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 migrations 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., boulders 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 consequences (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

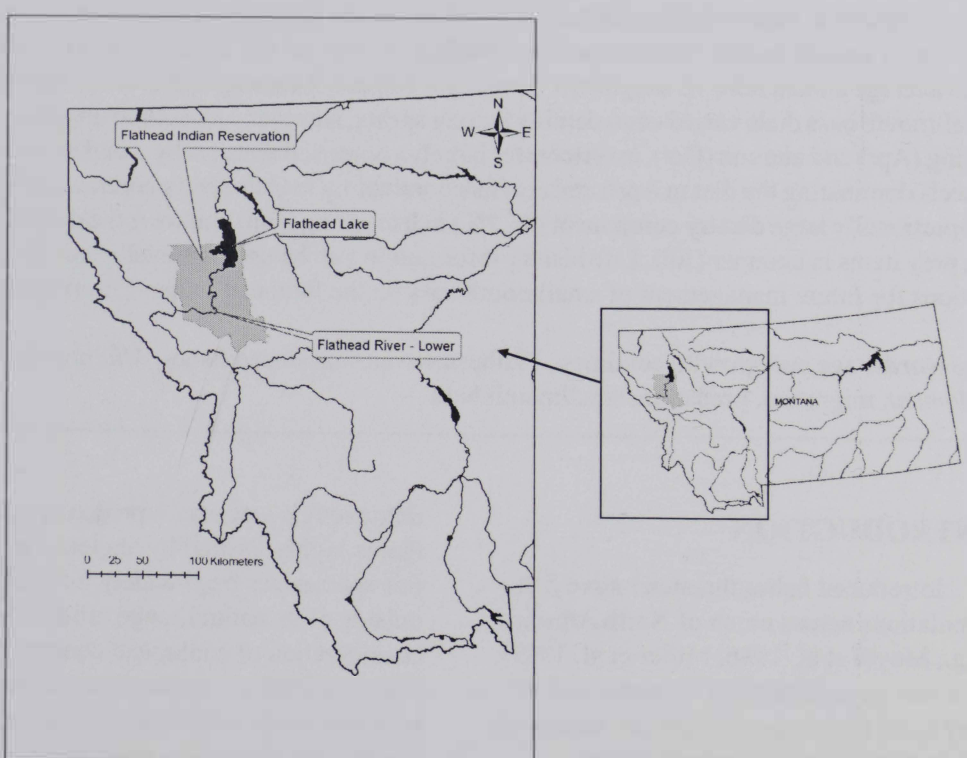

Figure 1. Map of Montana showing the location of the lower Flathead River, Flathead Lake, and Flathead Indian Reservation.

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.

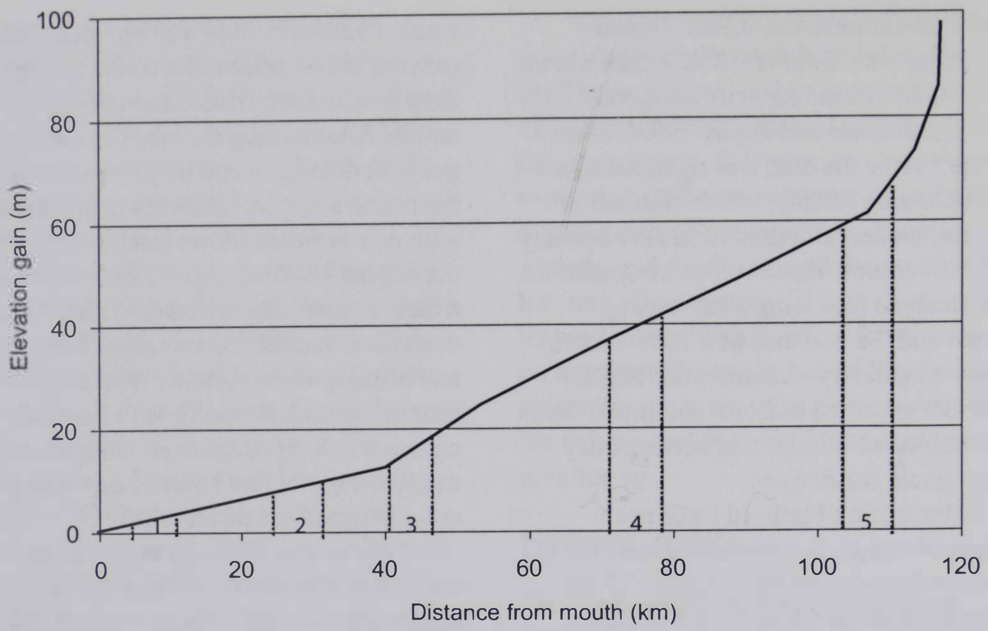

Figure 3. Longitudinal profile of the lower Flathead River, Montana, with locations of sample sections indicated by dashed lines.

