University of Alberta

Fall and Winter Movements of Arctic grayling (*Thymallus arcticus* (Pallas)) in the Little Smoky River, Alberta

by

Slawomir S. Stanislawski ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

Fall and winter movements of Arctic grayling from a 78 km reach of a river system were evaluated using radiotelemetry. The movements of 30 fish were monitored weekly from August 31 to November 16, 1993 and biweekly from November 16, 1993 to January 15, 1994. The mean total distance moved by the fish was 49.06 km and mean net distance moved was 23.54 km. Overall, the fish exhibited a downstream migration in fall and winter. Direction and amount of movements were different for the fish from upper study reaches as compared to the fish from middle study reaches. During overwintering migration from August 31 to October 19, most of the fish (46 - 73%) that showed movement between observations were moving downstream. The peak mean movement rate of 1.52 km/day was reached by September 21 as water temperatures and flows were decreasing. The migration subsided after October 19 as minimum water temperature reached 0.0°C for the first time on October 20. From October 19 to January 15, most of the fish (39 - 63%) that showed movement between observations were moving upstream. The fish did not stop moving after freeze-up. Consequently, overwintering grounds were not located in specific or restricted areas of the river. The mean length of overwintering ground was 2.98 km. The mean gradient in overwintering ground was in the 0.17 - 0.18% range.

ACKNOWLEDGMENTS

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INTRODUCTION

In lotic environments that do not dewater in winter, Arctic grayling (*Thymallus arcticus* (Pallas)) fall and winter movements are not influenced by loss of habitat. In these areas, overwintering movements of Arctic grayling may vary between distant reaches of a drainage depending on relative proximity of suitable overwintering habitat. However, little research has been done in this area.

Arctic grayling undergo extensive migrations to overwintering habitats (Craig and Poulin 1975; Tack 1980; Krueger 1981; Armstrong 1986; West *et al.* 1992). However, the timing and extent of fall migration of *T. arcticus* are poorly understood. This is especially true in drainages where fish are not excluded by ice in winter. From the limited number of studies done on overwintering of Arctic grayling in Alaska, one would expect that starting in September, these fish would migrate into springs, or larger river systems where there is higher potential for deep pools and connected lakes (Armstrong 1986; Hop *et al.* 1986; West *et al.* 1992). In Alaska, Arctic grayling migrate up to 101 km during the fall (Barber *et al.* 1985; Hop *et al.* 1986; West *et al.* 1992). However, movement this large might result from Alaskan streams freezing to the bottom in winter. In these streams, Arctic grayling migrate either upstream or downstream into overwintering sites that have input of ground water (Tack 1980; Armstrong 1986; West *et al.* 1992). In larger rivers, grayling inhabiting the upper reaches and tributaries migrate downstream to overwinter in deeper water of the main stem (Ward 1951; Tack 1980; Armstrong 1986). Grayling also overwinter in lakes, and may migrate upstream or downstream to reach them (Ward 1951;

Tack 1980; Armstrong 1986).

The problems that we face in studying Arctic grayling overwintering migrations stem from the fact that the natural range of grayling extends to areas with severe winter climates. Locating fish under ice, slush, and snow in sub zero temperatures can prove challenging both for investigator and for equipment.

The timing of Arctic grayling migration to overwintering sites appears to be influenced by dropping water temperatures and decreasing flows (Craig and Poulin 1975; Krueger 1981). Arctic grayling must migrate to their overwintering sites before streams become impassable due to low flows and ice buildup (Krueger 1981). In many drainages Arctic grayling can have a very limited winter distribution as a result of reduction in availability of suitable habitat. Many smaller streams and most of the summer rearing streams can freeze to the bottom in winter (Krueger 1981). It is likely that Arctic grayling would generally spend the winter in any place where sufficient depth and flow of water prevents the danger of freezing to the bottom (Ward 1951). Grayling have been observed to overwinter in beaver dams, in and near springs, in lakes, in open pools associated with springs and in very deep pools of ice covered streams and rivers (Ward 1951; Krueger 1981; West *et al.* 1992). Their relatively high tolerance for low dissolved oxygen levels also gives Arctic grayling an improved chance of overwintering under ice in lakes and isolated pools (Bendock 1980; Krueger 1981). Critical oxygen minima are from about 1.4 mg/l at 8°C to 1.8 mg/l at 20°C for grayling acclimated to 13°C (Hubert *et al.* 1985).

Arctic grayling winter distribution may also be limited by competitors and predators rather than by lack of suitable habitat. They appear to be generalists in terms of habitat and are displaced from different habitats by more specialized fish species. Arctic grayling may be poor competitors with other salmonids because their numbers tend to decline whenever rainbow trout (*Oncorhynchus mykiss* (Walbaum)), brook trout (*Salvelinus fontinalis* (Mitchill)) or brown trout (*Salmo trutta* Linnaeus) have been introduced (Bishop 1967; Liknes and Gould 1987).

Arctic grayling have different habitat requirements for spawning, summer rearing, and overwintering. Furthermore, different life stages (embryo, fry, juvenile, and adult) require different types of habitat that may or may not exist within a single stream or drainage. It is for these reasons that Arctic grayling populations can exhibit lengthy migrations and actually use a variety of streams and stream habitats over their life time.

The use of radio telemetry allows for the evaluation of fish migration independent of water or ice cover over the fish by permitting the observer to obtain a temporal series of locations of individual fish. While there remain certain technical limitations on the use of such systems (signal attenuation resulting from depth, distance, obstacles, etc.), radio telemetry is the most effective means of obtaining information about the activity of free-living fish (Kaseloo *et al.* 1992) and the only way to obtain this information on fish under ice cover.

The extent of fall migrations of Arctic grayling in Alaska were successfully determined using radio telemetry (West *et al.* 1992). They found grayling migrating up to 101 km to their overwintering grounds in deep pools, lakes and areas of year round ground water discharge. Migration rates peaked at 5-6 km/day in early September and reached near zero by November.

A significant statistical limitation in using radio telemetry is the lack of true replication in repeated observation of locations of the same fish (pseudo replication). However, there are some strengths as well. There is a commitment to a fixed number of fish and data from all fish is accepted equally. One should also be able to account for every fish initially tagged.

The use of a Global Positioning System (GPS) permits precise tracking of radio tagged fish by assigning latitude and longitude to fish locations with 1-5 meters accuracy (with differential correction). GPS is a satellite-based positioning system operated by the U.S. Department of Defense. GPS consists of space, control and user segments. The space segment has up to 24 satellites orbiting earth every twelve hours at an altitude of about 20,200 km which constantly transmit radio signals. The control segment consists of four ground-based monitor stations, three upload and one master control station. These stations track the satellites and calculate their ephemeris and clock correction coefficients. The user segment consists of various civilian and military GPS receivers.

GPS satellites transmit two radio signals called L1 and L2. The L1 signal is at 1575.42 MHz and the L2 is at 1227.60 MHz. L1 signal is modulated with the Precision (P) code which may be encrypted for military use, and the Coarse / Acquisition (CA) code which is not encrypted. The L2 signal is modulated with Precision code only. The L1 signals emitted by the GPS satellites are the only ones that are available for civilian use.

Modern GPS receivers can provide horizontal locations to within 100 meters. However, when used in combination with a ground base station, one can get horizontal location accurate to within 1-5 meters. The ground base station calculates and records the error in the GPS receiver's locations by knowing the exact location of the station and comparing it to the locations received from GPS satellites used at any given time. GPS locations can be combined with digitized maps and appropriate Geographic Information Systems (GIS) software to accurately map fish movements because GIS maps are geo-referenced in the same way as the GPS locations.

The Little Smoky River is home to the most productive southern Arctic grayling population in Alberta, and it is experiencing increasing angling pressure. This is the result of enhanced angler access as new roads are constructed due to increasing logging and oil-gas exploration in the area. In 1989, the upper 170 km of the river, which contains an abundant Arctic grayling population, was designated catch-and-release (no harvest). In the next lower 50 km, an angler could take two fish a day from June 16 to October 31 of each year. In 1996, the catch-and-release section of the river was extended further 25 km downstream.

The population of Arctic grayling in the Little Smoky River was of concern to fishery managers due to the large number and size of Arctic grayling found there, the increasing angler pressure, and the increasing human development in the area. No information existed on timing and extent of migrations or the location of overwintering grounds. The use of GPS and GIS proved invaluable in studying extensive fall and winter movements of *T. arcticus* over a large and inaccessible drainage like the Little Smoky. The location of overwintering grounds can also be readily determined when locations of radio tagged fish in winter are geo-referenced with GPS and GIS.

As winter approaches, large rivers like the Little Smoky might offer the only suitable overwintering habitat in a watershed. They tend to have more deep pools available and do not freeze to the bottom as much as smaller streams and tributaries. Fall migratory routes are also likely to remain open for longer periods of time since freeze-up usually starts in smaller tributaries and beaver dams which block migration are less likely to persist in larger rivers. Therefore, in larger rivers, Arctic grayling inhabiting the middle to upper reaches and tributaries during summer migrate downstream to overwinter in deeper water of the main stem (Ward 1951; Tack 1980; Armstrong 1986). Kamchatkan grayling (*T. a. mertensi*) were also found migrating into main rivers in autumn (Skopets and Prokop'yev 1990).

In this study, I tested the following hypothesis: as water temperatures and flows decrease in fall, Arctic grayling from distant reaches of the Little Smoky River migrate downstream to overwinter in pools that do not freeze to the bottom in winter. In testing this hypothesis, I determined the timing and extent of fall migration of Arctic grayling in the Little Smoky River and located overwintering sites in the drainage.

STUDY AREA

The Little Smoky River is located in north-west central Alberta and flows for about 550 km from its origin in the foothills of the Eastern Slopes of the Rocky Mountains (53° 51' N, 118° 21' W) to its confluence with the Smoky River. The study section extended from 54° 07' 59" N; 117° 51' 04" W to 54° 37' 24" N; 117° 06' 04" W, a distance of 215 km along the river (Figure 1). The study area is characterized by rolling terrain and boreal forest with extensive meadows and muskeg areas along the river. Summer range of Arctic grayling extends from the upstream end of the study section to the confluence of Tony Creek. Besides grayling, the river contains other sport fish which include bull trout (*Salvelinus confluentus* (Suckley)), mountain whitefish (*Prosopium williamsoni* (Girard)), northern pike (*Esox lucius* Linnaeus) and walleye (*Stizostedion vitreum vitreum* (Mitchill)). However, northern pike and walleye are mostly found downstream of the confluence with Tony Creek.

The habitat conditions for Arctic grayling appear to be different between the upper, middle, and lower parts of the study section. The average gradient in the study section is 0.21 %. However, atypical of normal gradient profiles, Arctic grayling upstream of site 3 are found in 0.19 % gradient whereas the gradient from site 3 to confluence of Tony Creek is 0.29 %. The latter part of the river is relatively shallow, wide and faster flowing with extensive cascade and riffle areas. Tony Creek's contribution to the Little Smoky River flow ranges from about 10 % to 15 % during open water season. Downstream of its confluence, the lower part of the study section has 0.16 % gradient and it is characterized by deep and highly meandering channel. Spring break-up of the river usually

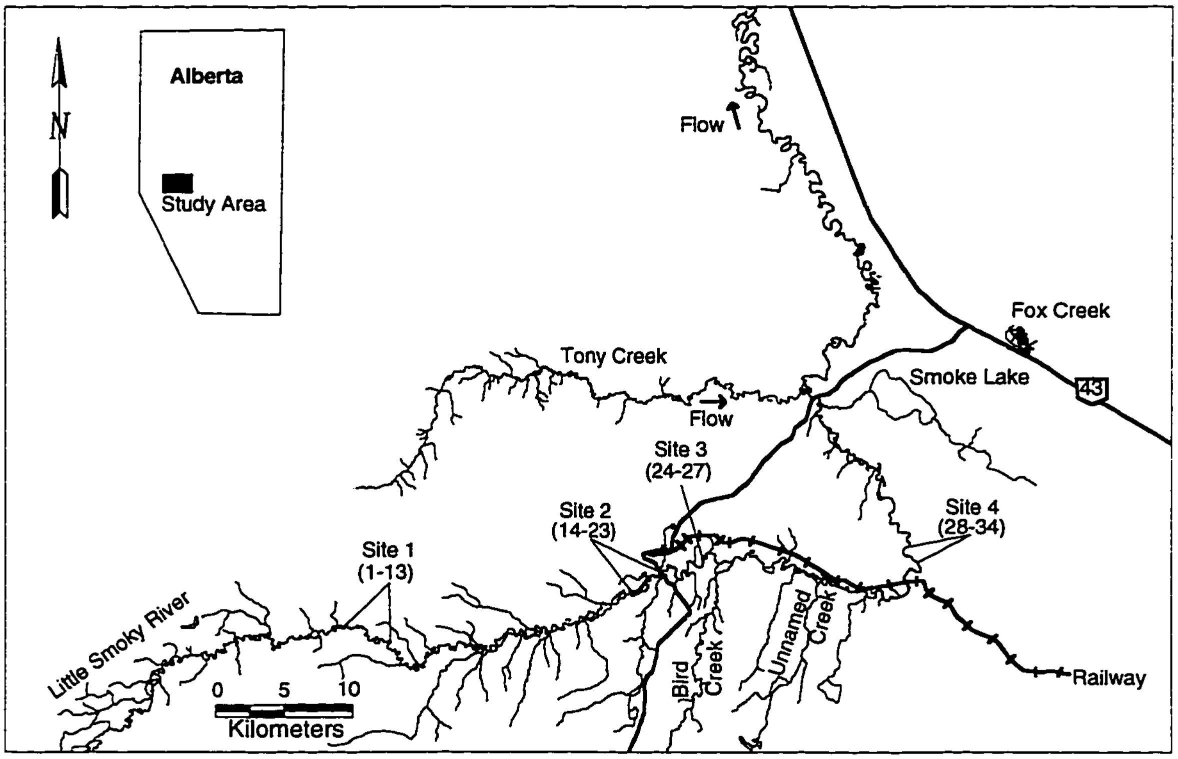

Figure 1. Map of the study section of the Little Smoky River, Alberta from 54° 07' 59" N; 117° 51' 04" W to 54° 37' 24" N; 117° 06' 04" W. The four capture / release sites of 34 radio tagged Arctic grayling are shown as a point (Site 3) or reaches along the river. The corresponding identification numbers of fish tagged and released at each of the sites are shown in parentheses. Fish were radio tagged from August 17 to November 3, 1993 and monitored from August 31, 1993 to January 15, 1994.

takes place in mid April and starts in the highest gradient, middle part of the study section. Freeze-up occurs from late October to early November. However, complete freeze-up of the middle part of the study section can take until the end of November.

The mean annual (March - October) discharge can vary from about 10 m^3/sec. to about 40 m^3/sec (Figure 2), based on historic data (1968-96) from Environment Canada water gauging station No. 07GG002 located 13.5 km downstream of the study section (54° 44' 24" N, 117° 10' 46" W). The maximum mean monthly discharge of 46.4 m^3/sec. occurs in May (Figure 3), based on historic data (1967-96) from the same station. The mean monthly discharge drops from 20.9 m^3/sec. in August to 3.7 m^3/sec. in March, decreasing the overall habitat available to the fish during fall migration and during the winter. In 1993, the mean monthly water discharge was below historic levels until August (Figure 3). However, from August to October, the monthly water discharge was similar to historic levels (Figure 4). Discharge data were not possible to obtain for flows after October due to freeze-up at the Environment Canada water gauge.

Figure 2. Mean annual (March - October) water discharge (m^3/sec.) in the Little Smoky River, Alberta. The water discharge was based on historic data (1968-96) from Environment Canada water gauging station No. 07GG002 located 13.5 km downstream of the study section at 54° 44' 24" N, 117° 10' 46" W.

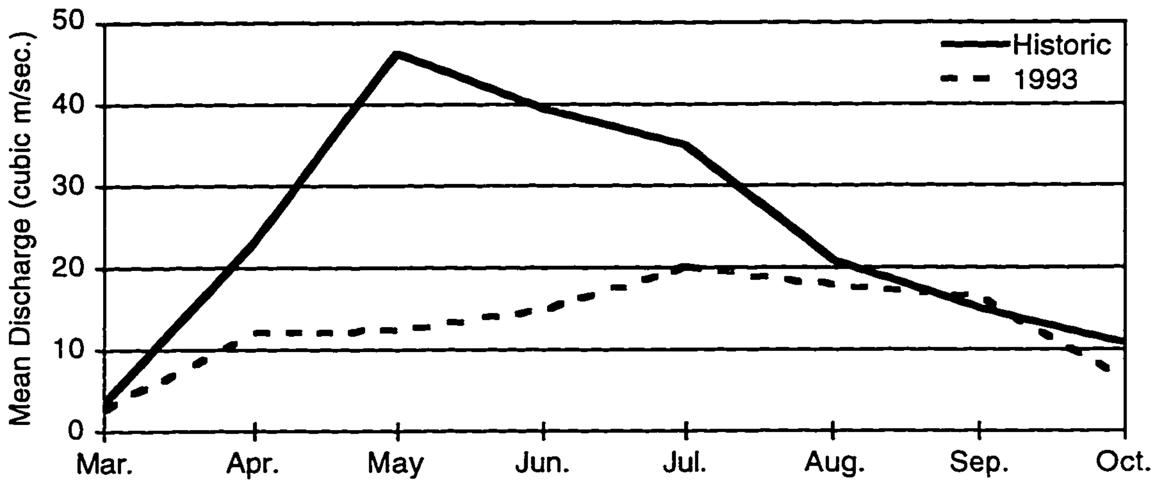

Figure 3. Mean historic and 1993 monthly water discharge (m^3/sec.) in the Little Smoky River, Alberta. The mean monthly water discharges were based on March - October historic data (1967-96) from Environment Canada water gauging station No. 07GG002 located 13.5 km downstream of the study section at 54° 44' 24" N, 117° 10' 46" W.

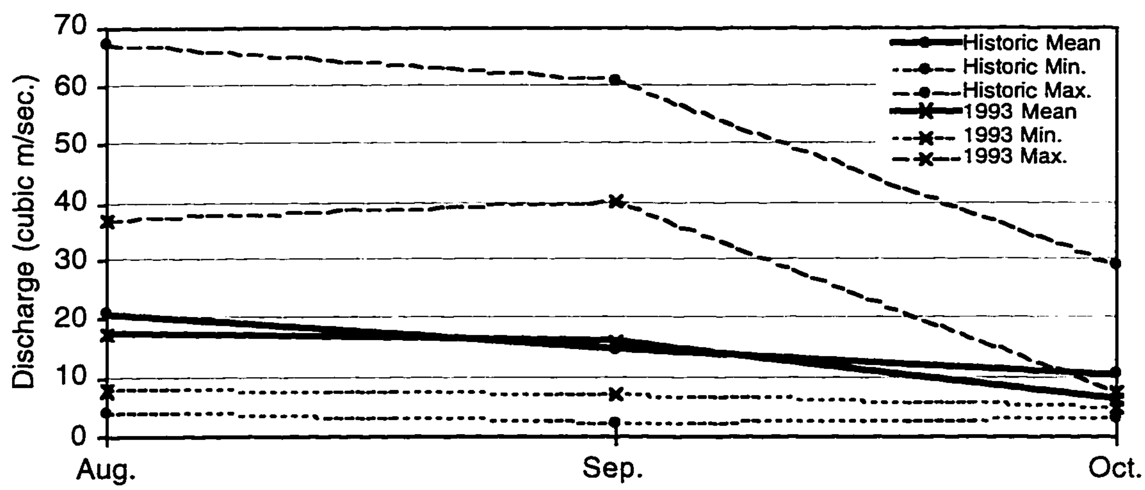

Figure 4. Historic mean, minimum, and maximum as compared to 1993 mean, minimum, and maximum monthly (Aug. - Oct.) water discharge (m^3/sec.) in the Little Smoky River, Alberta. The monthly water discharges for the period were based on historic data (1967-96) from Environment Canada water gauging station No. 07GG002 located 13.5 km downstream of the study section at 54° 44' 24" N; 117° 10' 46" W.

METHODS

Fall movements of Arctic grayling and the location of overwintering grounds in the Little Smoky River were determined by radiotelemetry. During the summer of 1993 (May - July), surveys of the river and surrounding terrain were conducted to determine the most suitable sites for capturing and early tracking of the fish. Cutlines and trails were surveyed and cleared in order to provide access to the transmitter implantation sites.

Arctic grayling can be successfully implanted with internal radio transmitters using the surgical techniques of Bidgood (1980) and McKinley *et al.* (1992). We implanted three spawning fish (>200 gm) with radio transmitters in early May, 1993 and monitored them for two weeks in a 2 m by 4 m enclosure placed in a 60 cm deep glide of Tony Creek. The fish remained alert and in good health.

Thirty-five Advance Telemetry Systems' (Isanti, Minnesota) (ATS) model 397 miniature radio transmitters were used in this study. The range of frequency used was from 150.000 MHz to 150.320 MHz. They were 3.5 cm X 1.5 cm cylinders, encapsulated with epoxy, with a 20 cm wire whip antenna extending from one end. The transmitters were powered by 1.5 volt silver oxide batteries and weighed approximately 4.0 gm in air and 2.6 gm in water. They were set to have a pulse rate of about 1 pulse per second (pps) which allowed the use of a scanning receiver from an aircraft with a scanning rate of at least 2 seconds per frequency. The transmitters were designed to last a minimum of 4 months with an expected life of 6 months, so that if fish were implanted in August, the transmitters would last until February of the following year. Thirty three transmitters were implanted into fish. Two reference transmitters were placed in the upper and lower part of the study section at exact known geographical locations. They were placed in burlap sacs filled with stones and submerged in 60 cm of water. These transmitters acted as temporal controls for the life of transmitters implanted in the fish and as stationary spatial controls to assess the precision of our locations and the mapping technique used. The reference transmitters were located without using visual cues. At the end of the study, we were able to obtain the accuracy by knowing the mean and standard deviation (m) for the distance of our aerial locations from the true location of the control transmitters. We were also able to obtain the precision of our locations by calculating the variance.

Thirty radio transmitters were implanted into Arctic grayling between August 17 and August 24, 1993 (Table 1). The four sites of fish capture were representative of summer habitat of Arctic grayling and were spread over 78 km of the study section (Figure 1). This allowed for the comparative evaluation of fall migration of fish having widely separated summer habitats. Additional radio transmitters were implanted on September 21, 1993 (1) and October 1, 1993 (2) as three radio tagged fish had moved out of the study area. Finally, one radio transmitter was reimplanted into another fish on November 3, 1993, after the original fish was caught by anglers and the intact transmitter returned to us.

As is the goal of all telemetry studies, we wanted to attach a transmitter to an animal to record its behavior, assuming that the mode of attachment would not influence the individual's behavior (McKinley *et al.* 1992). The transmitters were surgically implanted into the body cavity of Arctic grayling that were 200

Table 1. Identification number, fork length (mm), weight (gm), sex, date of implantation and location of capture / release sites of 34 radio tagged Arctic grayling from the Little Smoky River, Alberta, fall 1993. Fish locations were monitored from August 31, 1993 to January 15, 1994.

