni confidence intervals (Neu et al. 1974) were constructed around point estimates to determine whether a cover type was preferred, avoided, or used in proportion to availability. Preference or avoidance of a specific cover type occurred when percent cover availability did not overlap the confidence interval (Byers et al. 1984). Substrate preferences were compared using an electivity index (D) (Jacobs 1974):

$$D = \frac{r - p}{(r+p) - 2rp}$$

where r = proportion of substrate used by a species and p = proportion of substrate available. This index varies between -1.0 (strong avoidance) and +1.0 (strong selection). Values can be subdivided to describe the magnitude of avoidance or preference (Moyle and Baltz 1985):

-1.00 to -0.50	strong avoidance
-0.49 to -0.26	moderate avoidance
-0.25 to +0.25	neutral selection
+0.26 to +0.49	moderate selection
+0.50 to +1.00	strong selection

A discriminant function analysis similar to that conducted by Dolloff and Reeves (1990) was used to examine diel differences in microhabitat use displayed by four groups of fish (cutthroat trout day, cutthroat trout night, bull trout day, bull trout night) according to four microhabitat variables (depth, focal point velocity, focal point elevation, and distance to the nearest cover). Observations of juvenile and adult fish were combined by species and time of day; however, assumptions of multivariate normality and homogeneity of variance were violated despite log transformation of variables. Thus, the robust nature of discriminant analysis permitted a descriptive rather than predictive interpretation of the data (Morrison et al. 1992).

Nighttime habitat unit densities were compared between species using Mann-Whitney U-tests. Daytime densities were not compared statistically due to the small number of fish observed. Simple linear regression was used to examine the relationship between diel density and water temperature.

Results

A total of 4,959 fish (4,598 westslope; 361 bull trout) were observed during 12 autumn and winter snorkeling surveys in Meadow Creek. Individual microhabitat measurements were recorded for 1,220 cutthroat trout, 205 bull trout, and 154 aggregations. A total of 2,179 fish (1,620 cutthroat trout; 559 bull trout) were observed during 21 autumn and winter snorkeling surveys in Daly Creek. Individual microhabitat measurements were recorded for 1,307 cutthroat trout, 559 bull trout, and 38 aggregations. Consult Appendix Table 3 for specific snorkeling dates, times, water temperatures, and number of fish observed.

Microhabitat observations from the two autumn/winter seasons of the study were tested for significant differences between years. Significant differences occurred in two variables (focal point elevation and distance to cover) for Daly Creek cutthroat trout, but all other variables did not differ. I therefore pooled observations from both years for each stream. I believe the unseasonably cold water temperatures (< 10 C) in summer 1993 triggered earlier daytime hiding behavior (1992 = early October; 1993 = early September) which resulted in more observations of cutthroat trout lower in the water column (1992 mean = 4.3 cm, 1993 mean = 2.8 cm; $P < 0.0001$) and closer to cover (1992 mean = 20.2 cm, 1993 mean = 12.0 cm; $P < 0.0001$). Although similar numbers of cutthroat trout were observed during both years (1992 N = 660; 1993 N = 647), a greater percentage of 1993 observations were made at night further suggesting that winter behavior was triggered earlier in 1993 than in 1992.

Daytime Habitat Use

Daytime microhabitat use showed only slight differences between bull trout and westslope cutthroat trout. On autumn and winter days, westslope cutthroat trout in both streams occupied positions higher in the water column than bull trout (Table 3.3). Focal depth, distance to cover, and velocity was similar for both species.

Large woody debris was the dominant cover type used by cutthroat trout in both streams during autumn and winter days. Cutthroat trout preferred LWD jams and undercut banks in Meadow Creek (Figure 3.3), and LWD jams and boulder interstices in Daly Creek as cover (Figure 3.4). Bull trout did not display daytime cover preferences in either stream. Aggregations in Meadow Creek preferred LWD jams during the day (Table 3.4). Daytime aggregations in Daly Creek were uncommon and displayed no distinct cover preferences.

Substrate preferences were generally not evident for aggregations or individuals of either species (Figure 3.5). However, bull trout in Meadow Creek strongly selected boulder substrate.

Table 3.3. Diel differences (within & between species) in focal positions selected by bull trout and cutthroat trout in Daly Creek and Meadow Creek. Day and night observations are combined. FPE = Focal point elevation (cm); Depth (cm); DTC = Distance to the nearest cover (cm); FPV = Focal point velocity (cm/s); SE = Standard Error.

		Bull Trout			Cutthroat trout			Between Species Differences	
	Variable	Day Mean (SE)	Night Mean (SE)	P-value	Day Mean (SE)	Night Mean (SE)	P-value	Day	Night
DALY	FPE	2.7 (0.33)	1.2 (0.05)	0.0001 *	5.5 (0.30)	3.0 (0.08)	0.0001 *	0.0001 *	0.0001 *
	Depth	38.7 (1.39)	33.4 (0.50)	0.0006 *	38.6 (0.81)	34.5 (0.35)	0.0001 *	0.7666	0.0576
	DTC	9.6 (4.11)	12.6 (1.29)	0.6532	8.6 (1.86)	15.4 (0.86)	0.0001 *	0.1508	0.0030 *
	FPV	8.5 (0.007)	5.2 (0.002)	0.0001 *	8.1 (0.005)	6.5 (0.002)	0.0001 *	0.3069	0.0022 *
MEADOW	FPE	1.8 (2.67)	1.2 (0.10)	0.0001 *	3.9 (0.18)	1.6 (0.06)	0.0001 *	0.0001 *	0.0001 *
	Depth	45.6 (3.71)	39.9 (1.52)	0.2241	39.6 (0.62)	37.5 (0.64)	0.0006 *	0.3064	0.2075
	DTC	17.8 (7.25)	46.7 (5.98)	0.0001 *	8.1 (1.01)	33.7 (2.37)	0.0001 *	0.2389	0.0567
	FPV	5.6 (0.008)	4.8 (0.004)	0.1732	6.6 (0.002)	5.3 (0.002)	0.0001 *	0.3235	0.5789