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's 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 surgeries, 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 also 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 Computer Corp. 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 types 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 sections. We typically sampled once each spring and autumn in all sections, although we sometimes were unable to sample all five sections each season. We measured (TL; mm), weighed (g), and released all smallmouth bass 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 fish 150 mm TL or longer (relative weight [W_r]; Kolander et al. 1993, Anderson and Neumann 1996), and catch-per-unit-effort indices (CPUE; fish/h). We calculated CPUE 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 Mission Creek (Fig. 2). Relatively large numbers of juvenile salmonids move from these spawning tributaries into the Flathead River during spring and early summer, with a second 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) catostomids; (7) ictalurids; (8) salmonids; 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.

Results

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 was 356 mm (range = 290-445 mm) and median weight was 676 g (range = 380–1620 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 locations for an individual fish was 16 (range = 4-38). Median number of days at large was 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

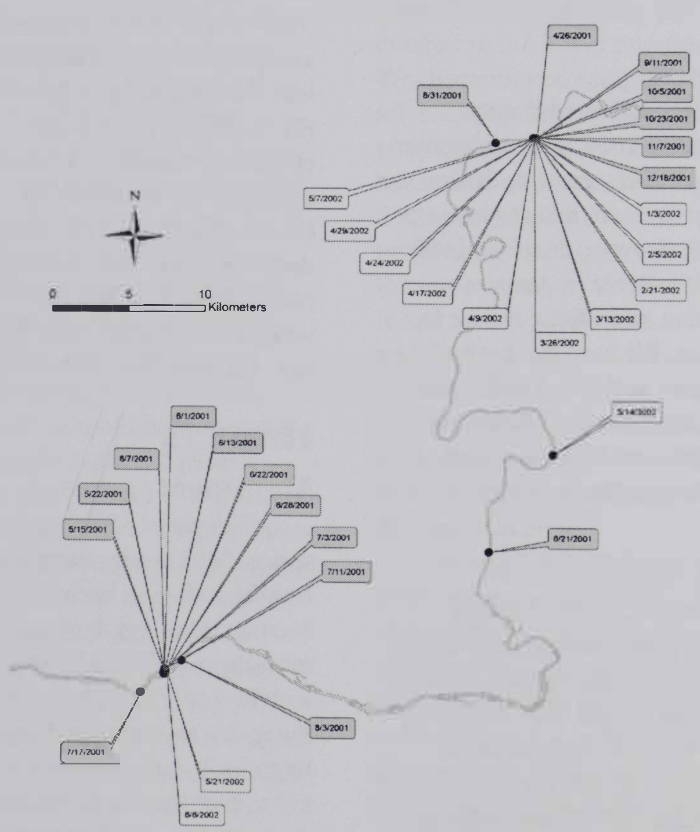

Figure 4. Example of extensive migratory behavior displayed by radio-tagged smallmouth bass (fish 149.70026) in the lower Flathead River, Montana.

