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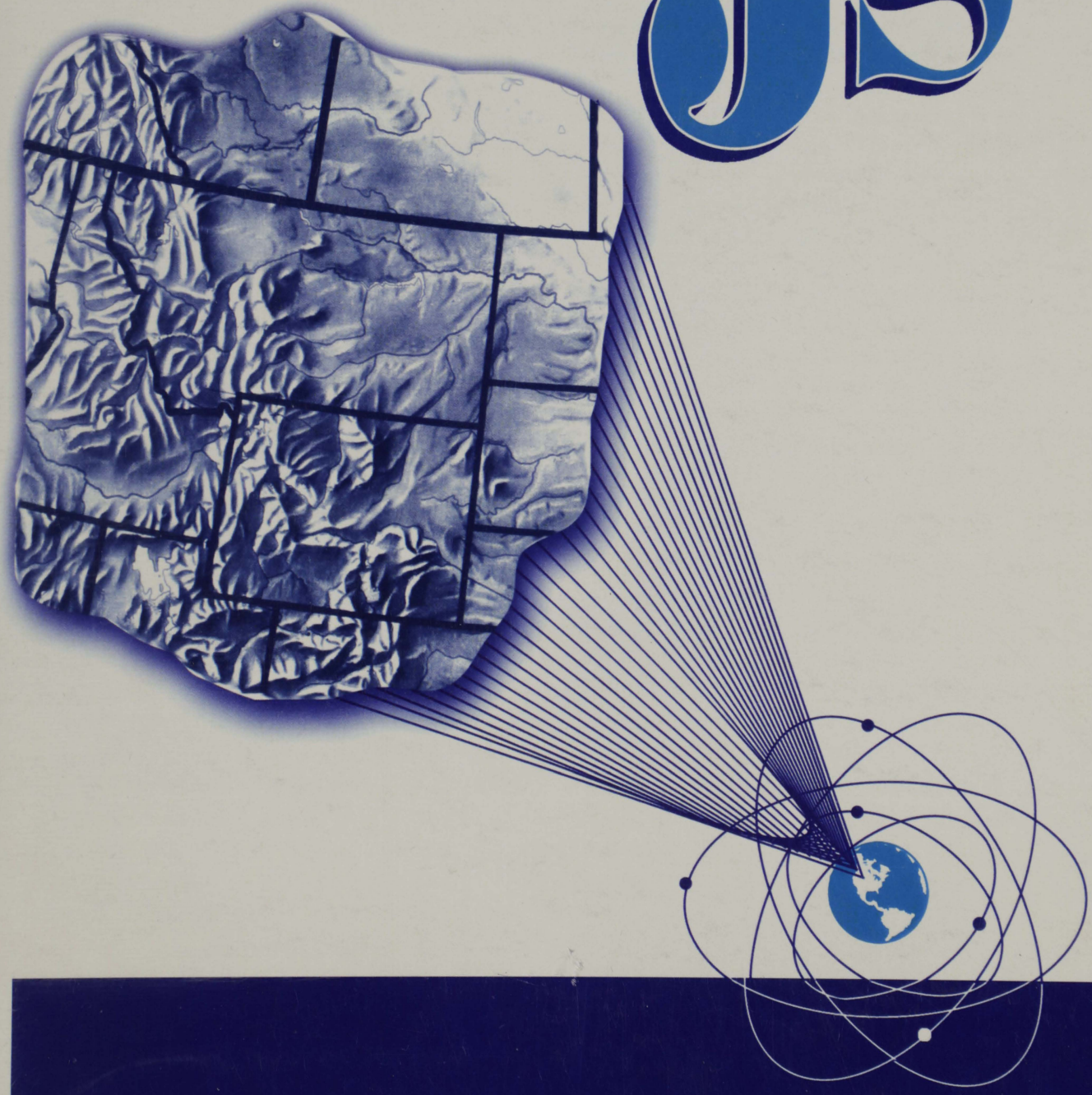

INTERMOUNTAIN JOURNAL OF SCIENCES

The Intermountain Journal of Sciences is a regional peer-reviewed journal that encourages scientists, educators and students to submit their research, management applications, or view-points concerning the sciences applicable to the intermountain region. Original manuscripts dealing with biological, environmental engineering, mathematical, molecular-cellular, pharmaceutical, physical and social sciences are welcome.

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Three hard copies of the submitted manuscript, with copies of the "Guidelines and checklist for IJS referees" attached are forwarded to the appropriate Associate Editor. The Associate Editor retains one coy of the manuscript and guidelines for his/her review, and submits a similar package to each of two other reviewers. A minimum of two reviewers, including the Associate Editor, is required for each manuscript. The two other reviewers are instructed to return the manuscript and their comments to the Associate Editor, who completes and returns to the EIC a blue "Cover Form" and all manuscripts and reviewer comments plus a recommendation for publication, with or without revisions, or rejection of the manuscript. This initial review process is limited to 30 days.

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Each manuscript that is rejected for publication is returned by the EIC to the corresponding author along with the reasons for rejection. The author is also advised that the manuscript may be resubmitted, provided all major criticisms and comments have been addressed in the new manuscript. The new manuscript may be returned to the initial review process if deemed appropriate by the EIC. If the manuscript is rejected a second time by either the EIC or the Associate Editor and reviewers, no further consideration will be given for publication of the manuscript in IJS. The corresponding author will be notified of this decision.

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The identity of all reviewers shall remain anonymous to the authors, called a blind review process. All criticisms or comments by authors shall be directed to the EIC; they may be referred to the ME or the Editorial Board by the EIC for resolution.

Ecology of a Recently Established Smallmouth Bass Population in the Flathead River, Montana

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Abstract

We studied life history and ecology of smallmouth bass (*Micropterus dolomieu*) in the Flathead River on the Flathead Indian Reservation, Montana, from 1998 through 2005. Smallmouth bass are relatively newly established in the Flathead River, and thus our goals were to better understand the life history of the species and to examine their effects on the Flathead River fish assemblage. We investigated smallmouth bass movements and broad patterns of habitat use with radio telemetry, as well as spatial and temporal patterns of relative abundance, age and growth, condition factors, and food habits. We observed two broad patterns of movement, primarily related to migration between spawning and overwintering habitats. Patterns of movement included (1) extensive (> 60 km) migrations between widespread spawning habitats in the lower river and abundant overwintering habitats in the upper river; and, (2) more restricted movements between spawning and overwintering habitats within close proximity to one another. Smallmouth bass abundance increased rapidly over our 8-year study. We documented highest relative abundances of young fish (< 180 mm TL) during autumn in low-gradient downstream river sections adjacent to spawning habitats, and highest abundances of larger fish (≥ 180 mm TL) in autumn in higher-gradient upper reaches of the river with deep pools and abundant large substrates, e.g., boulder and fractured bedrock. Growth of smallmouth bass after age 2 in our study area was relatively fast compared to other smallmouth bass populations in the Rocky Mountain West but moderate relative to growth across North America. Smallmouth bass in the Flathead River were robust, with average annual relative weights (W_r) usually > 100 in both spring and autumn. We found that smallmouth bass diets varied considerably among spring, summer, and autumn months. In early spring (Apr) and autumn (Oct), invertebrates largely comprised diets (% by weight), with aquatic insects dominating the diet in April and crayfish dominating in October. In contrast, fishes were a proportionally large dietary component (46.7%) in late spring (Jun) and were the dominant (58.2 %) prey items in summer (Jul). Life history information will be used to develop and recommend options for future management of smallmouth bass on the Flathead Indian Reservation.

Key words: age and growth, condition, Flathead River, introduced fishes, *Micropterus dolomieu*, migration, predation, smallmouth bass

Introduction

Introduced fishes threaten native fish populations across much of North America (e.g., Moyle et al. 1986, Miller et al. 1989). Non-native species often compete with or prey upon native species and can negatively affect populations of endemic fishes (e.g., Whittier and Kincaid 1999, Warner 2005). The smallmouth bass (*Micropterus dolomieu*) is a common predatory sport fish that is highly desired by anglers. As such, this species has been widely introduced far outside of its natural range, often with little consideration of ecological consequence (Jackson 2002). Negative interactions between smallmouth bass and native fishes can be both direct, i.e., primarily predation, and indirect. Predation on native fishes by introduced smallmouth bass has been

documented in a variety of ecological settings (e.g., Poe et al. 1991, Reiman et al. 1991, Tabor et al. 1993, Fayram and Sibley 2000, MacRae and Jackson 1999, Jackson 2002, Fritts and Pearsons 2004) although overall effects appear to be variable. Indirect effects have been less well studied.

Smallmouth bass were introduced into waters of the Flathead Indian Reservation in the mid-1980s. The species was initially stocked into Crow Reservoir, an irrigation storage reservoir in the Crow Creek drainage that has a direct tributary outlet to the Flathead River. Smallmouth bass quickly moved to the Flathead River and rapidly colonized the river downstream of Flathead Lake. The rapid expansion of smallmouth bass and the lack of understanding of population behavior and dynamics in the Flathead River necessitated research on the species in particular because of the Confederated Salish and Kootenai Tribes' ongoing efforts to restore native migratory salmonid populations in the Flathead River drainage.

We undertook our study to better understand smallmouth bass life history in the Flathead River and to examine potential direct effects of the species on the existing fish assemblage. Our specific objectives were to describe movements; describe and monitor population structure; document age, growth, and condition; and determine food habitats of the species. This research will be used to establish baseline information on smallmouth bass in one of Montana's largest rivers, to assist in management of the fishery, and to guide future research and monitoring.

Study Area

The Flathead River downstream from Flathead Lake, hereafter referred to as the lower Flathead River, is one of Montana's largest rivers (Fig. 1); average annual discharge is ~ 330 m^3/sec (Jourdonnais and Hauer 1993). Flows are regulated by Kerr Dam (Fig. 2), which is located downstream of the natural lake outlet and

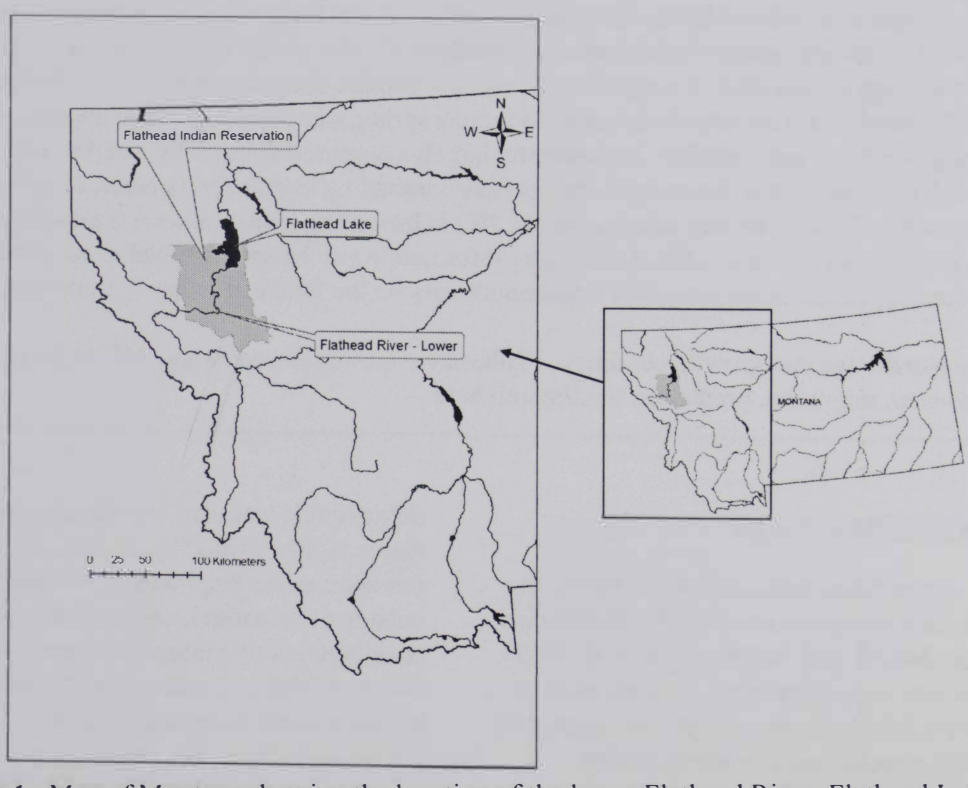

Figure 1. Map of Montana showing the location of the lower Flathead River, Flathead Lake, and Flathead Indian Reservation.

began operations in the 1930s. Turbine capacity of Kerr Dam is ~ 380 m^3/sec; flows greater than turbine capacity are passed as spill (Jourdonnais and Hauer 1993). Until the late 1990s, the dam was operated as a load-following facility, which resulted in frequent, unnatural within- and between-day flow fluctuations. However, these operations were changed following a relicensing process and the issuance of a 1997 Federal Energy Regulatory Commission (FERC) order that specified seasonal minimum flows and established within- and between-day ramping rate restrictions.

After exiting Flathead Lake near Polson, Montana, the lower Flathead River flows south and west for roughly 117 km before joining the Clark Fork River near Paradise, Montana (Fig. 2). Approximately 110 km of this distance lies within the Flathead Indian Reservation. The character of the river, which is modified by local geology and gradient, varies considerably over its length. Habitat of the uppermost reach, confined within a steep, rock-walled canyon, is comprised of a series of large, deep pools, steep riffles, and occasional rapids. After exiting the canyon, the stream gradient decreases and the river widens but maintains a single, relatively deep channel with non-turbulent flows interspersed with occasional shallow, high-velocity runs and riffles. Farther downstream, gradient again decreases, and the river channel becomes increasingly more variable with single channel meanders, multiple or braided channels, island complexes, sloughs, and extensive backwater habitats depending upon longitudinal position (Fig 3).

This habitat diversity supports an array of fish species. Historically, the river supported a variety of both resident and migratory native fishes, including four species of cyprinids [northern pikeminnow (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), longnose dace (*Rhinichthys cataractae*), and redside shiner (*Richardsonius balteatus*)], two

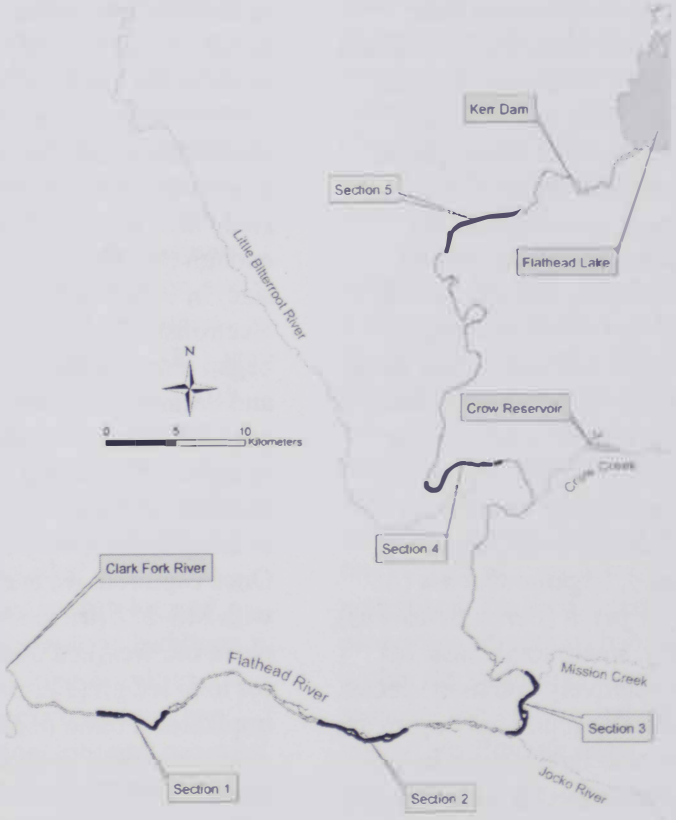

Figure 2. Map of study area showing locations of sample sections (darkened) along the lower Flathead River, Montana.

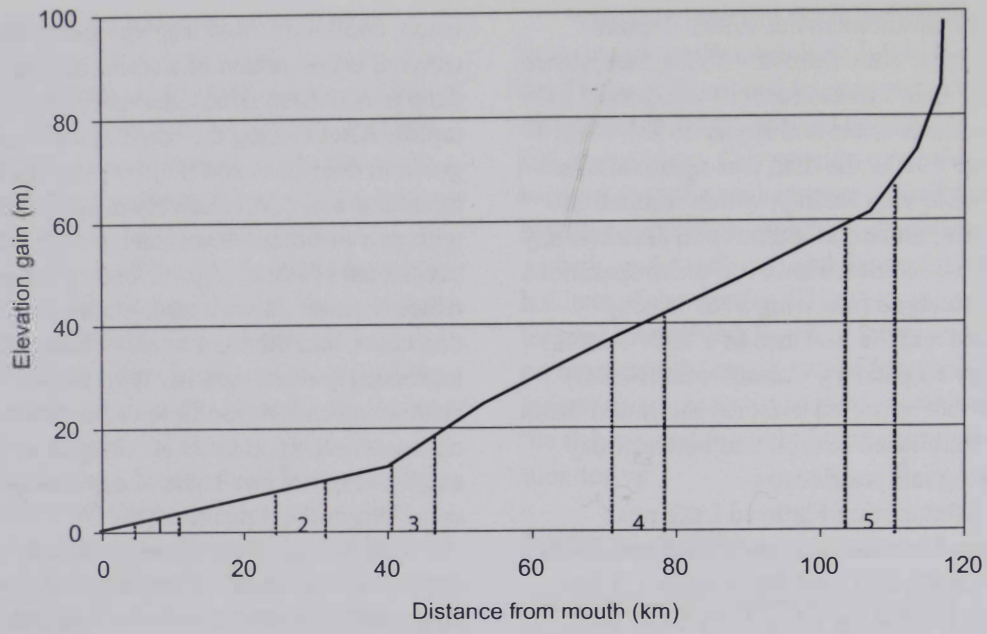

Figure 3. Longitudinal profile of the lower Flathead River, Montana, with locations of sample sections indicated by dashed lines.

species of catostomids [longnose sucker (*Catostomus catostomus*) and large-scale sucker (*C. macrocheilus*)], three species of salmonids [bull trout (*Salvelinus confluentus*), westslope cutthroat trout (*Oncorhynchus clarki lewisi*), and mountain whitefish (*Prosopium williamsoni*)], and one species of cottid, the slimy sculpin (*Cottus cognatus*). Some of these species have declined greatly in abundance because of land management activities and the introduction of non-native fish species. The river now supports a mixture of both native and introduced fishes. Introduced coldwater, coolwater, and warmwater fishes include yellow bullhead (*Ameiurus natalis*), black bullhead (*A. melas*), northern pike (*Esox lucius*), rainbow trout (*O. mykiss*), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), pumpkinseeds (*Lepomis gibbosus*), largemouth bass (*M. salmoides*), yellow perch (*Perca flavescens*), and, most recently, smallmouth bass. In addition to these relatively common species, three species, typically found only upstream in Flathead Lake, also rarely occur in the lower river: the native pygmy whitefish (*P. coulteri*), and the introduced lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*).