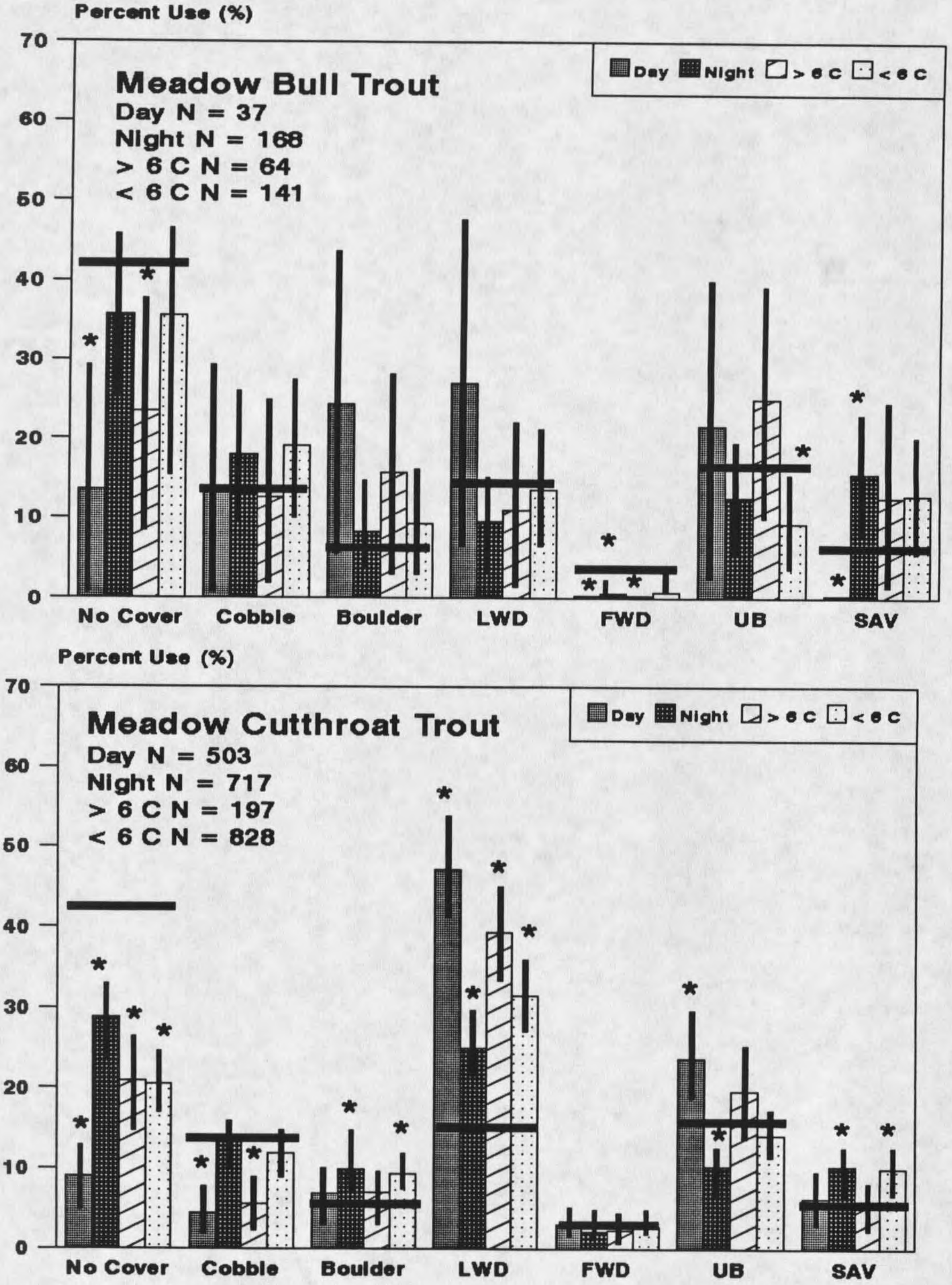


Figure 3.3. Cover use displayed by bull trout and westslope cutthroat trout in Meadow Creek. LWD = large woody debris; FWD = fine woody debris; UB = undercut bank; SAV = submerged aquatic vegetation; Horizontal lines = % availability; Vertical bars = 95% use interval; * = significant.

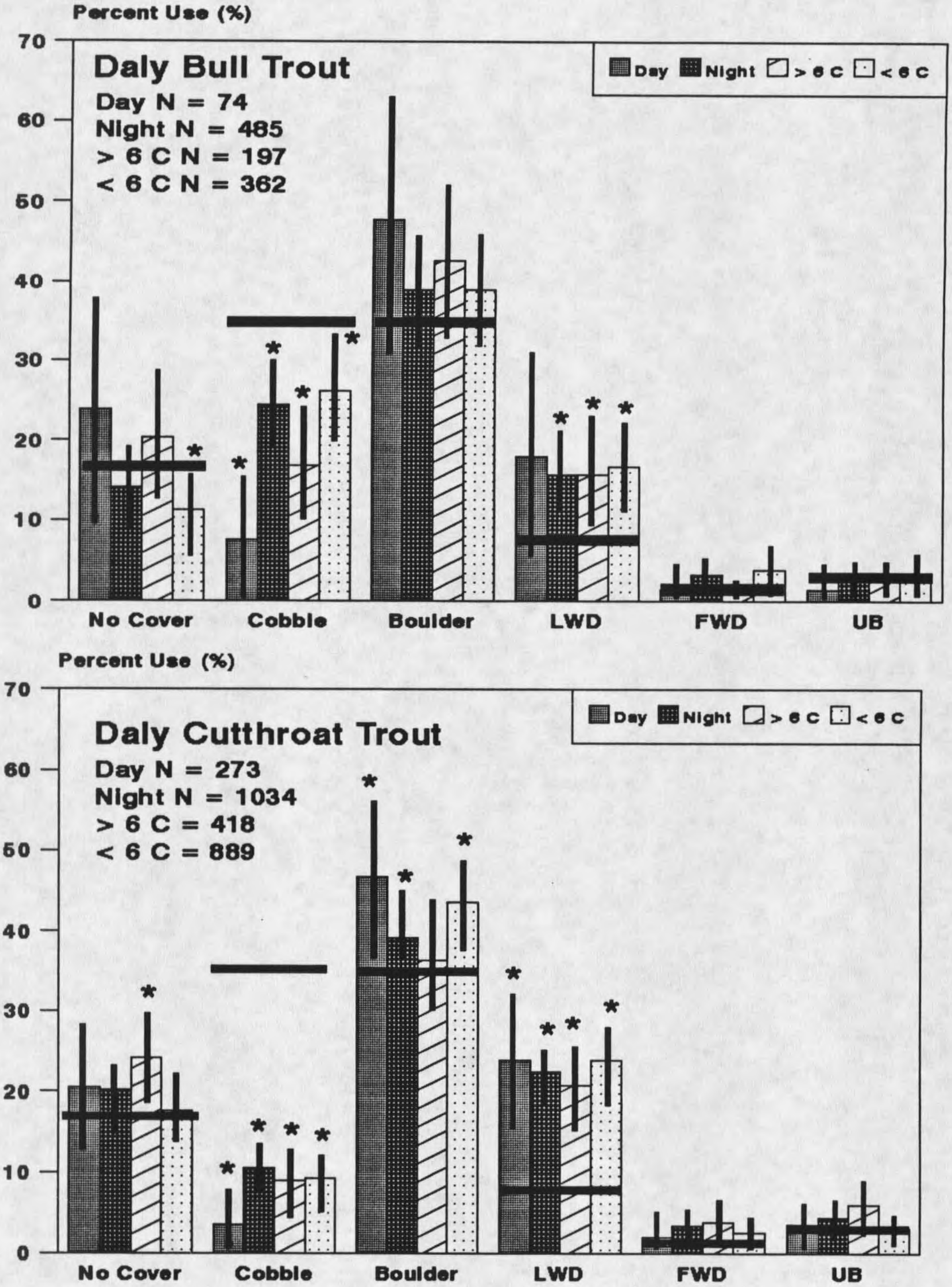


Figure 3.4. Cover use displayed by bull trout and westslope cutthroat trout in Daly Creek. LWD = large woody debris; FWD = fine woody debris; UB = undercut bank; Horizontal lines = % availability; Vertical bars = 95% use interval; * = significant.