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

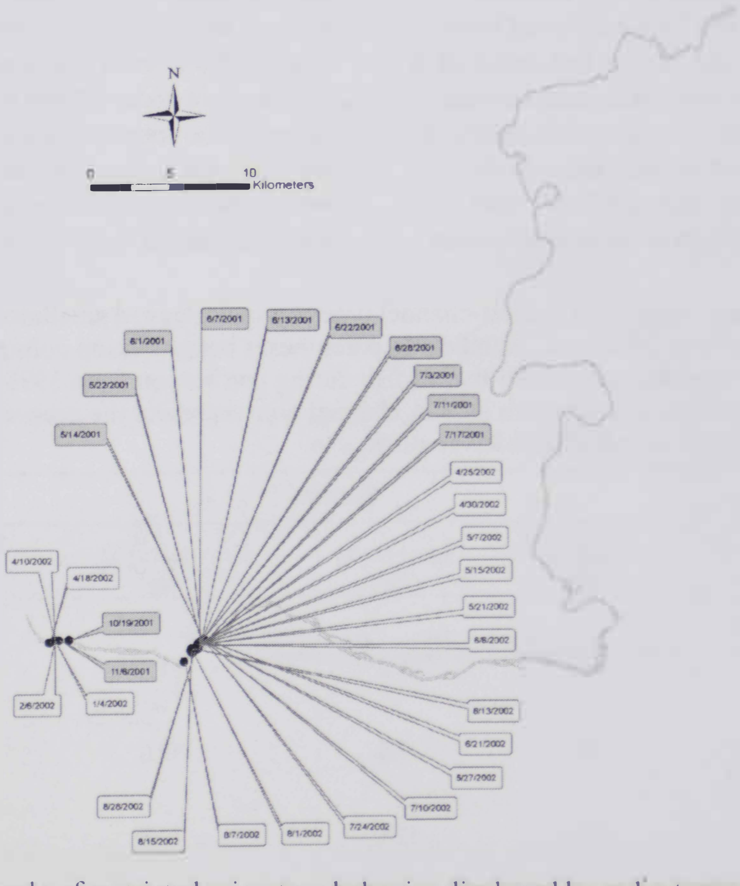

Figure 5. Example of restricted migratory behavior displayed by radio-tagged smallmouth bass (fish 149.70033) in the lower Flathead River, Montana.

temperatures ranged from ~ 13 to 20 ºC. 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 ºC. 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 ºC. 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

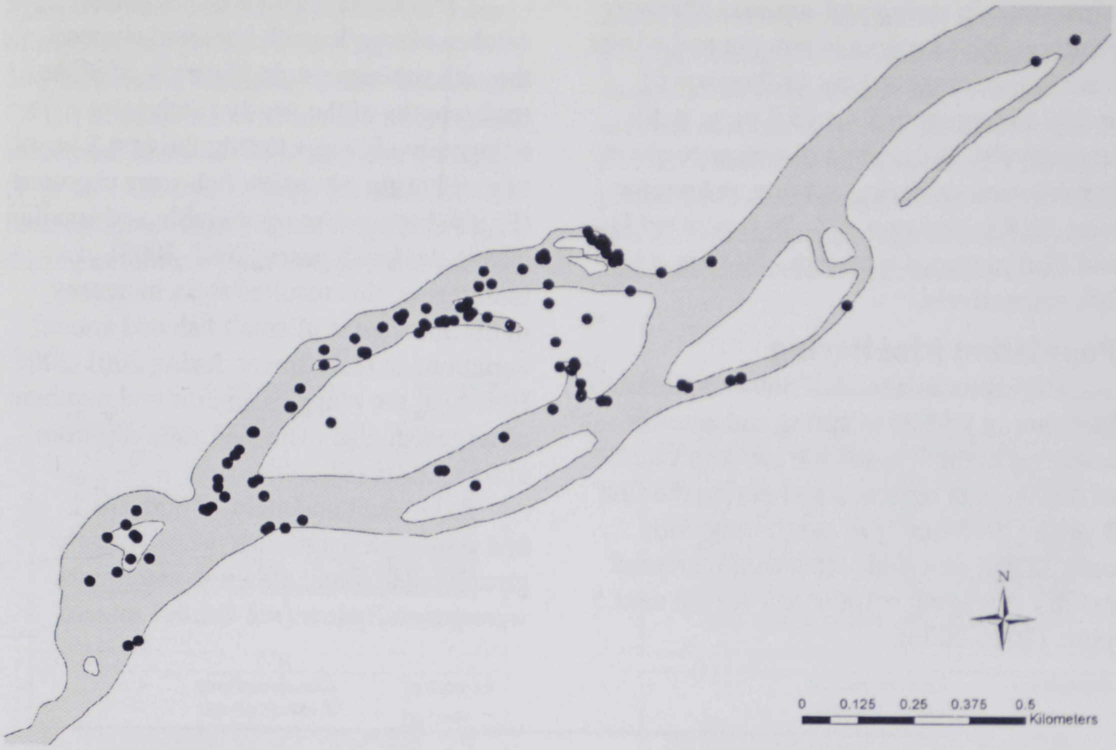

Figure 6. Example of the use of typical smallmouth bass spawning habitat in a braided reach of the lower Flathead River (rkm 11-14), Montana, by radio-tagged smallmouth bass. Dots indicate individual fish locations from 1999 to 2003.