Fish ID Number	Site	Date Implanted	Fork Length (mm)	Weight (g)	Sex
1	1	Aug.17	265	222	Female
2	1	Aug.18	280	266	Female
3	1	Aug.18	284	268	Female
4	1	Aug.18	291	290	Male
5	1	Aug.18	292	298	Male
6	1	Aug.17	296	314	Female
7	1	Aug.17	300	306	Female
8	1	Aug.18	312	310	Male
9	1	Aug.18	315	342	Male
10	1	Oct.1	330	440	Female
11	1	Sep.21	330	360	Female
12	1	Aug.18	350	528	Male
13	1	Oct.1	372	534	Male
14	2	Aug.20	282	274	Female
15	2	Aug.20	290	300	Female
16	2	Aug.20	292	300	Female
17	2	Aug.20	298	290	Male
18	2	Aug.21	298	310	Female
19	2	Aug.21	310	326	Male
20	2	Aug.21	318	370	Male
21	2	Nov.3	320	322	Male
22	2	Aug.20	332	366	Male
23	2	Aug.20	337	432	Male
24	3	Aug.23	278	272	Female
25	3	Aug.23	307	330	Male
26	3	Aug.23	337	500	Male
27	3	Aug.23	368	590	Male
28	4	Aug.24	280	210	Female
29	4	Aug.24	285	270	Male
30	4	Aug.24	290	256	Female
31	4	Aug.24	295	316	Female
32	4	Aug.24	295	310	Female
33	4	Aug.24	310	348	Female
34	4	Aug.24	320	386	Male

gm or more in weight (>300 mm total length). These transmitters did not exceed 2% of body weight (in air), which is the recommended figure for these fish (Hop *et al.* 1986). Internal transmitters do not cause drag, can not become snagged, and are less likely to cause abrasions than externally attached tags (Winter 1989). Arctic grayling are able to adjust their buoyancy with their swim bladder to compensate for the transmitter weight, as demonstrated by successful radio telemetry studies in Alaska (Barber *et al.* 1985; West *et al.* 1992).

In this study, precautions were taken to minimize stressing Arctic grayling during radio tagging. All fish were captured by angling using fly rods with barbless dry flies. After their capture, the fish were quickly landed, measured, weighed, and fish suitable for transmitter implantation were placed in a 20 L bucket of river water containing about 200 mg/L solution of anesthetic (MS-222). The surgery was conducted using a procedure similar to Bidgood (1980) and McKinley *et al.* (1992). A 1-2 cm incision was made on the ventral side of the fish, anterior and slightly dorsal to either of the pelvic fins. Beeswax dipped transmitters were inserted into the body cavity with the antenna threaded outside posterior to the pelvic fins. The transmitters were dipped in beeswax before insertion to reduce irritation. The incision was closed with three individual sutures using non-absorbable 00 silk thread. This was to prevent suture material from weakening prematurely and causing the incision to reopen before primary wound healing had occurred (Nemetz and MacMillan 1988). The individual frequency of each transmitter implanted into a specific fish was recorded. After surgery, each fish was released into a low velocity part of the river near the site of capture and left undisturbed until able to swim away on its own. Fish that failed to swim away (1) or showed signs of slow recovery (1) were sacrificed and other fish were substituted. Finally, the location of release of each fish was recorded as well.

As with any radio telemetry study, there are difficulties that one has to foresee before starting a study. Signal strength and range of 150 MHz transmitters can be reduced by water depth greater than 5 m, water conductivities greater than 400 µmho/cm, and slushy ice (Winter 1989). From a preliminary inspection of the river, we did not expect to find pools deeper than 5 m. Environment Canada records for the Little Smoky indicate that in winter, water conductivity reaches about 300 µmho/cm. As we were interested in where fish were found throughout the winter, we did not expect slushy ice conditions during ice formation in November to seriously affect our ability to locate fish. Losses of signal strength can occur when signals are deflected off terrain or from noise produced by powerlines, citizen band radios and telecommunication repeater towers (Winter 1989). We are confident that as experienced trackers, we were able to recognize echoed signals. The noise problem was also minimized by preliminary determination of the best time of day to track fish, for example, when the interference from other devices was minimal, and through directional antenna control.

The locations of radio tagged fish were monitored from ground and air in order to determine the health of fish, the occurrence and timing of movements, and the location of overwintering grounds. Checking for health of fish that had not exhibited much movement was done throughout the study using a Challenger R2000 scanning receiver and a YAGI 3 element antenna from ATS.

However, most of the tracking of radio tagged fish was done from the air starting on August 31, 1993 and ending on January 15, 1994. Aerial tracking was done due to the large size of the study area, inaccessibility, and Arctic grayling exhibiting large movements between tracking events (in excess of 1 km/day until freeze-up) (West *et al.* 1992). In 1993, aerial tracking was performed on August 31; September 7, 16, 21 and 28; October 5, 14, 19 and 26; November 2, 9, 16 and 30; and December 16 and 30. In 1994 radio tagged fish were located on January 15.

There are some problems associated with tracking a low power transmitter signal from a fixed wing aircraft. From a physical mounting perspective, one has to deal with the reflective surfaces of a fixed wing as well as the "hard mounted" antenna's lack of directional control. From an operational aspect the interface between the receiver operator and the pilot further complicates the scenario. The typical fixed wing mission would involve cross flying at the receiver operator's directions the location of each radio tagged fish. By the end of the required second pass a total of at least three minutes would have elapsed. The ability to place the fish's location using a fixed wing aircraft was less accurate than by using a helicopter, which can stop and hover over radio tagged fish, based on the high speed of the fixed wing aircraft, the fish's movement and the lapsed time between crossings. Based on preliminary flights with a fixed wing, at best, we were able to obtain the location of a tagged fish to within 200 m.

The most precise and economical method of tracking transmitter fish from the air was by using a small R-22 (Robinson) helicopter equipped with a

Corvallis Microtechnology Inc. MC-GPS datalogger (Corvallis, Oregon), R2000 scanning receiver from ATS, and an operator controlled moveable three element YAGI antenna. The MC-GPS is a 6-channel, waterproof, hand-held GPS receiver / data collector with the power of an 80C88-based computer. The helicopter and Global Positioning System hardware were provided by Aerial Recon Surveys (Whitecourt, Alberta). The GPS receiver used was able to provide geo-referenced locations every second. The antenna was mounted below the aircraft and it was possible for the operator to direct it 360 degrees in the horizontal plane and 85 degrees in the vertical plane from the cockpit.

The study section was flown twice on each mission. During the first pass over the study area, the R2000 scanning receiver scanned the 34 preprogrammed transmitter frequencies at a rate of 2 seconds per frequency with audio provided to both the pilot and the operator, assisting the pilot with gross directional control. This assured that if a specific transmitter was in receiving range, its 1 pps would be picked up at least once during the 2 second period. The scan frequency of 2 seconds was chosen to start with in order to minimize over running some transmitters due to the long 1 minute 6 seconds turnover rate for all the transmitter frequencies. During the second pass over the study area, the scan rate was changed to 4 or more seconds per frequency as there were few transmitters left to find.

The R22 helicopter would take off from the town of Fox Creek near the lower end of the study area and fly at less than 80 km/hr. The helicopter did not over run the location of radio tagged fish as a fixed wing aircraft would thus permitting continuous and accurate scanning of up to 33 transmitters. The typical flight mission was planned to provide a minimum of two passes over the range of radio tagged fish, at an altitude of 150 m above ground level and would take approximately 3.5 hours. Upon reception of a specific frequency, the scanning of other frequencies was stopped and the aircraft was slowed and lowered to hover directly above the transmitting fish for about 10 seconds. The receiver operator would then communicate the frequency of the specific transmitter to the pilot so that he could assign the frequency to the cluster of 10 positions (one per second) in the GPS datalogger (Figure 5). Average time from signal acquisition to fixing the location was 2.0 minutes. Once a fish was located, that particular frequency was dropped from the scanning list.

The GPS datalogger was able to record the location of each radio tagged fish using the strongest signal from four out of six GPS satellites by averaging the ten positions recorded during hovering over each fish. This was possible because the GPS datalogger also had all the individual fish frequencies pre-programmed into it. Therefore, the pilot could simply scroll through individual fish frequencies and assign geo-referenced position (attribute) to the hovering location.

Using Aerial Recon's GPS base station, we were able to post-process differentially correct the locations of radio tagged fish in the Little Smoky River. The base station is located in Whitecourt, Alberta about 80 km south of the study area. The station covers a region of 500 km around Whitecourt and it constantly receives all in-view satellites. The GPS receiver in MC GPS datalogger used was a TANNS unit receiving L1/CA code signal. By recording 4 satellites out of a possible 6 observable, typical accuracies were in the 1 to 5 meter range

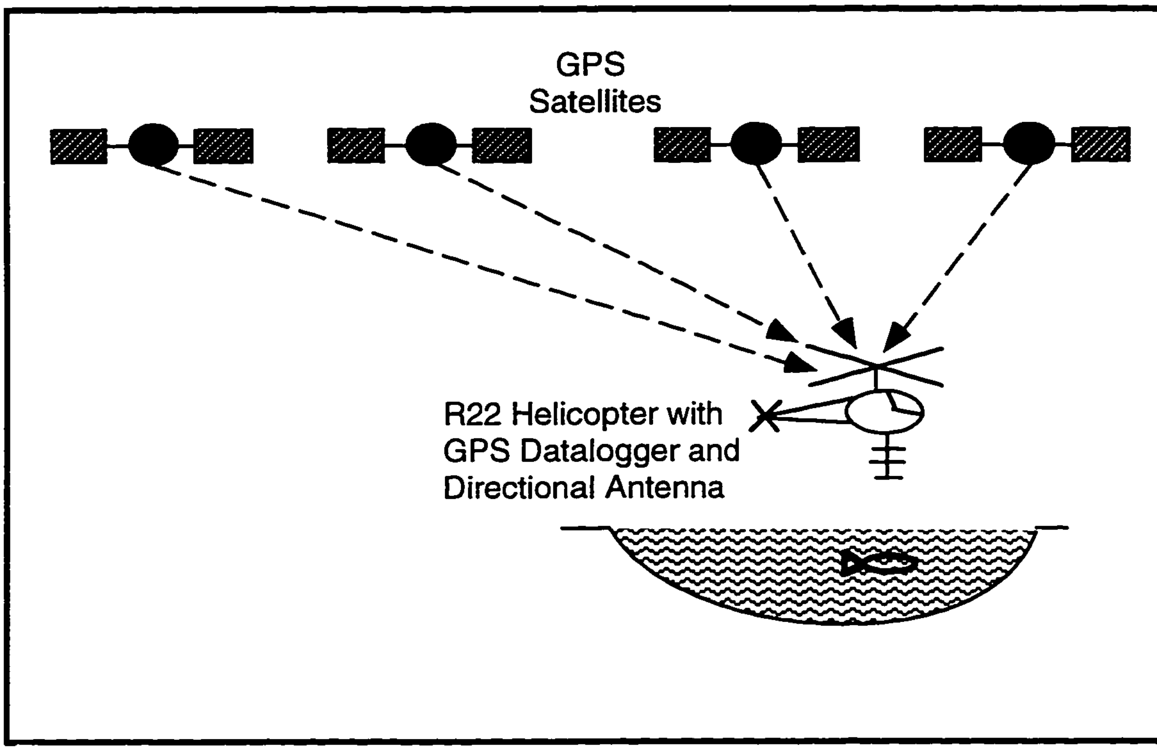

Figure 5. Example of how each radio tagged Arctic grayling was located in the Little Smoky River, Alberta from August 31, 1993 to January 15, 1994. The helicopter's Global Positioning System (GPS) datalogger was used to assign geo-referenced position to each of the fish. This was done after the fish was pinpointed using a 3 element directional YAGI antenna and the GPS datalogger was positioned directly above each of the fish.

horizontally when post-processed with differential correction systems.

The differential correction process required a second GPS receiver located at an exact known geographic location - the base station. As the base station records signals from the satellites, determined position errors are recorded. These differences in GPS determined position versus known geographic position are recorded for each satellite observed. Provided that both GPS units receive signals from the same satellites at the same time, the locations of the helicopter can be corrected (Figure 6). Files collected by the field unit (GPS datalogger), referred to as the rover, are reviewed by the processing computer and the differential values are applied to correct the locations calculated by the rover unit. This was accomplished using GPS Pathfinder software from Trimble Navigation Ltd. (Sunnyvale, California).

The resolved data sets contain digital data which can be readily transferred to a variety of industry recognized GIS formats. In the data sets collected during each flight, we assigned 2 attributes to individual recorded positions. These were individual radio tagged fish frequency and date of location.

The next step was to export the files into a GIS type environment in order to analyze the movement data. This was possible since the source data were spatially referenced, that is, they could be related to some location on earth and could be mapped. Using desktop mapping software - MapInfo 3.0 for Macintosh from MapInfo Corp. (Troy, New York) and a 40 MHz Macintosh computer, we were able to place the locations of all the radio tagged fish onto digitized maps of the Little Smoky drainage. Corrected data from the GPS datalogger were

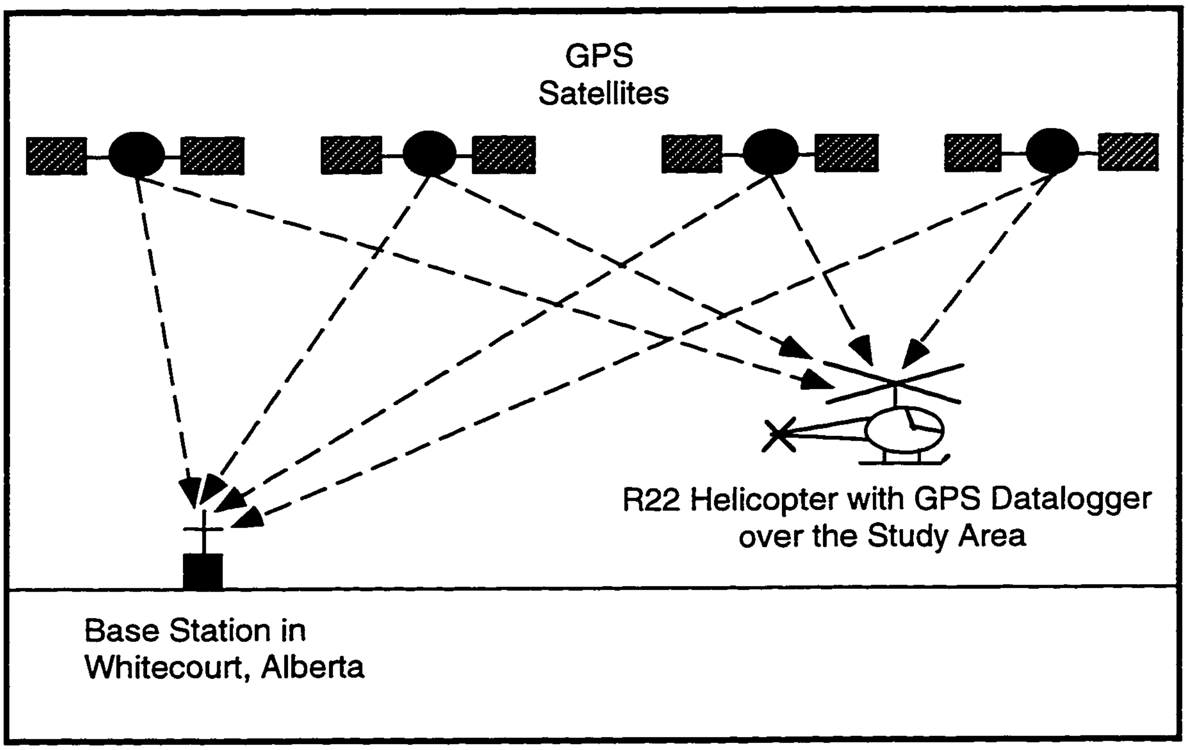

Figure 6. Example of how post-processed differential correction was applied to the helicopter's Global Positioning System (GPS) datalogger files using a base station in Whitecourt, Alberta. The base station kept track of reported position inaccuracies by the satellites used to locate radio tagged fish. The location of fish could then be corrected by applying base station values to the helicopters GPS files.

simply downloaded into MapInfo using the GPS Pathfinder software. The 1 : 20,000 digitized hydrology maps of the study area were obtained from the Alberta Fish and Wildlife Division GIS database and also imported into MapInfo using AutoCad DXF format so that we were able to overlay locations of the individual radio tagged fish onto the river.

The resultant maps of movement of radio tagged fish can only be as good as the digitized maps used. The near absolute positioning of GPS maps can be undermined by inaccurate digital map sheets. Alberta Fish and Wildlife Division has a good selection of well maintained digitized 1 : 20,000 maps of Alberta with a published accuracy of at least ± 5 m which provided an acceptable final product.

The fish movement database was constructed using MapInfo 3.0 as the software can be used to measure distances along a watercourse. It contained locations of radio tagged fish with the following attributes attached to these locations: 1) fish identification number, 2) date of location, 3) amount (km) and direction (+ upstream, - downstream) of fish movement, and 4) latitude and longitude. All maps in this thesis were produced using the digitized hydrology layer of the Little Smoky River drainage and the database.

Over the duration of the study, the geo-referenced database of temporal fish locations which was constructed, provided us with information on the amount and rate of movement of all radio tagged fish and locations of overwintering grounds. Using GPS and MapInfo, we were able to effectively and efficiently gather precise data on fish movements. This was an important consideration in the design of this study because, one had to consider that the animal in this study has the potential for exhibiting extensive movement. The database also permitted spatial analysis of the data. The distances moved by transmitter fish were measured as minimum mid-channel river kilometers using the digital hydrology layer of the Little Smoky River installed on MapInfo 3.0. All measurements were made at the same map scale.

In order to compare the amount of movement exhibited by the fish with the hypothesized "master" control factor - temperature; daily water temperatures (°C) were obtained. Water temperatures were measured to the nearest 0.1°C using three Hobo-Temp dataloggers from Onset Computer Corp. (Pocasset, Massachusetts). Each datalogger measured and recorded ten water temperatures on a daily basis. The dataloggers were placed about 60 cm underwater beneath logs and out of direct sunlight, in site 1, site 2 and just upstream of confluence of Tony Creek. As there was no significant difference (P>0.05; N=4140) in the water temperatures recorded between the three sites, temperature data were averaged from all sites. Local inflows of groundwater between the dataloggers may have been missed by this approach. However, no open water leads were observed after freeze-up of the study section. Small local inflows of groundwater might have existed under ice cover. The locations of these inflows could not be confirmed as the large amount of snowfall in winter of 1993/94 created hazardous travel conditions on the river. Changes in daily water discharge (m^3/sec.) were also monitored using data from the Environment Canada water gauging station. The data were obtained until November 4, 1993, by which time freeze-up occurred at the gauge.

Overwintering locations and their sizes were reported for radio tagged fish tracked after November 30, by which time all parts of the river had completely frozen over. This prevented fish movement data from being influenced by the developing ice cover, ice scouring or anchor ice forming in and below fast flowing riffles.

The gradient was obtained from 1 : 20,000 digitized maps using the elevation and hydrology layers. Using MapInfo 3.0, the length of the river containing a section in question was measured between the nearest 10 m contour intervals crossing the river.

Using the differentially corrected GPS locations of the two reference transmitters from 16 flights (August 31,1993 - January 15, 1994), I determined that the mean distance from true transmitter location was 5 m (N = 32; SD = 2 m; variance = 4 m). Therefore, 95% of the time, the fish were within 4 m of the location recorded. However, the digitized hydrology layer of the Little Smoky River that was used to plot fish movements could have been off by 5 m at any one point. In light of these facts, the minimum distance considered a movement by radio tagged fish over a period of time was a conservative 18 m (5 m + 4 m for both locations).

Systat 5.2.1 was used to analyze movement data. Liliefort tests were used to test for normality of the movement data. If data were not normally distributed, Kolmogorov-Smirnov nonparametric tests were used. Data on direction of fish movement were analyzed with chi-squared tests. The movement data between tagging and first tracking event were omitted to make sure that results were not influenced by any stress due to internal transmitter implantation.

RESULTS

Movements and Directional Patterns

Arctic grayling tagged in August moved a mean total distance of 49.06 km (N=21; Range 0.83 - 156.12 km) and a mean net distance of 23.54 km (N=21; Range 0.03 - 76.19 km) from August 31, 1993 to January 15,1994 (Table 2). Of the thirty four radio tagged fish, twenty-five (74%) were followed until the end of the study on January 15, 1994. In site 1, of the thirteen fish tagged, four were lost (1, 4, 6, and 12). Three fish (1, 4, and 12) moved upstream of the study section and one fish (6) was lost to angler harvest. Of the three fish that had moved upstream following tagging, two fish (1 and 4) had moved between 5 and 10 km upstream by August 31, 1993 and all three were not found in the study section after September 16, 1993. These fish could not be located further upstream due to limited fuel supply in the helicopter. In site 2, of the ten fish tagged, four were lost (16, 17, 20, and 23). Two fish (17 and 20) were lost to angler harvest, one fish (16) was lost to osprey predation, and one fish (23) was lost for unknown reasons. In site 3, of the four fish tagged, only one (24) was lost for unknown reasons. In site 4, of the seven fish tagged, none was lost. Since only two fish were lost for unknown reasons, we could account for thirty two (94%) out of thirty four radio tagged Arctic grayling. Movement maps of individual radio tagged fish are presented in Appendix 1.

Arctic grayling from the upper study reaches moved less than fish from the middle study reaches during this study. There was a significant difference ($P<0.05$; N=21) in net distances moved by upper fish (from sites 1 and 2) and those from middle study reaches (sites 3 and 4) from August 31, 1993 to

Table 2. Direction and distances (km) moved by radio tagged Arctic grayling in the Little Smoky River, Alberta, August 31, 1993 - January 15, 1994. The fish identification numbers correspond to those given in Table 1.