Table 3.4. Cover use displayed by aggregations in Daly Creek and Meadow Creek. Prefer/Avoid = significant; - = cover selected in proportion to availability (sample size in parenthesis).

Cover Type	Day	Night
Daly Creek	(N=9)	(N=21)
No Cover	-	Prefer
Cobble	-	-
Boulder	-	Avoid
Large woody debris	-	-
Fine woody debris	Avoid	Avoid
Undercut bank	Avoid	-
Meadow Creek	(N=78)	(N=76)
No Cover	-	Prefer
Cobble	Avoid	Avoid
Boulder	Avoid	Avoid
Large woody debris	Prefer	-
Fine woody debris	Avoid	Avoid
Undercut bank	-	Avoid
Aquatic vegetation	Avoid	-

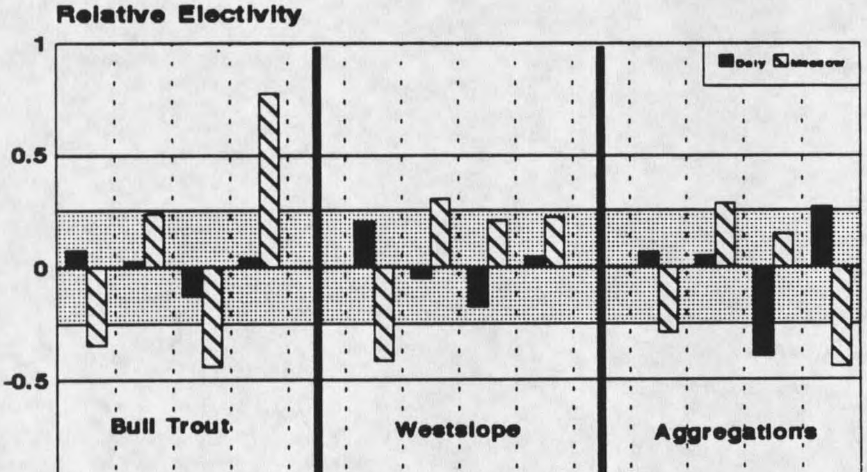


Figure 3.5. Electivity values (D) for substrate sizes selected by bull trout, cutthroat trout, and aggregations. Day and night observations are combined. Values within the shaded region (+0.25 to -0.25) indicate neutral selection.

Highest daytime densities of both species occurred in pools, although the type of pool differed by stream (Figure 3.6). In Meadow Creek, highest day densities of both species occurred in beaver ponds. Boulder-formed and LWD-formed pools contained the highest daytime densities of cutthroat and bull trout in Daly Creek.

Nighttime Habitat Use

Both species displayed similar diel microhabitat shifts in both streams. Nighttime focal positions were located further from cover, in shallower water, facing lower current velocities, and closer to the substrate than daytime positions (Table 3.3). Cutthroat trout occupied nighttime positions significantly higher in the water column than bull trout in both streams. There was no distinct pattern among focal point velocities, depths, and distances to cover between the species. Aggregations in both streams preferred nighttime focal positions closer to the substrate and further from cover (Table 3.5).

Large woody debris remained an important component of cover for both species at night. In Meadow Creek, westslope cutthroat trout increased their use of boulder cover, and both species showed a significant preference for submerged aquatic vegetation (*Fontinalis* spp.) (Figure 3.3). In Daly Creek, nighttime cover preferences were similar to daytime preferences, but bull trout at night showed a significant

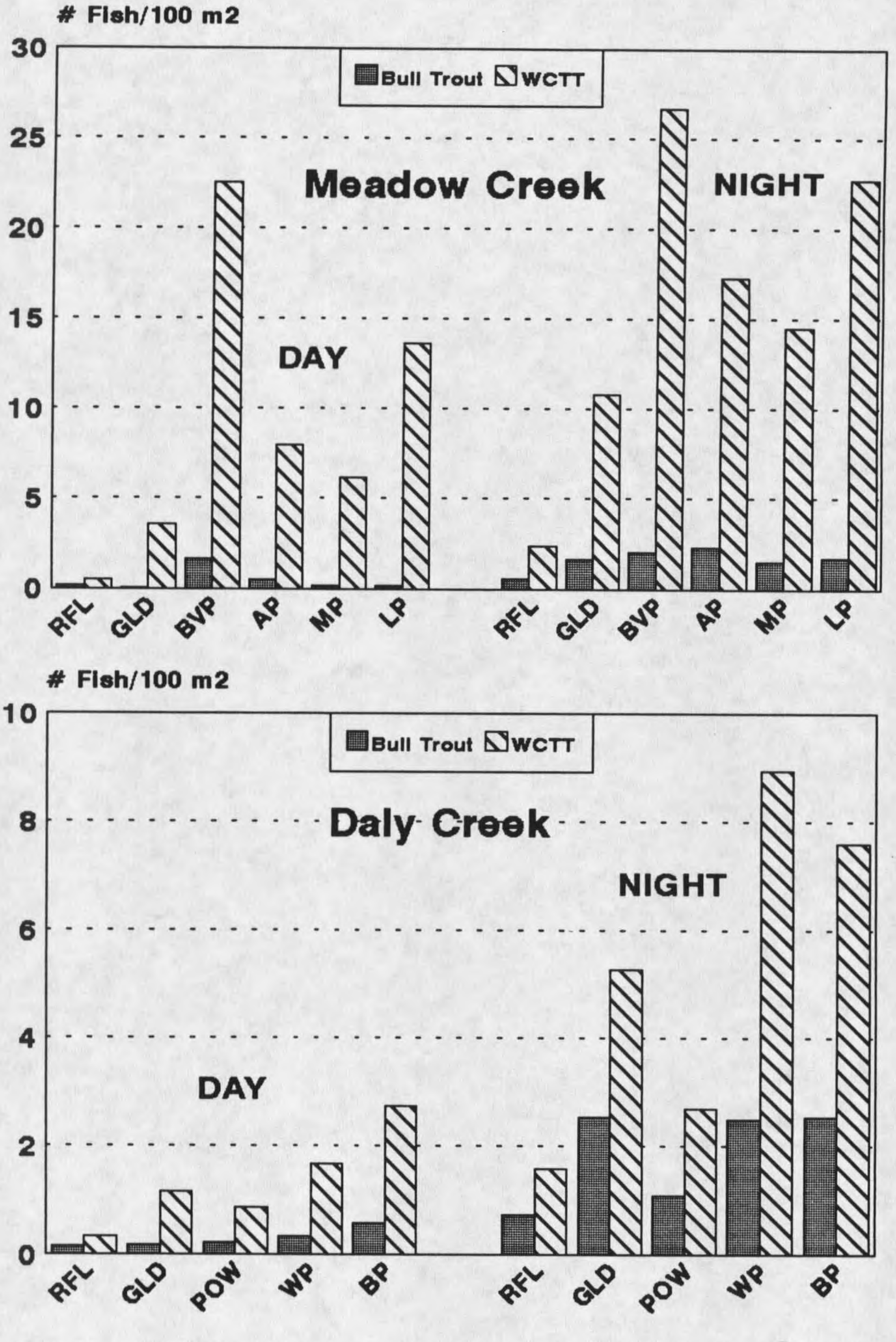


Figure 3.6. Diel habitat unit densities (#/100 m^2) of bull trout and westslope cutthroat trout (WCTT) observed by snorkeling in Meadow Creek and Daly Creek during autumn and winter, 1992-93. RFL = riffles; GLD = glides; BVP = beaver ponds; AP = pools with abundant LWD; MP = pools with moderate LWD; LP = pools lacking LWD; POW = pocket water; WP = LWD-dominated pools; BP = boulder-dominated pools.