Methods

Movements

Fish Tagging.—We used radio telemetry to describe movements and broad patterns of habitat use by adult smallmouth bass in the lower Flathead River. From spring 1999 through spring 2002 we used boat electrofishing and hook-and-line sampling at several locations throughout the 117-km study area to capture smallmouth bass large enough (> 385 g, depending on transmitter size) in which to implant transmitters. We electrofished primarily in the spring as fish began entering shallow shoreline areas and became vulnerable to our sampling gear. We also used hook-and-line sampling to capture fish during early spring when smallmouth bass used habitats too deep to sample effectively with electrofishing. Once captured, we anesthetized the fish with MS-222 (tricaine methanesulfonate) or clove oil, weighed them (g), measured them for total length (TL; mm), and surgically implanted a radio transmitter following methods similar to those of Ross and Kleiner (1982). We used uniquely coded radio transmitters (7.7 to 16.1 g; Lotek Engineering, Ontario, Canada), and avoided implanting fish when the weight of the

transmitter in air exceeded two percent of the fish' weight as recommended by Winter (1996). Transmitters were programmed with an on-off schedule (off 6 hr/night) to prolong battery life, which allowed transmitters an estimated operational life of 321-612 days, depending on transmitter size. After we completed urgeries, we allowed fish to recover their equilibrium in mesh cages positioned in slow velocity areas of the river before we released them near the point of capture.

Radio Tracking. We used a combination of boats, vehicles, and aircraft to monitor for presence of radio-tagged fish. We generally monitored transmitters at weekly intervals during daylight hours in spring, summer, and autumn and typically monthly or bimonthly intervals during winter. We used a Lotek SRX model 400 scanning receiver and three types of antennas (whip, three-element Yagi, and H-type) to locate radio-tagged fish. A whip antenna was initially used to obtain an approximate location of a fish when tracking by boat or vehicle; the accuracy of the position was then refined using a three-element Yagi antenna. We used an H-type antenna mounted on a wing strut when tracking by airplane. We generally conducted aerial and vehicle tracking infrequently and followed those efforts with boat tracking to refine fish positions. After we determined a fish's location, we recorded its position on high-resolution aerial photographs. Beginning in 2000, we also measured water depth to nearest 0.3 m over a fish's position with a fathometer. We used a laser rangefinder to measure distance (m) of the fish from the nearest shoreline. These data were inconsistently recorded, were not recorded in all years, and were only collected on fish located from a boat and that apparently had been undisturbed by our tracking activities. After completing a tracking session, we referenced aerial photographs and recorded the distance upstream from the mouth of the river (or tributary) for each fish's position using topographical maps with longitudinal distances marked to the nearest 0.16 km (0.1 mi) along a mid-channel line. We al o obtained movement data from angler recaptures of tagged fish.

Telemetry Data Analysis and Summary.—We digitized data from each radio-tagged fish into a geographic information system (GIS). We computed the number of locations as well as the total number of days at large, i.e., number of days between tagging and last location, for each radio-tagged fish. We then used location data to compute displacement distances (distance between furthest upstream and downstream locations) for each fish and to determine the timing of seasonal migrations, e.g., to spawning or overwintering areas, in relation to date and water temperature. We collected water temperature using four, hourly-recording thermographs (Optic Stowaway, Onset omputer orp. Pocasset, MA) located longitudinally throughout the study area (river kilometer [rkm] 18, 41, 73, 106). We used medians and ranges to describe all movement parameters because data were not normally distributed, and we used the average date of two contacts, i.e., to determine the date of movement between overwintering and spawning locations, as an estimate of when a fish initiated movement (Swanberg 1997). We discarded data from fish at large < 1 month post-implantation from our analyses.

To describe seasonal (spring = Apr Jun; summer = Jul–Sep; autumn = Oct–Dec; winter = Jan–Mar) habitat use by radio-tagged fish, we used a GIS and aerial photographs to delineate the 117-km study area into four broad habitat types based on modified descriptions of channel pattern from Mount (1995; Table 1). We digitized all segments along a thalweg trace to determine total length of river that each channel type comprised. We then determined the relative proportion of various habitat types present within the study area as well as proportional seasonal use of these habitat type by radio-tagged smallmouth bass.

Population Monitoring

We monitored smallmouth bass abundances in the lower Flathead River from

Table 1. Channel type descriptions modified from Mount (1995) used to classify habitat-channel types in the lower Flathead River.

Channel Type	Description
Straight	Single channel with sinuosity < 1.05
Sinuous	Single channel with sinuosity > 1.05 but < 1.50
Meandering	Single meandering channel with sinuosity > 1.50
Braided	Two or more active channels with numerous interchannel bars and small islands, and with sinuosity > 1.30

1998 through 2005 using boat electrofishing as part of a larger multi-species monitoring program required by the Department of Interior and the FERC as a condition of Kerr Dam relicensing. For comparative purposes, we collected these consistent with methods used in a study of the lower Flathead River done prior to relicensing (DosSantos et al. 1988). We sampled fishes at nighttime during spring and autumn in five stock-assessment reaches established by DosSantos et al. (1988). The sample reaches generally represented the variety of habitats located along the river continuum.

The stock assessment sample sections occurred along the stream gradient (Figs. 2 and 3) and had an average mid-channel length of ~ 6.1 km. Sample section 1 (rkm = 6.6-12.1; Figs. 2 and 3), the furthest downstream section, represented the lower reach of the river, and was characterized by a low-gradient, single channel except for one small mid-channel island. Substrates were mostly small gravels, sands, and silts, except for extensive riprap material over about a 2-km section where the stream bordered railroad and highway right-of-ways and a small section of bedrock at the upstream end. Sample section 2 (rkm = 25.8-32.4; Figs. 2 and 3) had a low-gradient, complex channel form with braided habitats and sloughs. Substrates ranged from gravels in the main channel to silts and sands in sloughs. This section also had areas of larger substrates in the form of riprap on railroad right-of-ways and small angular boulders originating from upslope colluvial materials in the most downstream end of the sample area. Section 3 (rkm = 40.7-46.4; Figs. 2 and 3) was similar to section 2, and also represented the low-gradient, braided channel type although off-channel habitats were not as extensive within this stock-assessment section. Two large coldwater tributaries (Jocko River and Mission Creek) entered this section. Section 4 (rkm = 71.1-77.9; Figs. 2 and 3), representative of the single-channel meandering reach of the lower Flathead River, was characterized by a moderate gradient and broad meanders bordered by steep cliffs of lacustrine sediments. Runs and glides interspersed with occasional higher gradient riffles mostly comprised the single channel. Substrate was diverse, and ranged from very large boulders to fine white lacustrine clays. One tributary, the Little Bitterroot River, entered in the lower one-third of the section. We discontinued sampling in this section after 2002 primarily because large boulders and shallow high-velocity habitats created hazardous nighttime boating conditions. Section 5 (rkm = 103.4-109.8; Figs. 2 and 3) represented the higher-gradient habitats in the upper reach of the lower Flathead River. It had a large, deep pool at the upper end, and then transitioned into a series of high-gradient runs and riffles. Substrate was large and comprised of boulders and bedrock in the upstream portions and a mixture of small boulders, cobbles, and gravels in downstream areas.

During 1998-2005 we conducted spring stock assessments in late April or early May and autumn stock assessments in early to mid-October. We sampled at nighttime by electrofishing the left and right banks of each section and netted all smallmouth bass. Electrofisher settings were approximately 300 V pulsed DC at 60 Hz and 5-6 A. Electrofishing times for each stream bank averaged 2.3 hr (SD = 0.54 hr) for all five

stock assessment section . We typically sampled once each spring and autumn in all section , although we sometime were unable to sample all five sections each season. We measured (TL; mm), weighed (g), and released all mallmouth bas except for a subsample of individuals that we sacrificed for food habits studies. From these data, we generated box plots showing length distributions of the yearly catch, a weight-length equation for fish >100 mm TL, condition factors for fi h 150 mm TL or longer (relative weight [W_r]; Kolander et al. 1993, Anderson and Neumann 1996), and catch-per-unit-effort indices (CP E; fish/h). We calculated P E indices for two length categories of fish: stock length (≥ 180 mm TL) and sub-stock length (<180 mm TL; Anderson and Neumann 1996). We used average CPUE of fish from the two shorelines of a sample section as our basic measure of relative abundance. To examine trends in relative abundances over the study period, we plotted CPUE of stock-length and sub-stock length fish by section, season, and year.

Age and Growth

We used scales collected during 2001-2002 and 2004-2005 to examine age and broadly characterize growth. Scales were removed, processed, and read using standard methods (Devries and Frie 1996, Klumb et al. 1999). Scale impressions were viewed with a microfiche reader at 24x magnification. We used the Fraser-Lee model (Devries and Frie 1996) and a standard intercept value of 35 mm as suggested by Carlander (1982) to back calculate length at age for each fish.

Food Habits

During 2002 through 2005 we sampled smallmouth bass food habits while conducting stock assessments during spring and autumn and during two separate sampling occasions in mid-July 2002 and mid-June 2005. We collected stomachs from a subsample of all fish captured during each sampling event. We added sampling during June and July periods because we wanted to examine if smallmouth bass were preying on juvenile salmonids that were migrating primarily out of the Jocko River and Mis ion reek (Fig. 2). Relatively large numbers of juvenile salmonids move from these spawning tributaries into the Flathead River during spring and early summer, with a econd peak in abundance occurring in late autumn (CSKT Fisheries Program unpublished data). Because we were particularly interested in predation on juvenile salmonids, we initially only sampled fish >200 mm TL (Zimmerman 1999); however, beginning in spring 2004 we expanded this sampling to include fish > 150 mm TL. (Fayram and Sibley 2000, Fritts and Pearsons 2004). We put stomach samples on ice in the field and later transferred them to ethanol for preservation and storage.

In the laboratory, we attempted to identify fish prey items to the lowest practical taxon. We used diagnostic bones (Frost 2000) to identify prey fish that were in an advanced state of digestion. After we identified an item, we blotted excess fluid from it and recorded its wet weight (Bowen 1996) to the nearest 0.001 g. For analysis, we categorized stomach contents into the following categories: (1) detritus; (2) insects; (3) non-insect invertebrates, e.g., crayfish Decapoda; (4) unidentified fish; (5) cyprinds; (6) catostomid ; (7) ictalurids; (8) salmonid ; and (9) cottids. For our data summary we calculated the average proportion of each major prey item by weight (Bowen 1996) in the monthly (Apr, Jun, Jul, and Oct) diet of smallmouth bass.

Result

Movement

Overview:—During spring 1999 through spring 2002 we implanted a total of 45 smallmouth bass with radio transmitters. Median total length of tagged fish wa 356 mm (range = 290-445 mm) and median weight was 676 g (range = 3 0 1620 g). Forty-one radio-tagged fish remaining at large for ≥ 1 month after tagging yielded 636 individual locations, but only two resulted from anglers. Median number of location for an individual fish was 16 (range = 4-38). edian number of days at large wa 355

(range = 34-588 days). Ninety-five percent (n = 39) had a total displacement distance of ≥1 km. Median displacement distance for tagged smallmouth bass was 27.4 km (range = 0.2–97.7 km).

Patterns of Movement.—Many (n = 27; 66%) radio-tagged smallmouth bass in the lower Flathead River had distinct migratory behaviors. We broadly classified radio-tagged smallmouth bass (n = 41 fish) into four groups based on their patterns of movement. The four groups were composed of fish displaying the following movements: 1) long-distance migrations between upper and lower river reaches (n = 11); 2) restricted migrations in upper river reaches (n = 4); 3) restricted migrations in lower river reaches (n = 12); and, 4) no discernable pattern of migratory movement (n = 14).

Fish in the long-distance migration group, i.e., fish with the largest total displacement distances, were those (n = 11) that overwintered in the upper one-third of the study area (Fig. 4) and spawned in the complex, low-gradient habitats of the lower one-half of the study area. These fish migrated (> 60 km) between spawning and overwintering areas. One individual made a documented round-trip migration of nearly 200 km. However, not all fish overwintering in the upper part of the study area displayed this extensive migratory pattern.

A low number (n = 4) of the radio-tagged fish in upstream areas of the lower Flathead River had a more restricted migration pattern (median displacement distance = 11.8 km; range = 6.9-30.1 km). These fish overwintered in the upper one-third of the study area and used the limited spawning habitat available in the upper river, and so did not migrate to downriver spawning habitats.

Fish in the other restricted migration group (n = 12) used the abundant spawning areas found in the lower one-half of the study area but moved downstream to overwintering habitats. These fish typically displayed distinct, but more restricted

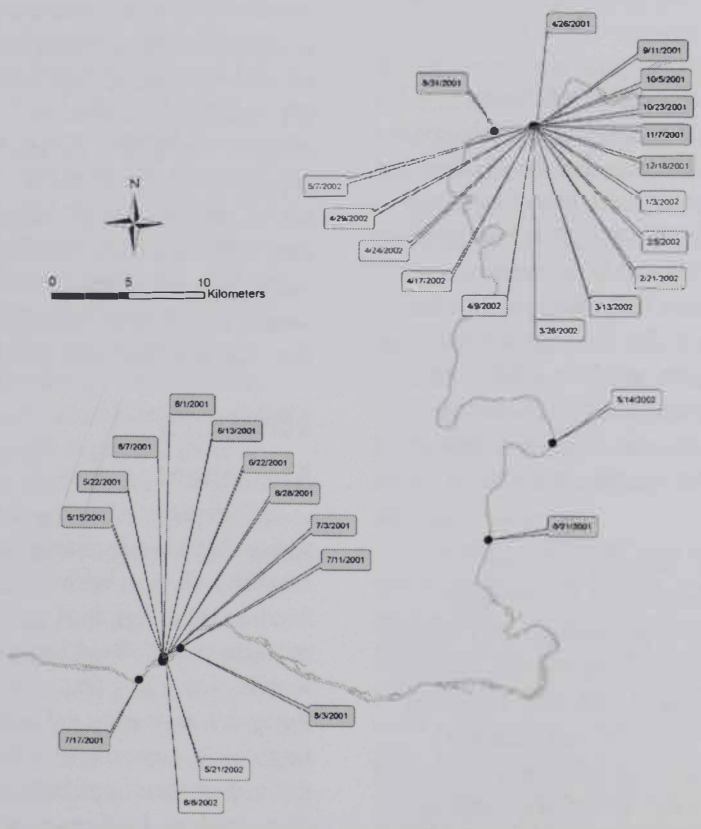

Figure 4. Example of extensive migratory behavior displayed by radio-tagged smallmouth bass (fish 149.70026) in the lower Flathead River, Montana.

migratory patterns compared to fish in the long-distance movement group that migrated between the upper and lower river (Fig. 5). Displacement distances for fish in this group were highly variable and ranged from ~ 4 to 40 km. Two of the 12 fish in this movement group moved from the lower Flathead River to the Clark Fork River (Fig. 2) during our study. One of these fish traveled 24.6 km downstream from the confluence of the Clark Fork and Flathead Rivers. We tagged this fish during spring 2000 in the lower Flathead River (rkm 13), where it presumably spawned and then moved downstream into the Clark Fork River until late August 2000. It then moved back into the lower Flathead River, overwintered, and, presumably spawned in spring 2001. The fish again returned to the Clark Fork River in early July 2001 where it remained into the winter. The other fish that entered the Clark Fork River did so in early June 1999 after it presumably spawned in the lower Flathead River in May 1999.

We were unable to clearly define the movement patterns of 14 radio-tagged fish due to several factors, including our inability to locate many radio-tagged fish during autumn and winter, resulting in limited periods of record for some fish. We assume this was because fish were in deep-water habitats that attenuated radio signals. Tests with transmitters suspended in Flathead Lake indicated that signal strength diminished at depths > 9 m. Many individuals in this group were therefore tracked for relatively short amounts of time (10 of 14 were tracked < 4 months). The remaining four fish in this group were tracked for longer periods (230-476 days), but displayed non-patterned movements.

Timing Of Movements.—Most (62%) smallmouth bass initiated spring spawning movements from mid-April to early May when average daily water temperatures ranged from ~ 6 to 12 °C. We observed radio-tagged males on nests from early June through early July when average daily water

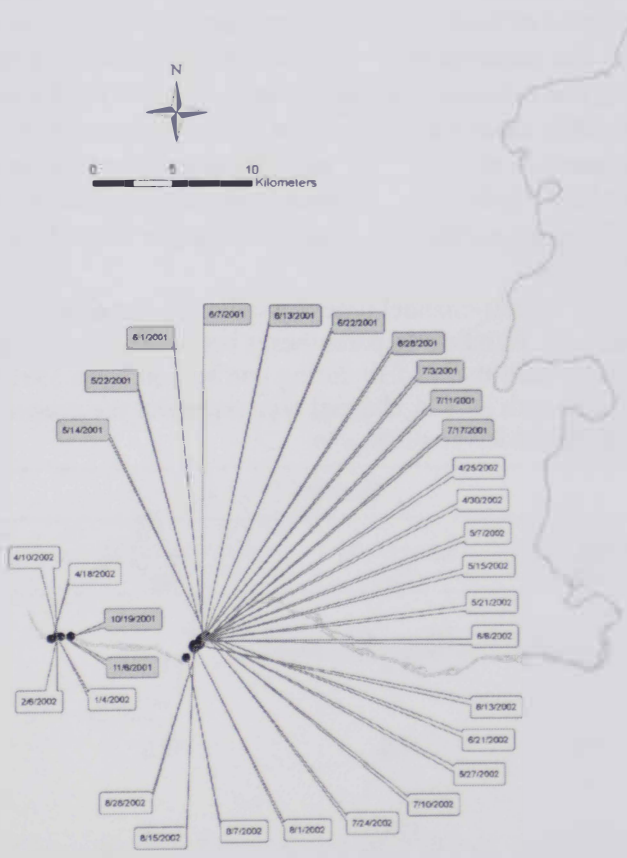

Figure 5. Example of restricted migratory behavior displayed by radio-tagged smallmouth bass (fish 149.70033) in the lower Flathead River, Montana.

temperatures ranged from ~ 13 to 20 °C. Radio-tagged smallmouth bass remained near areas used for spawning for periods typically > 2 months.

Most smallmouth bass initiated movements from spawning areas to overwintering habitats during mid-to-late July. During this period, average daily water temperatures ranged from ~ 17 to 23 °C. After late August, radio-tagged smallmouth bass generally exhibited only localized movements. However, we documented one fish that moved 3 km during mid-December when mean daily water temperature was ~ 4 °C. This apparently unique behavior was rarely observed among other radio-tagged fish.

Habitat- And Channel-Type Use.— During spring and summer (Apr–Sep) we found radio-tagged fish predominately in braided channel types (Table 2, Fig. 6) associated with island complexes and backwater sloughs. Braided channel types represented ~ 24 percent of total habitat in the lower Flathead River (Table 2). However, 66.1 and 56.6 percent of total relocations of radio-tagged fish occurred in these habitats during spring and summer, respectively (Table 2). We often observed many fish located in these areas on or near nests during June and July. Nests were typically constructed in quiet waters over gravel substrates. Median depths at fish locations in spring and summer were 2.4 m (range = 1.1 - 12.0 m; n = 86) and 3.0 m (range = 0.9 - 12.0 m; n = 30), respectively. Median distances to shore at fish locations during spring and summer were 10.5 m (range = 1.5 - 97.0 m; n = 145) and 19.5 m (range = 0.3 - 113.0 m; n = 64), respectively.