Fish ID Number	Site	Total Distance Moved (km)	Net Distance Moved (km)	Net Direction	Date of Last Location	Number of Days Monitored
1	1	0.49	0.49	up	Sep.07/93	7 *
2	1	56.49	26.69	down	Jan.15/94	137
3	1	15.80	0.03	up	Jan.15/94	137
4	1	0.35	0.35	down	Sep.16/93	16*
5	1	21.91	2.30	up	Jan.15/94	137
6	1	11.76	11.76	down	Sep.07/93	7 #
7	1	40.64	30.92	down	Jan.15/94	137
8	1	33.52	0.30	up	Jan.15/94	137
9	1	16.11	0.18	down	Jan.15/94	137
10	1	5.89	0.46	up	Jan.15/94	102
11	1	19.86	6.61	up	Jan.15/94	109
12	1	10.32	10.32	up	Sep.16/93	16*
13	1	24.29	12.22	up	Jan.15/94	102
14	2	12.37	8.14	down	Jan.15/94	137
15	2	10.96	10.62	down	Jan.15/94	137
16	2	0.00	0.00	none	Aug.31/93	0^
17	2	19.54	4.07	down	Oct.19/93	49#
18	2	21.41	8.69	up	Jan.15/94	137
19	2	13.32	10.11	down	Jan.15/94	137
20	2	37.49	3.36	down	Sep.16/93	16#
21	2	10.92	10.86	up	Jan.15/94	67
22	2	0.83	0.18	down	Jan.15/94	137
23	2	17.53	17.53	up	Sep.16/93	16^^
24	3	0.00	0.00	none	Aug.31/93	0^^
25	3	92.84	69.72	down	Jan.15/94	137
26	3	83.30	76.19	down	Jan.15/94	137
27	3	86.28	50.28	down	Jan.15/94	137
28	4	33.36	2.62	up	Jan.15/94	137
29	4	156.12	51.70	down	Jan.15/94	137
30	4	63.77	44.21	down	Jan.15/94	137
31	4	103.73	24.92	down	Jan.15/94	137
32	4	79.75	26.69	down	Jan.15/94	137
33	4	23.31	21.53	down	Jan.15/94	137
34	4	64.43	28.22	down	Jan.15/94	137

*Fish moved upstream of study area #Fish lost to anglers ^Fish lost to predation ^^Fish was lost

January 15, 1994. Upper fish migrated a mean net distance of 8.92 km (N=11; Range 0.03 - 30.92 km), whereas fish from middle reaches migrated a mean net distance of 39.61 km (N=10; Range 2.62 - 76.19 km) (Table 2). Movement data of individual radio tagged fish are presented in Appendix 2.

Radio tagged fish moved both upstream and downstream during overwintering migration but overall, fish exhibited a downstream migration in fall and winter. There was a significant difference ($P<0.05$; N=21) in the number of fish that had moved downstream and those that moved upstream from August 31, 1993 to January 15, 1994. Sixteen (76%) of the fish had moved downstream and only five (24%) of the fish had moved upstream (Table 2). However, the direction of fish overwintering migration appeared to be influenced by sites of capture. There was no significant difference ($P>0.05$; N=11) in number of fish that had moved downstream and those that moved upstream for fish from upper study reaches (sites 1 and 2). Seven (64%) of these fish had moved downstream as compared to four (36%) that had moved upstream. The same was true if one included the three fish that were suspected of moving upstream and out of the study area. In this case 50% would have moved downstream and 50% upstream. There was a significant difference ($P<0.05$; N=10) in the number of fish that had moved downstream and those that had moved upstream for fish from the middle study reaches (sites 3 and 4). Nine (90%) of these fish had moved downstream as compared to only one (10%) that had moved upstream.

Fish moved longer distances downstream than upstream. There was a significant difference ($P<0.05$; N=21) in net distances moved by Arctic grayling that migrated downstream and those that migrated upstream from August 31, 1993 to January 15, 1994. Fish that migrated downstream moved a mean distance of 30.02 km (N=16; Range 0.18 - 76.19 km), whereas fish that migrated upstream moved a mean distance of 2.79 km (N=5; Range 0.03 - 8.69 km) (Table 2).

Radio tagged Arctic grayling did not stop moving in the Little Smoky River after water temperatures reached 0.0°C. Both minimum and maximum daily water temperatures recorded in the study section reached 0.0°C on November 4 (Figure 7). The temperatures remained at 0.0°C from November 4, 1993 to end of the study on January 15, 1994. Of the 24 to 25 radio tagged fish monitored after November 2, 68 to 79 % showed movement between observations (Figure 8). However, the proportion of fish not moving increased as well after November 2 from 22% between November 2 and November 16 to 32 % between December 30 and January 15.

Arctic grayling fall migration in the Little Smoky River peaked as water temperatures and flows were decreasing in September. Radio tagged fish migrated at a mean rate of 0.42 km/day (N=359; Range 0.00 - 5.86 km/day) from August 31, 1993 to January 15, 1994. The peak of fall migration was reached by September 21 when fish were moving at a mean rate of 1.52 km/day (N=20; Range 0.00 - 5.86 km/day) (Figure 9). The movement rate increased from a mean of 0.28 km/day (N=26; Range 0.00 - 2.44 km/day) by September 7 to peak by September 21 as mean water temperatures decreased from 12.5 °C to 8.0 °C (Figure 10). This also coincided with the greatest decreases in flows as water discharge in the river dropped from a peak of 40.3 m^3/sec. on September

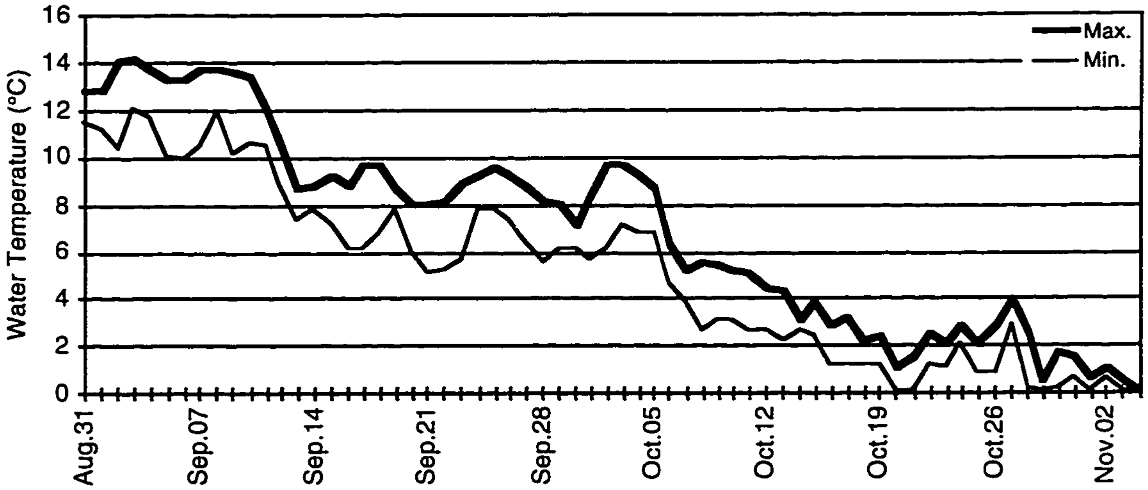

Figure 7. Maximum and minimum daily water temperatures (°C) recorded in the study section of Little Smoky River, Alberta, fall 1993. Data were collected by Hobo-Temp dataloggers from Onset Computer Corp. (Pocasset, Massachusetts). The temperatures remained at 0.0°C from November 4, 1993 to end of the study on January 15, 1994.

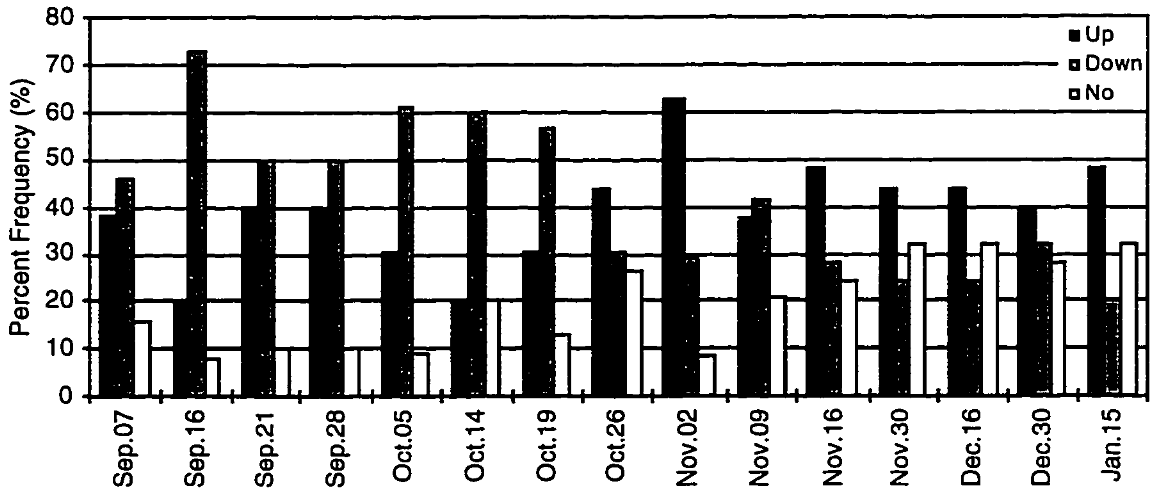

Figure 8. Percentage of radio tagged Arctic grayling exhibiting movement upstream, downstream and no movement since previous observation. Locations of radio tagged fish were monitored in the Little Smoky River, Alberta, from August 31, 1993 to January 15, 1994.

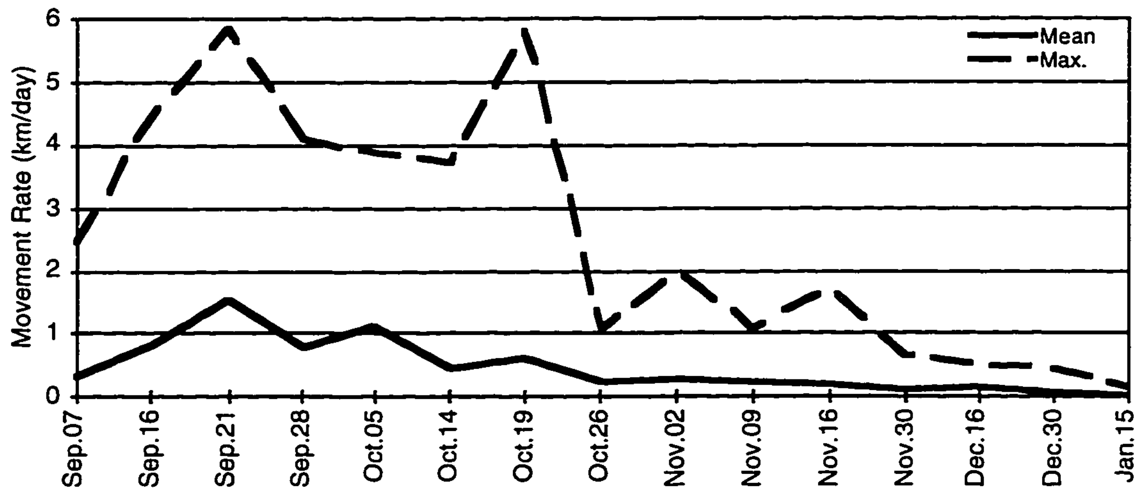

Figure 9. Maximum and mean movement rates (km/day) of radio tagged Arctic grayling in the Little Smoky River, Alberta, fall 1993 - winter 1993/94. Fish locations were monitored from August 31, 1993 to January 15, 1994. The rates of movement were calculated for monitoring dates shown using distances moved by fish since previous observation.

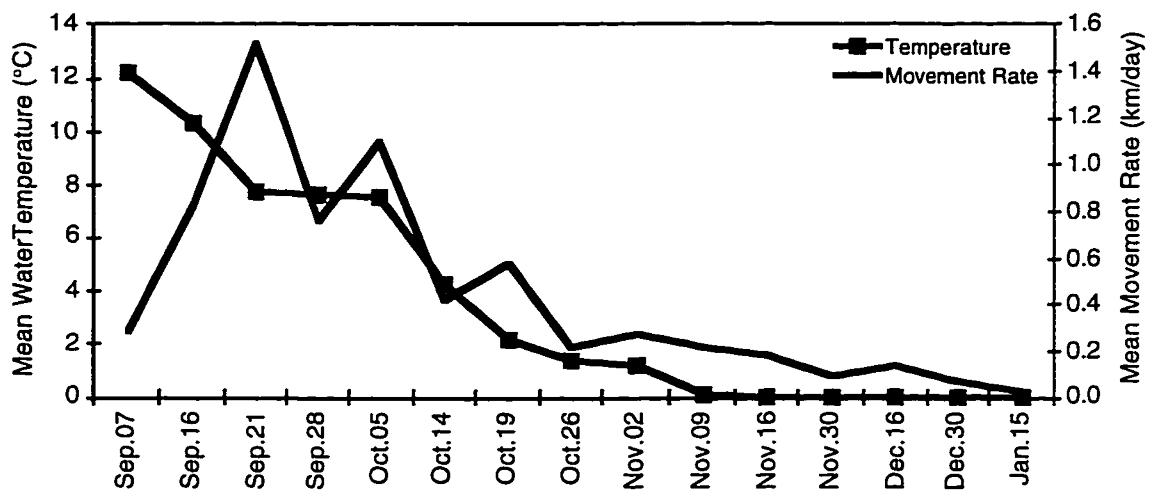

Figure 10. Mean water temperatures (°C) for periods of time since last fish monitoring date and mean movement rates (km/day) of radio tagged Arctic grayling in the Little Smoky River, Alberta, fall 1993 - winter 1993/94. Fish locations were monitored from August 31, 1993 to January 15, 1994. The rates of movement were calculated for monitoring dates shown using distances moved by fish since previous observation.

3 to 9.5 m^3/sec. on September 21 (Figure 11). Mean movement rates decreased with falling water temperatures after September 21 (Figure 7 and 10). They reached a low of 0.02 km/day (N=25; Range 0.00 - 0.15 km/day) by January 15. Flows remained below 10 m^3/sec. after September 21.

Radio tagged Arctic grayling from the upper study reaches moved at lower rates than fish from middle study reaches. Mean movement rates were significantly different (P<0.05; N=359) between radio tagged fish from sites 1 and 2, and those from sites 3 and 4. The mean movement rate for Arctic grayling from sites 1 and 2 was 0.24 km/day (N=217; Range 0.00 - 3.71 km/day) whereas for fish from sites 3 and 4, it was 0.71 km/day (N=142; Range 0.00 - 5.86 km/day) from August 31, 1993 to January 15, 1994.

It appears that most of the fall migration occurred by October 19 with fish moving downstream between August 31 and October 19, 1993. The mean movement rate decreased from 0.58 km/day (N=23; Range 0.00 - 5.84 km/day) by October 19 to 0.21 km/day (N=23; Range 0.00 - 1.04 km/day) by October 26 (Figure 9). This coincided with minimum water temperatures reaching 0.0 °C for the first time on October 20 and 21 (Figure 7). During fall migration (until October 19), significantly (P<0.05; N=143) more fish showed movement downstream than upstream between observations. From August 31 to October 19, 46 - 73 % of radio tagged fish showed movement downstream between observations (Figure 8). However, after October 19, significantly (P<0.05; N=146) more fish showed movement upstream than downstream between observations. From October 19, 1993 to January 15, 1994, 38 - 63 % of the fish showed movement upstream between observations.

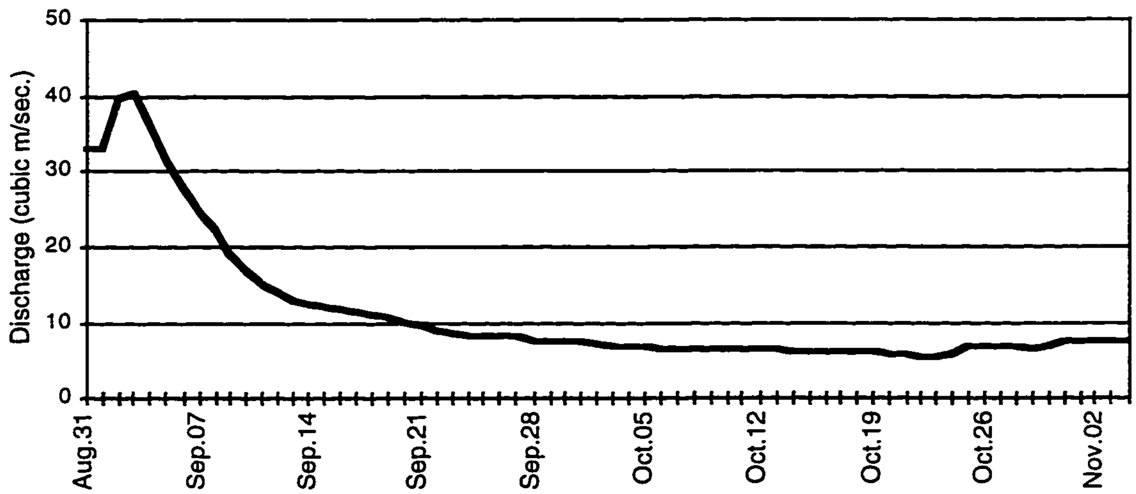

Figure 11. Daily water discharges (m^3/sec.)in the Little Smoky River, Alberta, fall 1993. The discharge data were obtained until freeze-up (November 4) from Environment Canada water gauging station No. 07GG002 located 13.5 km downstream of the study section at 54° 44' 24" N, 117° 10' 46" W.

Habitat Use Observations

There was a transition period in the use of mesohabitat by radio tagged fish during this study. In August, Arctic grayling were maximizing their food intake by positioning themselves close to relatively fast flowing water. All radio tagged fish were observed utilizing riffles and heads of pools, close to the entering riffles during the time of transmitter implantation. However, by October, as water temperatures started to drop drastically (Figure 7 and 10), the fish were observed using more deep pools and glides with cover in the form of logs, log jams, beaver caches, and bridges. Freeze-up started on October 19 as surface ice was observed on the edges of stagnant water for the first time. Minimum daily water temperature dropped to 0.0°C on October 20. By October 26, the fish were moving out of deep pools and glides and started to utilize the edges of surface ice as cover. Water temperatures dropped again to 0.0°C on November 4 and anchor ice was periodically observed in and below fast flowing riffles that remained open until November 30. This was especially true for the high gradient, middle reaches of the study section between site 3 and confluence with Tony Creek.

Overwintering Grounds

Arctic grayling overwintering grounds were not located in specific or restricted areas of the Little Smoky River. After the river completely froze over, 21 out of 25 (84 %) radio tagged fish moved at least once (Range 0.02 to 8.32 km) from November 30, 1993 to January 15, 1994. The mean size of overwintering area was 2.98 km long (N=25; Range 0.00 - 12.22 km) as defined by the range of the river that fish were found in after November 30 (Figure 12).

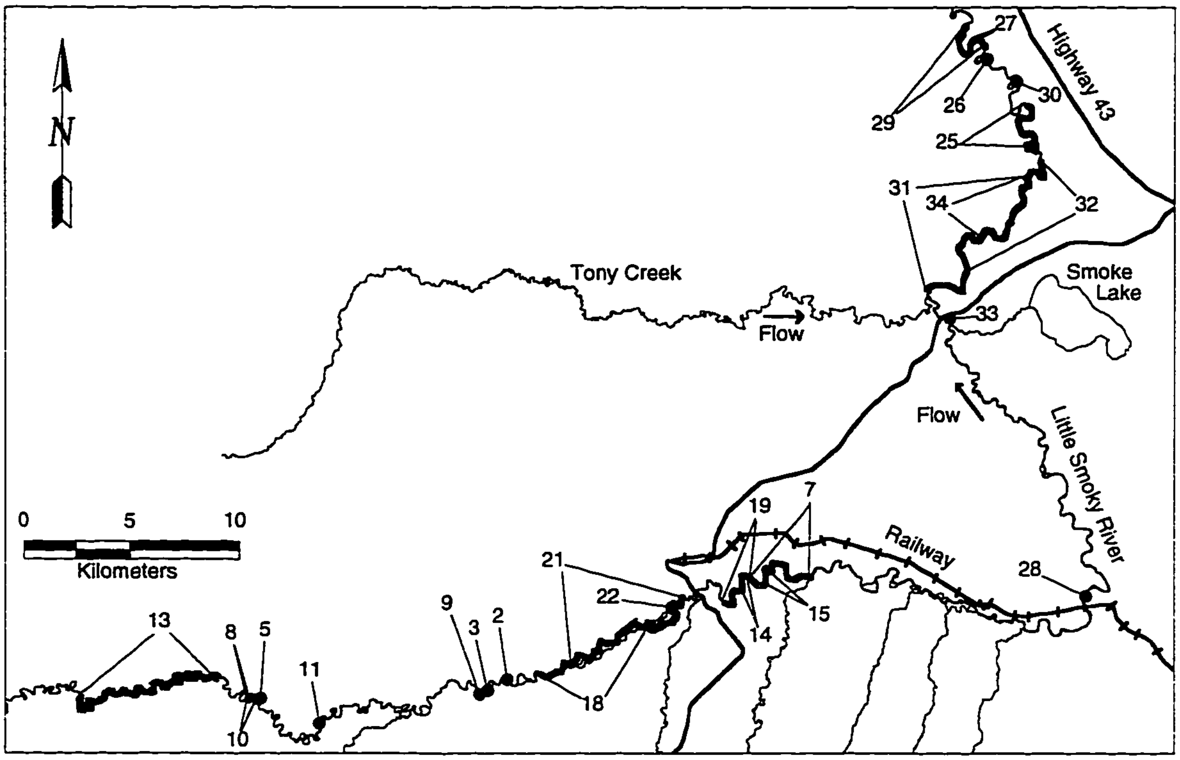

Figure 12. Map of overwintering grounds of 25 radio tagged Arctic grayling in the Little Smoky River, Alberta, November 30, 1993 - January 15, 1994. Overwintering grounds are shown as bold section of the river. Overwintering grounds that were less then 0.1 km in length are shown as solid circles. The fish identification numbers correspond to those given in Table 1.

Arctic grayling from the upper (sites 1 and 2) part of the study section overlapped in their overwintering ground locations. The same was true for fish from middle (sites 3 and 4) part of the study section. However, the two groups did not overwinter in the same parts of the river. Radio tagged fish from sites 1 and 2 overwintered both upstream and downstream of their release sites (Figure 12). They were found to be using the upper (0.19 % gradient) part of the study section and overwintered at a mean gradient of 0.18 % (N=15; Range 0.11 - 0.29 %). Radio tagged fish from sites 3 and 4 overwintered by and below the confluence of Tony Creek. These fish migrated downstream and out of the middle (0.29 % gradient) part of the study section to overwinter at a mean gradient of 0.17 % (N=9; Range 0.08 - 0.33 %) in the lower part of the study section. The only exception was fish 28 which overwintered close to its release site at a gradient of 0.31 %. However, this fish was found using one of few pools in the area to overwinter in. Fish 7, 14, 15 and 19 from sites 1 and 2 overwintered near site 3 and fish tagged at this location (25, 26 and 27) overwintered below Tony Creek.

DISCUSSION

Radio tagged fish exhibited two distinct overwintering migration patterns in the Little Smoky River. Fish from the middle study reaches (sites 3 and 4) migrated greater distances and at greater rates than fish from upstream reaches (sites 1 and 2). Furthermore, grayling from sites 3 and 4 migrated to different reaches of the river as compared to fish from sites 1 and 2. Radio tagged fish from sites 3 and 4 migrated downstream towards and below confluence of Tony Creek. Fish from sites 1 and 2 did not have a clear direction of migration with fish overwintering both upstream and downstream from their sites of capture.