Table 3.5. Diel focal points selected by aggregations in Daly Creek and Meadow Creek. FPE = Focal point elevation (cm); Depth (cm); DTC = Distance to the nearest cover (cm); FPV = Focal point velocity (cm/s); SE = Standard error.

Microhabitat Variable	Day Mean (SE)	Night Mean (SE)	P-value (* = Significant)
Daly Creek	**(N=9)**	**(N=29)**	
FPE	14.7 (2.11)	3.4 (0.43)	0.0002 *
Depth	48.8 (3.62)	48.2 (1.84)	0.8906
DTC	15.1 (11.90)	38.0 (6.00)	0.0157 *
FPV	11.0 (0.03)	5.7 (0.01)	0.0536
Meadow Creek	**(N=78)**	**(N=76)**	
FPE	11.5 (0.95)	1.5 (0.13)	0.0001 *
Depth	66.4 (2.53)	65.6 (2.16)	0.9813
DTC	64.7 (8.31)	110.0 (9.28)	0.0001 *
FPV	5.0 (0.01)	3.4 (0.01)	0.0526

preference for LWD (Figure 3.4). Nighttime aggregations in both streams typically occurred in exposed areas lacking cover (Table 3.4).

Highest densities of both species were observed in pools, beaver ponds, and glides on autumn and winter nights. In Meadow Creek, the highest nighttime densities of cutthroat trout were observed in beaver ponds whereas bull trout were most often observed in pools with abundant LWD (Figure 3.6). In Daly Creek, LWD-formed pools contained the highest nighttime densities of cutthroat trout and boulder-formed pools, LWD-formed pools, and glides contained the highest bull trout densities (Figure 3.6).

Overall, nighttime densities in both streams were 5 to 6 times higher than during daytime (Figure 3.7). Although Meadow Creek densities were 3 to 4 times higher than those in Daly Creek and cutthroat trout densities were approximately 3 times those of bull trout in both streams (Figure 3.6), differences closely conform to those observed in annual electroshocking surveys (C. Clancy, MDFWP, personal communication). Increases in bull trout densities at night were most pronounced in glide (16-30 fold increase) and pool (4-11 fold increase) habitats in both streams (Figure 3.6). Differences in cutthroat trout day and night densities across habitat types were much less marked (1-5 fold increase).

At night, aggregations most commonly occurred in Meadow Creek beaver ponds and Daly Creek pools. Size of aggregations in beaver ponds differed considerably between day (mean = 46.6 fish) and night (mean = 21.9 fish), and was strongly correlated with declining autumn water temperature (day $r^2=0.84$, $P=0.001$; night $r^2=0.96$, $P=0.018$). At night, pond aggregations were significantly more numerous than during the day (mean = 1.2 vs 0.5 aggregations/100 m^2, $P=0.004$). However, nighttime aggregations usually consisted of fewer fish (< 20) that were resting directly on the pond bottom. Daytime aggregations, in contrast, consisted of large mixed schools (50-120 fish) of cutthroat trout and

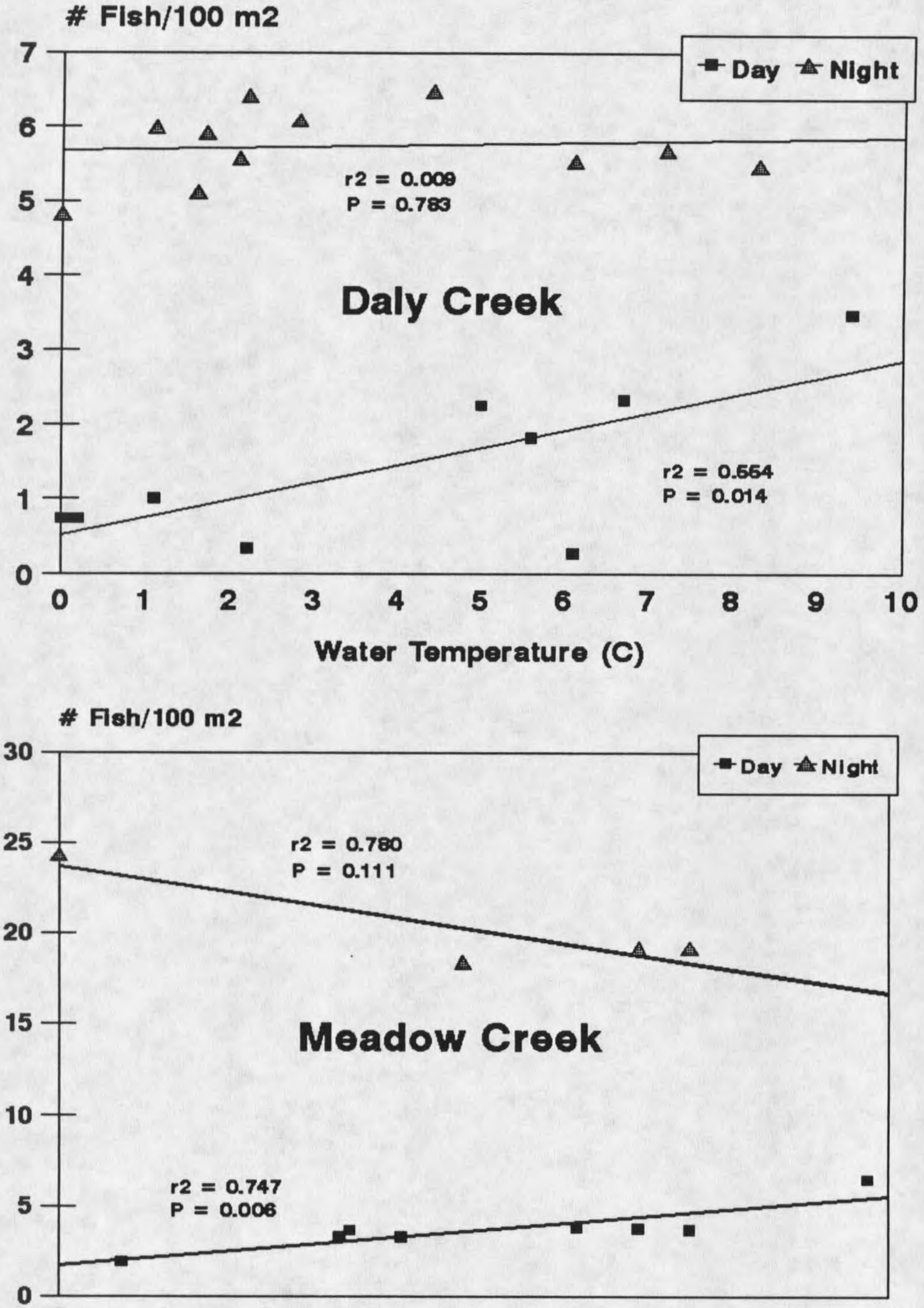


Figure 3.7. Relationship between diel fish density (bull trout and cutthroat trout combined) and water temperature during autumn and winter, 1992-93.

bull trout swimming in mid-water column in the deepest sections of the pond.