During autumn and winter (Oct–Mar), the majority of radio-tagged fish used deep pools (Table 2, Fig. 7), which in the lower Flathead River generally occurred in meandering or straight-channel reaches (Table 2). Deep pools were relatively uncommon except for limited amounts in the lower 11 km of the river and also in the upper one-third of the study area where this habitat type was most abundant. Deep-water habitats used by radio-tagged smallmouth bass in autumn and winter usually had large substrates, i.e., boulders and fractured bedrock, and slow water velocities. We collected very few depth and distance-to-shore measurements at fish positions in autumn and winter because many fish were unavailable to track and presumably because they were in water depths too great for our radio-tags to transmit through. Data that we collected showed that smallmouth bass were generally associated with deeper water and were farther from shore in autumn and

Table 2. Seasonal use (%) of habitat-channel types by radio-tagged smallmouth bass in the lower Flathead River, Montana. Numbers in parentheses below season columns represent the total number of relocations of radio-tagged fish during that season from 1999 through 2003. Numbers in parentheses under each habitat-channel type represent the proportions (%) of each channel type in the lower Flathead River study area.

	Season			
Channel Type	Spring (%) (389)	Summer (%) (198)	Autumn (%) (42)	Winter (%) (37)
Straight (30.2 %)	17.0	21.2	21.4	43.2
Sinuous (32.0 %)	3.9	10.6	19.0	10.8
Meandering (14.0 %)	13.1	11.6	47.6	43.2
Braided (23.8 %)	66.1	56.6	11.9	2.7

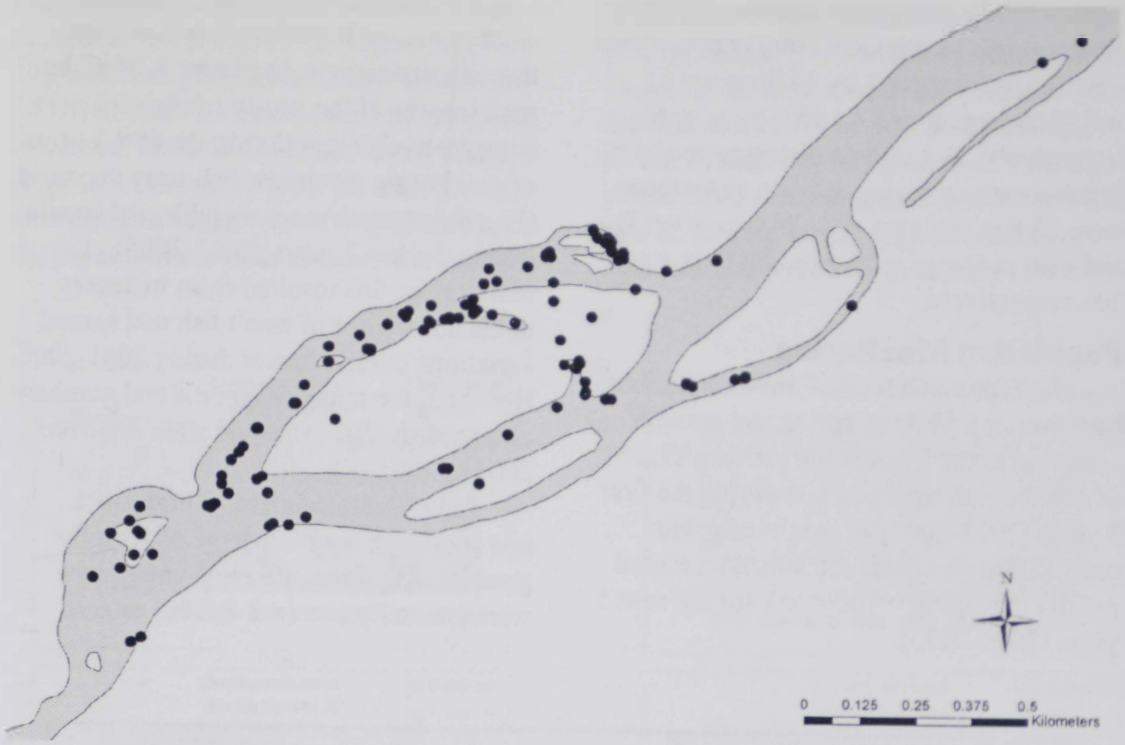

Figure 6. Example of the use of typical smallmouth bass spawning habitat in a braided reach of the lower Flathead River (rkm 11-14), Montana, by radio-tagged smallmouth bass. Dots indicate individual fish locations from 1999 to 2003.

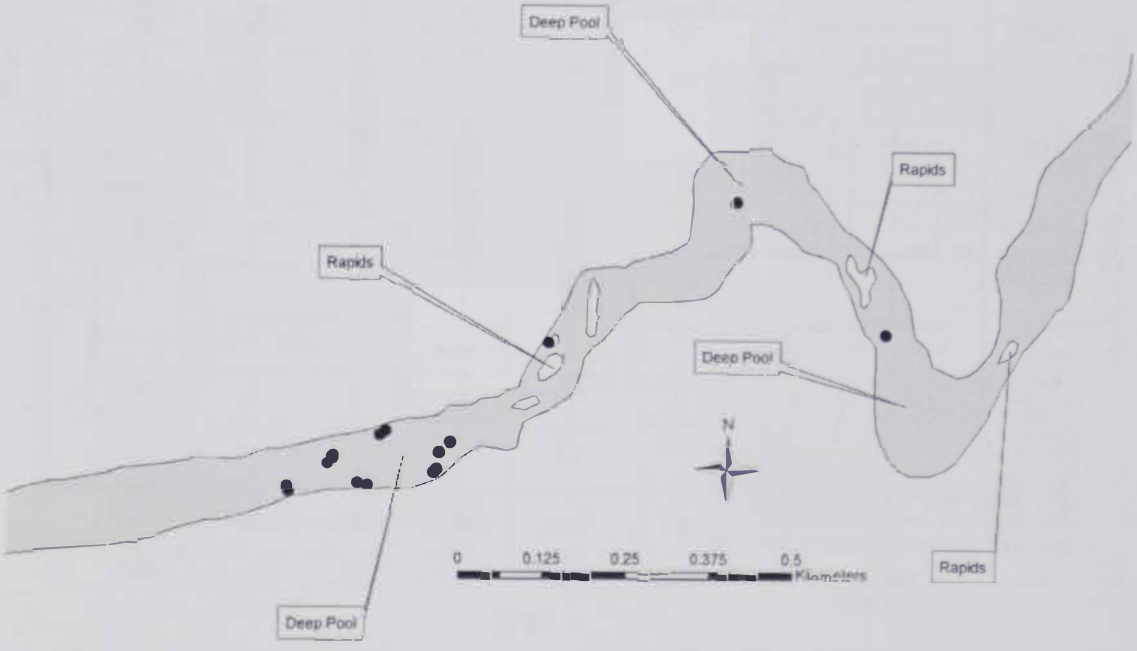

Figure 7. Example of the use of typical smallmouth bass overwintering habitat in a deep section of the lower Flathead River (rkm 110-112), Montana, by radio-tagged smallmouth bass. Dots indicate individual fish locations from 1999 to 2003.

winter than in spring and summer. Median depths at fish locations in autumn and winter were 9.8 m (range = 3.6 - 15.0 m; n = 6) and 12 m (range = 5.4 - 15.3 m; n = 9), respectively. The median distances to shore at fish locations during autumn and winter were 22.8 m (range = 6.0 - 74.0 m; n = 18) and 41.0 m (range = 10.5 m - 82.0 m; n = 20), respectively.

Population Monitoring

We captured a total of 5694 smallmouth bass during 8 years of spring and autumn sampling in the five sample sections Catch of smallmouth bass was low during the first 3 years (1998-2000) of monitoring with only 52 fish captured; catch then increased rapidly averaging > 1000/year for the next 5 years (2001-2005).

Length distributions of the annual catches of smallmouth bass and changes through time appear in Figure 8. Median total lengths of the yearly catch were comparatively large during the first 3 years of monitoring when few fish were captured (Fig. 8) but were more variable and smaller during the last 5 years (2001-2005) of monitoring; this resulted from increases in the abundance of small fish and annual variations in recruitment during 2001-2005. However, the range of lengths and numbers of large fish also increased annually from 2001 to 2005 (Fig. 8).

Relative abundances of both stock and sub-stock length fish were typically greatest in autumn, although catch rates were generally low (< 3 fish/hr) or zero

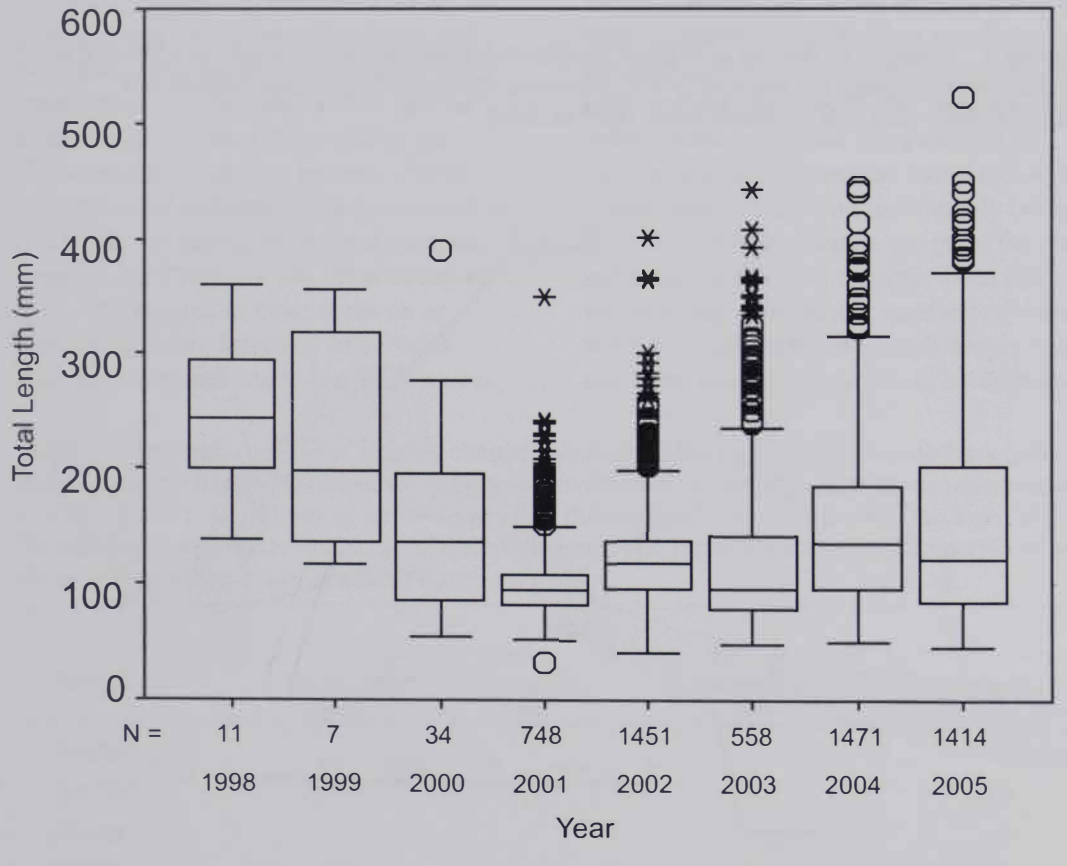

Figure 8. Box plots of the total lengths (TL) of smallmouth bass captured each year in the lower Flathead River, Montana, during eight years (1998-2005) of monitoring. The box corresponds to the interquartile (IQR) range of TL and the median TL is represented by a line through the box. Whiskers show the range of TL values that are not outliers. Outlier values (> 1.5 IQR from the box) are denoted by circles and extreme values (> 3.0 IQR from the box) are indicated by stars. N = numbers of fish captured each year.

in all five sections during the first 3 years of monitoring (1998-2000; Figs. 9 and 10). Beginning in autumn 2001, however, CPUE of substock smallmouth bass rapidly increased, particularly in sections 1 and 2 (Fig. 10). Catches of substock smallmouth bass remained high (exceeding 25 fish/hr) during autumn in both of these sections after 2001, but varied considerably from year-to-year, particularly in section 1, where catches of small fish were always high relative to other sections (Fig. 10). Mean autumn CPUE of substock fish in section 1 for the period 2001-2005 ranged from 45.1 to 173.7 fish/hr. During spring, highest catches of substock fish were also in section 1, but

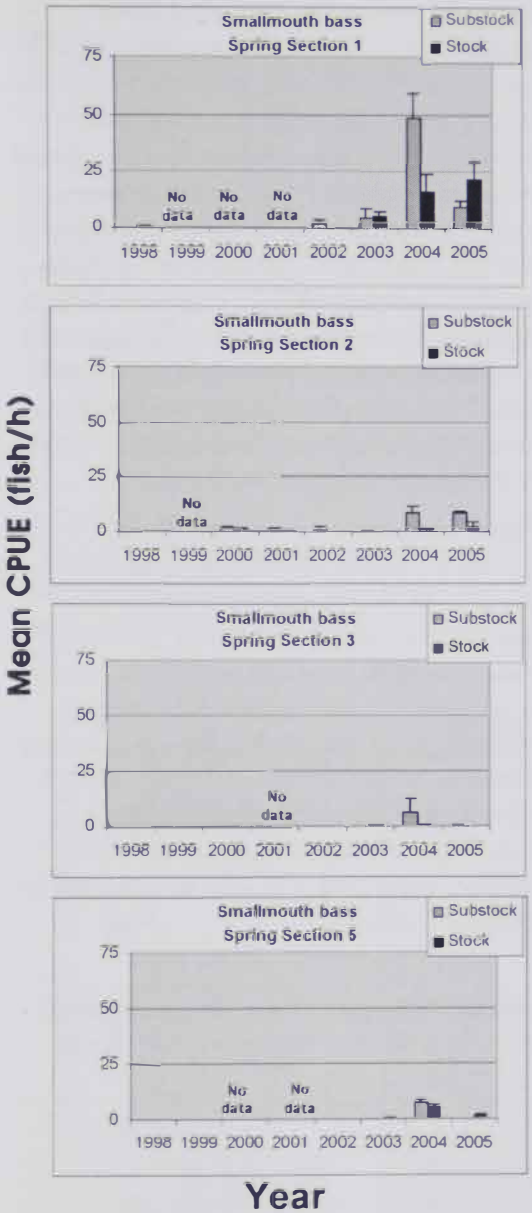

Figure 9. Mean catch per unit effort (CPUE; fish/h) of smallmouth bass during spring in four study sections of the lower Flathead River, Montana, 1998-2005. Vertical lines are one standard error. Note: section 4, where we discontinued sampling in 2002, is not shown.

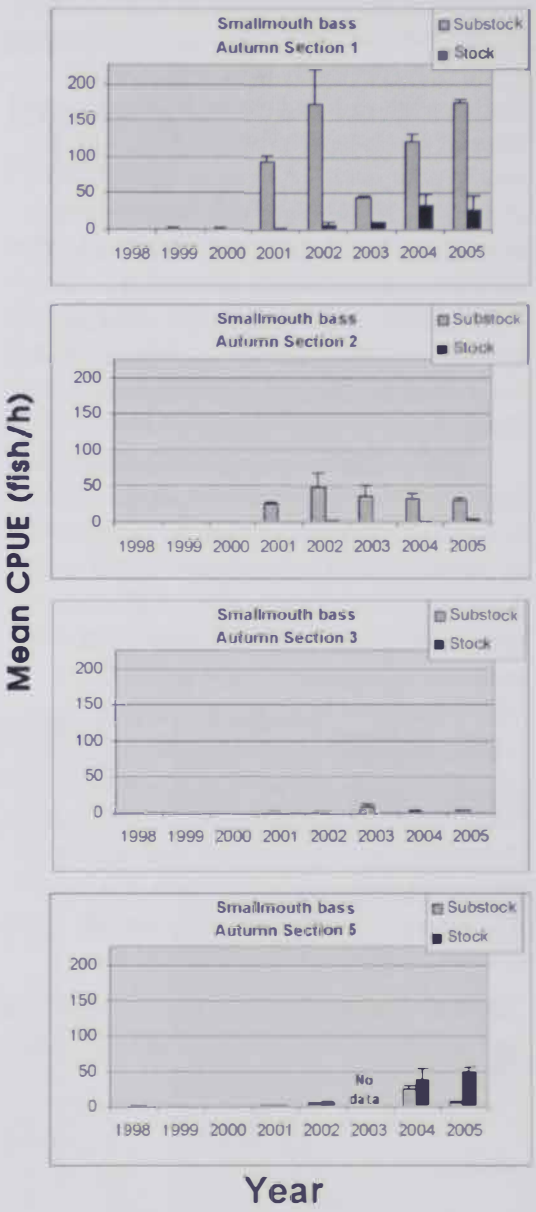

Figure 10. Mean catch per unit effort (CPUE; fish/h) of smallmouth bass during autumn in four study sections of the lower Flathead River, Montana, 1998-2005. Vertical lines are one standard error. Note: section 4, where we discontinued sampling in 2002, is not shown.

CPUE values were typically lower than in autumn (Figs. 9 and 10).

We observed highest relative abundances of stock-length fish in sections 1 and 5 in autumn (Fig. 10). Abundances of these larger fish generally showed increasing trends in both of these sections from 2002-2005 (Figs. 9 and 10). Average CPUE of stock-length fish in autumn 2002 was 7.4 fish/hr in section 1 and 5.4 fish/hr in section 5, whereas in autumn 2005 average CPUE values were 28.4 and 50.8 fish/hr in sections 1 and 5, respectively (Fig. 10). During spring, section 1 had the highest catch rates of stock-length fish (Fig. 9), which was in contrast to patterns of abundance in autumn when larger fish were generally most abundant in section 5. Catch rates for both size classes of fish were always low (< 10 fish/hr) in sections 3 and 4, regardless of season. However, as discussed in methods, we discontinued sampling in section 4 after 2002.

The weight-length equation developed from 1545 fish ≥ 100 mm TL (max size = 524 mm TL) captured over the duration of our study was: log10 Wt = -5.359 + 3.220 (log10[TL]), $r^2 = 0.98$. Fish were relatively robust, with only two mean seasonal W_rs (autumn 1998 and 2003) < 100. Mean annual spring W_rs ranged from 101 to 118, whereas average autumn W_rs ranged from 94 to 117 with no consistent trends over the 8 years of our study. Overall, average condition generally increased with increasing fish length for fish > 300 mm TL, whereas condition factors for fish < 300 mm TL were generally similar and averaged below 105.

Age and growth

We obtained age estimates using scales from 282 fish ranging in size from 58 to 524 mm TL. Scale samples from 18 fish captured in autumn and ranging in size from 58 to 117 mm TL (mean = 78 mm TL) did not have annuli; only two of these fish were > 100 mm TL. The remaining 264 fish were from 1 to 10 years in age. Mean back-calculated total length at age ranged from 83 mm at age-1 to 507 mm at age-10 (Table 3). Most fish represented in our scale samples (94%) were < 6 years old because few larger fish were available for sampling. Mean annual growth was highest during the first year (83 mm), remained relatively similar ages 2 to 4 (range 63 = 67 mm), and then declined (Table 3). Two anomalous growth increments occurred at ages-7 (6 mm) and age-10 (63 mm). Both may be related to small sample sizes, $n = 5$ and 1, respectively, or misinterpretation of annuli.