Based on movement data and location of overwintering grounds, one could argue for the existence of two sub-populations of Arctic grayling in the relatively large and productive Little Smoky River. Skopets and Prokop'yev (1990) indicated that in large salmon rivers, Kamchatkan grayling do not move more than a few tens of kilometers forming separate populations 70 to 100 km apart. These fish have adapted to live in large, deep rivers with moderate flows where abundant food is provided by salmon eggs and carcasses. There is also an absence of extensive migrations as compared with other subspecies of Arctic grayling. This would be similar to fish from sites 1 and 2 which migrate relatively short distances (mean = 8.92 km) and live in more stable, lower gradient section of the river than fish from sites 3 and 4. The latter moved longer distances (up to 76.19 km) and are more typical of other migratory Arctic grayling populations in Alaska.

Movements by fish from the middle study reaches of the Little Smoky River were similar to those reported for Arctic grayling elsewhere. In Alaska, grayling were found to migrate over 100 km to reach overwintering grounds in lakes, deep pools of streams and rivers, and spring-fed areas (Craig and Poulin 1975; Krueger 1981; Barber *et al.* 1985; Hubert *et al.* 1985; Hop *et al.* 1986; West *et al.* 1992). West *et al.* (1992) reported radio tagged grayling migrating into larger streams at a mean rate of 0.94 km/day from early August to mid - December. They found that most migration took place during August and September as the reported maximum migration rates of 5 - 6 km/day occurred about September 1. This was similar to migration by fish from sites 3 and 4 of this study. These fish migrated at a mean rate of 0.71 km/day from August 31, 1993 to January 15, 1994 with maximum rates of 5.86 km/day recorded on September 21. However, most migration took place in September and the first half of October due to the longer open water season.

Extensive overwintering migrations might be due to necessity rather than lack of suitable overwintering habitat. Often, lack of deep water habitat can cause streams to freeze to the bottom in winter forcing fish out of these areas (Ward 1951; Krueger 1981). Furthermore, as might be the case for fish from sites 3 and 4, fish living in relatively wide, shallow and fast flowing parts of a drainage might be forced out in winter due to frazil and anchor ice occurrence (Brown *et al.* 1993). Anchor ice was observed between Site 3 and confluence with Tony Creek after November 4. The unusually high gradient in middle study reaches of the Little Smoky River might have facilitated relatively more frazil ice production than in other study reaches. This might have forced fish from sites 3 and 4 to move from areas of higher gradient (middle study reaches) in summer to areas of lower gradient (lower study reaches) in winter. It was striking that most fish overwintered in water with a mean gradient in the 0.17-0.18% range.

The unexpected upstream movement of Arctic grayling during winter, when the river was completely frozen over and water temperatures were at 0.0°C, can not be easily explained. One could argue that in some areas, ice was becoming too thick and it was displacing fish from relatively shallow habitats. Another explanation could be that since these fish are well adapted to overwintering in marginal habitats, they do not seek out specific winter habitat but rather use available habitat on an opportunistic basis. Furthermore, fish from sites 3 and 4 overwintered in an area where northern pike and walleye are found. Winter movements of these fish could have been related to predator avoidance. In general, overwintering grounds were not restricted in the Little Smoky River as they are in Alaskan streams (Krueger 1981).

Erratic movements around the time of freeze-up can possibly be explained by the dynamics of developing ice. Arctic grayling were observed using the edges of developing surface ice which would offer them cover and the ability to feed in well lit open water. Since anchor ice was observed, Arctic grayling could have also been forced out of pools where anchor ice enveloped logs, log jams and beaver caches that the fish were using as cover. Anchor ice was found to exclude cutthroat trout from pools containing submerged woody debris as cover (Brown and Mackay 1995).

Since the Little Smoky River is located in southern part of Arctic grayling range, it should come as no surprise that the fish exhibited complex movements in fall. Studies in more southern regions of *T. arcticus* range suggest complex and varying patterns of movements to overwintering grounds (Craig and Poulin

1975). In general, Arctic grayling in the Little Smoky River migrated downstream in fall as water temperatures and flows were decreasing. This is similar to what Craig and Poulin (1975), Tack (1980) and Hubert *et al.* (1985) found in their studies in Alaska. Ward (1951), Tack (1980) and Armstrong (1986) also mentioned that in larger rivers, grayling inhabiting the middle to upper reaches and tributaries migrate downstream to overwinter in deeper waters of the main stem.

The three radio tagged Arctic grayling suspected of moving upstream of the study section might have migrated to spring areas. The exceptions to grayling downstream migration in fall can occur if spring-fed streams and input areas are found upstream of summer rearing habitat (Stanislawski 1994). No spring areas were found in the study section as there were no open leads observed, with the exception of riffles and cascades, after water temperatures reached 0.0 °C on November 4. Furthermore, the study section froze over completely after November 30. However, spring areas could possibly exist closer to head waters of the Little Smoky River. Tack (1980), Armstrong (1986) and West *et al.* (1992) reported Arctic grayling migrating upstream into overwintering sites that have input of ground water.

CONCLUSIONS

This study found several new aspects that pertain to Arctic grayling migration to overwintering grounds. Arctic grayling fall and winter movements in a large river system are more complex than previously thought. The existence of sub-populations of grayling within a single drainage might not be new knowledge, but two distinct movement patterns within the same drainage is. In large productive rivers like the Little Smoky, grayling overwintering migration patterns vary between distant reaches of the drainage. These fish do not simply migrate downstream in fall to overwinter in deeper water of the mainstem. One should not be looking at grayling movements from just one part of their range within a drainage. To get the full picture of grayling migrations, care should be taken to examine movements of fish from as distant reaches as possible.

To explain some of the movements that grayling exhibited during their migration in fall, physical parameters like water depth and velocity, water temperature and ice production should be monitored more closely. One should find a way to relate local movements to local physical parameter changes. Do fish move in winter due to changes in physical parameters, predator avoidance or simply act opportunistically in terms of habitat selection? Do they start migration to spawning grounds in winter and under ice?

LITERATURE CITED

Armstrong, R. H. 1986. A review of Arctic grayling studies in Alaska, 1952 - 1982. Biological Papers of the University of Alaska 23:3-17.

Barber, W. E., H. Hop and J. B. Reynolds. 1985. Autumn movements of Arctic grayling on the Arctic National Wildlife Refuge as determined by radio telemetry. Proceedings of the 1985 Arctic Science Conference 36: 218-219.

Bendock, T. N. 1980. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game. Federal Aid in Fish Restoration Annual Performance Report, 1979-1980. Project F-9-12, 21(G-I-I). 31 pp.

Bidgood, B. F., 1980. Field surgical procedures for implantation of radio tags in fish. Alberta Fish and Wildlife Division, Fisheries Research Report No. 20. 9 pp.

Bishop, F. G. 1967. The biology of the Arctic grayling, *Thymallus arcticus* (Pallas), in Great Slave Lake. M.S. Thesis, University of Alberta, Edmonton. 166 pp.

Brown, R. S., S. S. Stanislawski and W. C. Mackay. 1993. Effects of frazil ice on fish. Proceedings of the Workshop on Environmental Aspects of River Ice, In T. D. Prowse (Editor), National Hydrology Research Institute, Saskatoon, Saskatchewan, 1993, NHRI Symposium Series No. 12, p. 261-278.

Brown, R. S. and W. C. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124:873-885.

Craig, P. C. and V. A. Poulin. 1975. Movements and growth of Arctic grayling (*Thymallus arcticus*) and juvenile Arctic char (*Salvelinus alpinus*) in a small Arctic stream, Alaska. Journal of the Fisheries Research Board of Canada 32:689-697.

Hop, H., W. E. Barber and J. B. Reynolds, 1986. Telemetry study of autumn migration and winter distribution of Arctic grayling on the Arctic National Wildlife Refuge. Final report to Fishery Resources, Alaska Region, U. S. Fish and Wildlife Service, Unit Cooperative Agreement 14-16-0009-1532. Alaska Cooperative Fishery Research Unit, University of Alaska Fairbanks, Fairbanks. Unit Contribution No. 21. 72 pp.

Hubert, W. A., R. S. Helzner, L. A. Lee and P. C. Nelson. 1985. Habitat suitability index models and instream flow suitability curves: Arctic grayling riverine populations. U. S. Fish and Wildlife Service Biological Report 82(10.110). 34 pp.

Kaseloo, P. A., A. H. Weatherley, J. Lotimer and M. D. Farina. 1992. A biotelemetry system recording fish activity. Journal of Fish Biology 40: 165-179.

Krueger, S. W. 1981. Freshwater habitat relationships: Arctic grayling (*Thymallus arcticus*). Alaska Department of Fish and Game. 65 pp.

Liknes, G. A. and W. R. Gould. 1987. The distribution, habitat and population characteristics of fluvial Arctic grayling (*Thymallus arcticus*) in Montana. Northwest Science 61:122-129.

McKinley, G. Power and H. E. Kowalyk. 1992. Transmitter attachment / implant - Laboratory manual. Ontario Hydro Research and University of Waterloo, Biology Department. 15 pp.

Nemetz, T. G. and J. R. MacMillan. 1988. Wound healing of incisions closed with a cyanoacrylate adhesive. Transactions of the American Fisheries Society 117: 190-195.

Skopets, M. B. and N. M. Prokop'yev. 1990. Biological characteristics of subspecies of the Arctic grayling in northeastern Asia. I. The Kamchatkan grayling - *Thymallus arcticus mertensi*. Journal of Ichthyology 30(5):43-58.

Stanislawski, S. 1994. What defines an Arctic grayling (*Thymallus arcticus*) stream? A review of literature. Department of Zoology, University of Alberta, Edmonton, Alberta. 42 pp.

Tack, S. L. 1980. Migrations and distribution of Arctic grayling, *Thymallus arcticus* (Pallas), in interior and Arctic Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, 1979-1980. Project F-9-12, 21(R-I). 32 pp.

Ward, J. C. 1951. The biology of the Arctic grayling in the southern Athabasca drainage. M.S. Thesis, University of Alberta, Edmonton. 71 pp.

West, R. L., M. W. Smith, W. E. Barber, J. B. Reynolds and H. Hop. 1992. Autumn migration and overwintering of Arctic grayling in coastal streams of the Arctic National Wildlife Refuge, Alaska. Transactions of the American Fisheries Society 121:709-715.

Winter, J. D. 1989. Underwater biotelemetry. In L. A. Nielsen, D. L. Johnson and S. S. Lampton (eds.) 1989. Fisheries Techniques. American Fisheries Society, Southern Printing Company, Inc., Blacksburg, Virginia. pp. 371-395.

APPENDIX 1

Movement maps of 34 radio tagged Arctic grayling in the Little Smoky River, Alberta. The fish were radio tagged from August 17 to November 3, 1993 and monitored from August 31, 1993 to January 15, 1994.

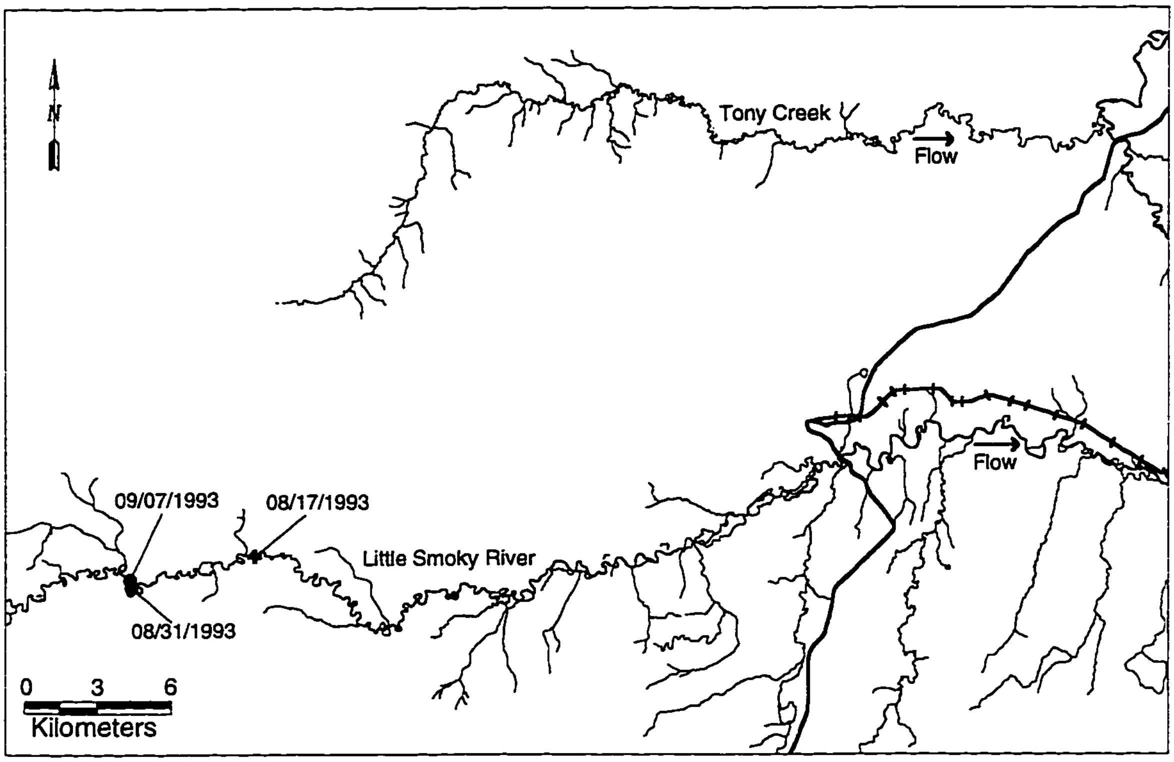

Figure A-1. Movement map of fish #1 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles). The fish was not located after September 7, 1993 as it moved upstream and out of the study reach.

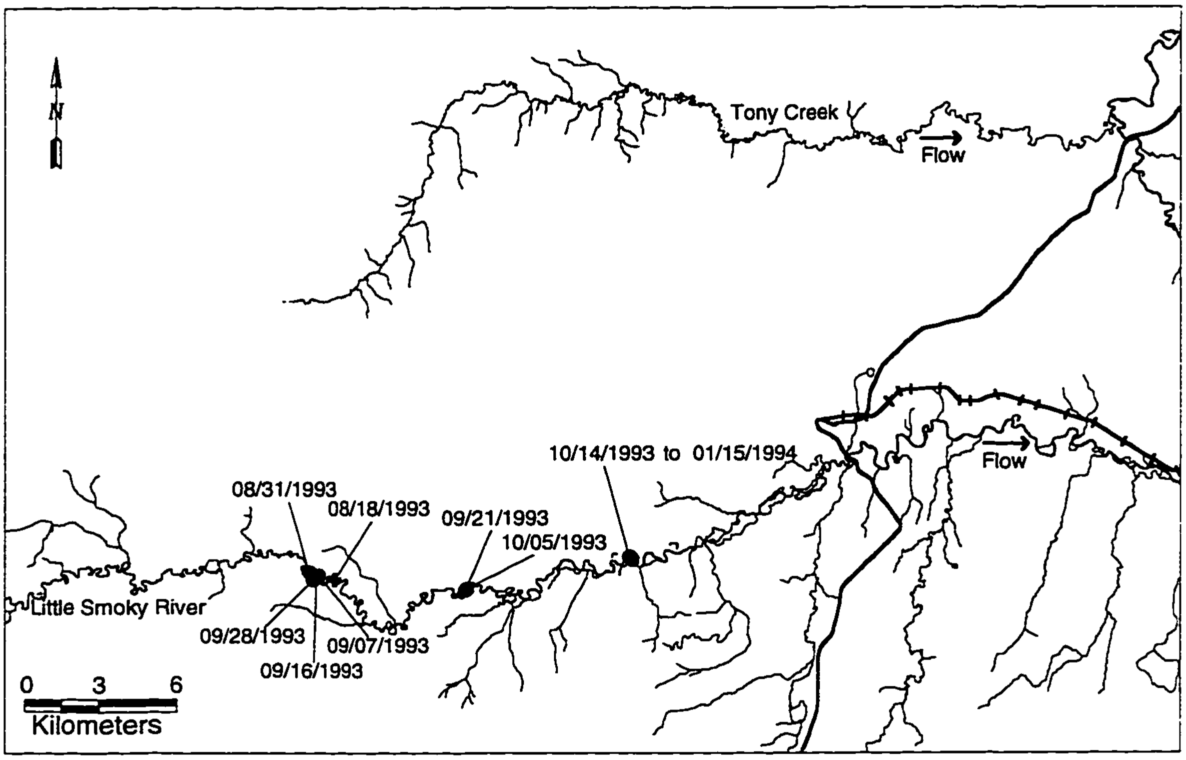

Figure A-2. Movement map of fish #2 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

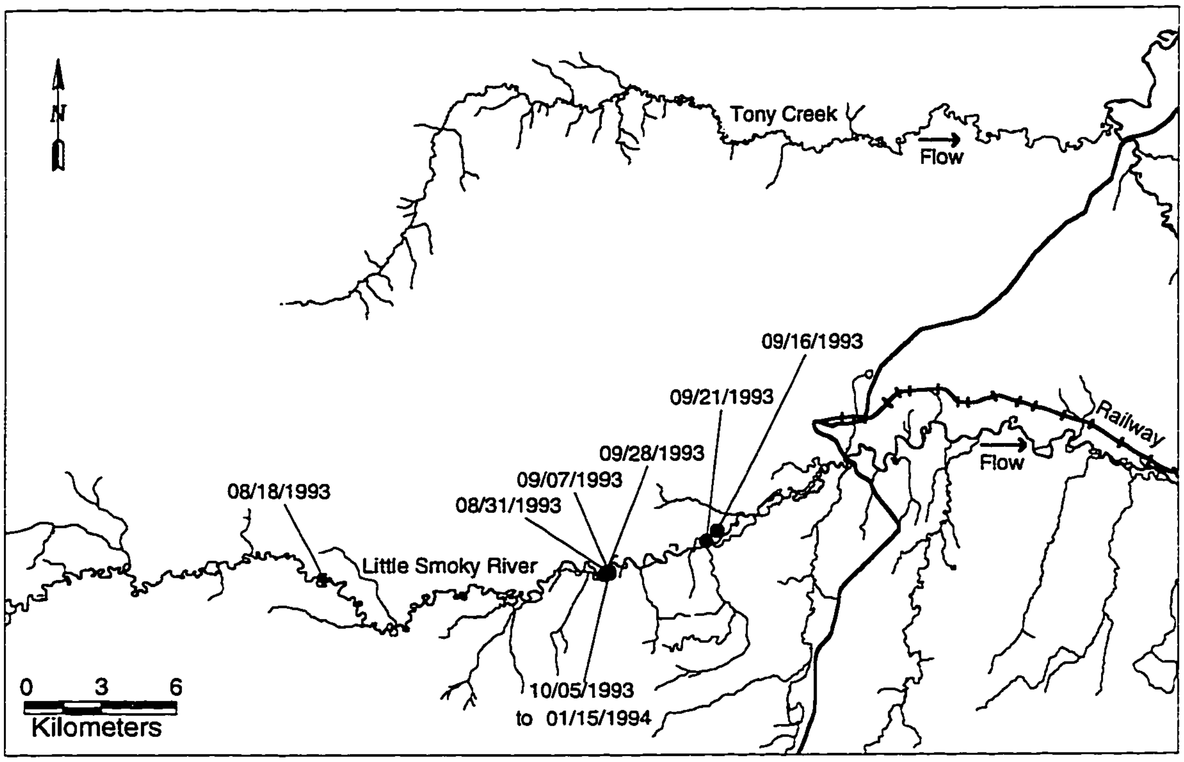

Figure A-3. Movement map of fish #3 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

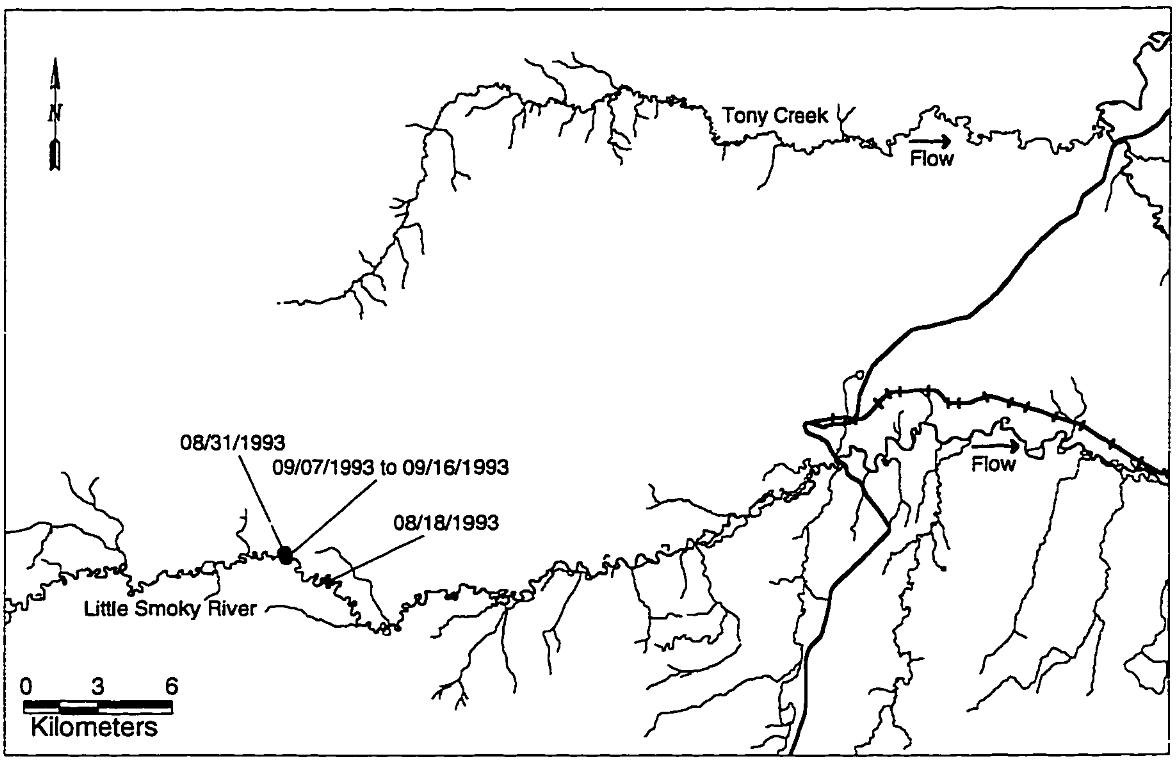

Figure A-4. Movement map of fish #4 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles). The fish was not located after September 16, 1993 as it moved upstream and out of the study reach.