Seasonal Differences

Westslope cutthroat trout and bull trout displayed similar microhabitat shifts in response to water temperature declines. Both species moved significantly closer to the substrate and cover, selected shallower depths, and faced slower current velocities at temperatures < 6 C (Table 3.6).

Table 3.6. Focal points selected by bull trout (Bull) and westslope cutthroat trout (WCTT) in Daly Creek and Meadow Creek at water temperatures > 6 C and < 6 C. Day and night observations are combined in this table. FPE = Focal point elevation (cm); Depth (cm); DTC = Distance to the nearest cover (cm); FPV = Focal point velocity (cm/s); SE = Standard Error.

Microhabitat Variable	> 6 C Mean (SE)	< 6 C Mean (SE)	P-value (☆ = Significant)
Daly Bull	**(N=197)**	**(N=362)**	
FPE	1.6 (0.13)	1.3 (0.07)	0.0001 ☆
Depth	36.4 (0.81)	32.8 (0.57)	0.0006 ☆
DTC	22.5 (3.02)	9.5 (1.09)	0.0157 ☆
FPV	7.2 (0.004)	4.8 (0.002)	0.0001 ☆
Daly WCTT	**(N=418)**	**(N=889)**	
FPE	4.1 (0.19)	3.3 (0.11)	0.0001 ☆
Depth	37.9 (0.61)	34.6 (0.37)	0.0001 ☆
DTC	24.7 (2.09)	12.0 (0.78)	0.0001 ☆
FPV	8.8 (0.004)	6.1 (0.002)	0.0001 ☆
Meadow Bull	**(N=64)**	**(N=141)**	
FPE	1.1 (0.05)	1.4 (0.16)	0.9104
Depth	43.0 (2.39)	40.0 (1.75)	0.2318
DTC	30.6 (8.53)	46.4 (6.34)	0.0454 ☆
FPV	6.3 (0.006)	4.3 (0.004)	0.0011 ☆
Meadow WCTT	**(N=392)**	**(N=828)**	
FPE	3.1 (0.19)	2.3 (0.09)	0.0001 ☆
Depth	39.9 (0.76)	37.6 (0.56)	0.0036 ☆
DTC	25.6 (3.18)	22.0 (1.61)	0.1900
FPV	6.5 (0.003)	5.5 (0.002)	0.0043 ☆

The exception was bull trout in Meadow Creek that were observed mostly in beaver ponds at temperatures < 6 C. Thus, their microhabitat shift exhibited an unusual pattern, with fish moving further from cover and higher in the water column.

Large woody debris and surface ice margins were the preferred hiding covers of Daly Creek westslope cutthroat trout at temperatures < 6 C (Figures 3.4, 3.8). Daly Creek bull trout, in contrast, avoided surface ice margins and preferred LWD (Figures 3.4, 3.8). Meadow Creek bull trout generally used cover in proportion to availability, whereas cutthroat trout preferred LWD, boulder interstices, and submerged aquatic vegetation at temperatures < 6 C (Figure 3.3).

Water temperature strongly influenced daytime fish density but had little effect on nighttime density. In both streams, daytime density (cutthroat trout and bull trout combined) was positively correlated with water temperature but night density was not correlated (Figure 3.7). By contrast, daytime density in Meadow Creek beaver ponds was negatively correlated with water temperature (r^2=0.79, P=0.003). Mean size of daytime aggregations in beaver ponds increased from < 16 fish (7.8 C) to approximately 73 fish (0.0 C) as declining water temperatures triggered movement of large numbers of fish into beaver ponds.