Food Habits

We collected stomach samples from 156 fish ranging in size from 152 to 445 mm TL. Our sample sizes were not equal among months. June had the largest number of samples and July the fewest (Table 4). Percentages of smallmouth bass with empty stomachs ranged from zero in July to 62.9 percent ($n = 22$) in October (Table 4). In contrast, average weights of stomach contents were lowest in July and greatest in October (Table 4).

Table 3. Estimated mean back-calculated total length (mm) at age and mean annual growth increments (mm) for smallmouth bass in the lower Flathead River. Numbers below age in parentheses are sample sizes.

	Age (yrs)									
	1 (264)	2 (222)	3 (126)	4 (81)	5 (33)	6 (12)	7 (5)	8 (2)	9 (2)	10 (1)
Mean TL (mm)										
	83	146	213	280	328	372	378	416	444	507
SE	0.88	1.79	3.30	4.74	7.16	9.30	6.29	15.99	16.75	NA
Mean growth increment (mm)										
	83	63	67	67	48	44	6	38	28	63

Table 4. Numbers of smallmouth bass stomachs examined (*n*), percentage of empty stomachs, and average wet weight (g) of predator stomachs. Average stomach weights do not include zeros for empty stomachs.

Month	*n*	% Empty	Average weight of stomach contents
April	54	35.2	0.541
June	55	23.6	1.076
July	12	0.0	0.828
October	35	62.9	3.170

We observed considerable differences (average % by weight) in monthly diets of smallmouth bass (Fig. 11). During April, smallmouth bass stomachs contained primarily (77.3%) insects. In contrast, fishes (combined average weights of all fish categories) became increasingly more important in June (46.7%), and were the dominant prey items in July (58.2%). Non-insect invertebrates, principally crayfish, were the major diet item by weight (50.9%) in October (Fig. 11).

Collectively, identifiable fish in the diet of smallmouth bass were primarily native cyprinids, catostomids, and cottids; introduced bullheads only occurred in the diet during April and October (Fig. 11). However, salmonids were the primary identifiable prey fish (by weight) in both June (3.1%) and July (14.0%; Fig 11). The bulk (% by weight) of salmonids in the diet was native mountain whitefish. The rest were members of the genus *Oncorhynchus* that could not be conclusively identified as native westslope cutthroat trout, introduced rainbow trout, or westslope cutthroat trout x rainbow trout hybrids.

Discussion

Movement

Smallmouth bass radio-tagged in the lower Flathead River from 1999 to 2002 exhibited a diversity of movement patterns although the majority of fish were mobile and moved at least 1 km. In general, movement behavior of smallmouth bass in rivers and streams has been shown to be highly variable. Several studies have suggested that smallmouth bass are rather sedentary, moving less than a few km during the course of a year (Fajen 1962, Munther 1970, Todd and Rabeni 1989, VanArnum et al. 2004). For example,

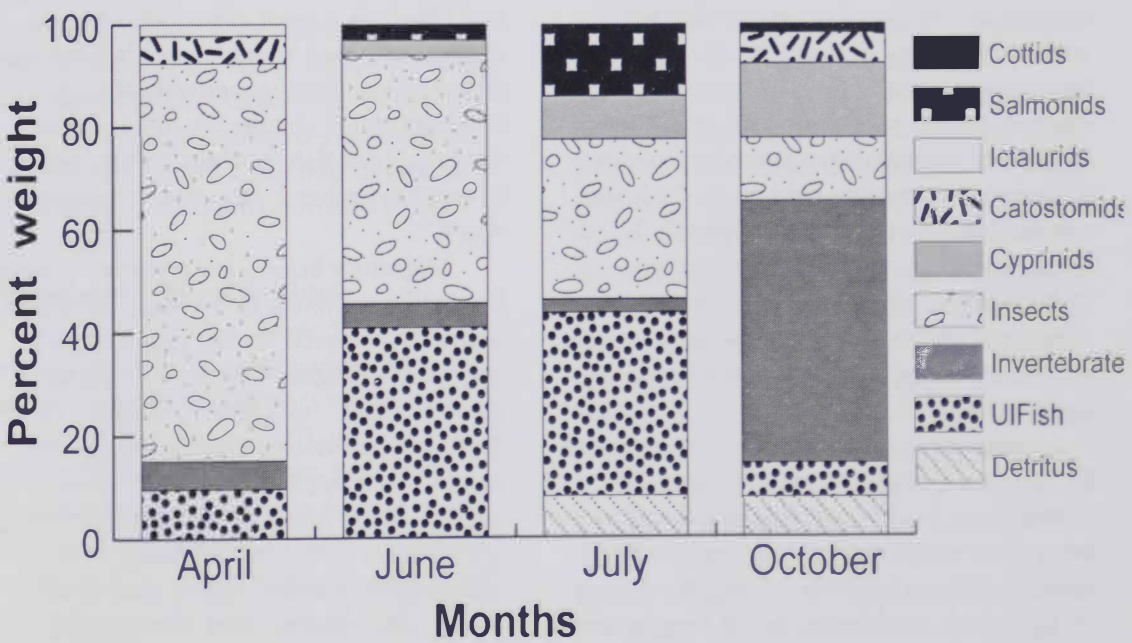

Figure 11. Monthly diet composition (percent by weight) of smallmouth bass 150 mm TL or longer in the lower Flathead River, Montana.

Munther (1970) found that most smallmouth bass in the Snake River, Idaho, remained within the confines of a single pool. In contrast, minimum displacement distance we observed for fish tracked for at least 1 year was 4.3 km. In general, we found that radio-tagged smallmouth bass in the lower Flathead River were seasonally migratory, and most non-localized movements occurred between spawning and overwintering habitats. The extent of migration varied among individual fish, but nearly one-third (29%) moved > 60 km. The largest displacement distance was 97.7 km. The migratory behavior we documented appeared somewhat unique for lotic populations of smallmouth bass. To our knowledge, only Montgomery et al. (1980) and Langhurst and Schoenike (1990) reported similar large-scale migrations by smallmouth bass. Montgomery et al. (1980) noted radio-tagged smallmouth bass in the Columbia River, Washington, moving downstream as far as 61 km in autumn. Langhurst and Schoenike (1990) observed smallmouth bass in the Embarrass River, Wisconsin, making extensive downstream autumn migrations (35 to 109 km) into the larger Wolf River to overwinter. In each of these studies, predominant direction of autumn movement to overwintering areas was downstream. In contrast, we observed radio-tagged smallmouth bass making both upstream and downstream movements in autumn. Fish that overwintered upstream of abundant spawning habitats in the lower one-half of our study area undertook the most extensive migrations. This pattern of large-scale, upstream migration to overwintering locations appears to be unique among other studied smallmouth bass populations.

Large-scale movements by radio-tagged fish generally centered around migrations to spawning locations in mid-April and early May and migrations to overwintering areas in mid- to late July. Montgomery et al. (1980) observed smallmouth bass in the Columbia River entering sloughs to spawn in mid-March and early April as water temperatures increased. Fish remained in these locations (sloughs) into August before migrating out to the main channel and back downriver. Water temperature is an important variable triggering seasonal movement by smallmouth bass (Munther 1970, Langhurst and Schoenike 1990). We found that smallmouth bass in the lower Flathead River generally initiated movements to spawning areas when mean daily water temperatures were ~ 6 to 12 °C. They initiated movements to overwintering locations when mean daily water temperatures were around 17 to 23 °C. Lyons and Kanehl (2002) and Langhurst and Schoenike (1990) reported spring spawning migrations by smallmouth bass in Wisconsin when water temperatures were between 10 and 16 °C. As spawning concluded and winter neared, Langhurst and Schoenike (1990) observed smallmouth bass migrating to downstream overwintering areas when water temperatures began to fall below 16 °C in autumn. Similarly, Munther (1970) found that smallmouth bass in the Snake River moved into deep (> 3.6 m) pools when water temperatures dropped below 15.5 °C in autumn. Smallmouth bass activity generally decreases with declining water temperature (Munther 1970, Todd and Rabeni 1989). Consistent with this, we found that after late August, most radio-tagged smallmouth bass in the lower Flathead River only had localized movements after entering overwintering habitats. We did, however, document one fish moving downstream 3 km in mid-December when water temperature was 4 °C.

Migratory behavioral patterns exhibited by smallmouth bass in our study appeared related to seasonal habitat requirements and the distribution and availability of those habitats. Specifically, habitats used for reproduction and overwintering were typically not in close proximity to one another in the lower Flathead River. During spawning in spring and summer, smallmouth bass tended to select nesting sites over gravel substrates in areas of negligible velocity (Edwards et al. 1983). In the lower Flathead River, this habitat type occurs mainly in the lower 55 km of the study area

where numerous braided sections with island complexes, backwaters, gravel substrates, and few deep-water habitats characterize the low-gradient channel. During our study, spawning smallmouth bass used braided channel areas extensively during spring and summer. Montgomery et al. (1980) noted similar use of backwater and island habitats during spring and summer in an unimpounded section of the Columbia River.

Winter habitat requirements of smallmouth bass are not well understood. However, some believe that availability of overwintering habitat can be a limiting factor for many populations in northern latitudes (Langhurst and Schoenike 1990). During winter, smallmouth bass occupy deep pools with boulder substrate exclusive to most other habitat types (Munther 1970, Todd and Rabeni 1989). Smallmouth bass likely seek out deep pools as refugia from high water velocities and as buffers against winter ice effects in northern latitudes. Although we did not measure water velocity at locations of radio-tagged fish in the lower Flathead River, Todd and Rabeni (1989) found that smallmouth bass prefer habitat with velocities less than 0.2 m/sec. In the lower Flathead River, deep water associated with boulder substrate was relatively sparse but most common in the high-gradient upper portion of the study area. Consistent with habitat requirements of smallmouth bass, our findings indicated that many fish overwintered in the upper one-third and reproduced in the lower one-half of the study area.

Population Monitoring

Our relative abundance (CPUE) data suggest that smallmouth bass increased rapidly over the period that we monitored the population (1998-2005), particularly after 2001. We are uncertain how long smallmouth bass have been present in the lower Flathead River, but we believe bass emigrated from Crow Reservoir sometime after the reservoir was stocked with smallmouth bass in July 1987 (R. Wagner, USDI Fish and Wildlife Service, personal communication). However, little sampling was conducted in the Flathead River during this time. The only other extensive sampling done on the lower Flathead River in addition to our study occurred during the early and mid 1980s and smallmouth bass were not reported during this period (DosSantos et al. 1988). Limited sampling conducted during May 1992 in river sections 1 and 5 did not detect smallmouth bass although these two sections had the highest relative abundances of smallmouth bass during our study (CSKT Fisheries Program unpublished data). Earliest records of smallmouth bass in the lower Flathead River were from 1998, the first year of our study, when 11 fish were captured primarily in sections 1 and 5.

We are unaware of other research documenting similar expansions of smallmouth bass in the intermountain west. However, McNeill (1995) suggested that a combination of fish introductions and natural colonization into connected waters facilitated a large expansion in abundance and distribution of smallmouth bass over a 15-year period in Nova Scotia. We postulate that mobility of this species, at least in the population we studied, may allow smallmouth bass to expand into new suitable areas.

Our catch rates from electrofishing smallmouth bass were comparable to other well-established populations despite the fact that the population became established relatively recently in the lower Flathead River. Autumn 2005 CPUE of stock-length (> 180 TL mm) fish in section 5 was 50.8 fish/hr. At Hells Canyon of the Snake River, Idaho, Nelle (1999) reported highest mean CPUEs of 67.8 fish/hr for fish ≥ 250 mm fork length (FL). Fritts and Pearsons (2004), in a study on the Yakima River, Washington, reported CPUEs ranging from 16.56 to 55.02 fish/hr for smallmouth bass ≥ 150 mm FL. Similarly, smallmouth bass CPUEs in a reach of the Tennessee River, Alabama, with a nationally acclaimed fishery averaged 21.0 fish/hr for fish ≥ 250 mm TL (Slipke et al. 1998). Capture efficiencies undoubtedly differed among these areas making comparisons difficult. However, we believe catch rates from our

study were likely biased low and represent minimums for the lower Flathead River, particularly for larger fish. The lower Flathead River is a large, wide river with relatively steep shorelines, particularly in the upper sections, and smallmouth bass abundances can be underrepresented by electrofishing in these habitats (Lyons 1991). Additionally, we monitored lower Flathead River fish populations in early spring and autumn when average water temperatures ranged from ~ 8-12 ºC. At these temperatures smallmouth bass activity is generally low, and fish often occupy deeper habitats farther from shore (Munther 1970), depending upon time of year. Thus, if our monitoring had taken place in late spring or summer when water temperatures were warmer, CPUEs probably would have been even higher. Nonetheless, we believe our electrofishing data represent, at a minimum, spatial variations in relative abundances and a pattern of increasing smallmouth bass distribution and abundance over the last 8 years in the lower Flathead River.

Overall, patterns of smallmouth bass distribution and abundance that we derived from electrofishing were consistent with movement information gained from our radio-telemetry. Many radio-tagged adult smallmouth bass were highly migratory, spawning in the lower river (sections 1 and 2) and overwintering in deep habitats with large substrates in the upper river. Consistent with this, we documented highest CPUEs of large fish in section 1 during spring. Similarly, we found highest CPUEs of small fish (< 180 mm TL) during autumn in our two lowermost sample sections, which were close to or within habitats where we observed spawning by many of our radio-tagged fish. Also consistent with movement information, we observed highest relative abundances of stock-length (> 180 mm TL) smallmouth bass in our uppermost sample section during autumn, where many radio-tagged fish spent late summer through winter. We captured few smallmouth bass in the two middle-river sample areas (sections 3 and 4), a finding that also concurs with movement studies; we generally observed that most radio-tagged fish only moved through these river reaches as they traveled between spawning and wintering habitats.

Age and Growth

Smallmouth bass growth was relatively fast after age-2 in the lower Flathead River relative to values reported for other populations in nearby Rocky Mountain states, but moderate compared to populations throughout North America (Beamesderfer and North 1995; Fig. 12). For example, by age-5 average total length of smallmouth bass in the lower Flathead River was 328 mm, compared to an average of 255 mm for two populations in Wyoming and an average of 287 mm for six populations in Idaho (Beamesderfer and North 1995). We hypothesize that relatively warm thermal regimes and possibly recent colonization may be responsible for this comparatively fast growth in the lower Flathead River relative to populations in Wyoming and Idaho.

Growth and population dynamics of smallmouth bass are strongly influenced by water temperature (Armour 1993, Beamesderfer and North 1995, Patton and Hubert 1996). Thermal regimes in the lower Flathead River downstream of Flathead Lake are somewhat unique for a large western Montana River because water temperatures are relatively high during the summer months. This is primarily due to warming of surface waters in the expansive shallow southern end of Flathead Lake. Although lower Flathead River temperatures generally do not reach the optimum for smallmouth bass growth (25-27 ºC; Coutant and DeAngelis 1983), they frequently exceed 20 ºC and thus, may be partially responsible for the relatively high growth rates that we observed. Patton and Hubert (1996) studied a slow growing smallmouth bass population in the Laramie River, Wyoming, and found that average daily temperatures only exceeded 20 ºC for 16-38 days depending on longitudinal stream position during the summer. In contrast, average daily temperatures in our study area exceeded 20 ºC an average of 47 days (range = 20-66) during 2000-2004. Our scale data

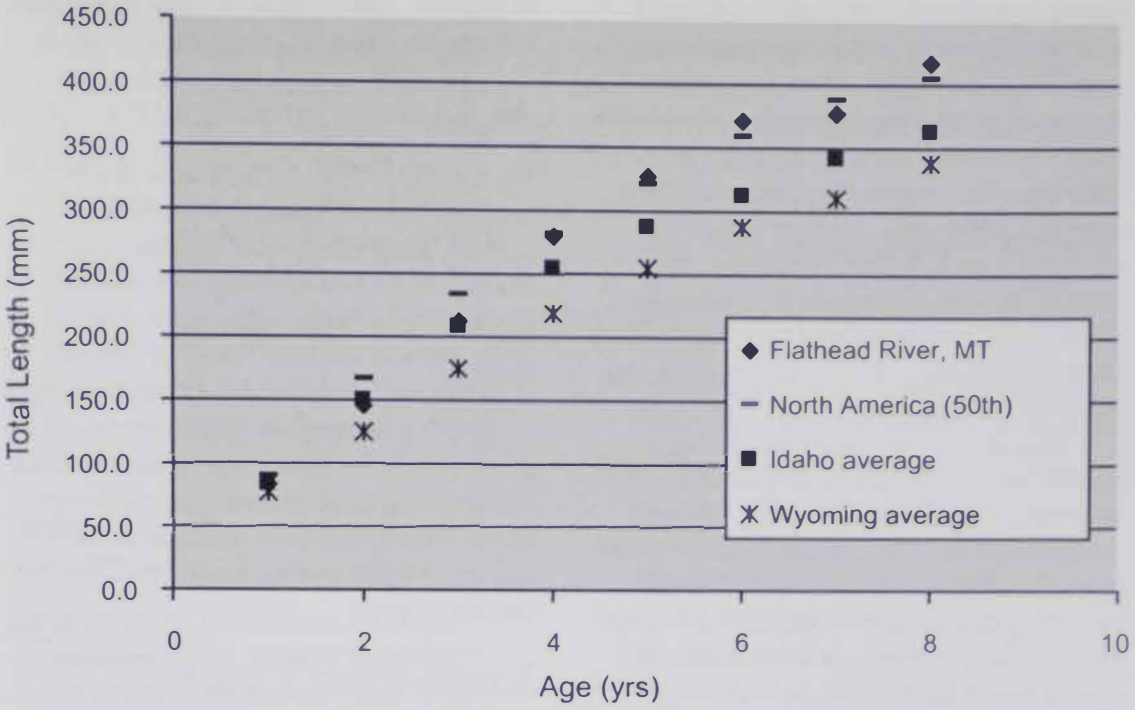

Figure 12. Average back-calculated total lengths at age for smallmouth bass in the lower Flathead River, Montana, and for populations in the Rocky Mountain states of Wyoming and Idaho and the median total length at age for populations across North America (Beamesderfer and North 1995).

were limited, however, and insufficient to examine annual differences in growth related to variations in thermal regimes or other factors because we pooled samples from several years for analysis.

In addition to thermal regimes, recent colonization of the lower Flathead River by smallmouth bass might also have contributed to relatively fast growth and high condition factors that we observed. Smallmouth bass may be better competitors than other fishes in the river, or they may be exploiting different resources than other fishes that allowed them to maintain comparatively high condition factors and growth rates. However, we did not test these hypotheses.