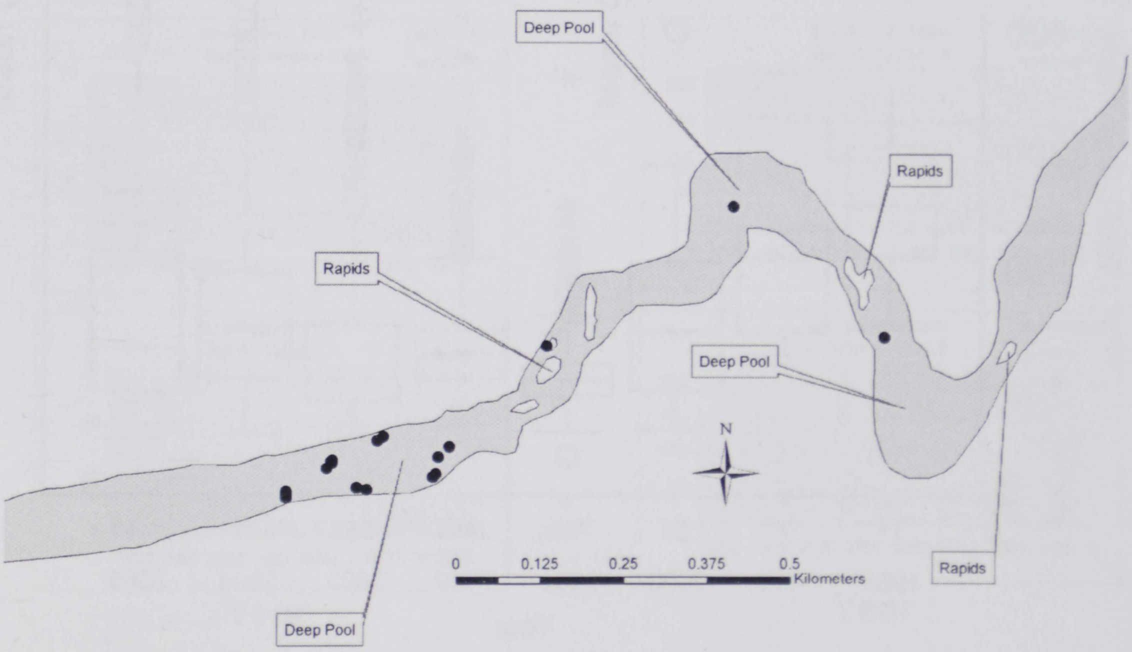

Figure 7. Example of the use of typical smallmouth bass overwintering habitat in a deep section of the lower Flathead River (rkm 110-112), Montana, by radio-tagged smallmouth bass. Dots indicate individual fish locations from 1999 to 2003.