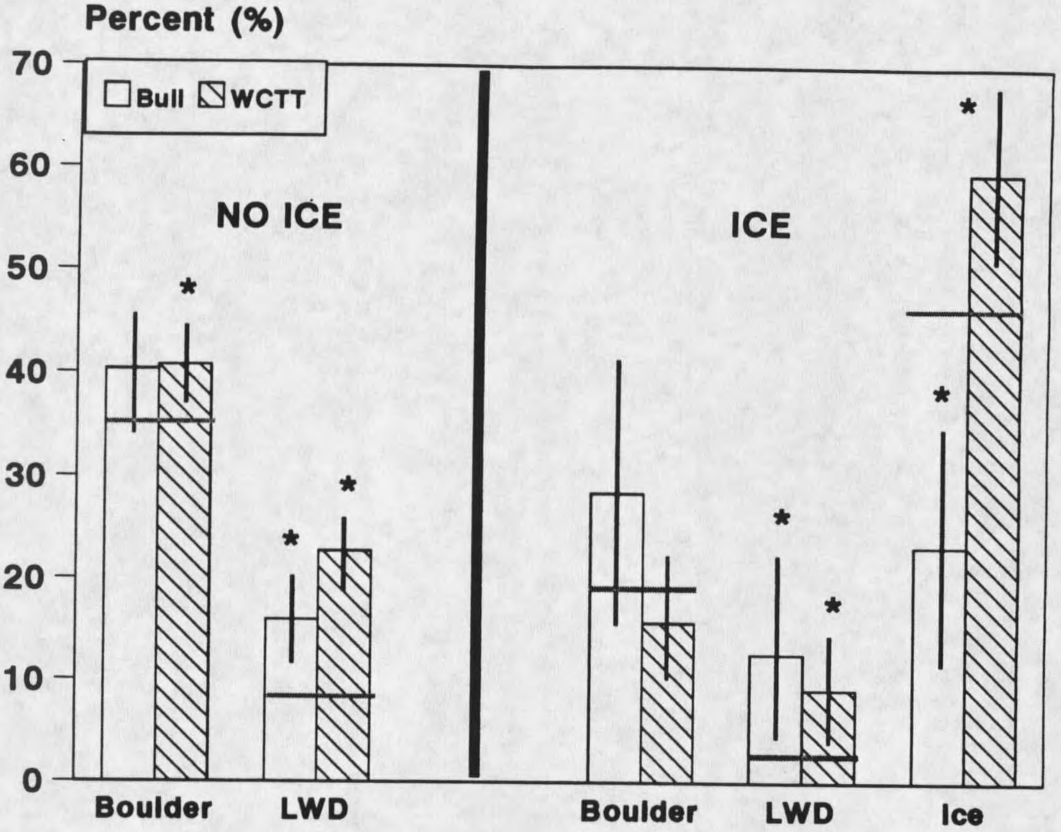
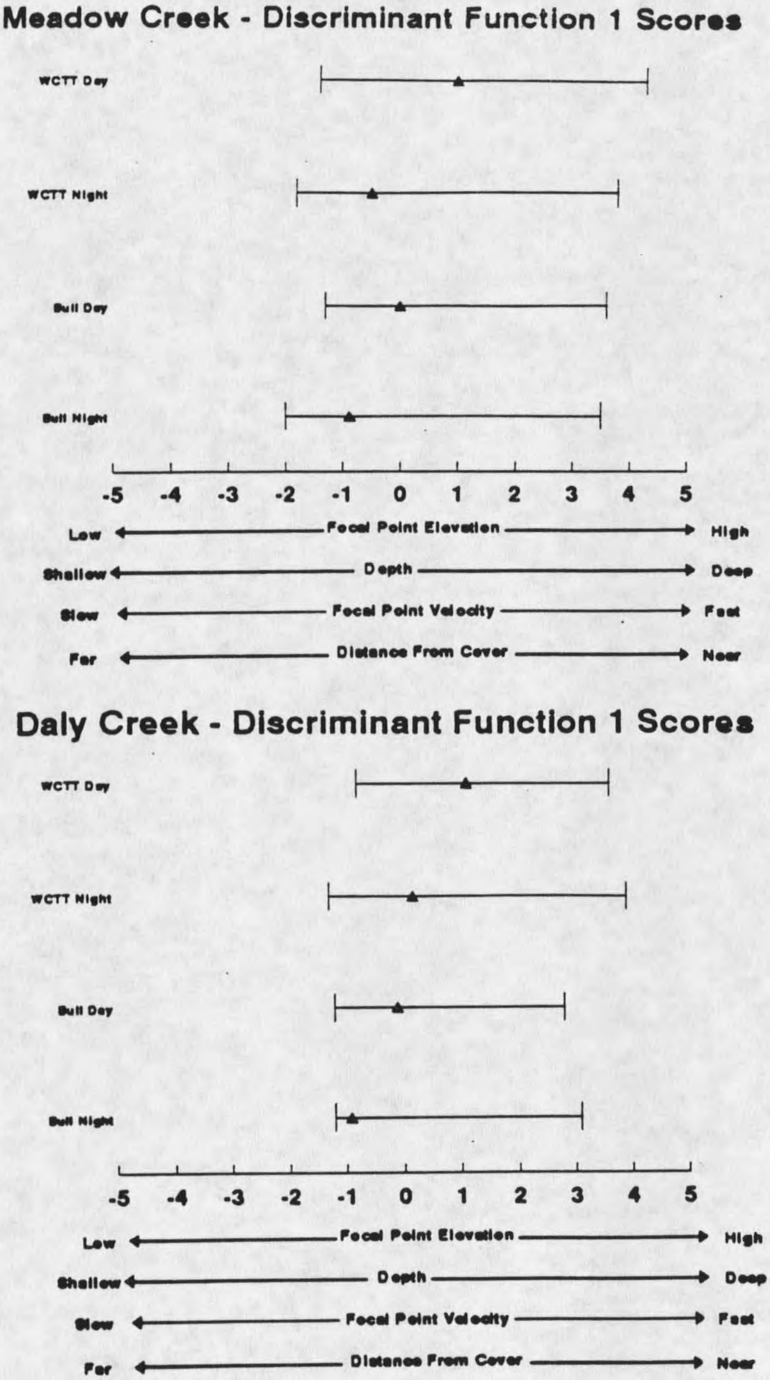


Figure 3.8. Use of boulders, large woody debris, and surface ice by bull trout and westslope cutthroat trout in Daly Creek during autumn and winter, 1992-93. Day and night observations are combined. LWD = large woody debris; Horizontal lines = % availability; Vertical bars = 95% use interval; * = significant.

Discriminant Analysis

Results of multivariate analysis showed minor differences in microhabitat use between streams and similar diel shifts between species. Nighttime microhabitat use of both species in Meadow Creek was similar whereas differences in daytime use were more apparent (Figure 3.9). In Daly Creek, diel shifts were similar in magnitude for both



Meadow Creek - Discriminant Function 1 Scores

Daly Creek - Discriminant Function 1 Scores

Figure 3.9. Group centroids (triangles) and ranges of position on the first discriminant function for 4 groups of fish (cutthroat day, cutthroat night, bull trout day, bull trout night) observed while snorkeling in Meadow Creek and Daly Creek. WCTT = westslope cutthroat trout; Bull = bull trout.

species and between-species differences were more apparent regardless of day or night (Figure 3.9). In both streams, differences were only apparent on the first discriminant function. Focal position in the water column (elevation) was the most important variable separating groups in both streams (Table 3.7). Distance to cover, focal point velocity, and depth varied in importance in both streams; however, all were less important at separating groups than focal point elevation.

Table 3.7. Standardized discriminant function coefficients and percent of variation explained by the first discriminant function (DF I) for Meadow Creek and Daly Creek microhabitat use observations.

Variable	**Meadow Creek DF I**	**Daly Creek DF I**
Focal point elevation	0.79051	1.02871
Distance to cover	-0.58163	-0.08030
Depth	0.12940	-0.03881
Focal point velocity	0.02340	-0.08765
Percent of variance	96.84%	92.31%

Daytime westslope cutthroat trout observations in both streams were correctly classified 60-62% of the time; misclassifications were mostly daytime bull trout observations (Table 3.8). Night cutthroat trout observations were most often classified as night bull trout observations. Day bull trout observations were correctly classified 24% (Daly Creek) and 51% (Meadow Creek) of the time (Table 3.8). In Daly Creek, day bull trout

Table 3.8. Proportion of group membership predicted by discriminant function analysis for four groups of bull trout (Bull) and westslope cutthroat trout (WCTT) in Meadow Creek (M) and Daly Creek (D). The number of correct classifications is enclosed in parenthesis.

Actual Group	Sample size N	WCTT Day	WCTT Night	BT Day	BT Night
		Predicted group membership			
M-WCTT Day	503	59.6% (300)	9.2% (46)	28.4% (143)	2.8% (14)
M-WCTT Night	717	13.5% (97)	23.4% (168)	22.3% (160)	40.7% (292)
M-Bull Day	37	16.2% (6)	10.8% (4)	51.4% (19)	21.6% (8)
M-Bull Night	168	2.4% (4)	20.2% (34)	22.6% (38)	54.8% (92)
D-WCTT Day	273	62.3% (170)	11.4% (31)	15.0% (41)	11.4% (31)
D-WCTT Night	1034	29.7% (307)	20.7% (214)	17.3% (179)	32.3% (334)
D-Bull Day	74	21.6% (16)	13.5% (10)	24.3% (18)	40.5% (30)
D-Bull Night	485	2.3% (11)	3.7% (18)	5.8% (28)	88.3% (428)

observations were usually confused with night observations. The discriminant model correctly classified night bull trout observations 55% (Meadow Creek) and 88% of the time (Daly Creek).

Snorkeling Efficiency

Night snorkeling was more accurate than day snorkeling in cold water temperatures. Day snorkeling counts consistently underestimated cutthroat trout by 75% and bull trout by 90-95%. Night snorkeling, in contrast, overestimated cutthroat trout by approximately 35% and underestimated bull trout numbers by approximately 20%.