Food Habits

We found that smallmouth bass diets varied considerably among spring, summer, and autumn. In early spring (Apr) and autumn (Oct) diets largely included invertebrates with aquatic insects dominating in April and crayfish being the most important prey in autumn. Fishes were proportionally more important (by weight) in the June diet than in either April or October and were the dominant prey items in July. These seasonal differences may be related to temporal changes in habitat use and variations in prey abundances among different habitat types. For example, smallmouth bass in the lower Flathead River fed more on crayfish in October than during other months from which samples were available. We suspect this occurred because during autumn smallmouth bass used areas with boulder substrates, and these habitat types often support comparatively high numbers of crayfish (Munther 1970, Edwards et al. 1983). In contrast, we found that smallmouth bass fed primarily upon fishes during June and July. This dietary pattern might also have resulted from variation in prey availability related to habitat use by smallmouth bass. During June and July, smallmouth bass used a diversity of habitats and often occupied complex braided channel types. In the lower Flathead River, as in other large river systems (e.g., Koel 2004), these habitats support a diversity of fishes, particularly younger

age classes of both native and introduced taxa, but generally lack rocky substrate suitable for crayfishes. Thus, we postulate that smallmouth bass preyed more heavily upon small fishes during late spring and early summer because they were the most abundant prey items. Zimmerman (1999) also found considerable variation in the diets of smallmouth bass in the Columbia River basin, and speculated that this resulted from differences in prey abundances among different habitats.

Because of ongoing salmonid conservation and restoration efforts in lower Flathead River tributaries, we were interested in smallmouth bass predation and potential effects on salmonids. We found no incidence of predation on salmonids during April or October, but smallmouth bass fed on salmonids during both June and July. The proportion of salmonids in smallmouth bass diets, however, was relatively low (< 15%). However, a high proportion (36.6-40.7%) of unidentifiable fish in the stomachs of fish collected in both months, particularly in July, and the limited numbers of samples collected, somewhat confounded interpretation of these results. Others (Tabor et al. 1993, Fayram and Sibley 2000, Fritts et al. 2004, Naughton et al. 2004) reported that overall effects of smallmouth bass predation on juvenile anadromous salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*) in the Pacific Northwest were variable and may depend on a variety of factors. Differences in smallmouth bass diets and potential effects on migratory salmonid populations in these studies appeared related to abundance and size of available salmonid prey, environmental conditions when the predators and prey are sympatric, and the potential for spatial and temporal overlap of smallmouth bass and migratory juvenile salmonids. Our study suggested that predation on salmonids in the lower Flathead River may be relatively moderate. However, additional sampling during key times identified in this study (late spring and early summer) is required to more thoroughly describe potential effects, examine annual differences in predation on salmonids, and examine for any size-related differences in predation by smallmouth bass.

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Fluvial Westslope Cutthroat Trout Movements and Restoration Relationships in the Upper Blackfoot Basin, Montana

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Abstract

We telemetered fluvial westslope cutthroat trout (*Oncorhynchus clarki lewisi,* WSCT*)* to relate migratory life history traits to restoration opportunities in the upper Blackfoot Basin (upstream of the North Fork confluence) of Montana. Telemetry confirmed life-history similarities to fish of the lower basin but also identified higher fidelity to spawning areas and mainstem pools as well as movements through intermittent channels to headwater spawning areas. Anthropogenic influences limit fluvial WSCT abundance and their ability to reproduce and thus, place sensitive areas of the Blackfoot River environment at increased risk. Road crossings, riparian grazing, and irrigation practices, primarily in tributaries of the Garnet Mountains, adversely influence fluvial WSCT from the tributary to sub-basin scales. Localized life history characteristics demonstrated in the upper Blackfoot River environment confirm the value of fisheries investigations at reach and regional fisheries scales. Understanding local life history strategies is vital when planning fluvial native fish recovery in watersheds of geo-spatial and anthropogenic variability. Telemetry results indicated that WSCT conservation and recovery in the upper Blackfoot basin will rely on restoration of tributaries, protection of intermittent channels, changes in grazing and timber harvest practices on alluvial stream channels, and careful management of private ponds (to avoid hybridization). These assessments identified a fundamental need to work with private landowners for fluvial WSCT recovery at a metapopulation scale to be effective.

Key words: fluvial westslope cutthroat trout, movement, *Oncorhynchus clarki lewisi*, private land, tributary restoration, telemetry, upper Blackfoot River

Introduction

Concern over declines in both abundance and distribution of westslope cutthroat trout (*Oncorhynchus clarki lewisi*) (WSCT*)* throughout the subspecies range have prompted fisheries managers to attempt to identify mechanisms responsible for declines and develop effective conservation and recovery programs (Behnke 1992, Shepard et al. 1997, 2003, Pierce et al. 2005). Historical accounts suggest WSCT were once abundant in river systems of western Montana (Lewis 1805, Behnke 1992, Shepard et al. 2005), where populations expressed a range of migratory (fluvial and adfluvial) and stream-resident life history traits (Behnke 2002, Shepard et al. 2003). Fluvial WSCT often occupy large home ranges, spawn in tributaries where the young rear for ≤ 3 years, migrate to a large river to mature, and then return as adults to their natal tributaries to spawn (Schmetterling 2001, Behnke 2002). Fluvial WSCT have become increasingly rare as a result of habitat loss and degradation, competition with non-native fishes, genetic introgression, and fish passage barriers (McIntyre and Reiman 1995, Shepard 2003) of which all are common in the Blackfoot watershed (Pierce et al. 2005).

Radio telemetry has recently been used to elucidate migratory life history traits of native trout species in the lower Blackfoot basin, i.e. from the North Fork downstream (Swanberg 1997, Schmetterling 2001), such as extensive spawning migrations (>80 km) to natal tributaries by WSCT (Schmetterling

2001, 2003). Telemetered native trout have also helped identify specific population recovery and protection actions at critical sites; validate restoration assumptions; and monitor fluvial use of completed restoration projects (Swanberg 1997, Schmetterling 2001, Pierce et al. 2004). Two examples of these applications include Dunham Creek and hamberlain reek, both recently restored tributaries to the lower Blackfoot River. Dunham reek involved a bull trout *(Salvelinus confluentus)* tagged in the lower Blackfoot River, tracked to an unknown and severely altered (channelized) spawning site, and then entrained in an irrigation ditch during the out-migration (Swanberg 1997). This information, generated during the formative years of bull trout recovery planning, led to restoration of the channelized site and screening of the Dunham ditch (Pierce et al 2002), and contributed to designation of Dunham Creek as *proposed critical habitat* for bull trout under the Endangered Species Act (USDI Fish and Wildlife Service 2002). The second example is Chamberlain Creek, a tributary to the lower Blackfoot river where, after chronic issues such as dewatering, entrainment, grazing and channel alterations were remediated (Pierce et al 1997), telemetered WSCT indicated that fluvial adults began to use the tributary for spawning in greater numbers (Schmetterling 200 I). And higher numbers (densities) of WSCT continue to persist in this stream, years after the restoration efforts (Pierce et al. 2006). Results from these and other telemetry-based investigations have been integrated into monitoring and restoration planning that allows these activities to be targeted more efficiently. However, these applications have focused primarily on the lower Blackfoot basin, and other sub-basins within the Blackfoot watershed (Clearwater River basin and upper Blackfoot River basin) have not been emphasized.

Because of the successful interface between understanding life history traits through applied research and restoration planning and implementation in the lower Blackfoot basin, we investigated fluvial adult WSCT movement and related our finding· to anthropogenic impairments in the upper Blackfoot basin where WSCT occur (Pierce et al. 2004). We hypothesize the physical and human environment of the upper Blackfoot basin would locally influence WSCT movement patterns, and areas with low dens1t1es of fluvial WSCT therein would reflect human disturbance or aquatic habitat. Study objectives were to 1) describe movement patterns of fluvial WSCT in the upper Blackfoot basin following Schmetterlin, (2001), and 2) discuss restoration implications by comparing known upper basin impairments (Pierce ct al 2004) with movement or adult WSCT as well as spawning, summering, and wintering needs in the upper Blackfoot basin. The purpose of this study is to characterize seasonal movements over a sub-basin scale so that specific recovery actions can be directed at important, but anthropogenically impaired habitat and movement corridors with the goal of conserving and restoring the fluvial WSCT life history in the upper Blackfoot basin.

Study Are

The Blackfoot River, a 5th order tributary (Strahler 1957) of the upper Columbia River, lies in west-central Montana and flows west 211 km from the Continental Divide to its confluence with the Clark Fork River at Bonner, Montana (Fig. 1). The Blackfoot River drains a 3728-km^2 water hed through 3040 km of perennial streams and discharges a mean annual flow of 45.2 m3/sec (United States Geological Survey 2004). High-elevation, glaciated mountains to the north and a low-relief, nonglaciated landscape to the south define the physical geography of the Blackfoot watershed. Northem tributary streams begin in high cirque basins and flow through alluviated glacial valleys where sections of stream are often seasonally intermittent. The Garnet Mountains to the south of the Blackfoot River produce small streams that are naturally perennial to the Blackfoot River although most are anthropogenically

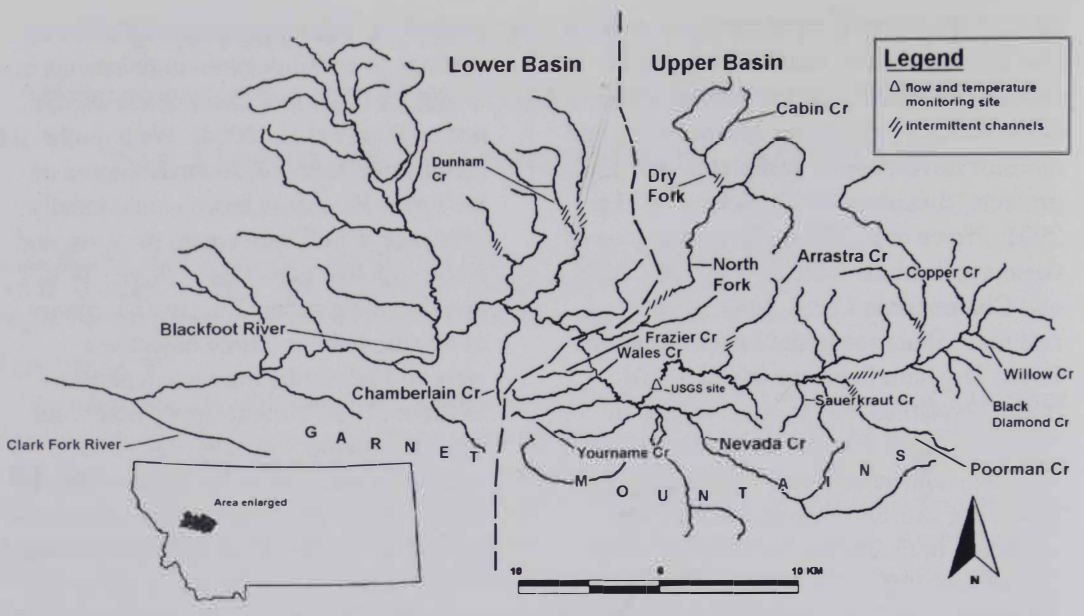

Figure 1. Study area: upper Blackfoot River basin with water temperature and flow monitoring station and intermittent stream channels

degraded or dewatered during the irrigation season. Lands in the upper Blackfoot Basin are mostly public (65%) headwater areas, with private lands consisting primarily of timbered foothills and agricultural bottomland.

The regional (natural and human-induced) variability of the basin is further expressed within the valley of the Blackfoot River. The upper Blackfoot River occupies a low-gradient, alluvial channel with long segments without tributary input, and tributaries that are present are often seasonally intermittent or degraded in lower reaches often as a result of agricultural activities. The upper river supports low instream (secondary) productivity and water quality impairment from non-point agricultural sources increases between Nevada Creek and the North Fork Blackfoot River (Ingman et al. 1990). At the junction of the North Fork, the divide between the upper and lower basins, the lower Blackfoot River receives a large influx of cold water, which reduces summer water temperature, improves water quality and approximately doubles the base flow of the lower Blackfoot River (Ingman et al. 1990, Pierce et al 2006, United States Geological Survey 2006). Contained by glacial boulders and bedrock, the lower river channel is steeper, geomorphically stable and bedrock controlled. The lower Blackfoot River has high secondary productivity (Ingman et al. 1990) and much higher densities of WSCT than the upper Blackfoot River (Pierce et al. 2004). The density of adult WSCT in the upper mainstem Blackfoot River near Nevada Creek are as low as 4/km compared to 58/km in the lower Blackfoot River near Chamberlain Creek and few, if any, fluvial WSCT from the lower Blackfoot River migrate to the upper Blackfoot basin upstream of the North Fork confluence (Schmetterling 2001, 2003, Pierce et al. 2006).

Unlike the lower Blackfoot basin and despite no isolating mechanism, the upper Blackfoot Basin is absent of fluvial rainbow trout (*O. mykiss*) reproduction with the exception of Wales Creek (Shepard et al. 2003, Pierce et al. 2005). Here, WSCT occupy about 90 percent of headwater tributaries although population abundances usually decrease in the downstream direction due to tributary alterations (Pierce et al. 2004). The loss of spawning areas has been identified as a major reason for the decline and low abundance of WSCT within the upper Blackfoot River. Correcting

anthropogenic impairments in the upper Blackfoot basin is increasingly a restoration focus (Blackfoot Challenge 2005), but prior to this study no attempt was made to identify problems specifically affecting fluvial WSCT.

Within the upper Blackfoot basin, the first 88 km of upper mainstem Blackfoot River above the confluence of the North Fork Blackfoot River is naturally stratified into three (hereafter upper, middle and lower) reaches, among which anthropogenic impairments are spatially variable (Pierce et al 2004). The upper reach extends 33.4 river kilometers (rkm) from Poorman Creek (rkm 174.2) to Arrastra Creek (rkm 140.8) and is a densely wooded C4 alluvial channel-type (Rosgen 1996). This reach begins at the downstream end of an intermittent section of the mainstem where groundwater and spring creek inflows re-enter the mainstem Blackfoot River. The middle reach, also a C4 channel-type, extends 32.5 km from Arrastra Creek downstream to Nevada Creek (rkm 108.3). The channel in this less-wooded reach loses slope, becomes highly sinuous, prone to bank erosion, and deposition of fine sediment. Riparian livestock grazing is more common in downstream areas (Marler 1997, Confluence Consulting 2003), and the lower section of this reach is increasingly dewatered during the irrigation season (Pierce et al 2005). Other than at reach boundaries no tributaries enter the middle reach. The lower reach extends 22.3 km from Nevada Creek, a water quality (nitrate, phosphate, total suspended solids and temperature) impaired tributary, to the mouth of the North Fork (rkm 86) (Ingman et al. 1990, Pierce et al. 2006). Below Nevada Creek, the Blackfoot River transitions from a low gradient alluvial (C4) channel to a more confined, higher gradient geologically controlled (B3 and F3) channel (Rosgen 1996). Several small but degraded and dewatered tributaries enter this reach from the Garnet Mountains (Pierce et al. 2005).

Methods

Radio Telemetry

WSCT were captured in the upper Blackfoot River, phenotypically identified, implanted with continuous radio Lotek™ transmitters between 13 March–18 April 2002 and 18 March– 3 April 2003 and tracked fish through one full spawning migration cycle. Visual identification was later verified through genetic analysis of fin clips using 17 fragments of nuclear DNA at the University of Montana, Trout and Wild Salmon Genetics Laboratory (Boecklen and Howard 1997). We evenly distributed transmitters (10-11/reach) within each of the three study reaches. Fish were captured prior to spring run off, presumably prior to spawning migrations by angling or electro-fishing in suspected wintering pools. Individually coded transmitters, which did not exceed 2 percent of fish weight, weighed 7.7 g, had an estimated life of 450 days, (Winters 1997) and were implanted following standard surgical methods (Swanberg 1997, Schmetterling 2001).

We located fish from the ground using either an omni-directional whip antenna mounted on a truck or a hand held three-element Yagi antenna when walking. When ground tracking failed to locate a fish, we relied on fixed-wing aircraft equipped with a three-element Yagi antenna attached to the wing strut flying ~ 100-200 m above the river. Similar to Schmetterling (2001), we located fish at least three times/ week immediately prior to and during spring migrations and spawning, once/ week while holding in tributaries or the Blackfoot River following spawning, and once/month thereafter. For each ground-based relocation within a habitat unit, we triangulated the fish's location to within an estimated 5 m and recorded its location using GPS.

Within tributaries and the Blackfoot River, we expressed locations as distances upstream from the mouth in river kilometers (rkm). Following Schmetterling (2001), we assumed fish to have spawned if they ascended a stream (or river reach) with suitable spawning habitats during a spring

spawning period, and the upper-most location was the assumed spawning site. Because of high flows and poor instream visibility, we were unable to visually validate spawning at most assumed spawning areas. We therefore relied on the presence of juvenile (age-0 and I) WSCT within < 2 km of all identified spawning areas (FWP unpublished data) to support spawning site assumptions. The mean date between two contacts surrounding an event, such as a migration start or spawning date was used to estimate the date of an event (Schmetterling 2001). We considered relocations from November through April to represent winter habitat use, whereas a spring spawning-migration period was delineated from May through 14 July and summer habitat use from 15 July through October.

Blackfoot River daily discharge data were obtained from U.S. Geological Survey (USGS) gauging station (No. 12335100) located in the middle reach at rkm 115.5 to examine potential relationships between discharge and fish movement. We also placed thermographs (Onset™) at the USGS gauge to evaluate effect of maximum daily water temperature on onset of migration and spawning. We used the FWP "dewatered stream list" to identify naturally intermittent reaches (Pierce et al. 2005) and compared basin area above intermittent channels between lower and upper Blackfoot subbasins.

Because of small sample size, we grouped all first-year WSCT spawners from 2002 and 2003 by reach. We then tested between-reach differences by dates that migrations began and dates WSCT entered tributaries using a Kruskal-Wallis one way analysis of variance (ANOVA) on ranks. To explore between-year (2002 and 2003) differences influencing onset of movement and spawning, we compared daily water temperatures for the May through 14 July spawning migration period using a paired *t*-test. Mann-Whitney rank sum tests were then used to test between-year differences in the dates migrations began and the date first year WSCT spawners entered tributaries. Potential associations between date migrations began and total pre-spawning distance moved, and spawning tributary size (drainage area) and number of days WSCT spent in each of these tributaries was assessed with linear regressions. Second-year (repeat) spawners were tracked in 2003 but not included in our analyses because of limited transmitter life during the second migration/spawning period. All results were tested at the $\alpha = 0.05$ level of significance.

Results

Over the course of this study we tagged and tracked 31 WSCT to spawning sites, and those fish with active transmitters were then tracked to summering and wintering areas. These 31 fish were located each an average of 39 times (range = 17-88) between March 2002 and December 2004. We tracked four spawners tagged in 2002 as repeat spawners in 2003 and used these fish to identify spawning site fidelity. Twenty-nine (94%) of 31 fish tested genetically pure WSCT. Two fish (6%) contained all WSCT genetic markers plus two of seven rainbow trout genetic markers and were classified as post-F1 generation hybrids (Martin 2004). Because of their visual WSCT features the low level of hybridization, we included these fish in our analyses. Overall, 28 (90%) fish migrated to tributaries, whereas three migrated to spawning sites in the upper main stem Blackfoot River during the 2-year study (Fig. 2, Table 1).