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

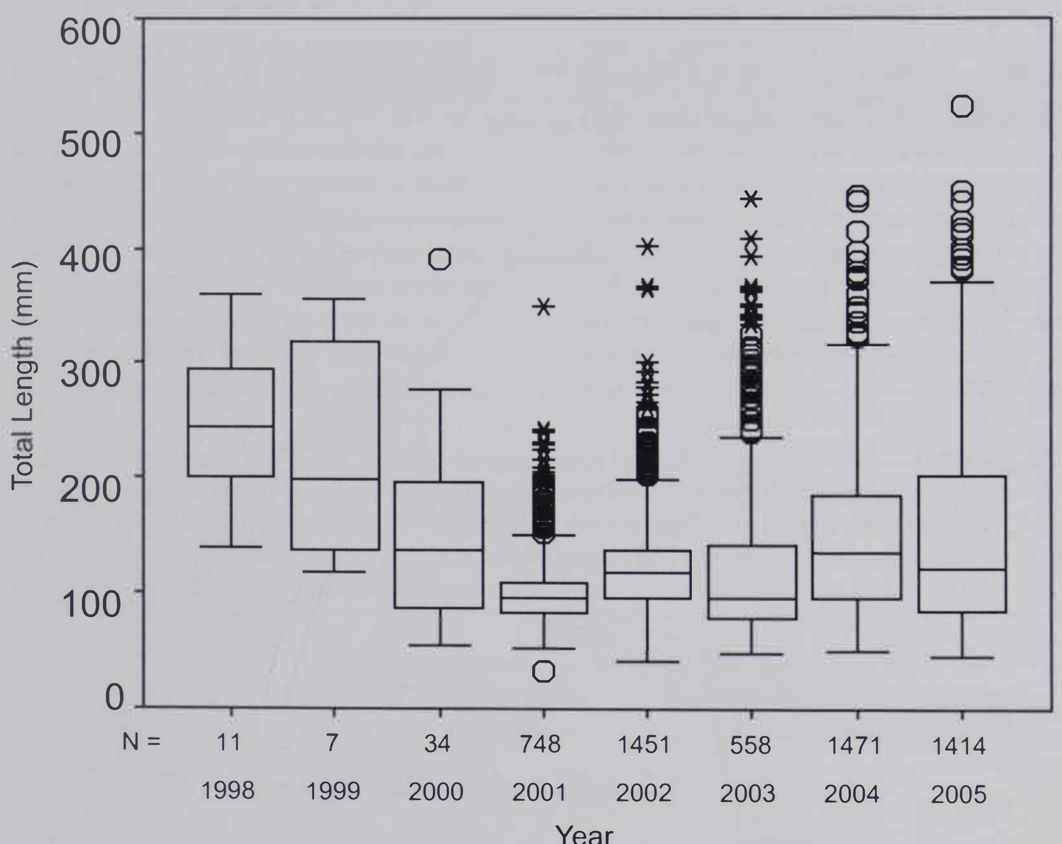

Figure 8. Box plots of the total lengths (TL) of smallmouth bass captured each year in the lower Flathead River, Montana, during eight years (1998-2005) of monitoring. The box corresponds to the interquartile (IQR) range of TL and the median TL is represented by a line through the box. Whiskers show 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

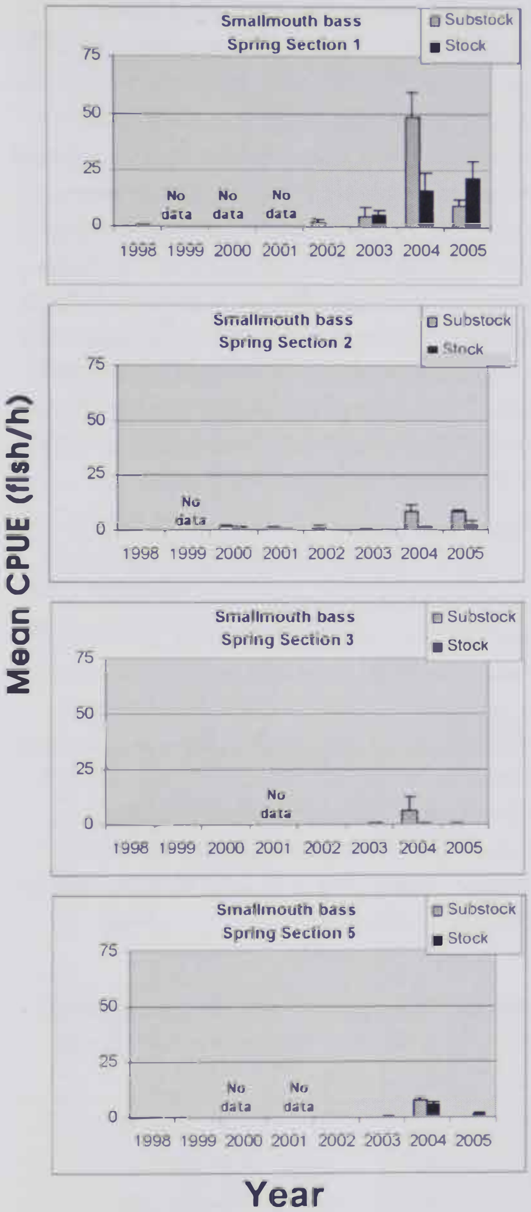

Figure 9. Mean catch per unit effort (CPUE; fish/h) of smallmouth bass during spring in four study sections of the lower Flathead River, Montana, 1998-2005. Vertical lines are one standard error. Note: section 4, where we discontinued sampling in 2002, is not shown.