Discussion

Diel Behavior and Habitat Use

Heggenes et al. (1993) and Griffith and Smith (1993) report that trout use different diel behavioral strategies during winter based on fish size. During the day, small trout conceal in the substrate, LWD jams, submerged vegetation, or undercut banks, and are rarely active. Trout too large to find suitable hiding cover aggregate in deep, slow pools during the day. At night, fish of all sizes move into the water column away from cover.

My findings confirm the use of these diel behaviors by resident bull trout and westslope cutthroat trout. During the day, small (< 200 mm) cutthroat trout and bull trout of all sizes concealed in the interstices of large substrate and complex LWD accumulations. Large (> 200 mm) cutthroat trout aggregated in deep, low velocity pools. At night, bull trout and cutthroat trout of all sizes abandoned daytime concealment cover and moved into more exposed positions. Fish remained active on or above the substrate throughout winter at night, even during extreme temperatures and ice conditions. Heggenes et al. (1993) and Campbell and Neuner (1985) observed similar nocturnal winter movements away from daytime concealment cover for brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), respectively.

Densities of cutthroat trout and bull trout observed at night were generally 5-6 times greater than those of daytime. Other researchers report 2-15 fold increases in the density of cutthroat trout and bull trout on autumn and winter nights (Goetz 1991; Vore 1993; Bonneau 1994). Diel densities were most similar in early September when water temperatures exceeded > 7 C; however, differences became more apparent as water temperatures declined. Schill (1991) observed no difference in day and night bull trout densities at water temperatures between 8-13 C, but was unable to locate bull trout in the water column in temperatures < 2 C on autumn days. In this study, water temperature declines below an approximate 7 C threshold appeared to trigger daytime concealment behavior by both species. Other researchers have observed juvenile bull trout, cutthroat trout, and rainbow trout entering the substrate at water temperatures ranging from 7.0 to 8.5 C (Bustard and Narver 1975; Shepard et al. 1984; Campbell and Neuner 1985; Contor 1989; Schill 1991; Riehle and Griffith 1993).

Several hypotheses have been forwarded to account for this nocturnal shift in winter. One hypothesis is that at low water temperatures, reductions in swimming ability and critical holding velocity profoundly affect a fish's ability to avoid predators (Rimmer et al. 1983, 1984). By hiding during daylight, trout reduce their vulnerability to endothermic predators such as otter and mink while also minimizing energy expenditure (Erlinge 1972; Heggenes and Borgstrom 1988). Another hypothesis suggests that trout abandon concealment cover at night to avoid being trapped by anchor ice formation. Dynamic changes in ice formation typically occur at night during winter in streams of high latitudes and altitudes (Power et al. 1993); therefore, a nocturnal activity strategy protects stream salmonids from habitat exclusion or microhabitat inclusion by sub-surface ice formation (Heggenes et al. 1993).

Trout also shift to primarily foraging at night during winter. Although trout are considered visual foragers (Henderson and Northcote 1985), winter feeding is thought to occur primarily at night when fish are presumed to become photonegative (Cunjak 1988b; Rimmer and Paim 1990). Fraser et al. (1993) demonstrated that physiological adaptations paralleling diel behavioral shifts occur in response to water temperature. As water temperatures decline, the ratio of porphyropsin to rhodopsin visual pigments in the retina of salmonids increases which heightens sensitivity in red light and enhances the ability of salmonids to see and feed at night (Allen et al. 1973). At night, approximately half of the cutthroat trout I observed appeared to be feeding on drifting invertebrates, while the remainder rested on the substrate in exposed, shallow (< 30 cm), low velocity (< 5 cm/s) areas near stream margins. Campbell and Neuner (1985) observed rainbow trout of all sizes occupying similar resting habitats on winter nights. Nighttime feeding positions, in contrast, were located on or slightly above (1-3 cm) the substrate in deeper, mid-channel areas of stream. I did not observe bull trout preying on other fish at night; however, it has been reported by Bonneau (1994). At night, juvenile bull trout (100-200 mm TL) often maintained resting positions adjacent to numerous small cutthroat trout, which may reflect a predator/prey relationship. Use of shallow resting habitats at night may be influenced by moonlight intensity. Contor (1989) demonstrated that fewer juvenile trout emerge from daytime hiding cover on full moon nights than on moonless nights. I did not observe noticeable moonlight effects on nocturnal behavior and densities in either stream; however, dense riparian canopy cover blocked much of the light.

Bull trout and westslope cutthroat trout displayed similar diel microhabitat shifts during autumn and winter. At night, both species moved closer to the substrate, further from cover, into shallower water, and faced slower current velocities. The similarity of nocturnal microhabitat shifts was probably caused by both species utilizing similar diel behavioral strategies (moving into exposed, low velocity resting and feeding positions at night) in response to similar winter habitat requirements. With the exception of focal point elevation, Bonneau (1994) observed similar diel shifts for bull trout and westslope cutthroat trout in Idaho streams. Nighttime focal positions were higher in the water column than daytime focal positions for both species (Bonneau 1994). Most fish in his study were concealed 5-10 cm within cobble substrate during the day and moved into the water column at night. Fraser et al. (1993) also observed nocturnal upward movement out of the substrate by juvenile Atlantic salmon (*Salmo salar*). Because I was unable to find large numbers of fish concealed in the substrate in either stream, most winter daytime observations were made on a small number of fish (mostly cutthroat trout) hiding in LWD jams 5-10 cm above the streambed. Thus, I observed a downward shift in focal elevations at night. All bull trout observed in my study rested directly on the substrate at night and most cutthroat were within 3 cm of the substrate.

Influence of Stream Morphology

The type and abundance of dense winter hiding cover available for trout was influenced by stream size and channel morphology. Pool habitats, which provided an important combination of complex cover, low velocities, and depth, were the preferred habitat types for both species in both streams throughout autumn and winter. Type of pool, however, was strongly influenced by channel morphology. In Daly Creek, occupied pools possessed a combination of abundant boulders and moderate amounts of LWD. Although pools are reported to be highly preferred autumn and winter bull trout habitats (Goetz 1991; Bonneau 1994), the relative importance of large substrate and LWD cover within pools is not well understood. Shepard et al. (1984) and Bonneau (1994) report that juvenile bull trout tend to favor substrate interstices in pools, whereas larger fish prefer complex LWD cover in pools. Goetz (1991), conversely, observed a more substantial use of LWD than substrate interstices by juvenile bull trout. Based on diel habitat densities and cover preferences, the presence of complex LWD in pools appeared to add important daytime hiding cover and was possibly the critical element which separated good bull trout winter habitat from excellent habitat in Daly Creek.