During migration and spawning periods, river temperatures were similar between 2002 and 2003 ($P = 0.29$), and WSCT migrations began on the rising limb of the hydrograph as temperatures approached 4 °C (Fig. 3). Twenty-two WSCT migrated upstream, nine moved downstream and one repeat spawner (fish No. 8) moved upstream in 2002 and downstream in 2003 before ascending spawning streams. The period of migration in the Blackfoot River averaged 16 days and fish moved an average of 21 km in the Blackfoot River before reaching spawning tributaries or main stem spawning sites (Table 1). Tributary spawners

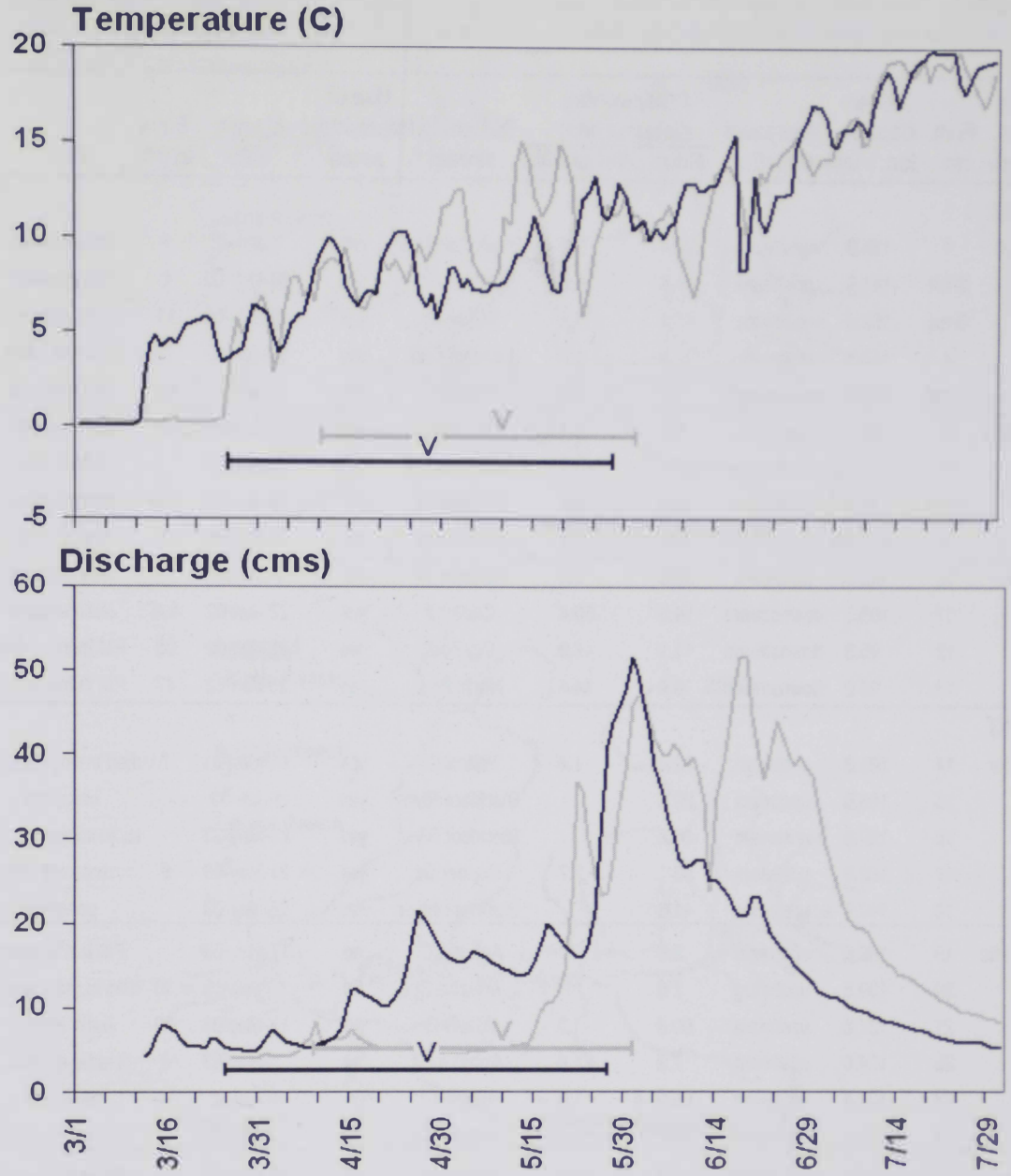

Figure 2. Relationships of water temperature (top) and discharge (bottom) to dates WSCT began migrations (range and median) in 2002 (gray) and 2003 (black). The range is shown by the horizontal bar and median migration start date by vertical arrows.

entered spawning streams at mean water temperatures of 6-7 °C and migrated another 8 km to spawning sites.

Among the three reaches, the start of spawning migrations incrementally increased in the upstream direction from 29 April in the lower reach, to 1 May in the middle reach, to 4 May in the upper reach; however, differences were not significant (ANOVA, $P = 0.89$). Between years, WSCT began their spawning migrations 17 days later (13 Apr vs. 26 Mar) in 2002 (range = 54 days) than in 2003 (range = 61 days). Although slight annual variation was detected ($P = 0.085$) differences were not significant. Likewise, the starting dates of WSCT migrations were not associated with the distance moved ($R^2 = 0.08$, $P = 0.24$).

Overall, WSCT spawning occurred in nine tributaries varying from 1st to 4th

Table 1. Summary of capture locations, spawning movements sites and dates, time spent in tributaries and fate of postspawning WSCT, 2002 and 2003; PM = post spawning mortality.

Year and reach	Fish no.	River Capture loc. (rkm)	Prespawn direction	Prespawning distance (km) River	Prespawning distance (km) Tributaries	Spawning stream	Use of intermittent reach	Spawn date	Days in trib.	Fate
2002										
upper	1	165.3	upstream	25.4	2.1	Black Diamond	yes	1-Jun-02	7	radio expired
	2-rpt	163.5	upstream	34.4	0.6	Willow Cr	yes	24-May-02	6	radio expired
	3-rpt	152.8	upstream	45.1	1.1	Willow Cr	yes	30-May-02	11	radio expired
	4	148.3	upstream	37.5	1.3	Landers Fork	yes	23-Jun-02	12	summer mort
	5-rpt	142.4	downstream	0.3	3.4	Arrastra Cr	no	9-Jun-02	60	radio expired
middle	6	139	upstream	3.5	1.1	Arrastra Cr	no	7-Jun-03	47	radio expired
	7	132.3	upstream	31	3.7	Sauerkraut Cr	no	3-Jun-02		PM in trib
	8-rpt	131.4	upstream	10.8	4.2	Arrastra Cr	no	29-Jun-02	153	radio expired
	9	113.8	downstream	27.5	4.5	North Fork	no	11-Jul-02	142	died in river
lower	10	103.5	upstream	38.6	5.4	Arrastra Cr	no	7-Jun-02	12	radio expired
	11	103.5	downstream	14.3	50.4	Cabin Cr	yes	27-Jun-02	406	radio expired
	12	95.8	downstream	11.1	41.9	Dry Fork	yes	23-Jun-02	93	PM in trib-avian
	13	94.2	downstream	6.4	14.4	North Fork	yes	25-Jun-02	47	PM in trib-avian
2003										
upper	14	165.8	upstream	32.2	1.4	Willow Cr	yes	14-May-03	7	died in original pool
	15	165.6	upstream	22.6		Blackfoot River	yes	1-Jun-03		unknown
	16	152.8	upstream	36.2		Blackfoot River	yes	21-May-03		radio expired in trib
	17	152.8	upstream	33	7.7	Copper Cr	yes	21-May-03	5	radio expired
	18	147.7	upstream	41.8		Blackfoot River	yes	25-May-03		poached
middle	19	139.5	upstream	2.6	2.7	Arrastra Cr	no	17-May-03		PM in trib-avian
	20	139.5	upstream	2.6	1.1	Arrastra Cr	no	10-Jun-03	30	died in original pool
	21	137.6	upstream	60.3	1.3	Willow Cr	yes	17-May-03	29	radio expired
	22	134.6	upstream	7.2	1.6	Arrastra Cr	no	25-May-03	6	radio expired
	23	131.4	upstream	66.9	1.3	Willow Cr	yes	4-Jun-03	4	poached
	24	115.4	upstream	26.7	1	Arrastra Cr	no	19-May-03		PM in trib-avian
lower	25	101.4	downstream	13.8	0.3	Wales Cr	no	19-May-03		PM in trib-avian
	26	96.2	upstream	45.9	1	Arrastra Cr	no	29-May-03		PM in trib
	27-hyb	96	upstream	2.9	0.6	Wales Cr	no	21-Apr-03	13	PM in river
	28	96	downstream	10.9	43.2	Dry Fork	yes	19-Jun-03		PM in trib
	29	95.7	downstream	9.8	12.2	North Fork	yes	10-Jun-03	80	PM in trib-avian
	30	95.2	downstream	9.3	28.5	North Fork	yes	19-Jun-03		radio expired in trib
	31-hyb	94.2	upstream	2	1.1	Wales Cr	no	19-Jun-03		PM in trib

rpt=repeat spawner
hyb=hybrid

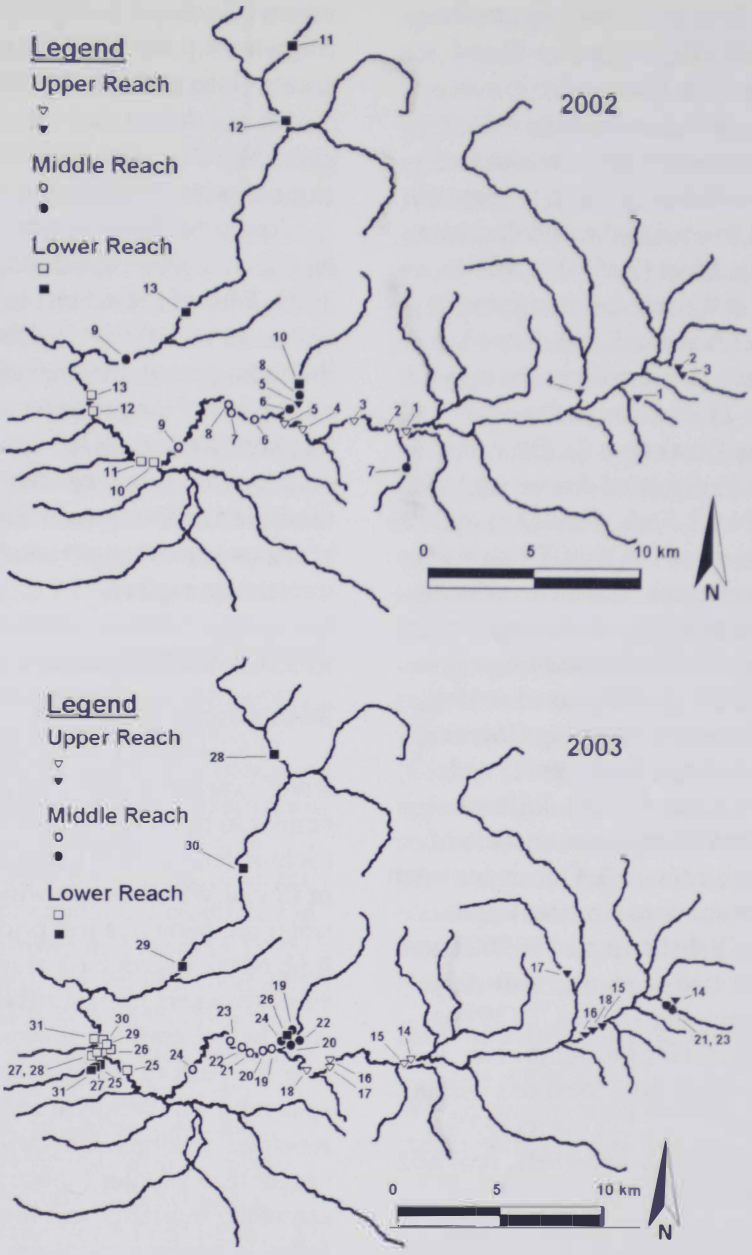

Figure 3. Capture locations (open symbols) and assumed spawning sites (closed symbols) of telemetered WSCT for 2002 (left) and 2003 (right). Numbers refer to individuals in Table 1.

order (see Table 1 and Fig. 2 for locations). Arrastra Creek and Willow Creek supported the highest proportion of telemetered spawners (9 or 29%, and 5 or 16%), respectfully, and each of these tributaries also had at least one 2002 repeat spawner return in 2003. WSCT entered tributaries from mid-April through mid-June (mean date = 16 May). We detected no significant differences in the date WSCT entered spawning tributaries either among reaches (ANOVA, $P = 0.42$) or between years ($P = 0.17$). WSCT spent an average 51 days in tributaries (range = 4-402) and spent significantly different amounts of time in the seven different spawning tributaries ($R^2 = 0.36$, $P = 0.002$), staying the longest in the largest tributary, the North Fork.

The majority of WSCT tagged in the lower river reach (6 of 11 or 55%) migrated downriver to the lower reach boundary before ascending the North Fork for

spawning (n = 3) or two tributaries to the upper North Fork (Dry Fork (n = 2) and Cabin Creek (n = 1). Three other lower-reach fish entered Wales Creek (n = 3), a tributary adjacent to the lower reach; two ascended the middle river reach to spawn in Arrastra Creek located at the middle-upper reach boundary. Most (9 of 10 or 90%) WSCT tagged in the middle river moved upriver to either Arrastra Creek (n = 6), Sauerkraut Creek (a tributary to the upper river reach, n = 1), or through the upper reach to Willow Creek (n = 2). Only one middle-reach fish migrated downriver before ascending the North Fork. Similar to middle-reach fish, most (9 of 10) WSCT originally in the upper river reach migrated upriver; however, unlike the concentrated spawning of most middle reach fish, spawning of upper-reach WSCT was dispersed among several spawning sites including Copper Creek (n = 1), Landers Fork (n = 1) and Black Diamond Creek (n = 1), Willow Creek (n = 3) and the upper main stem of the Blackfoot River (n = 3). One upper reach fish moved downriver to Arrastra Creek.

Of 31 WSCT that spawned in 2002 and 2003, 13 (42%) died soon after spawning. Seven of the surviving 18 WSCT (39%) returned from tributaries to summer in their original capture pool locations within 1-55 days (mean = 22). Six others (33%), including two mainstem spawners, returned to summer within an average of 4.3 km (1.1-11.4 km) of their mainstem capture locations. Five (28%) remained in their spawning tributaries during the summer.

Of 18 tagged WSCT that survived into summer, we monitored 11 at wintering locations (1 Nov-30 Apr). Most (6) WSCT that summered at original captures remained there into winter, and two additional fish that summered upstream moved downstream to (or within < 1.0 km) of their original pool capture site; two (18%) over-wintered 11.2 and 25.1 km from their original capture sites. One WSCT, originally captured in a pool in the Blackfoot River near rkm 103.5 in 2002, over-wintered in the North Fork (rkm 31.8) the following year, a distance of 51 rkm between wintering sites. We observed a majority of wintering WSCT using large pools with complex wood associations and fish exhibited very little movement during the winter. The remaining seven WSCT either died or their transmitters expired prior to winter.

Ten WSCT (40%) captured in 2002 remained alive with working transmitters in 2003. Four of these fish (40%) were repeat spawners with three returning to spawn in the same stream they had used in 2002, and all ≤ 1 km of the previous year's spawning location. The fourth fish returned to the mouth of the tributary (Willow Creek) it had used the previous year, within 1.1 km of the previous spawning site, at which point the transmitter expired.

Discussion

Movement patterns

Fluvial WSCT of the upper Blackfoot River expressed migratory characteristics similar to those in the lower Blackfoot River (Schmetterling 2001). Spawning movements of fluvial WSCT began with increasing water temperatures just prior to the rising limb of the hydrograph at which point adult spawners moved either up or down river before entering spawning tributaries near the peak of the hydrograph. Repeat spawning was common and spawners remained in larger tributaries significantly longer than smaller tributaries and post-spawning mortality was high. Telemetry failed to confirm mainstem spawning within the three study reaches; however, we observed spawning migrations to potential spawning sites in the upper-most Blackfoot River. Unlike other studies that showed more discrete use of lower-order tributary streams (Magee et al. 1996), our results identified spawning across 1st through 4th order tributary streams similar to the lower Blackfoot River study.

Despite many similarities to WSCT of the lower basin, we detected differences in certain spawning site and mainstem habitat use compared to Schmetterling (2001), i.e., higher adult WSCT fidelity to both spawning and main stem sites in our study. Spawning

site fidelity for WSCT has previously been documented (Magee et al. 1996), but was not apparent in the lower Blackfoot basin where two repeat spawning migrants did not return to their previous year's spawning location (Schmetterling 2001). However, the small sample size of repeat spawners in the lower Blackfoot basin limits the strength of this comparison. Nonetheless, all repeat spawners returned to or within 1.1 km of previous spawning sites. This suggests that spawning sites were more limiting in the upper Blackfoot basin, thus prompting higher fidelity, a premise supported by lower WSCT densities in the upper Blackfoot River. We also found higher fidelity to wintering sites with 73 percent of post-spawning fish returning to their original pool capture locations compared with 11 percent in the lower basin study. These differences suggested a lower number of preferred wintering pools in the upper river compared with the lower Blackfoot River where pools were larger and geologically stable. In our study, we observed wintering in larger pools, a pattern of habitat use confirmed in similar studies (Brown and Mackay 1995, Schmetterling 2001, Dare and Hubert 2002).

A majority of WSCT (55%) from the upper Blackfoot River ascended naturally intermittent reaches, i.e. channels dry during base flows, to access upstream spawning sites, compared with 4 percent in the lower river study (Schmetterling 2001). Including the North Fork basin, 48 percent of the upper basin lies upstream of naturally intermittent channels, compared to 10 percent of the lower basin. This use of natural intermittent channels likely reflected both a higher number of intermittent channels in the upper Blackfoot Basin and more suitable spawning sites found in smaller streams upstream of intermittent reaches. Interestingly, all telemetered WSCT migrating through naturally intermittent reaches from spawning sites returned prior to no flow periods without related mortality.

Spatial/temporal migration patterns of WSCT were inconsistent among reaches and seemingly reflected both natural and anthropogenic influences. As an example, upriver migrations for a majority of middle reach spawners to Arrastra Creek suggested a pattern influenced by lack of natural tributaries downstream. Conversely, lack of spawning at several tributaries in the area of Nevada Creek suggested that anthropogenic loss of natal connections influencing lower-reach WSCT. Although not significantly different, lower-reach WSCT began migrations earlier, and these migrations were on average longer in both distance (4.3 km) and duration (8 days) compared to the combined upper reaches despite the near proximity to several tributaries. Unlike the upper two reaches, lower-reach fish exhibited a downriver movement pattern, and spawners sustained a surprisingly high level of post-spawning mortality (73%) compared with middle and upper reaches (combined total = 27%). Similar to an evaluation with Yellowstone cutthroat trout (Clancy 1988), lower reach difference appeared influenced by loss of recruitment sources from adjacent Garnet Mountains tributaries and coincided with impaired water quality and very low densities of fluvial WSCT in the Blackfoot River near Nevada Creek (Pierce et al. 2004).