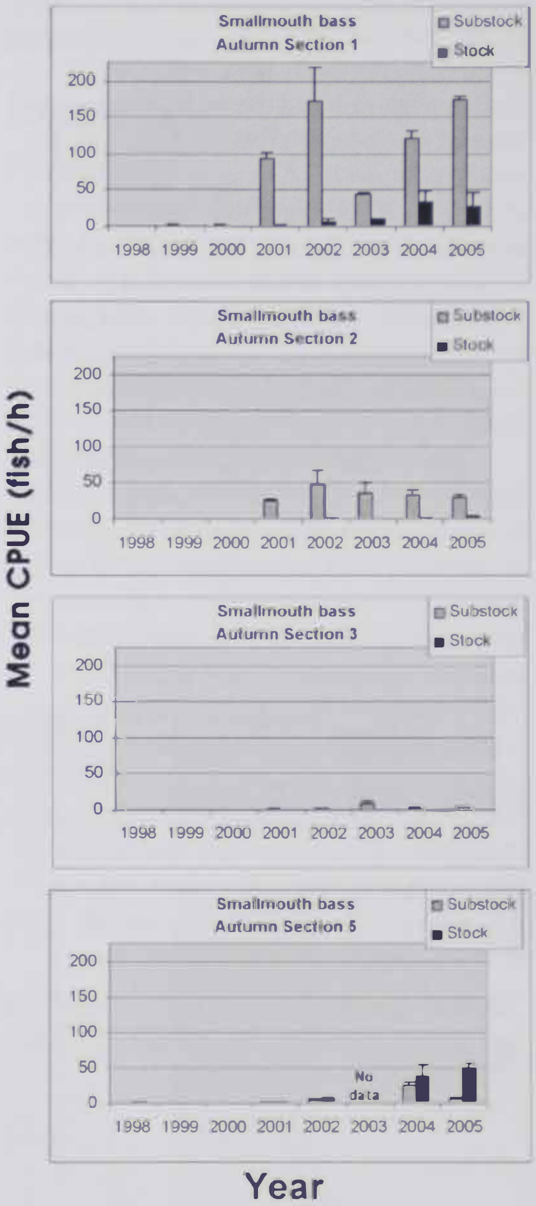

Figure 10. Mean catch per unit effort (CPUE; fish/h) of smallmouth bass during autumn in four study sections of the lower Flathead River, Montana, 1998-2005. Vertical lines are one standard error. Note: section 4, where we discontinued sampling in 2002, is not shown.