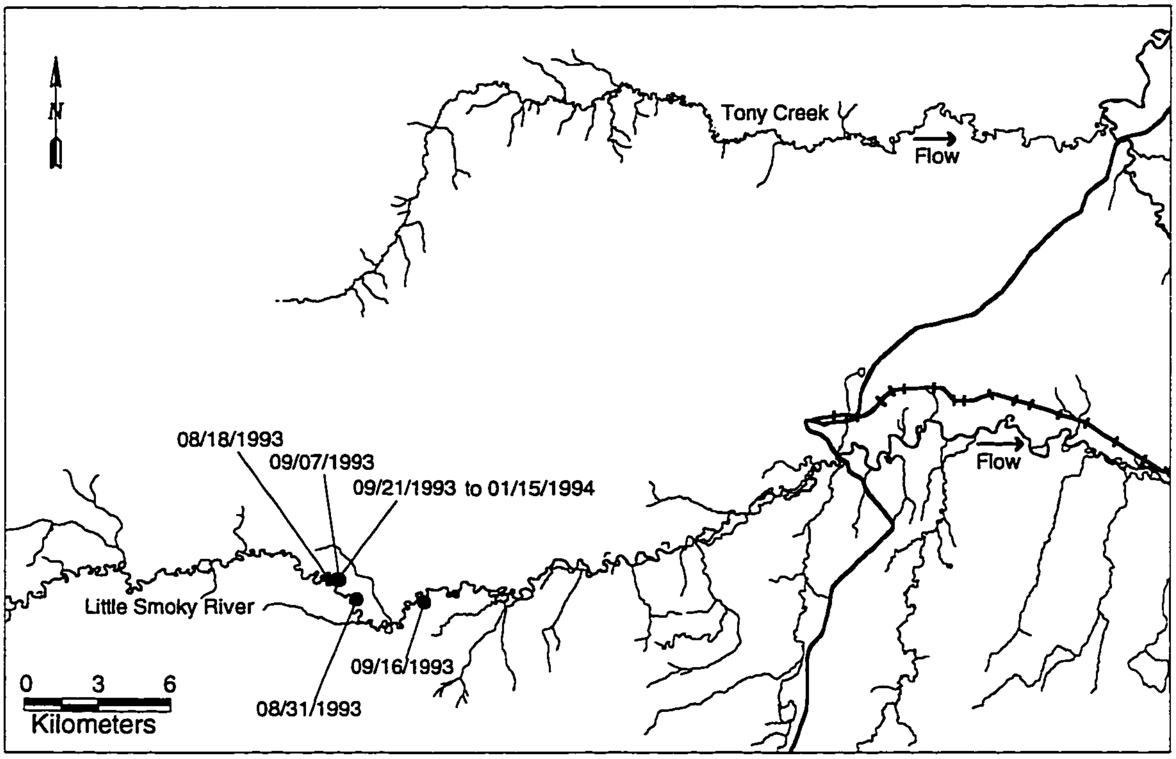

Figure A-5. Movement map of fish #5 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

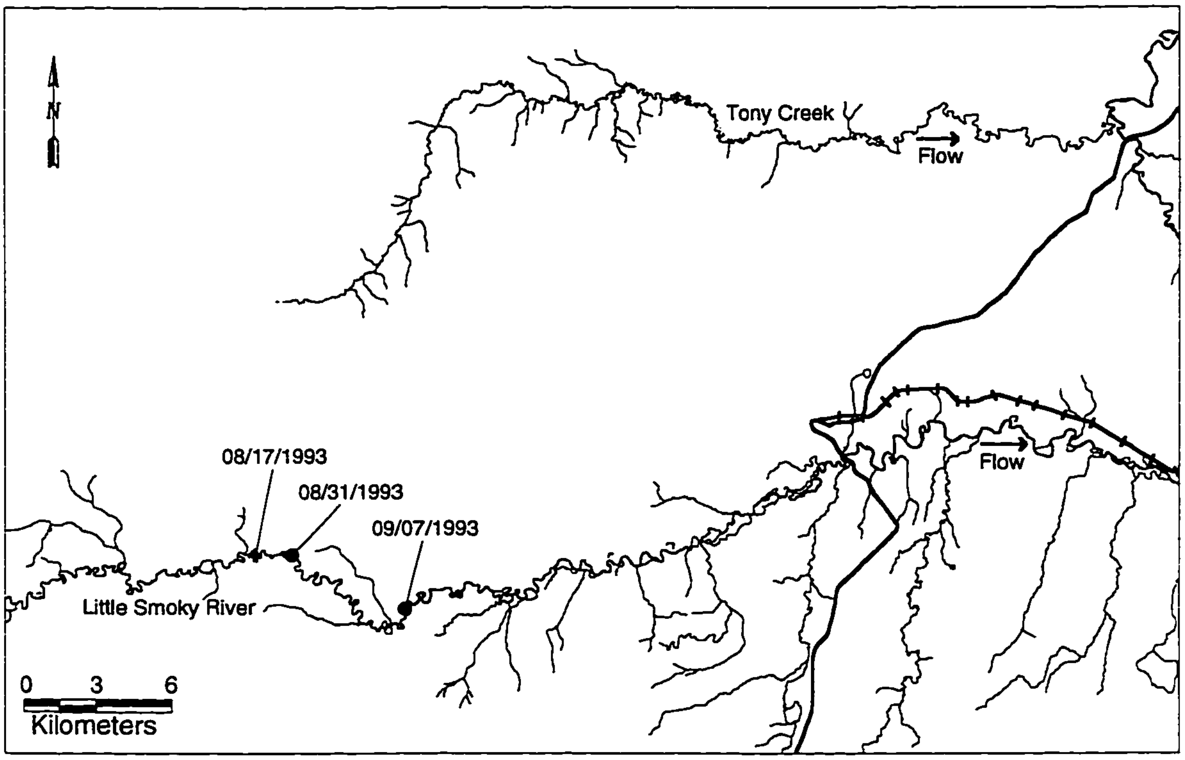

Figure A-6. Movement map of fish #6 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles). The fish was last located on September 7, 1993. It was caught by an angler on September 15, 1993.

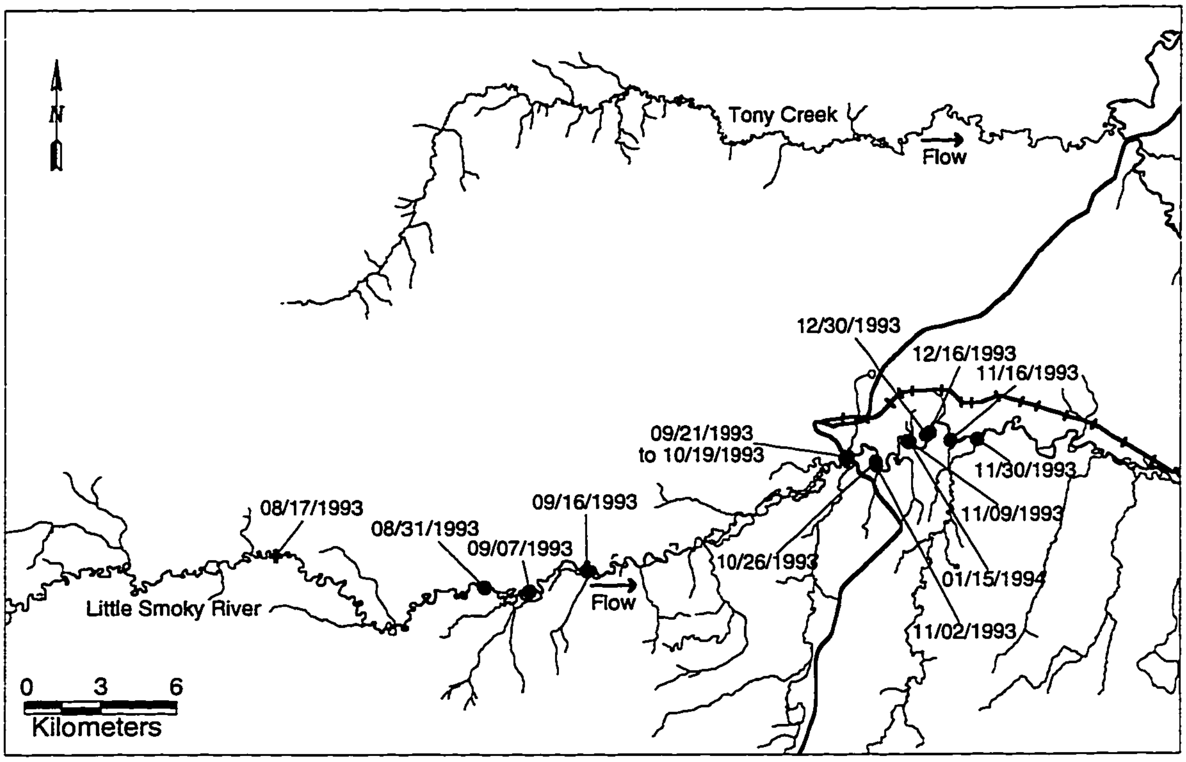

Figure A-7. Movement map of fish #7 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

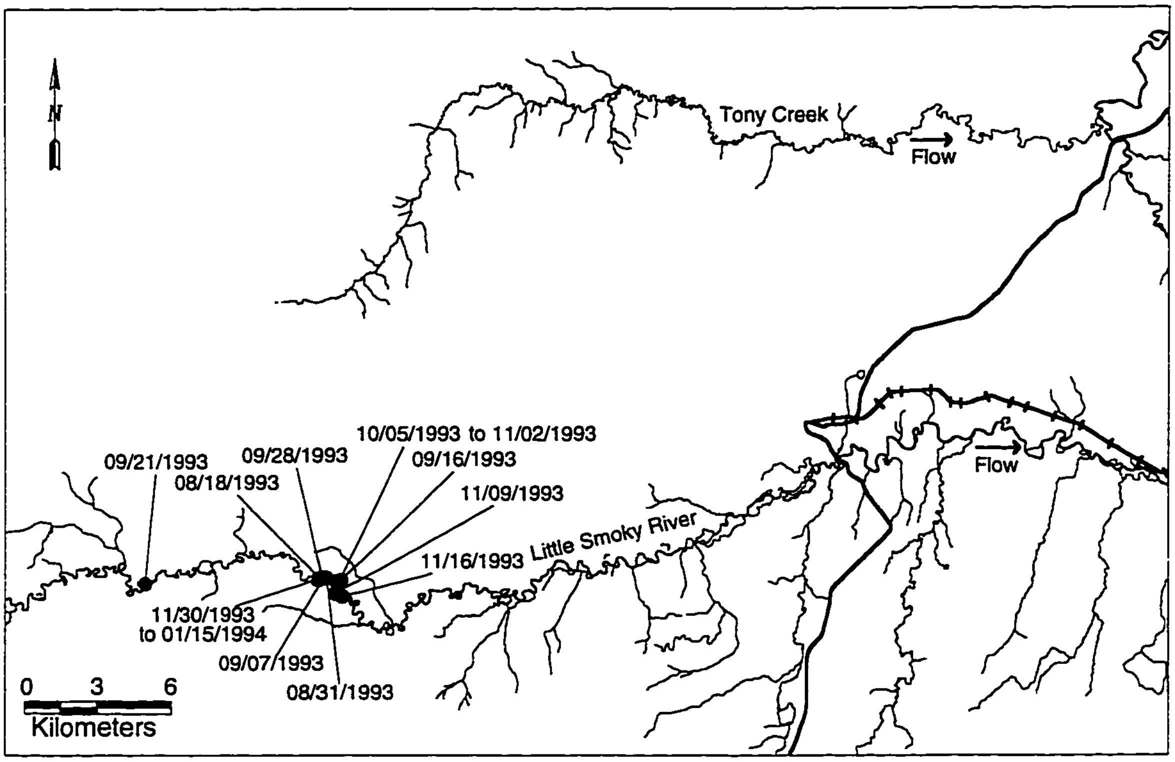

Figure A-8. Movement map of fish #8 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 18, 1993) and aerial tracking (solid circles).

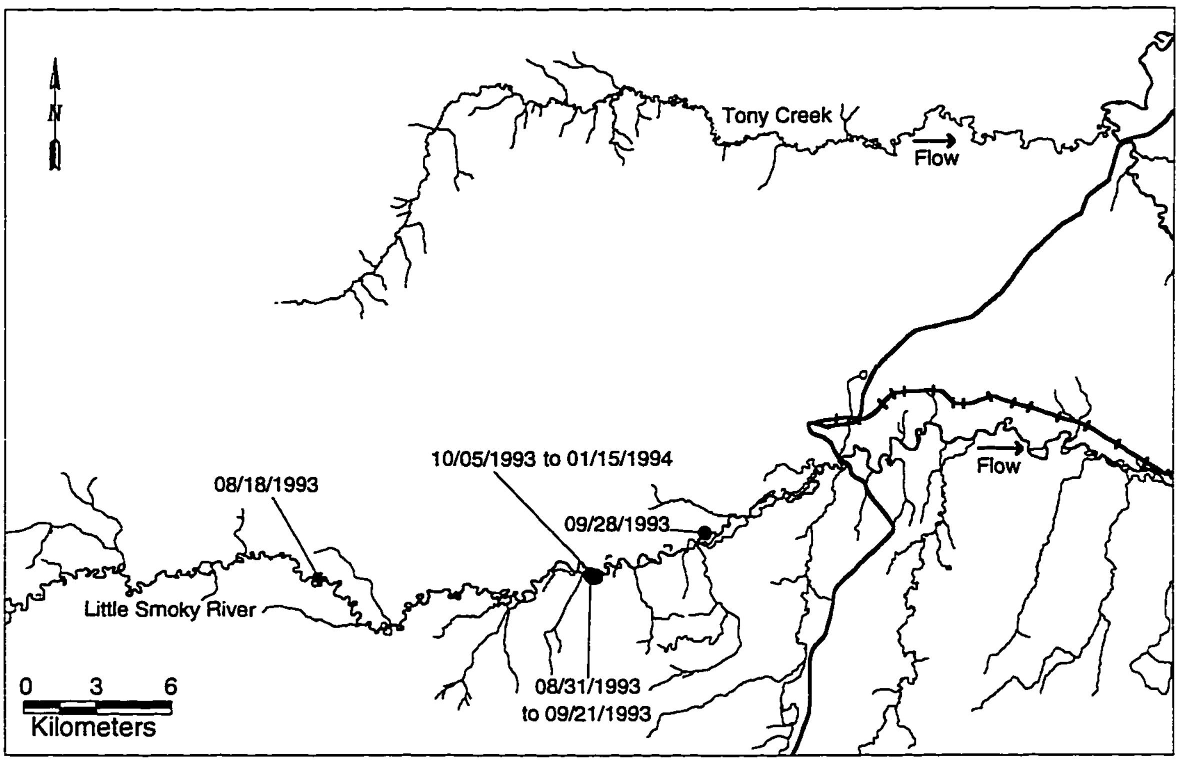

Figure A-9. Movement map of fish #9 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

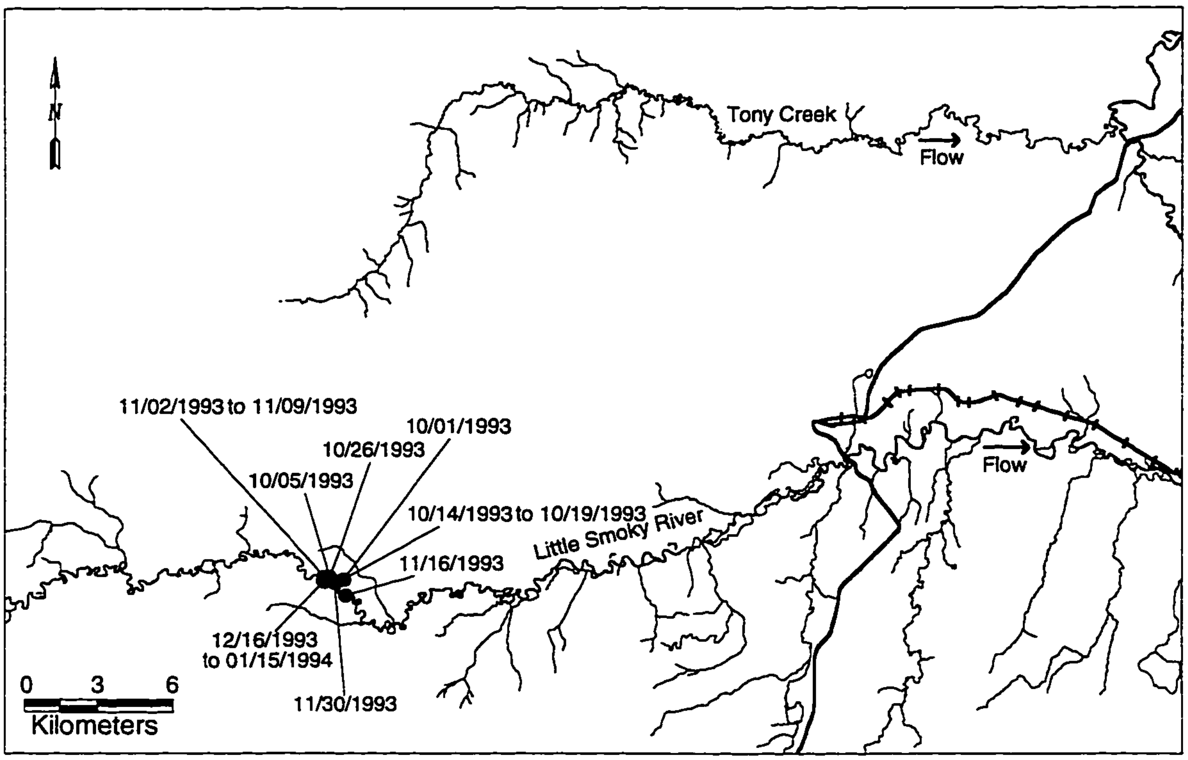

Figure A-10. Movement map of fish #10 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (October, 1, 1993) and aerial tracking (solid circles).

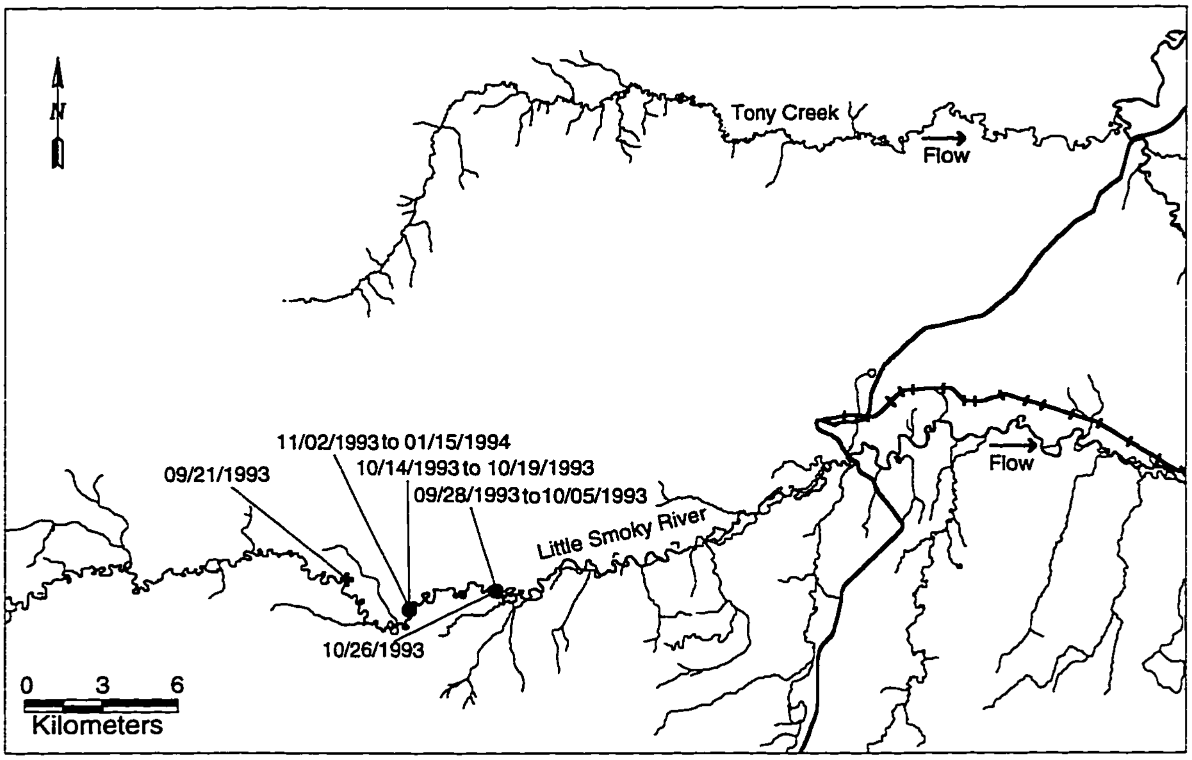

Figure A-11. Movement map of fish #11 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

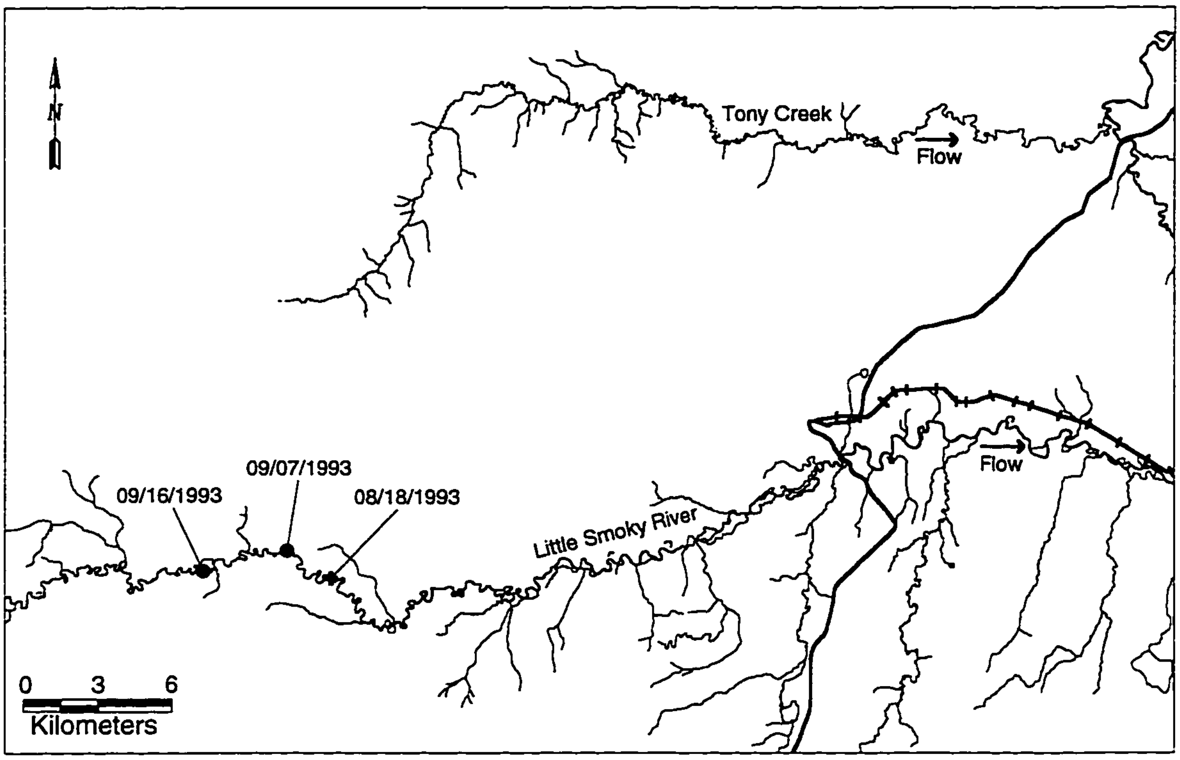

Figure A-12. Movement map of fish #12 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles). The fish was not located after September 16, 1993 as it moved upstream and out of the study reach.