Restoration Implications

The upper Blackfoot River fluvial WSCT conservation strategy calls for metapopulation function and enhancing "core" populations of genetically "pure" WSCT (Shepard et al 2003). This strategy relies on access between mainstem habitats in the upper Blackfoot River and suitable spawning tributaries over a large area. The majority of perturbations to WSCT habitat in the Blackfoot Basin, including altered habitat and passage issues, occurred in the lower reaches of most tributaries, primarily on private land (Pierce et al. 2004; 2005). These impairments included over-grazing in riparian areas (32 streams), road crossings (28 streams), irrigation structures (fish passage and entrainment) and irrigation-related flow problems (23 streams), and historical placer mining (12 streams) (Pierce et al. 2004, 2006). Although private lands in the upper Blackfoot basin comprise only 35

percent of the land base, they contained the majority of WSCT spawning sites (64%), migration corridors (69%) and wintering areas (80%) documented in this study. Thus, successful application of the conservation strategy includes correcting human-caused impairments affecting WSCT on private land.

Compared to the lower Blackfoot Basin, fidelity of fluvial upper River WSCT to pools and observations of cover associations suggest heightened preference to pool with instream wood as identified in other studies (Brown and Mackay 1995). Using a census of large instream wood as an index to these habitat requirements, Pierce et al. (2004) measured a significant (89%) decrease in amount of large instream wood between the upper and lower reaches. These findings identify a need to manage for the recruitment of large wood to the Blackfoot River channel between Arrastra Creek and the North Fork.

In a region where land use is dominated by traditional agriculture, tributary fish population inventories indicated a pattern of fewer WSCT in the lower reaches of 32 of 46 tributaries in the upper Blackfoot basin (Pierce et al. 2005). Our telemetered fluvial WSCT entered only one tributary (Wales Creek) between the North Fork and Arrastra Creek, a distance of 55.5 rkm. Consistent with recent population trends that show very little WSCT use in lower reaches of other tributaries to the lower river reach (Pierce et al. 2004), we found no fluvial use of Nevada Creek or its tributaries, Yourname Creek, and Frazier Creek, a large contiguous area comprising 43 percent of the upper Blackfoot Basin upstream of the North Fork, despite stream-resident WSCT widely distributed throughout headwaters of these streams. Between the mainstem Blackfoot River and resident WSCT populations in the upper tributaries, dewatering, habitat degradation, e.g. overgrazing, and low water quality have been identified as fisheries impairments (Ingman et al. 1990, Pierce et al. 2001, Blackfoot Challenge 2005) but correctable with alternative agricultural practices.

Between the North Fork and Arrastra Creek, only lower Wales Creek received limited spawning use by three WSCT, and this was downstream of an on-channel irrigation reservoir. Of these fish, two did not survive spawning potentially due to irrigation-induced low flows. Furthermore, Wales Creek, the lower-most spawning site identified in this study, occurred within the upper range of rainbow trout in the watershed and contained private fishponds with rainbow trout. Both of the WSCT that showed rainbow trout hybridization in our study entered Wales Creek. With exception of the North Fork, all other individual WSCT in our study spawned in tributaries supporting genetically unaltered WSCT stocks (Pierce et al. 2005). These findings confirm the risks of introducing hybridizing species into ponds and lakes within the range of WSCT in the upper Blackfoot basin.

Arrastra Creek, the next identified upstream spawning stream, 45.4 km upstream of Wales Creek, received the highest spawning use of all streams that included WSCT from all reaches as well as the majority of WSCT tagged in the middle reach. However, these fish all spawned downstream from a set of impassable culverts. Compared to concentrated spawning in Arrastra Creek, the majority of upper reach WSCT spawning was dispersed among headwater tributaries and the mainstem Blackfoot River upstream of an intermittent segment. As important migration corridors, intermittent reaches such as this should be managed within the context of migration and downriver recruitment. However, critical fisheries are not often associated with seasonally dry channels, and Montana's stream protection laws do not offer intermittent streams the same legal protection as perennial streams without consent of local conservation districts.

Conclusions

Variability within the physical and cultural landscape of the Blackfoot watershed influenced expression of fluvial

life histories and habitat use at various spatial scales. Understanding this variability within a context of anthropogenic limiting factors is vital towards developing concise restoration actions for fluvial WSCT. We believe that links between human impairments and spawning limitations in the upper Blackfoot River were supported by 1) reach-related low densities of WSCT in the River where adjacent spawning tributaries are no longer functional or accessible, 2) concentrated use of the few available nearby tributary spawning sites between the North Fork and Arrastra Creek, and 3) movement differences and high mortality of lower reach WSCT spawners. These links elucidated the value of the few existing spawning sites and a need to restore habitat and access at sites with high-quality spawning and recruitment potential, particularly those near the lower and middle reaches. This study identified a clear need to engage private landowners, county road departments, and conservation districts in restoration work. Based on the proven ability of the stakeholders within the Blackfoot watershed to find solutions to identified fisheries problems, we expect this information will facilitate development of specific fluvial WSCT restoration actions.

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Elk Habitat Selection and Winter Range Vegetation Management in Northwest Montana

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Abstract

We determined winter and spring habitat selection of a small (~100) resident elk (*Cervus elaphus*) herd from 1988 to 1998 including 3 years before to 6 years after timber harvest and/or prescribed burns. Sixty-nine elk were fitted with radio transmitters to document elk response to these habitat treatments. The study area was located on Firefighter Mountain along the west shore of Hungry Horse Reservoir in northwestern Montana. Treatments included burning 66 ha of shrubs in eight natural openings and removing coniferous overstory on 251 ha in 48 logging units. We detected no difference pre- to post-treatment in elk selection for the treatment area from within their seasonal home range. Habitat treatments did not influence elk habitat selection. However, snow negatively affected their selection for the treatment area, which suggested forest canopy cover was important to elk in this study area. Thus, opening the forest canopy to increase winter forage production seemingly did not benefit elk. Managers should use caution when managing forests to create forage openings on winter ranges with high snowfall.

Key Words: *Cervus elaphus*, elk, habitat management, Montana, snow, winter range.

Introduction

Managers commonly enhance forage production on elk (*Cervus elaphus*) winter range to increase elk productivity, survival, or change winter distribution. The Rocky Mountain Elk Foundation has funded > 2600 habitat enhancement projects in 27 states (Rocky Mountain Elk Foundation 2007). These projects included a variety of treatments, of which some were designed to increase forage production. Managers typically justify this work on the *a priori* assumption that winter forage is a limiting factor and that increasing forage will increase elk survival and population size. However, no studies have demonstrated increased elk production or survival as a result of habitat enhancement designed to increase forage production on forested winter ranges. In fact, past studies have warned that manipulation of cover on forested elk winter ranges may not improve elk habitat and should be designed with great care (Thomas et al. 1979, Lyon et al. 1985).

The effect of snow on elk habitat use in the vicinity of our Firefighter Mountain study area in northwestern Montana is well documented (Jenkins 1985, Singer 1979). Elk preferentially use timbered habitats at snow depths greater than 60 cm (Telfer and Kelsall 1971, Leege and Hickey 1977, Singer 1979, Peck and Peek 1991). Jenkins (1985) found that habitat use by elk was related to overstory density during a severe winter in the North Fork of the Flathead River. Martinka (1976) found elk densities west of the continental divide in Glacier National Park were highest on winter ranges in intermediate seral stages and stressed the importance of habitat structure in areas of deep snow.

The objective of our project was to evaluate a long-term management plan intended to improve winter range and thereby increase carrying capacity by an additional 133 elk (D. Casey and P. R. Malta 1990, unpublished report). Our approach used radio-equipped elk to test an assumption that poor interspersion of cover and forage and a deteriorating forage base (due to fire suppression and conifer density) limit elk population size on Firefighter Mountain in northwestern

Montana. Alternatively, elk populations may not respond numerically but may respond by changing their distribution to increase use of treated habitats. Montana Fish, Wildlife and Parks identified the project area for potential treatment based on preliminary field work conducted during 1987-89 (D. Casey and P. R. Malta 1990, unpublished report).

Study Area

The Firefighter Mountain study area is located on the northeast shore of Hungry Horse Reservoir along the South Fork Flathead River in northwest Montana (Fig. 1). USDA Flathead National Forest manages the land. During our study there were < 0.25 km/km^2 of road open to motorized vehicle use in the study area during the fall elk hunting season. Hunting regulations remained constant during the course of the study. A 6-week archery season allowed harvest of any elk, followed by a 5-week firearms season that allowed harvest of any elk during the first week and any antlered bull during the last 4 weeks.

A nonmigratory elk herd occupied the 19,847-ha study area, including Firefighter Mountain and adjacent range, during I December to 14 May from 1988 to 1997 (J. Vore, P. R. Malta and E. Schmidt 1995, unpublished report). Pacific maritime weather patterns prevailed on the study area (Daubenmire 1969). Mean annual precipitation at the Emery Creek Snow Telemetry (S OTEL) site 2.8 km northeast of the study area (elevation 1327 m) was I 06 cm (SE = 7.50 cm) during water years (I Oct- 30 Sep) 1988-1997 (USDA Natural Resource Conservation Service 1988-1997). SNOTEL sites were automated stations that collected and transmitted the daily snow water equivalent (SWE) from snow pillows, total precipitation (accumulated from 1 Oct each year), and daily air temperatures. Approximately half of annual precipitation fell as snow from October through March although winter rains were common. Snow was commonly > 1 m deep on this elk winter range. Elevation in the mountainous topography ranged from 980 to 2000 m.

A closed-canopy forest dominated the study area; there were relatively few natural openings and scattered clearcuts created by past logging. Clearcuts < 10 years old in the area had scattered trees < 2 m tall, whereas older clearcut were typically more densely vegetated with shrub and trees > 2 m tall. Lodgepole pine (Pinus contorta) and western larch (Larix occidentalis) were the dominant conifers, while Douglas fir (Pseudotsuga menziesii occupied more xeric south and southwest aspects below 1500 m. Subalpine fir (Abies lasiocarpa) was common above 1800 m. Pacific yew (Taxus brevifolia), alder (Alnus spp.), menziesia (Menziesia ferruginea) or globe huckleberry (Vacinnium globulare) locally dominated understory shrubs. Beargrass (Xerophyllum tenax) and pinegrass (Calamagrostis rubesens) were ubiquitous throughout the study area

Ungulates on the study area included elk, mule and white-tailed deer (Odocoileus hemionus and O. virginianus), and moose (Alces alces). Large carnivores included black and grizzly bear (Ursus americanus and U. arctos), mountain lion (Felis concolor, wolverine (Gulo gulo). and coyote (Canis latrans). Wolves (C. lupus) have been sighted, but no known resident packs have become established during the study period.

Methods

Habitat enhancement on Firefighter Mountain consisted of 56 treatment units totaling 317 ha on the south and west side of the mountain (Fig. l). Eight units totaling 66 ha (X - 8.4, range 1.2 - 14.3) were natural openings where shrubs were slashed and burned to stimulate forage production. The other 48 units totaling 251 h a (X = 5.3. range 0.9 - 8.4), were either logged or trees were slashed and then burned to open the canopy and stimulate brow ·e production. Timbered units were designed in which no point in a treatment unit was > 180 m from forest cover that was at least 180m wide. Hereafter, these 48 units are referred to as logging unts .

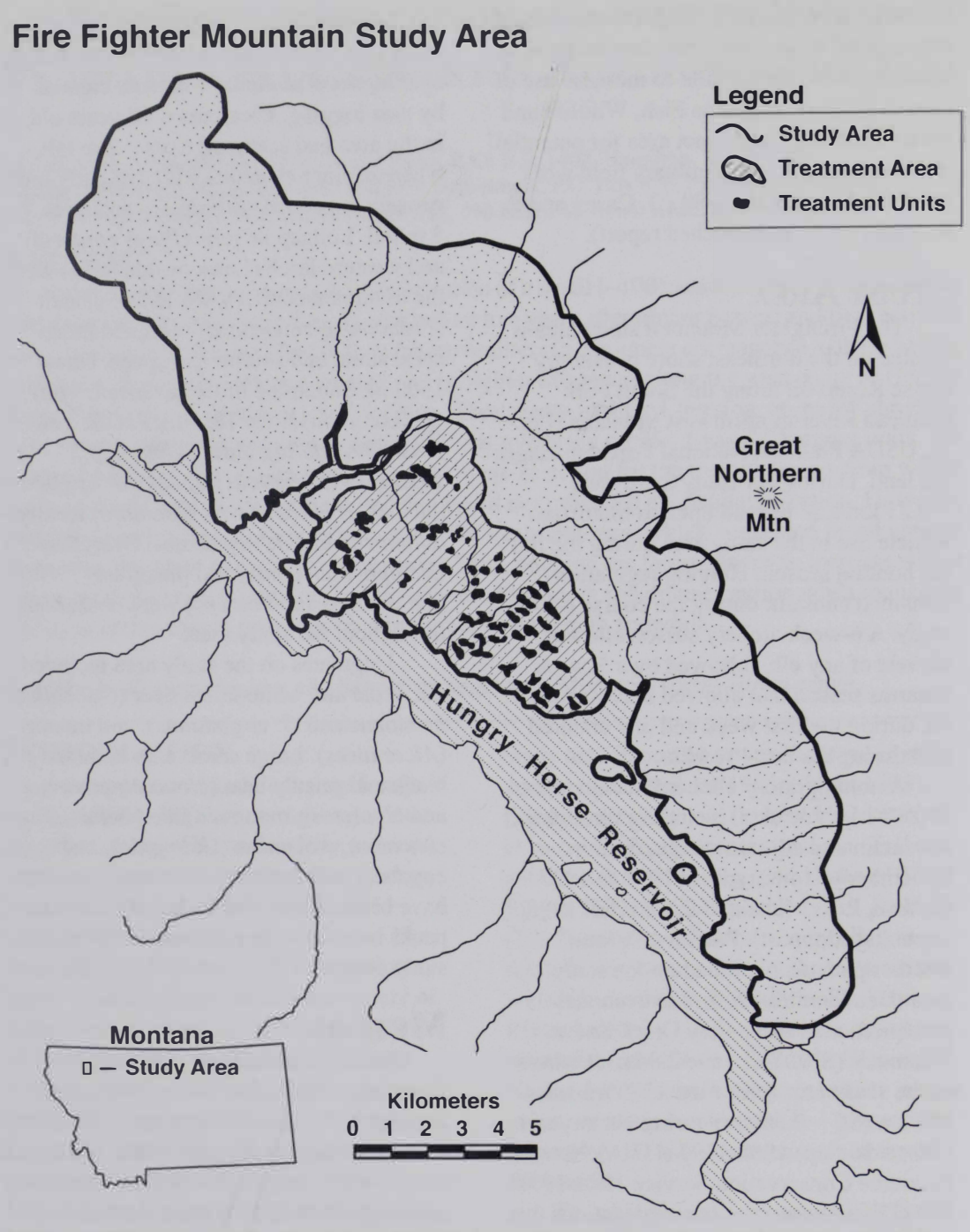

Figure 1. Elk range on the Firefighter Mountain study area in northwest Montana showing location of treatment area and individual treatment units.

With the exception of a single natural opening, closed-canopy forest of dense lodgepole pine with little understory forage production dominated the southern half (46%) of the study area. Pretreatment elk distribution showed little elk use of the southern half other than in the natural opening. Logging units were purposely concentrated (77% of logging units) in the south half to attract more use to this area of relative low forage production.

Habitat treatments began in 1991 and were mostly completed by summer 1995 except for burning of one unit. At the end

of the study during winter 1998, treatments on natural openings were 6 years old, and treated logging units ranged from 2 to 6 years old with 75 percent of units ≥ 4 years old.

Project personnel measured vegetation response to treatments in order to evaluate changes in forage production resulting from habitat enhancement efforts using standardized vegetation sampling methods from the USDA Forest Service ECODATA handbook (Hann 1987). We sampled at least 3 sites representative of each primary type of treatment for monitoring, including natural openings, dense seral forest stands, as well as random and control sites with no habitat treatments. We then sampled vegetation on five 0.25-m^2 plots along each of five 20-m transects at 11 permanently marked treatment sites and one control site. We calculated a forage production index by multiplying shrub height by shrub width and dividing the product by the average distance to shrubs along each transect.

Project personnel captured elk from December to mid-March in a corral trap, Clover traps (Thompson et al. 1989) or by net gunning from a helicopter (Helicopter Wildlife Management, Salt Lake City, UT) and fitted them with radio collars (Advanced Telemetry Systems, Inc., Isanti, MN). We located elk from a Cessna 185 aircraft and plotted locations on 7.5-min United States Geographical Survey topographic maps using Universal Transverse Mercator (UTM) coordinates. Mean telemetry error (±1 SE) of 24 locations on 17 radio collars either shed or on dead elk was 196 ± 72 m. We defined an elk group as ≥ 1 animal and it was not uncommon for >1 radio-collared elk to be in a group. In these cases, we used the geographic center of the group rather than coordinates of individuals in the group as our habitat point because the presence of conspecifics can bias an individual's choice of habitat (White and Garrott 1990). We used only locations that were separated by > 4 days (White and Garrott 1990) to insure independence of locations of individuals. This research was conducted using wildlife capture and handling protocols established by Montana Fish, Wildlife and Parks.

We used the Animal Movement extension in the Geographic Information System (GIS) program ArcView 3.1 (Environmental Systems Research Institute, Inc., Redlands, CA) to generate adaptive kernel herd home ranges (Worton 1989) for winter (1 Dec-15 Mar) and spring (16 Mar-14 May). We defined the total and core home ranges by the 100 percent and 50 percent isopleths, respectively, and excluded portions of home range polygons located in Hungry Horse Reservoir.

We defined the "treatment area" for analysis of elk use as that portion of Firefighter Mountain inside a 712-m buffer (mean daily movement of cow elk in spring and early summer [Vore and Schmidt 2001]) around each treatment unit (Fig. 1). The 3480- ha treatment area covered most of the west face of Firefighter Mountain. Few places within the treatment area were > 712 m from a treatment unit because units were designed to maximize interspersion of cover and openings (Fig. 1).

We determined habitat selection at three analysis levels during three time periods: pre-treatment (1988-1991), treatment (1992-1995), and post-treatment (1996-1998). The first level of selection determined selection for the treatment area from within the total home range. Second, because treatment units were concentrated in the southern portion of the treatment area, we evaluated selection between the north and south portions of the treatment area by elk groups located within it. Finally, we examined selection for the treatment units by elk within the treatment area. We buffered each unit by the mean telemetry error and used natural openings, logging units, and the remainder of the treatment area as habitat categories. We further categorized logging units as either cut or uncut during the treatment time period.

The close proximity of units to each other precluded analysis at the individual unit level. Because conversion of closed-canopy forest into forage openings was a primary purpose of the project, we further analyzed selection for logging units by excluding locations in natural openings.

Table 1. Selection by elk for the treatment area on Firefighter Mountain from within an elk herd's 100 percent kernel home range during winter and spring, 1991-1998.