Beaver ponds provided critical overwintering habitat for both species in Meadow Creek. In late autumn just prior to surface ice formation, substantial numbers of cutthroat trout and bull trout entered the ponds and formed large, mixed species aggregations (Chapter 2), providing further evidence that winter habitat preferences were similar for both species in Meadow Creek. In other habitat types, bull trout remained solitary and were not observed as members of nearby cutthroat trout aggregations. Beaver ponds provided a variety of favorable habitat characteristics throughout winter (e.g. complete surface ice cover; depths > 80 cm; velocities < 5 cm/s; lack of anchor ice; and stable water temperatures slightly above freezing), and most likely satisfied the winter habitat requirements of both species. Cutthroat trout appeared to be attracted to impoundments by the abundance of deep, low velocity water in conjunction with overhead cover, similar to their preference for mid-water column positions in streams (Nakano et al. 1992). Bull trout were possibly attracted by the abundance of small cutthroat prey in the ponds throughout winter.

The size and frequency of aggregations may be a function of habitat structure. Cunjak and Power (1986) documented an increased size and abundance of trout aggregations during winter in Ontario streams containing the fewest pools. In small streams such as Meadow Creek where overwintering habitats are limited, aggregations of trout are larger and more common as fish must share the few suitable habitats available. Cunjak and Power (1986) also observed increasing aggregation sizes with colder water temperatures, a phenomenon common to Meadow Creek beaver ponds in late autumn. Increased aggregative behavior at colder autumn water temperatures is a result of diminished aggression and territoriality (Hartman 1965), concurrent with a reduction in suitable habitat area (Cunjak and Power 1986).

Aggregative behavior involved considerable behavioral plasticity. In Meadow Creek beaver ponds, aggregations of cutthroat trout and bull trout altered their size and structure on a diel basis, perhaps as a means to minimize the risk of predation. In daylight (prior to surface ice formation), fish formed a single, large school in the deepest section of the pond. At night, however, fish dispersed into small feeding congregations (5-20 fish) and moved into shallow areas of the pond. Diel changes in aggregation size and location may have been a response to the risk of avian predators such as belted kingfishers (*Ceryle alcyon*) present in the vicinity of the ponds. In LWD-dominated pools in Daly Creek, aggregations (10-20 cutthroat trout) only formed at night. In boulder-formed pools, however, smaller aggregations (5-15 cutthroat trout) were present both day and night. The formation of nighttime cutthroat trout aggregations in LWD-formed pools suggests that fish either moved into these habitats from nearby areas, or hid in LWD jams during the day and moved out after dark. The latter explanation is probably most correct. Heggenes et al. (1993) only observed daytime brown trout aggregations in pools lacking adequate hiding cover. Cunjak and Power (1986) observed more aggregations in pools lacking substrate hiding cover than in those with abundant hiding cover.

Although stream morphology influenced the abundance of LWD and boulder cover, both species displayed considerable flexibility in their use of winter concealment cover. Large substrate and LWD are believed to be the most important cover types for overwintering cutthroat trout and bull trout

(Goetz 1991; Vore 1993; Bonneau 1994). Dolloff (1986) and Elliot (1986) documented significant reductions in overwintering juvenile Dolly Varden following the removal of LWD from Alaskan streams. My study confirms the importance of LWD to overwintering bull trout and cutthroat trout. Despite a relative lack of LWD, bull trout in Daly Creek displayed a stronger preference for LWD than boulder interstices during winter. Although LWD was much more common in Meadow Creek, it often occurred in marginal winter pool habitats. As a result, bull trout appeared to use LWD in Meadow Creek only in proportion to its availability. LWD was also the most important autumn and winter cover type for westslope cutthroat trout in both streams. LWD creates a myriad of low velocity pockets in conjunction with complex submerged cover, prevents displacement from winter freshets, and protects fish from the scouring effects of winter ice (Needham and Jones 1959; Tschaplinski and Hartman 1983; Cunjak and Power 1987b).

Both species preferred submerged aquatic vegetation cover at night in Meadow Creek. Fish resting in exposed areas on the bottom of beaver ponds often burrowed into thick mats of aquatic buttercup (*Ranunculus neomexicana*) when disturbed. In other habitats, fish hid in nearby mats of *Fontinalis* spp. adjacent to exposed nighttime resting positions. Contor (1989) and Heggenes et al. (1993) both observed large numbers of trout concealed in submerged aquatic vegetation on winter days; however, submerged aquatic vegetation in Meadow Creek was concentrated in shallow (< 20 cm) stream margins and was avoided during the day.

Overhead cover provided by surface ice was preferred by westslope cutthroat trout and avoided by bull trout in Daly Creek. Cutthroat trout were probably attracted by the overhead cover which allowed fish to maintain water column focal positions similar to those of summer (Nakano et al. 1992). Bull trout, in contrast, were much more substrate-oriented and did not appear to be attracted by overhead ice cover in depths > 20 cm. Fish become more photonegative during winter (Rimmer and Paim 1990), and cutthroat trout often maintain positions in slow water (< 10 cm/s) in almost total darkness beneath ice shelves (Vore 1993). If ice shelves were broken in this study, cutthroat trout did not return to the area until the ice had completely reformed.

Interspecific Interactions

The overlap in winter habitat use displayed in this study suggests that winter habitat requirements of bull trout and westslope cutthroat trout are similar. Focal point elevation and cover preferences accounted for the minor interspecific differences observed, and diel microhabitat shifts appeared to be more pronounced than between-species differences. Past efforts to prove that winter space is the focus of competition among salmonids have not produced clear results (Heggenes et al. 1993). Dolloff and Reeves (1990) demonstrated that Dolly Varden and juvenile coho salmon occupy the same microhabitats whether alone or in the presence of the other species during summer, suggesting that microhabitat selection is innately controlled and not caused by behavioral interactions. Although westslope cutthroat trout and bull trout prefer different microhabitats and are more territorial during summer (Nakano et al. 1992), aggression and territoriality break down at low water temperatures (Hartman 1965). Bull trout and westslope cutthroat trout in my study showed no signs of aggressiveness and did not appear to defend territories during winter. Both species maintained similar focal points whether alone or in the presence of the other species. Lack of aggression and use of similar microhabitats suggests that bull trout and westslope cutthroat trout respond to winter stresses in a similar manner and small differences are probably the result of a long evolutionary history of coexistence.

Conclusions and Management Implications

This research demonstrates that winter habitat use is relatively similar at both the microhabitat and habitat unit scales for westslope cutthroat trout and bull trout. Beaver ponds are critical overwintering habitats for resident bull trout in Meadow Creek, and deep pools possessing a combination of complex LWD and unembedded large substrate are critical to resident bull trout in Daly Creek. Westslope cutthroat trout in both streams required pools dominated by complex LWD during winter. Beaver ponds also function as important overwintering areas for cutthroat trout.

Further research is needed to quantify the use of substrate hiding cover by bull trout during autumn and winter. In order to accurately assess the relative importance of LWD versus substrate cover to bull trout during winter, we need to better understand the entire process of autumn concealment behavior. For instance, can the addition of LWD to heavily-sedimented streams provide adequate overwintering cover for bull trout where suitable interstitial cover has been lost? Why do larger bull trout overwinter in beaver ponds when LWD cover in pools may be suitable? Do bull trout return to the same daytime hiding spots throughout winter? How do bull trout adjust to different ice conditions?

The future management of threatened species such as bull trout may involve the artificial construction or enhancement of suitable overwintering habitat. In order to effectively create and manage winter habitat, we must have a better understanding of winter habitat requirements.

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