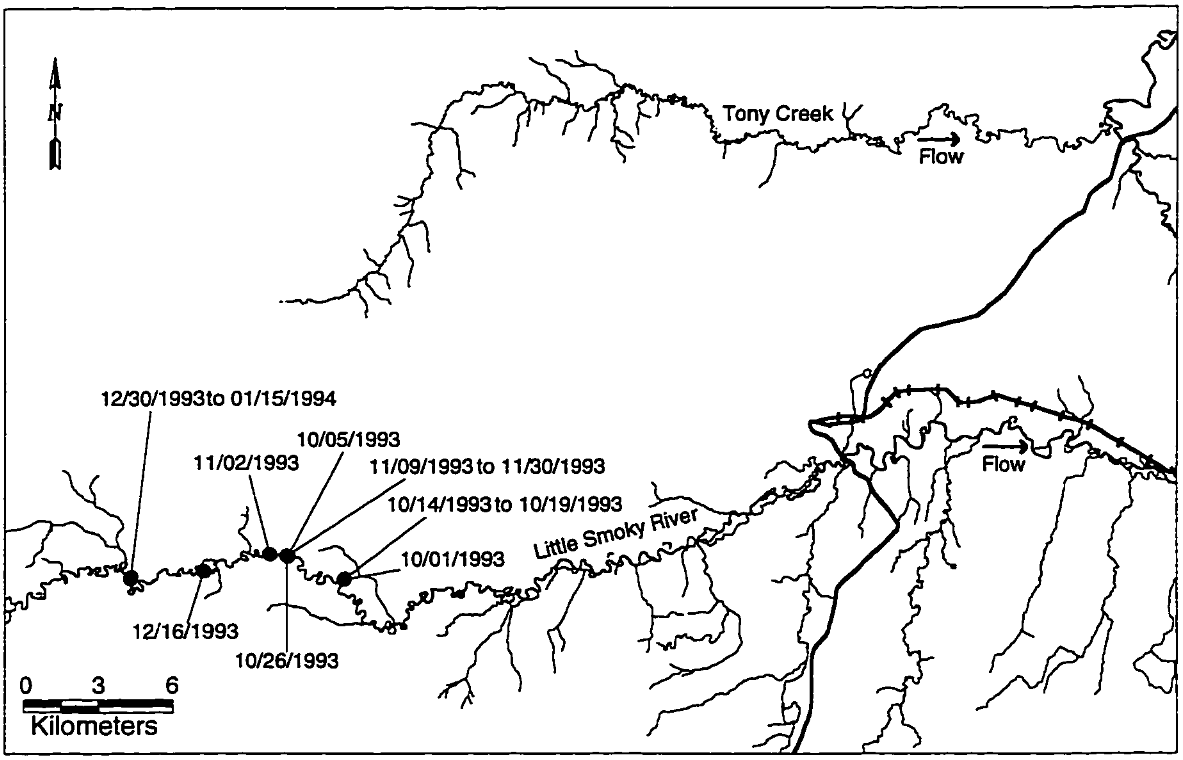

Figure A-13. Movement map of fish #13 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (October 1, 1993) and aerial tracking (solid circles).

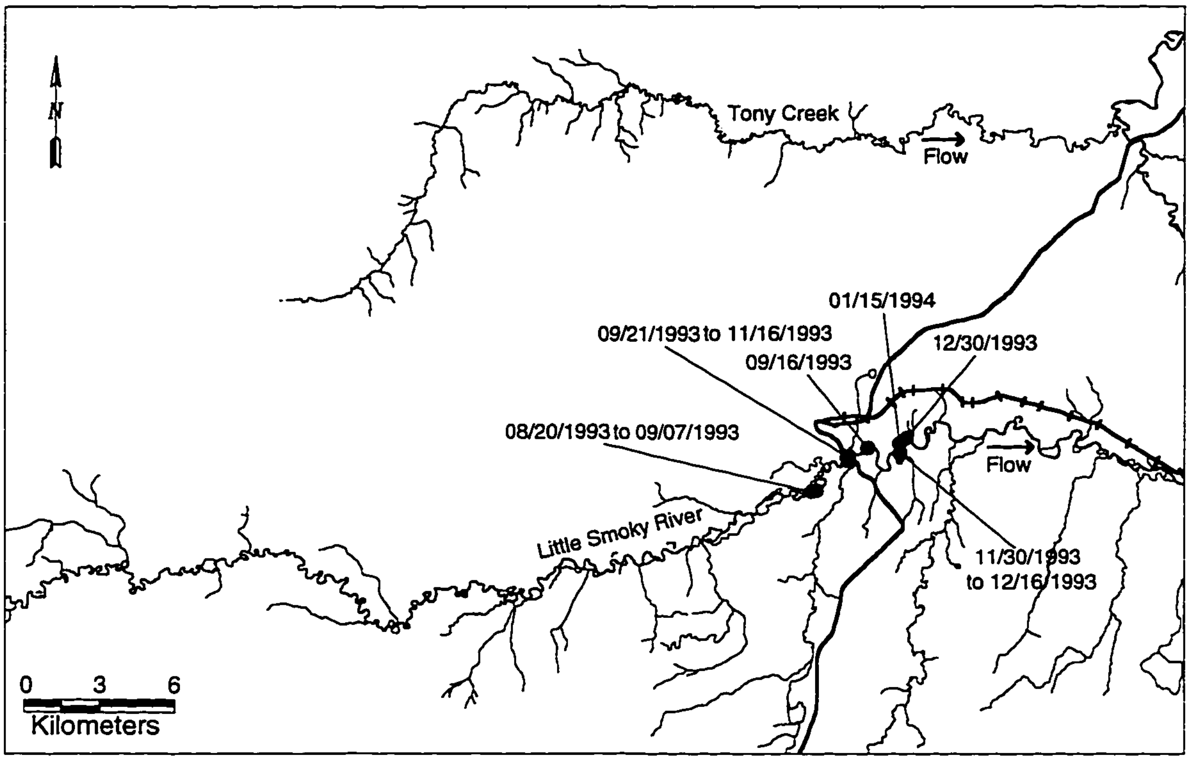

Figure A-14. Movement map of fish #14 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 20, 1993) and aerial tracking (solid circles).

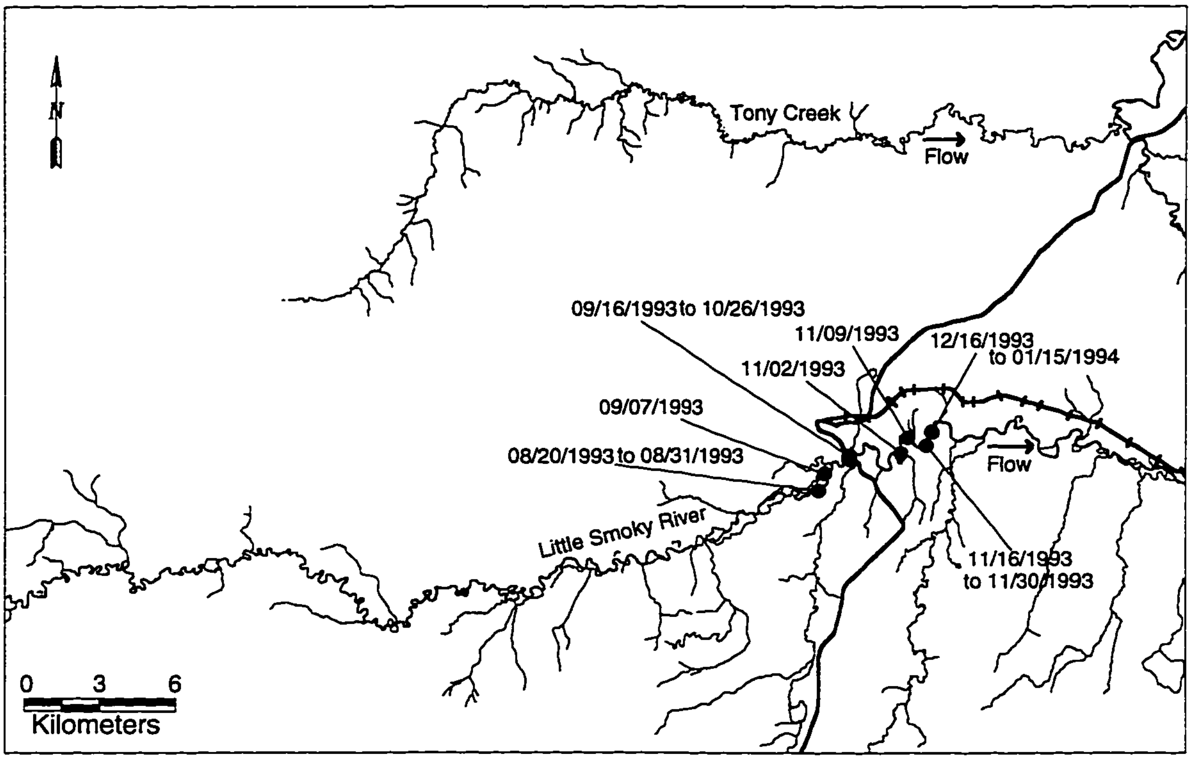

Figure A-15. Movement map of fish #15 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 20, 1993) and aerial tracking (solid circles).

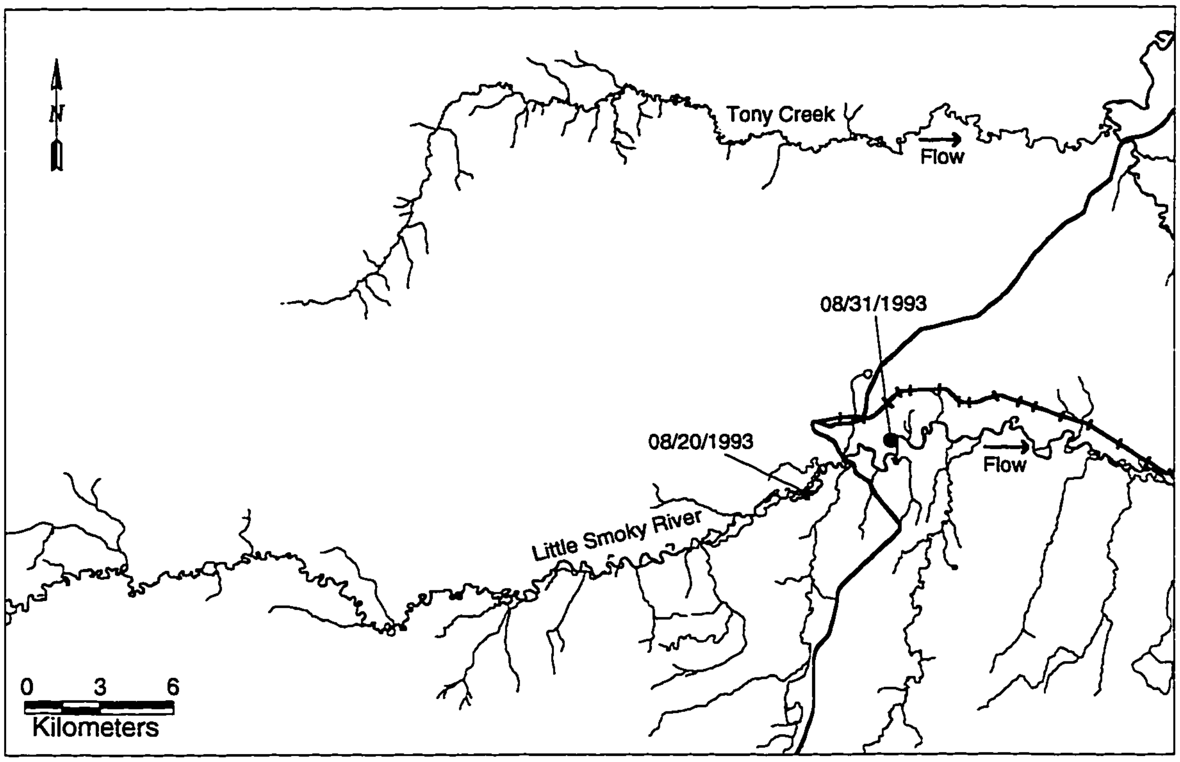

Figure A-16. Movement map of fish #16 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circle). The transmitter was last located in an osprey nest on August 31, 1993.

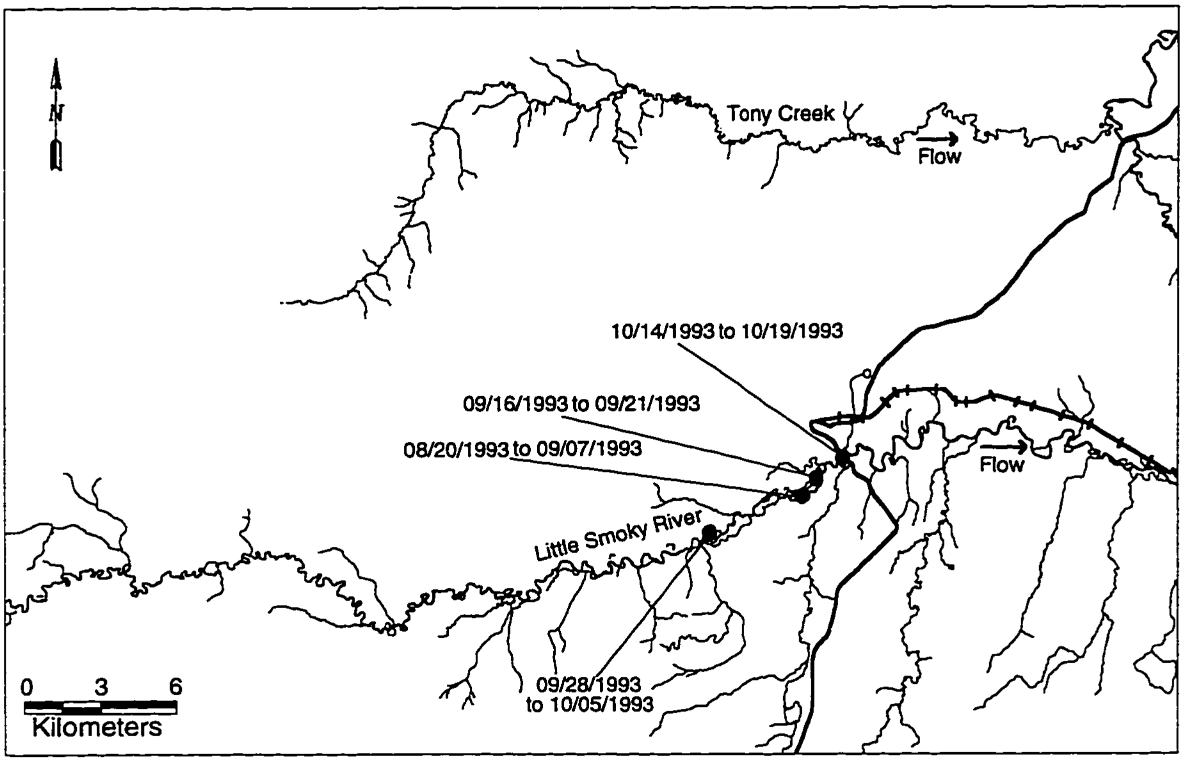

Figure A-17. Movement map of fish #17 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 20, 1993) and aerial tracking (solid circles). The fish was last located on October 19, 1993. It was caught by an angler on October 21, 1993.

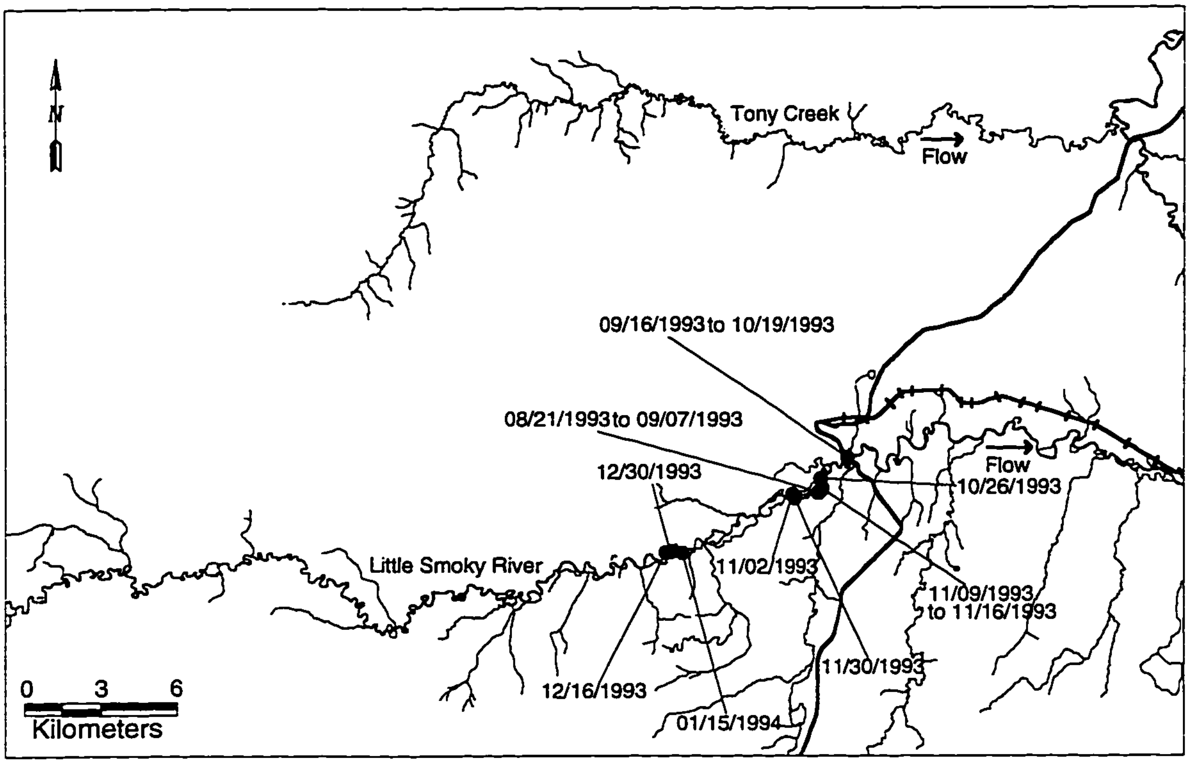

Figure A-18. Movement map of fish #18 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 21, 1993) and aerial tracking (solid circles).

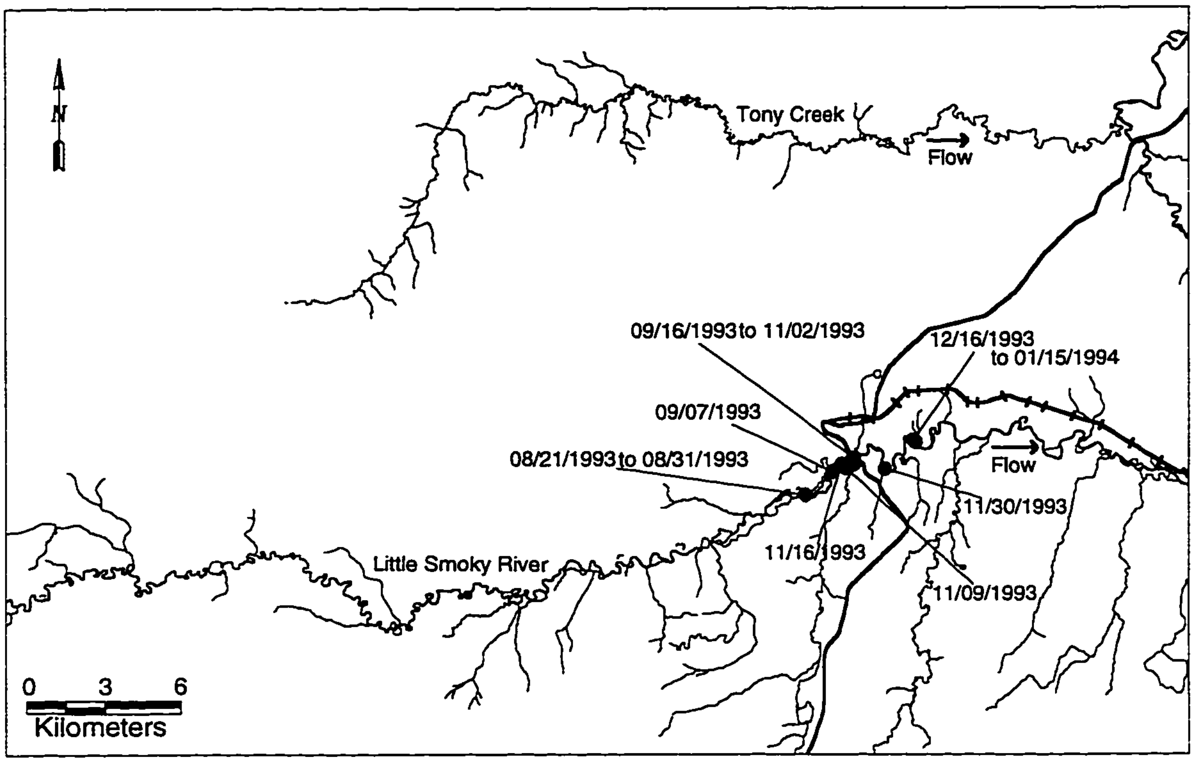

Figure A-19. Movement map of fish #19 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 21, 1993) and aerial tracking (solid circles).