Time Period	Treatment Area	North Herd						South Herd					
		Winter			Spring			Winter			Spring		
		Groups (%)	w[a]	P[b]	Groups (%)	w[a]	P[b]	Groups (%)	w[a]	P[b]	Groups (%)	w[a]	P[b]
Pre-treatment	Inside	28 (26)	1.070		50 (51)	1.943					0 (0)	0.000	
				0.685			0.000	No Data					0.000
	Outside	81 (74)	0.978		49 (49)	0.669					18 (100)	1.493	
During treatment	Inside	62 (38)	1.575		59 (44)	1.848		14 (13)	0.393		18 (22)	0.665	
				0.000			0.000			0.000			0.026
	Outside	102 (62)	0.818		74 (56)	0.732		94 (87)	1.299		64 (78)	1.165	
Post-treatment	Inside	19 (27)	1.147		24 (32)	1.215		13 (15)	0.453		15 (23)	0.699	
				0.506			0.277			0.000			0.075
	Outside	50 (73)	0.955		52 (68)	0.925		74 (85)	1.270		50 (77)	1.148	

[a] Selection Index indicating use less than (<1), greater than (>1), or equal to (=1) habitat availability.
[b] G-test of significance (Manley et al. 1993)

For this analysis we used only those groups that were either in logging units or on the remainder of the treatment area.

We calculated the distance to the nearest treatment unit for elk groups in the treatment area using The Analysis Extension for ArcView (SWEGIS, Göteborg, Sweden). This metric might document a geographic shift in elk distribution that may not be evident by the previous analysis of elk in or out of treatment units. We compared distances pre- vs. post-treatment for natural openings and logging units using Student's *t* test.

We used Programs for Ecological Methodology (Exeter Software, New York, NY) to determine habitat selection using Cock's (1978) selection index found in Krebs (1999:478):

$$w_i = \frac{o_i}{p_i}$$

where: w_i = Selection index for habitat *i*
o_i = Proportion of elk groups in habitat *i*
p_i = Proportion of habitat *i* available

An index of 1 indicates habitat use in proportion to availability whereas > 1 indicates selection for and < 1 selection against a habitat. We used the *G*-test recommended by Manley et al. (1993) to determine differences in habitat selection within a time period and x^2 to compare elk use among time periods.

To evaluate the effect of snow on elk distribution, we used the SWE recorded at the Emery Creek SNOTEL site for the dates on which elk were located (location-date SWE or LDSWE). We regressed the mean LDSWE for each winter against that winter's treatment area selection index. We used the program Statistica (StatSoft Inc., Tulsa, OK) for x^2, Student's t and linear regression analyses and identified significant differences at $P < 0.1$ for all statistical tests.

Results

Vegetation Response

Pretreatment forage production was generally highest in natural openings and lowest among control and treatment sites; random sites were intermediate (Fig. 2). This supported early rationale that forested areas chosen for forage-enhancing treatment were poor forage producers because of their dense forest canopy.

Vegetation response to treatment was greatest in natural openings. The forage production index decreased in response to initial treatment but returned to pre-treatment levels within 4 years. Lengths of unbrowsed twigs increased an average of 17-fold the year after treatment and declined an average of 50 percent/year thereafter. Shrubs in natural openings completely regained their former stature within 5 years post-treatment.

We documented little to no shrub production in the understory of dense forest stands prior to treatment and little shrub response ≤ 6 years following timber harvests. Established shrub communities in natural openings responded quickly to fire treatments. In contrast, forested treatment units did not establish new shrub communities during 2-6 years of monitoring during this study.

Elk Response

We obtained 1199 radio telemetry locations of 69 elk in 1023 groups (543 winter, 480 spring) from 1988 to 1998. Two small (~50 elk) but distinct herds used the treatment area, and we hereafter refer to these as the north herd and the south herd and reported them separately.

Selection for the Treatment Area from within the Herd Home Range

North herd.—The north herd had a 13,287-ha winter home range based on locations of 342 groups. Twenty-four percent of the home range was in the treatment area. Their core winter range was 1046 ha with 53 percent in the treatment area. These elk selected the treatment area over all winters combined ($w = 1.328$, $P = 0.003$), but this varied among time periods (Table 1). North herd elk showed no area preference during either the pre-treatment or post-treatment time periods, and the relative amount of use between the two periods was

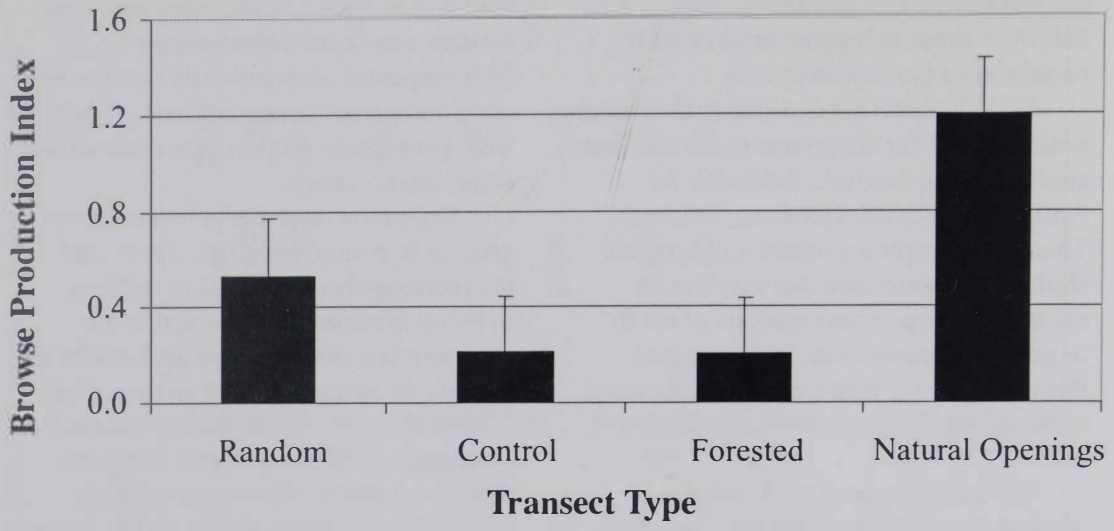

Figure 2. Browse production index ($\bar{x}$ + SE) on random, control and treatment transects on the Firefighter Mountain study area in northwest Montana.

the same ($x^2_1 = 0.07$, $P = 0.785$). These elk also selected the treatment area during the years treatment occurred.

Winter selection for the treatment area by the north herd was negatively correlated with the mean LDSWE ($F_{reg} = 12.6$, $P = 0.010$) (Fig. 3). When LDSWE was < 9, elk selected the treatment area ($w_t = 1.801$, $P = 0.000$, $n = 155$), but this value was exceeded on 48 percent of winter days during our study. When LDSWE was between 9 and 11, elk showed no selection ($w_t = 1.292$, $P = 0.107$, $n = 96$) and used their home range in proportion to availability. When LDSWE was >11, elk selected against the treatment area ($w_t = 0.550$, $P = 0.010$, $n = 91$) and 31

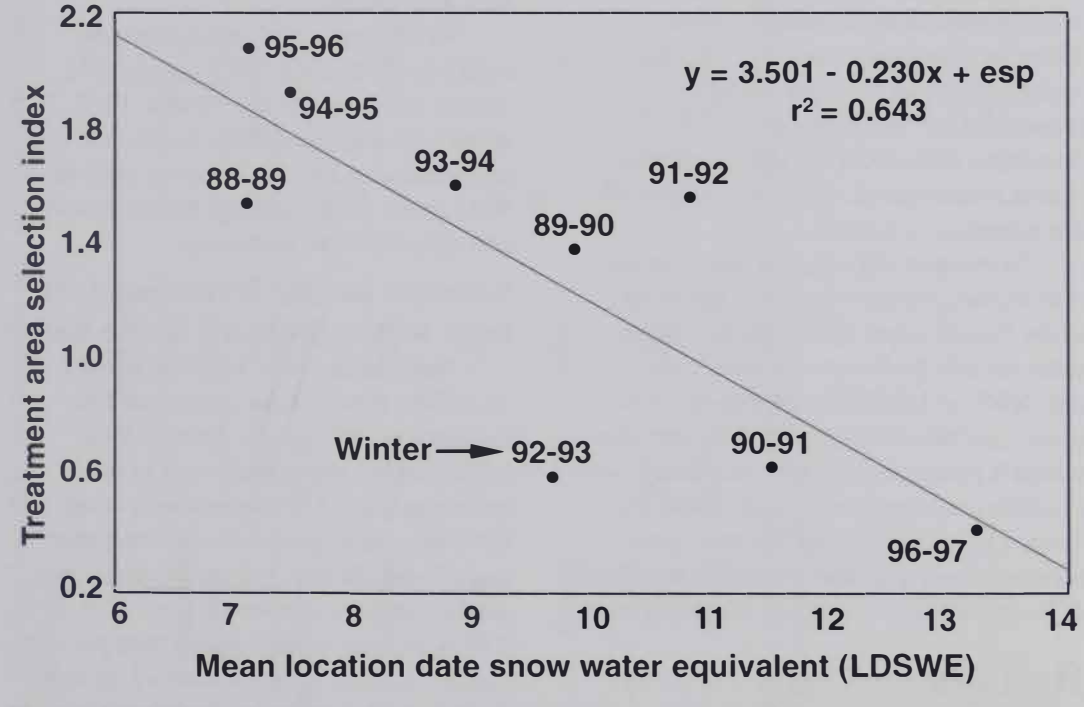

Figure 3. North herd winter selection index by elk for the treatment area as influenced by mean location-date snow water equivalent for winters 1988-89 through 1996-97 on the Firefighter Mountain study area in northwest Montana.

percent of all winter days during our study exceeded this value.

North herd elk responded similarly to snow during both pre-treatment and post-treatment years. Pre-treatment winter 1988-1989 and post-treatment 1995-1996 had the lowest mean LDSWEs ($\bar{x}$ = 7.1 for both), and elk used the treatment area to the same degree each year (x^2_1 = 0.97, P = 0.324). Likewise, we observed highest mean LDSWEs during pre-treatment winter 1990-1991 ($\bar{x}$ = 11.5) and post-treatment winter 1996-1997 ($\bar{x}$ =13.2), and again elk use did not differ between the two (x^2_1 = 0.51, P = 0.477).

In spring the north herd's total and core home ranges were 12,720 and 675 ha, respectively. Twenty-six percent of the total and 64 percent of the core home range was in the treatment area. Over all years elk used the treatment area more in spring than in winter (w^2_1 = 8.87, P = 0.003, Table 1). In the pre-treatment period and during treatment, elk selected the treatment area but showed no preference for it post-treatment. Spring use of the treatment area by elk was less post-treatment than it had been pre-treatment (x^2_1 = 6.31, P = 0.012).

South herd.—We based the south herd's 9608-ha winter home range on locations of 201 groups. Although 33 percent of the total home range was in the treatment area, none of the 926-ha core range included the treatment area. The winter core home range of the south herd was 1.5 km from the treatment area at its nearest point.

The south herd used the treatment area very little in winter. A mean of 14 percent (range = 0-21%) of groups were in the treatment area in winter, and elk selected against it in all winters (Table 1). We had no pre-treatment data for south herd elk because we did not begin trapping these elk until winter 1992. In post-treatment years, 15 percent of south herd groups were in the treatment area. We found no relationship between snow and treatment area selection for the south herd elk (F_{reg} = 0.273, P = 0.623, r^2 = 0.052).

In spring, the total range was 9369 ha with 33 percent in the treatment area. The 900-ha core range was 1.4 km from the treatment area. The south herd elk did not use the treatment area more in spring than in winter (x^2_1 = 2.44, P = 0.119).

Selection for North vs. South Portion of the Treatment Area

North herd.—North herd elk concentrated their use in the northern

Table 2. Selection for the north (2243 ha) vs. south (10598 ha) portion of the treatment area by north herd elk on Firefighter Mountain.

Time Period	Area	Winter			Spring		
		Groups (%)	w^a	P^b	Groups (%)	w^a	P^b
Pre-treatment	North	26 (93)	1.720	0.000	46 (92)	1.704	0.000
	South	2 (7)	0.155		4 (8)	0.174	
During treatment	North	34 (85)	1.574	0.000	38 (93)	1.716	0.000
	South	6 (15)	0.326		3 (7)	0.159	
Post-treatment	North	16 (84)	1.560	0.005	20 (83)	1.543	0.003
	South	3 (16)	0.343		4 (17)	0.362	

[a] Selection Index indicating use less than (<1), greater than (>1), or equal to (=1) habitat availability.
[b] *G*-test of significance (Manley et al. 1993)

Table 3. North herd habitat selection by elk within the treatment area for natural openings (13% of area), logging units (35%) or the remainder of the Firefighter Mountain herd range (52%).

Time Period	Area	Winter			Spring		
		Groups (%)	w^a	P^b	Groups (%)	w^a	P^b
Pre-treatment	Natural Openings	5 (18)	1.374		22 (44)	3.385	
	Uncut Logging Units	6 (21)	0.612	0.278	7 (14)	0.400	0.000
	Remainder	17 (61)	1.168		21 (42)	0.808	
During Treatment	Natural Openings	10 (16)	1.241		18 (31)	2.347	
	Cut Logging Units[c]	5 (8)	0.504	0.000	5 (8)	0.530	0.002
	Uncut Logging Units	27 (44)	2.292		6 (10)	0.535	
	Remainder	20 (32)	0.620		30 (51)	0.978	
Post-Treatment	Natural Openings	4 (21)	1.619		7 (29)	2.244	
	Cut Logging Units	5 (26)	0.752	0.542	7 (29)	0.833	0.112
	Remainder	10 (53)	1.012		10 (42)	0.801	

[a] Selection Index indicating use less than (<1), greater than (>1), or equal to (=1) habitat
[b] *G*-test of significance (Manley et al. 1993)
[c] Cut Logging Units = 16% of the area, Uncut Logging Units = 19%

portion of the treatment area throughout the study irrespective of the fact that treatment units were concentrated in the southern portion of the treatment area. Ninety percent ($n = 47$) of the north herd groups located in the treatment area were in the north portion during each time period (Table 2). The north herd's winter use of the north and south portions of the treatment area did not differ pre- vs. post-treatment ($x^2_1 = 0.89$, $P = 0.345$). In spring north herd elk selected the north portion (Table 2), and we detected no difference in the amount of pre- vs. post-treatment use ($x^2_1 = 1.26$, $P = 0.261$).

South herd.—South herd elk showed no preference for either portion of the treatment area ($w_{north} = 0.784$, $w_{south} = 1.254$, $P = 0.230$, $n = 27$). During all years combined, 56 percent of winter ($n = 27$) and 73 percent of spring groups ($n = 33$) were located in the south half of the treatment area.

Selection for Treatment Types within the Treatment Area

North herd elk using the treatment area in winter did not select from among natural openings, logging units, or the remainder of the treatment area during either pre- or post-treatment years (Table 3). However, during the years in which units were treated, elk selected for uncut areas scheduled for future treatment (uncut logging units). In spring elk selected natural openings pre-treatment and during treatment, and a small sample ($n = 24$) showed a similar tendency post-treatment (Table 3). Among north herd elk not associated with natural openings, there was no difference in distribution pre- vs. post-treatment during either winter or spring ($x^2_1 = 0.23$, $P = 0.630$ and $x^2_1 = 1.39$, $P = 0.256$ respectively). The small number of south herd groups using the treatment area and the lack of pre-treatment data precluded this analysis for the south herd.

Table 4. Distance of elk to nearest treatment unit pre- vs. post-treatment during winter and spring for north herd elk groups in the Firefighter Mountain treatment area.

Season	Treatment Type	Pre/Post Treatment	Distance (m) $\bar{x}$ ± 1SE	n	t - test P
Winter	Natural Opening	Pre	286 ± 41	17	0.448
		Post	224 ± 66	6	
	Logging Units	Pre	202 ± 75	11	0.485
		Post	266 ± 52	13	
Spring	Natural Opening	Pre	129 ± 33	24	0.229
		Post	210 ± 66	12	
	Logging Units	Pre	232 ± 42	26	0.871
		Post	219 ± 62	12	

Other Potential Responses

Lack of response by elk to habitat treatment was also evident from the distance between north herd elk groups and the nearest unit (Table 4). We found no difference in the distance to the nearest treatment unit in either winter or spring.

An alternative explanation to the lack of elk response might be that vegetation within treatment units did not have adequate time to develop post-treatment. To evaluate this possibility, we looked for a response by elk in only the 10 units that had developed shrub canopies > 15 percent and when SWE was < 11. Results of x^2 analyses showed no significant difference from all other areas in pre-treatment (n = 70 locations) during treatment (n = 34 locations) or post-treatment (n = 43 locations) time periods (P > 0.2).

Discussion

Snow depth greatly influenced elk habitat use in our study area where high snowfall (>1 m) was common. Typical winter ranges for elk in Montana are more open, grass-dominated, and receive and retain less snow compared to our study area. Snow depths at sites where elk had foraged on Firefighter Mountain during the 1997 winter averaged 89 cm and were 2 to18 times that measured on five other Montana and Wyoming winter ranges that received measurable snow (Pils et al. 1999). There was no measurable snow on these other ranges during 20 percent of the sampling periods.

The regression presented in Figure 3 suggested that excessive snow depths during 31 percent of the winter days during our study precluded the north herd from using treatment areas. Use of the treatment area by south herd elk was not influenced by snow because none of their core home range occurred in the treatment area. Elk shifted their distribution in response to changing snow depth, but neither herd responded to utilize habitat modified by the treatments. This suggested that snow depth, as influenced by forest canopy cover, was a primary driver of winter elk distribution and habitat use in this area.

In addition to snow intercept, conifer stands also provide forage. Conifers and associated arboreal lichen are important winter forage for elk in northwest Montana (Jenkins 1985, Jenkins and Wright 1987, Baty 1995). Jenkins (1985) and Baty (1995) considered conifers a winter dietary staple. Gaffney (1941) documented

heavily browsed lodgepole pine stands on elk winter ranges in the South Fork of the Flathead River in 1935-1937 prior to forest successional changes resulting from fire suppression. On Firefighter Mountain 33 percent of the elk winter diet included lodgepole pine, Douglas fir, and Pacific yew (J. Vore, P. R. Malta and E. Schmidt 1995, unpublished report). Nutritional quality of this diet was as good or better than that on grass winter ranges in Montana and Wyoming (Pils et al. 1999). Removal of the overstory also lowered availability of arboreal lichen. Stevenson (1979) found that even selective logging reduced lichens by 75 percent.

We documented no increase in use of treatment units in the Firefighter Mountain study area. Habitat use was regulated by deep snow conditions that persisted from late winter into early spring. By the time snow had melted and vegetation was readily available, elk had moved on to spring calving ranges leaving inadequate data to evaluate late spring or early summer use within treatment areas.

Management Implications

In deep snow environments where elk habitat use is influenced by snowfall, treatments intended to increase winter forage production at the expense of forest canopy cover may not be warranted. Thus, managers should explore silvicultural options that increase understory production but maintain snow intercept and forage including availability of coniferous browse and lichen production. These habitat conditions seemingly are key to maintaining higher elk densities through winter in a portion of the northern Rocky Mountains, such as northwest Montana, that typically receives a majority of its annual precipitation in the form of snow during winter.

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