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,

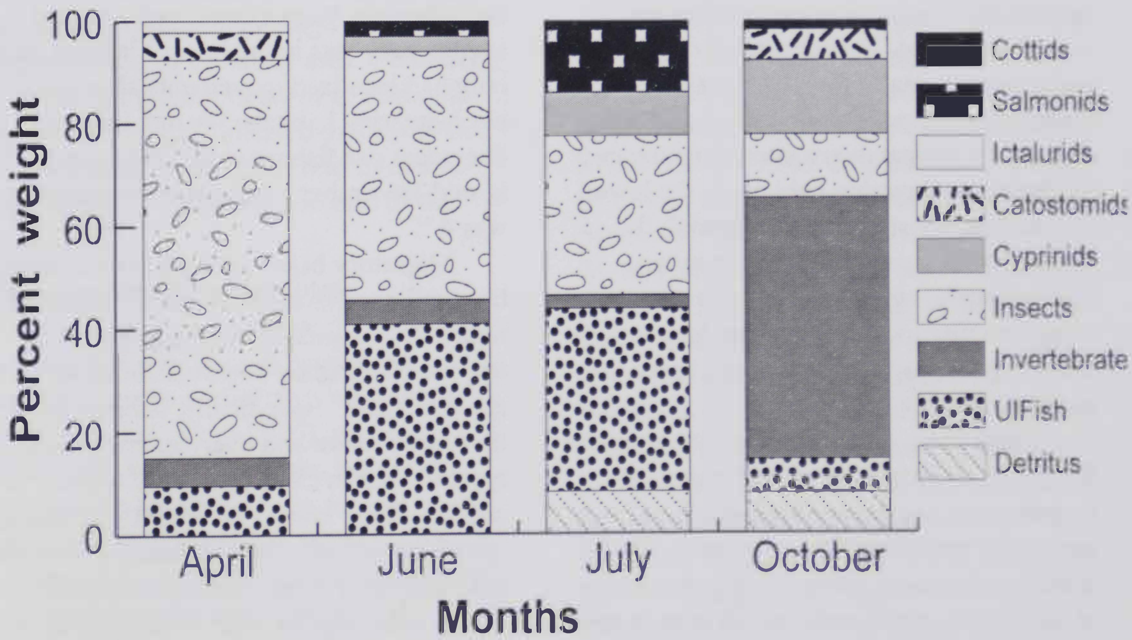

Figure 11. Monthly diet composition (percent by weight) of smallmouth bass 150 mm TL or longer in the lower Flathead River, Montana.

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 ºC. They initiated movements to overwintering locations when mean daily water temperatures were around 17 to 23 ºC. 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 ºC. 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 ºC 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 ºC 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 ºC.

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 °C. 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 °C; Coutant and DeAngelis 1983), they frequently exceed 20 °C 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 °C for 16-38 days depending on longitudinal stream position during the summer. In contrast, average daily temperatures in our study area exceeded 20 °C an average of 47 days (range = 20-66) during 2000-2004. Our scale data

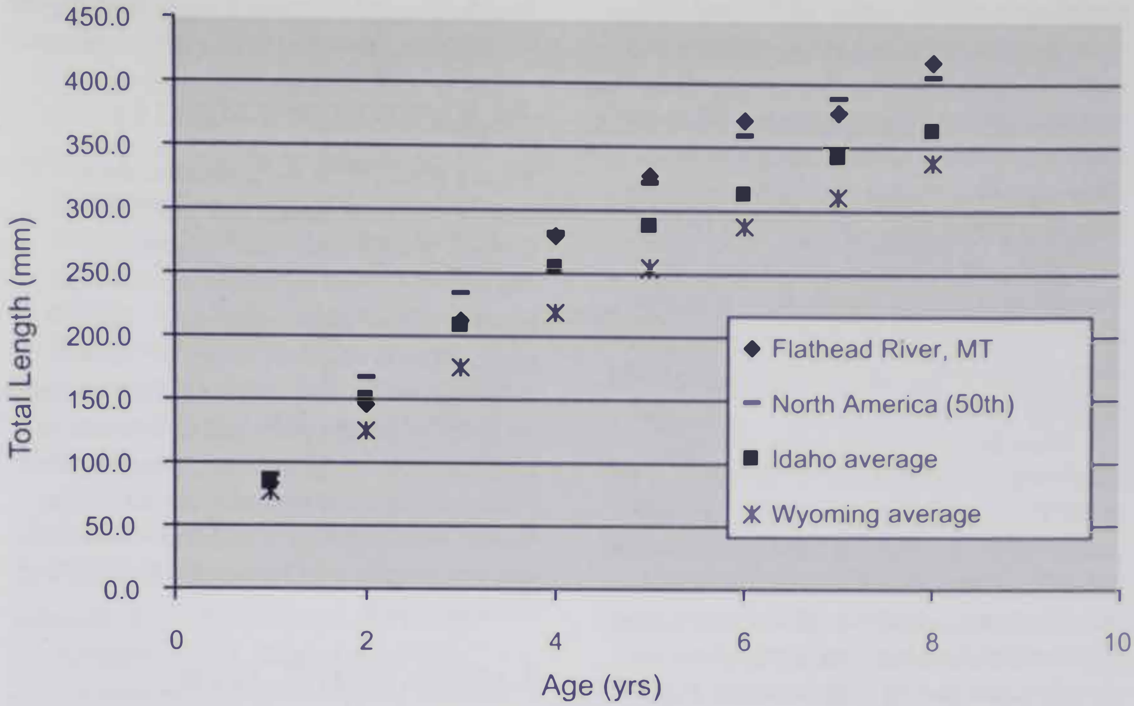

Figure 12. Average back-calculated total lengths at age for smallmouth bass in the lower Flathead River, Montana, and for populations in the Rocky Mountain states of Wyoming and Idaho and the median total length at age for populations across North America (Beamesderfer and North 1995).

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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