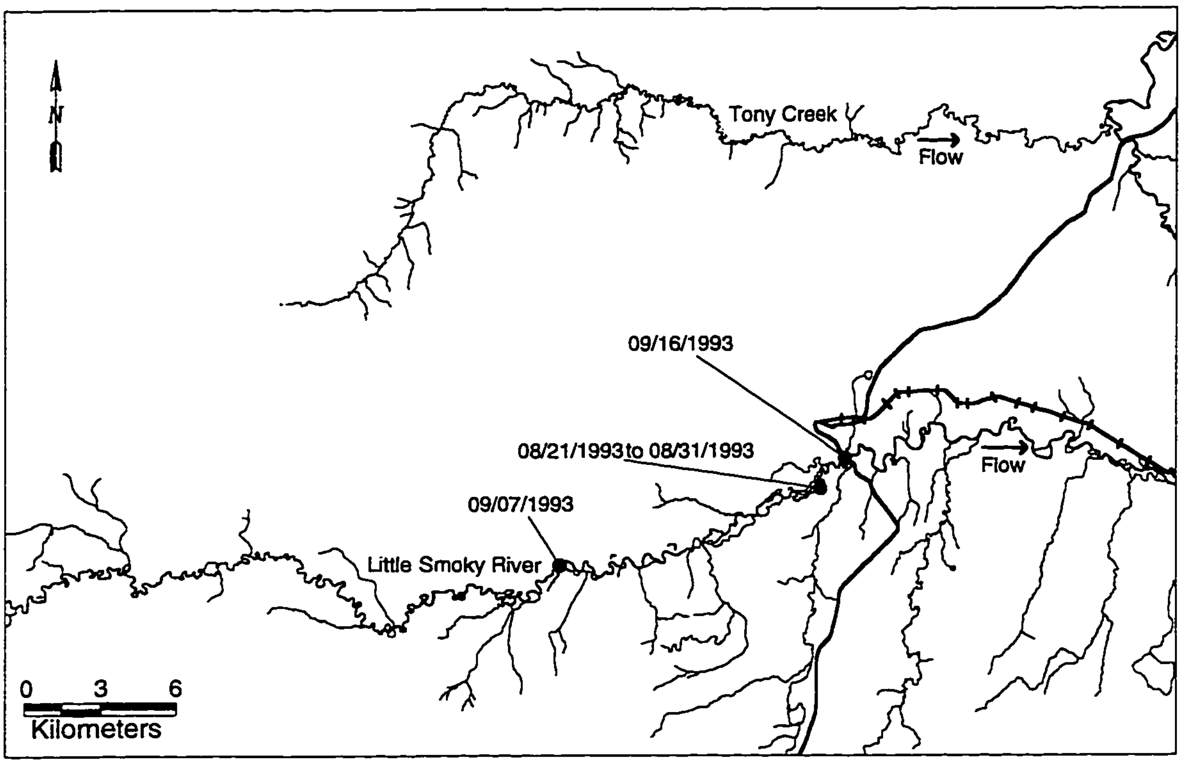

Figure A-20. Movement map of fish #20 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 21, 1993) and aerial tracking (solid circles). The fish was last located on September 16, 1993. It was caught by an angler on September 19, 1993.

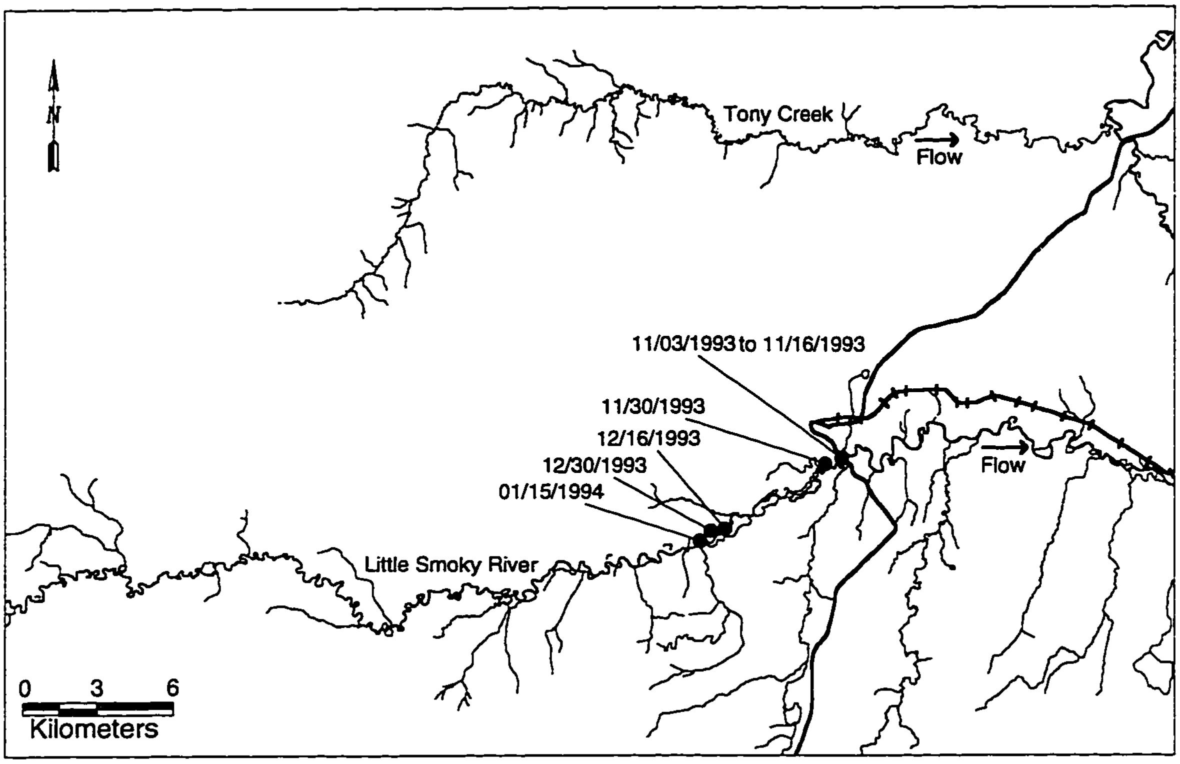

Figure A-21. Movement map of fish #21 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (November 3, 1993) and aerial tracking (solid circles).

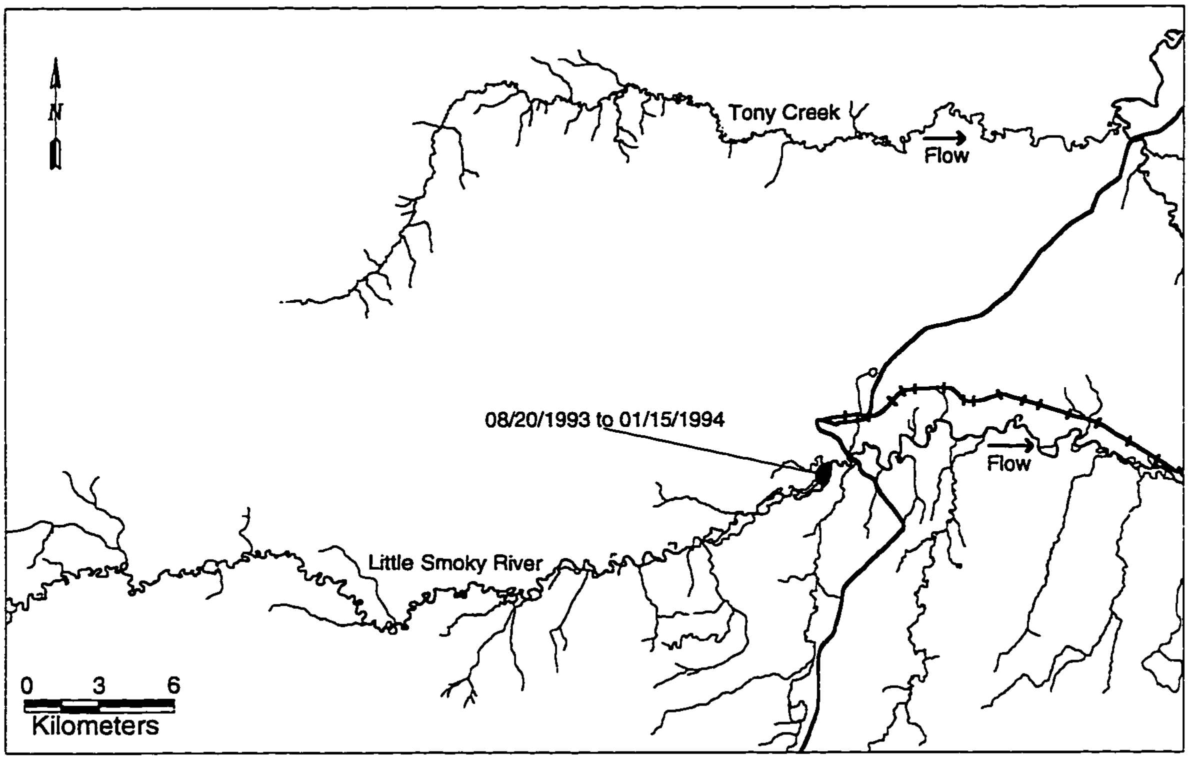

Figure A-22. Movement map of fish #22 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 20, 1993) and aerial tracking (solid circle).

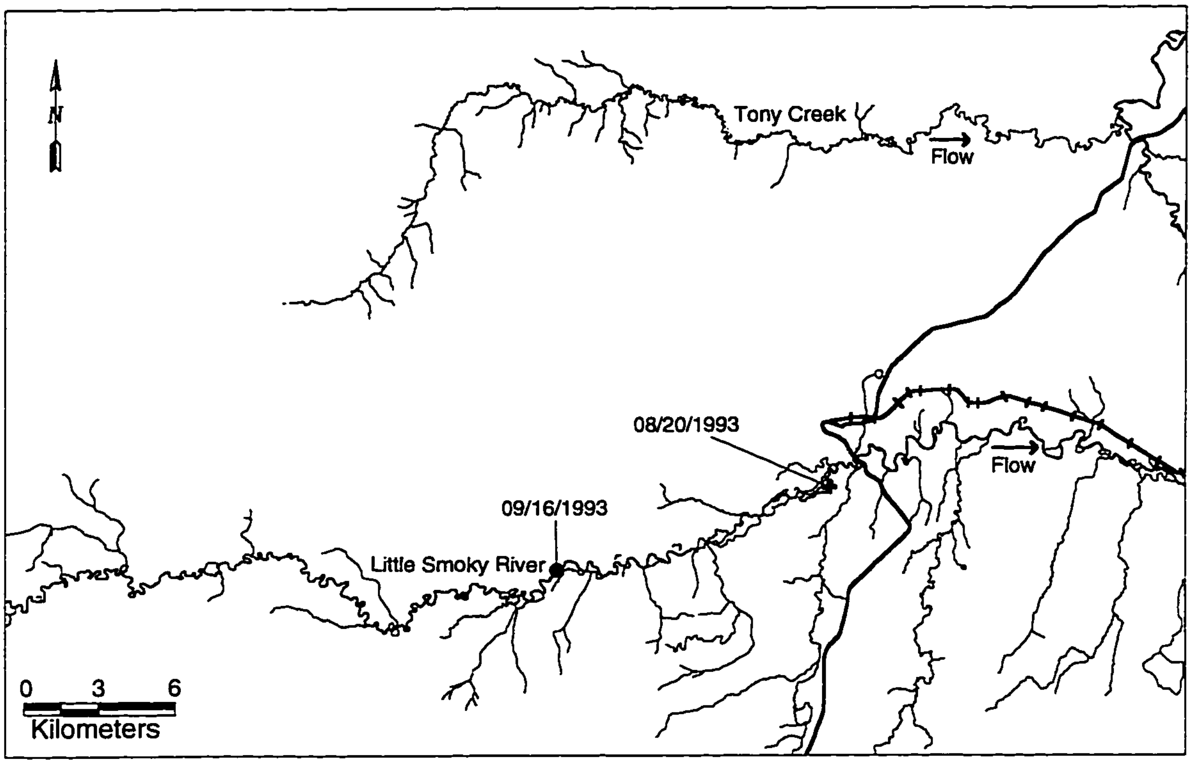

Figure A-23. Movement map of fish #23 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circle). The fish was not located after September 16, 1993 and its fate is unknown.

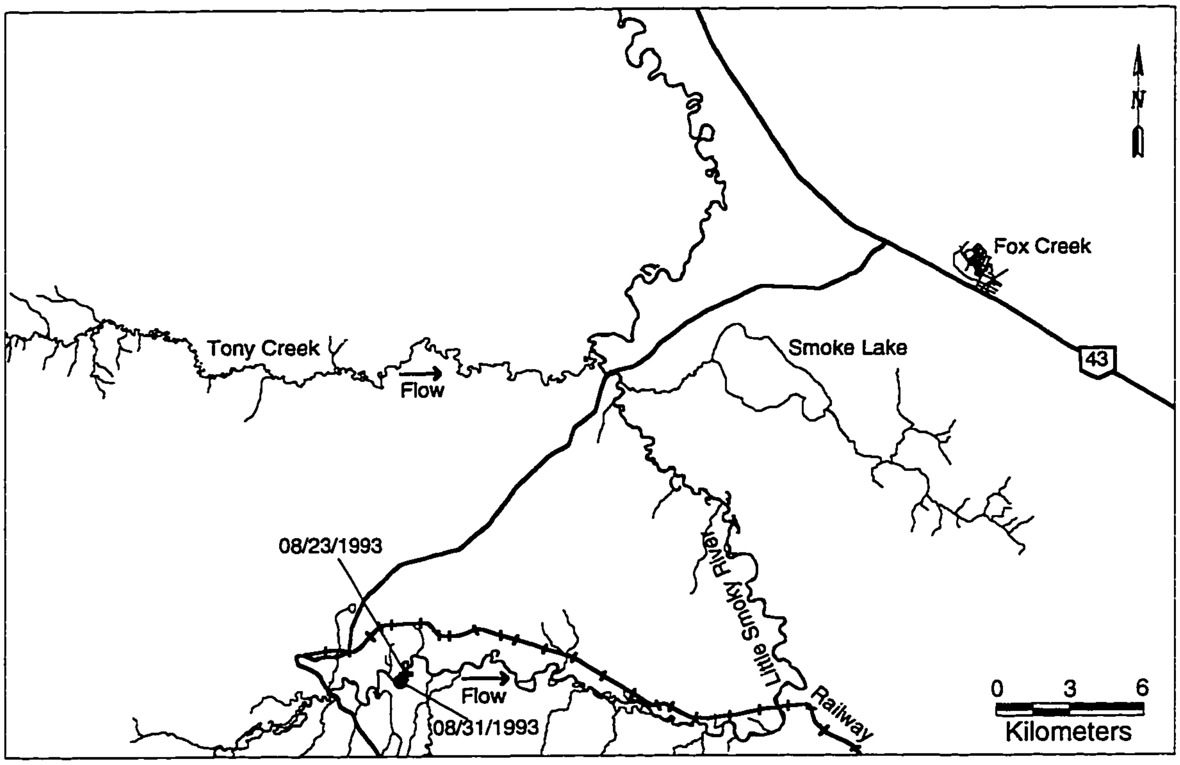

Figure A-24. Movement map of fish #24 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circle). The fish was not located after August 31, 1993 and its fate is unknown.

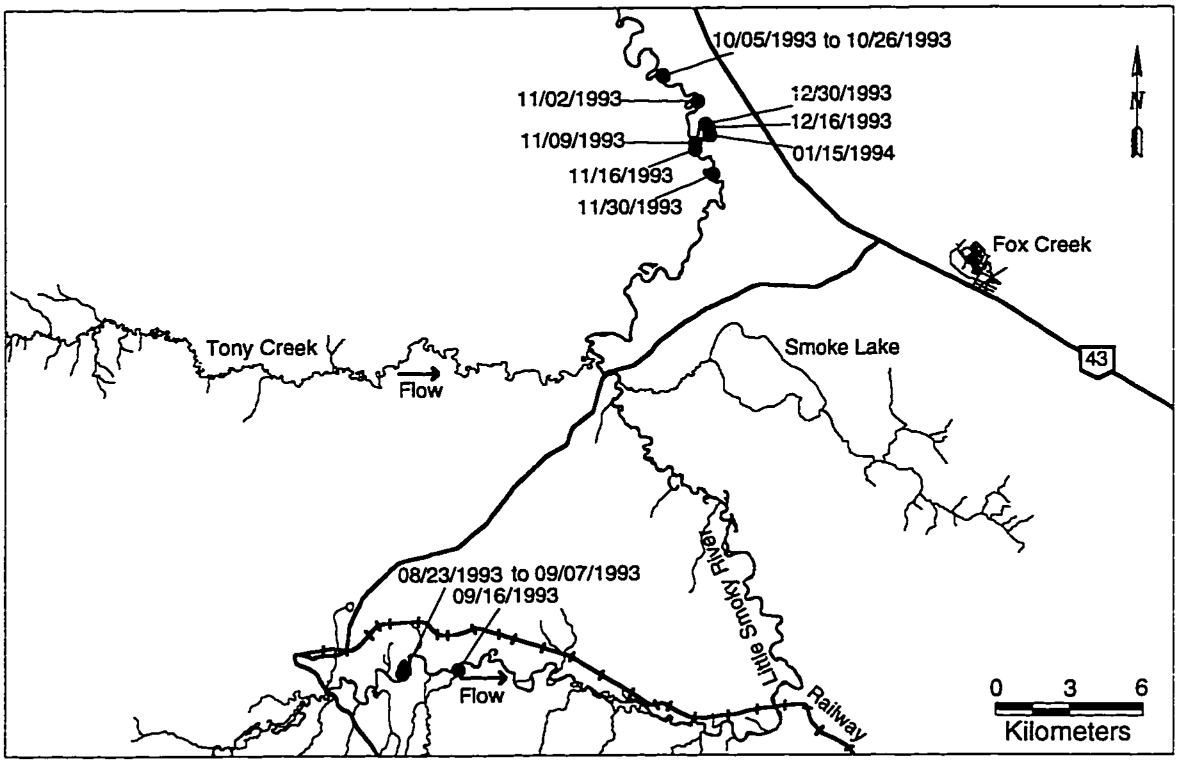

Figure A-25. Movement map of fish #25 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 23, 1993) and aerial tracking (solid circles).

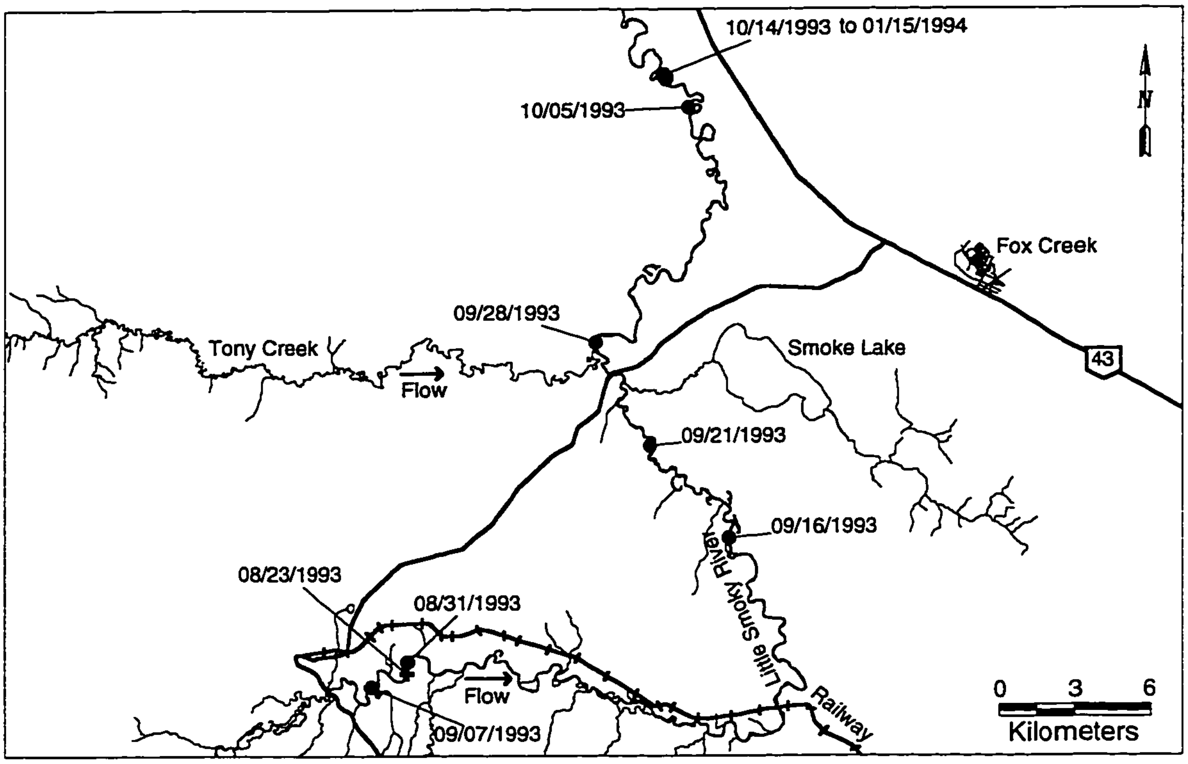

Figure A-26. Movement map of fish #26 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

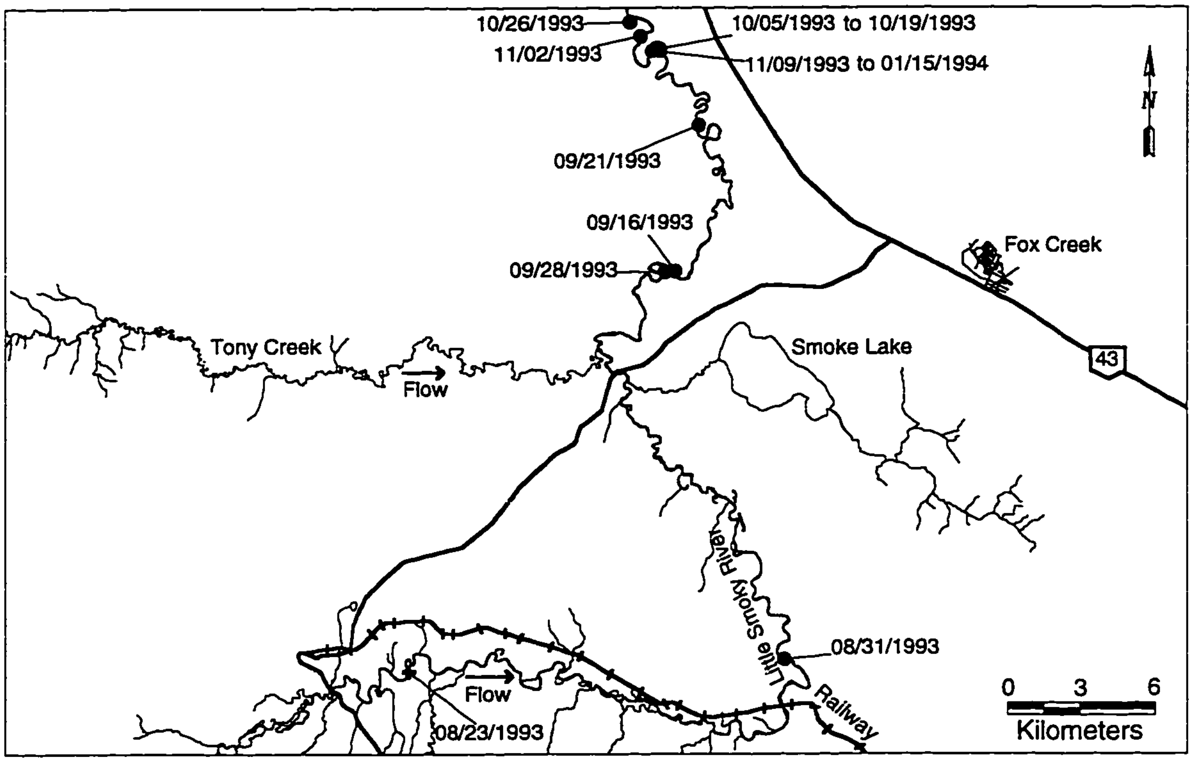

Figure A-27. Movement map of fish #27 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (solid cross) and aerial tracking (solid circles).

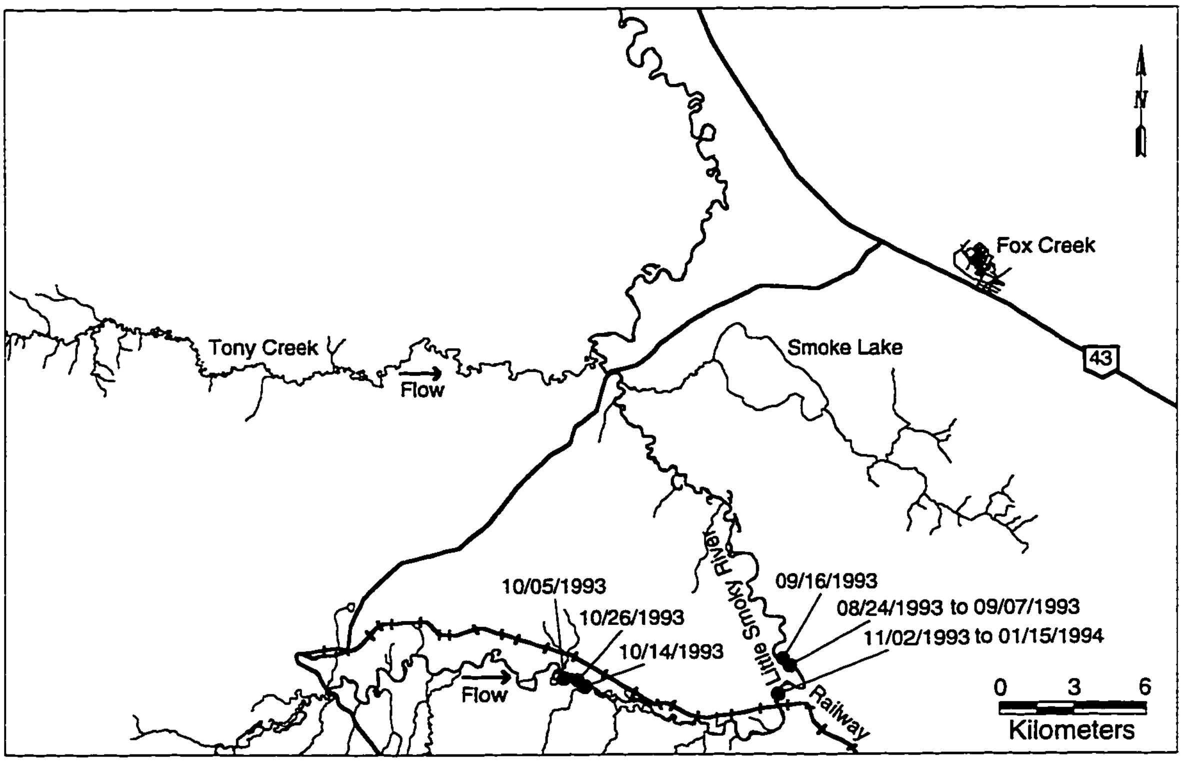

Figure A-28. Movement map of fish #28 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 24, 1993) and aerial tracking (solid circles).

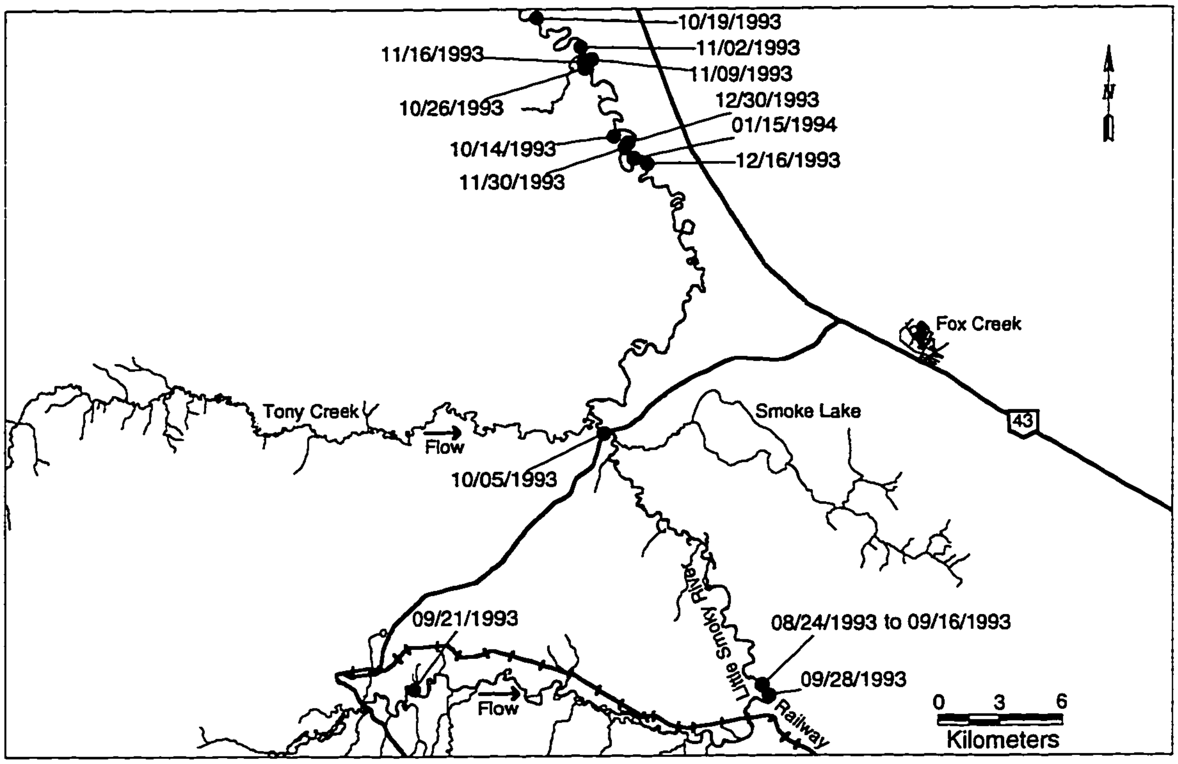

Figure A-29. Movement map of fish #29 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 24, 1993) and aerial tracking (solid circles).

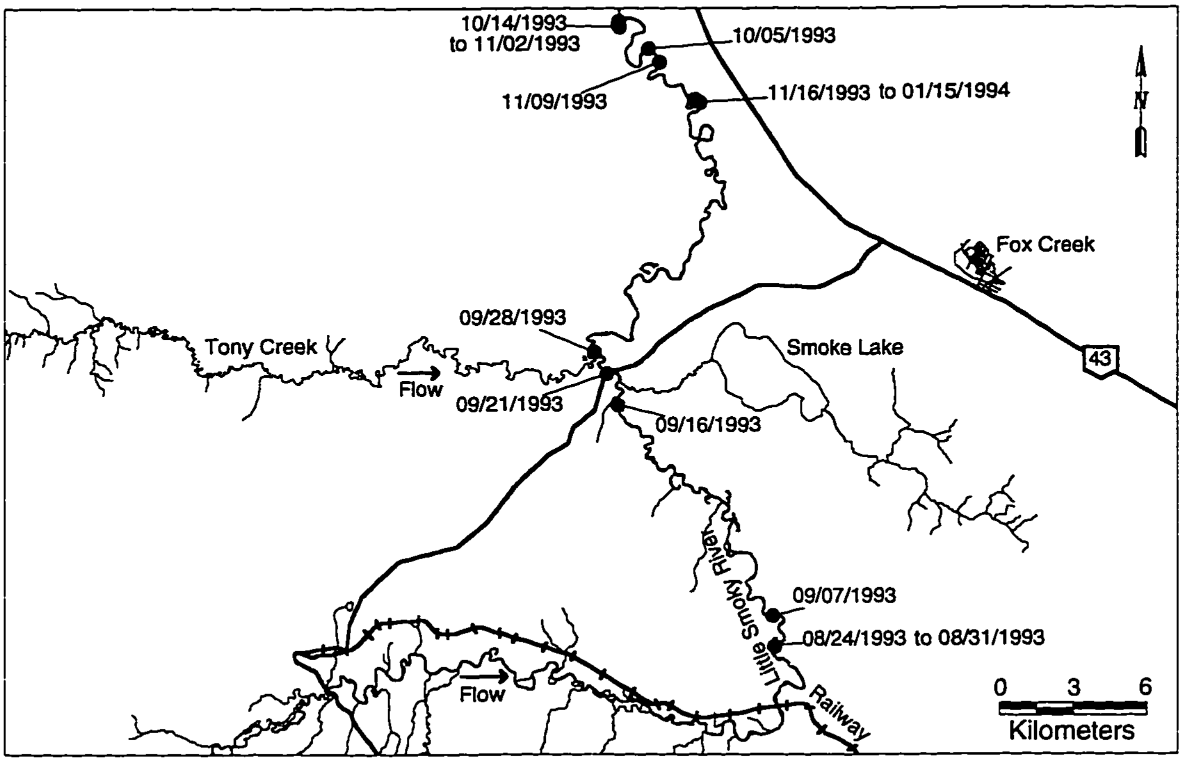

Figure A-30. Movement map of fish #30 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 24, 1993) and aerial tracking (solid circles).

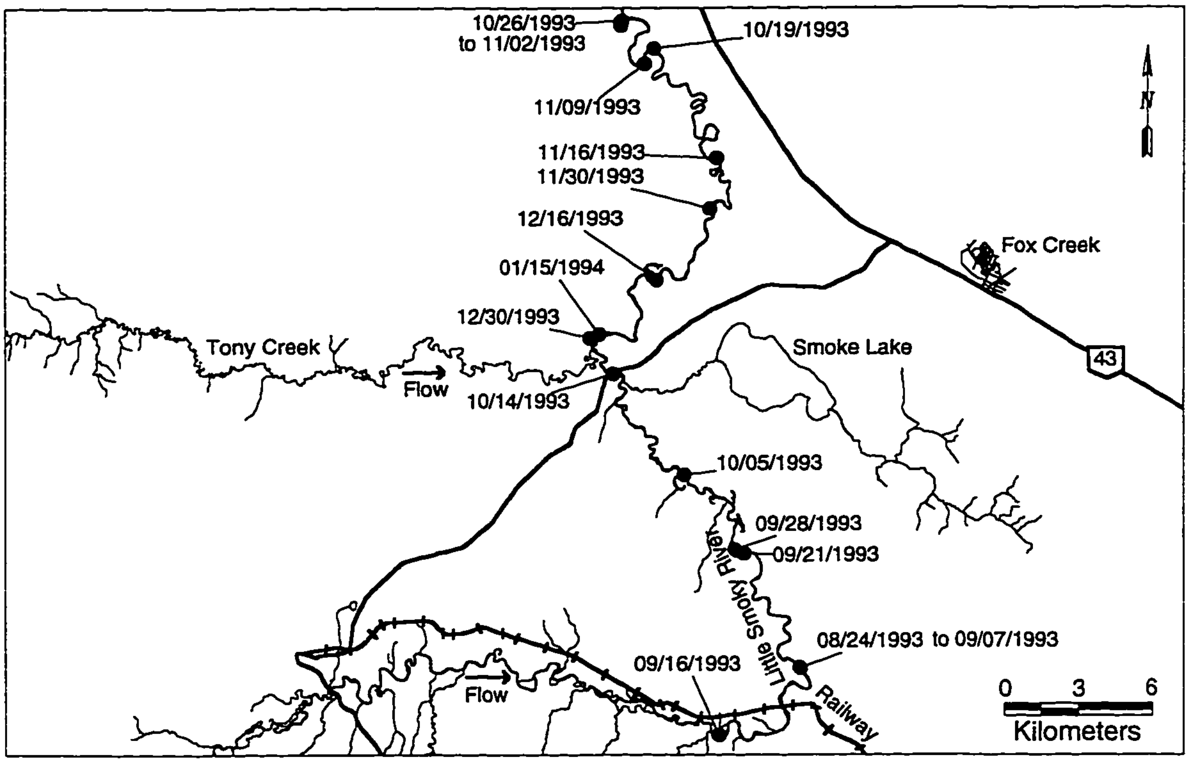

Figure A-31. Movement map of fish #31 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 24, 1993) and aerial tracking (solid circles).

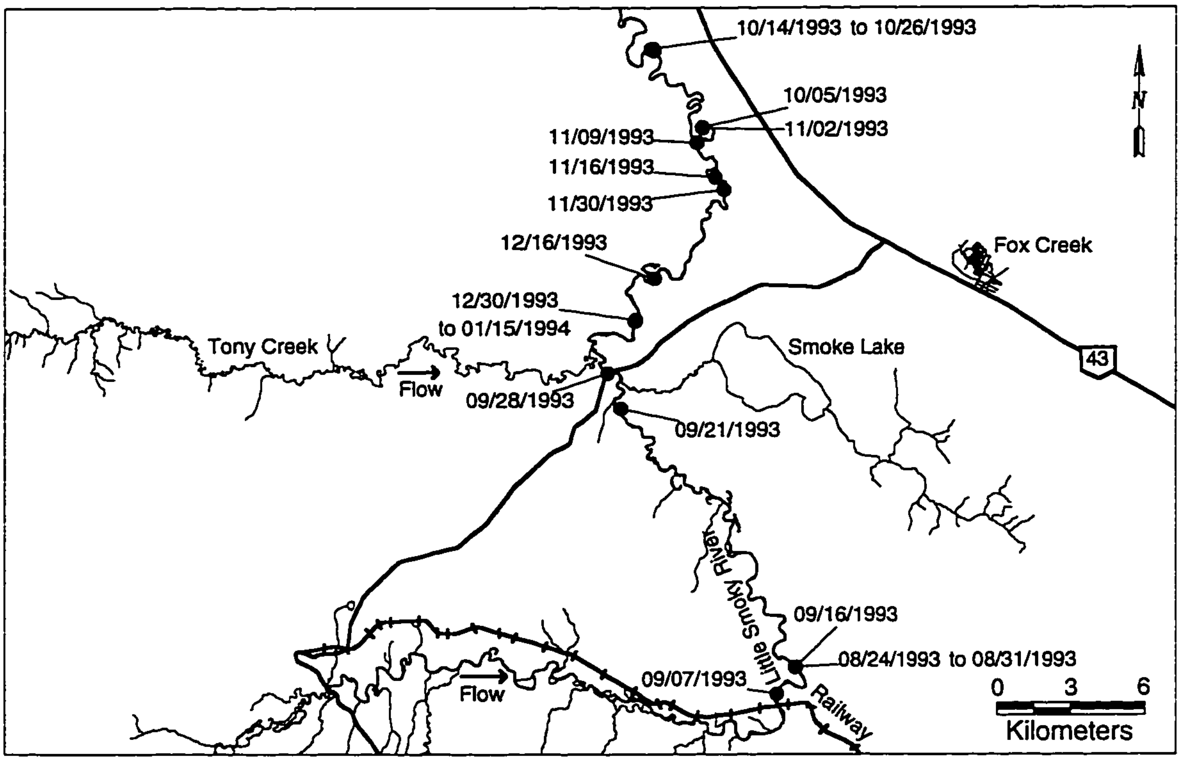

Figure A-32. Movement map of fish #32 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 24, 1993) and aerial tracking (solid circles).

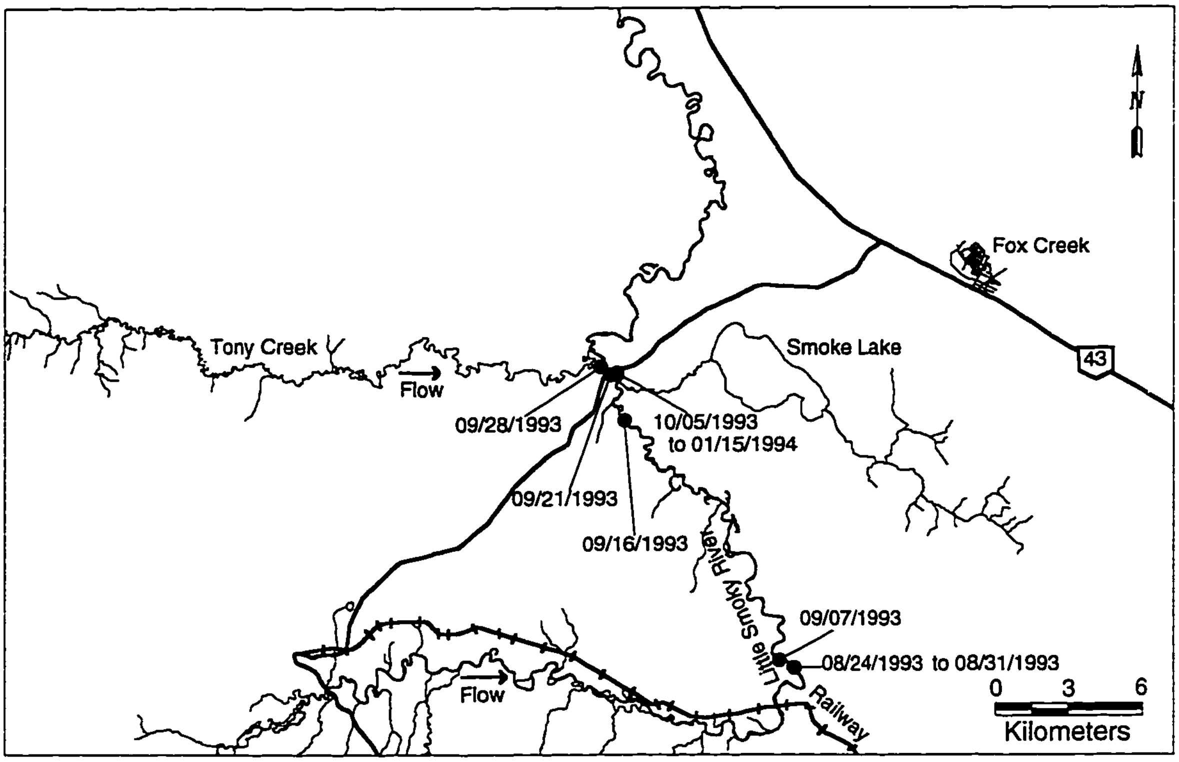

Figure A-33. Movement map of fish #33 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 24, 1993) and aerial tracking (solid circles).

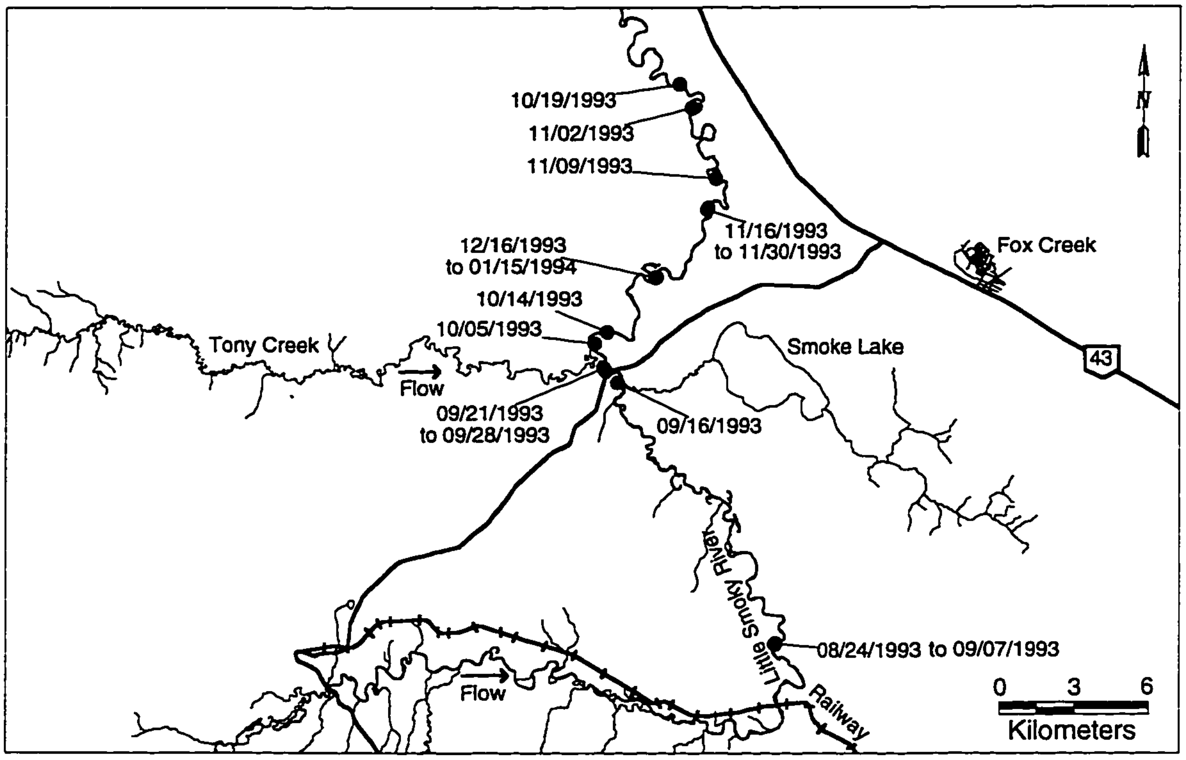

Figure A-34. Movement map of fish #34 in the Little Smoky River, Alberta. The temporal locations were determined by site of transmitter implantation (August 24, 1993) and aerial tracking (solid circles).

APPENDIX 2

Movement data of 34 radio tagged Arctic grayling in the Little Smoky River, Alberta. The fish were radio tagged from August 17 to November 3, 1993 and monitored from August 31, 1993 to January 15, 1994

Fish Number	Site	Date	Distance Moved (km)	Days Since Last Location	Movement Rate (km/day)	Direction
1	1	8/31/93	9.66	14	0.69	up
1	1	9/7/93	0.49	7	0.07	up
2	1	8/31/93	2.49	13	0.19	up
2	1	9/7/93	0.77	7	0.11	down
2	1	9/16/93	0.09	9	0.01	up
2	1	9/21/93	14.38	5	2.88	down
2	1	9/28/93	14.60	7	2.09	up
2	1	10/5/93	14.67	7	2.10	down
2	1	10/14/93	11.49	9	1.28	down
2	1	10/19/93	0.18	5	0.04	down
2	1	10/26/93	0.00	7	0.00	none
2	1	11/2/93	0.13	7	0.02	up
2	1	11/9/93	0.06	7	0.01	down
2	1	11/16/93	0.05	7	0.01	up
2	1	11/30/93	0.00	14	0.00	none
2	1	12/16/93	0.05	16	0.00	down
2	1	12/30/93	0.00	14	0.00	none
2	1	1/15/94	0.03	16	0.00	up
3	1	8/31/93	22.85	13	1.76	down
3	1	9/7/93	0.00	7	0.00	none
3	1	9/16/93	7.52	9	0.84	down
3	1	9/21/93	0.92	5	0.18	up
3	1	9/28/93	6.87	7	0.98	up
3	1	10/5/93	0.25	7	0.04	down
3	1	10/14/93	0.11	9	0.01	up
3	1	10/19/93	0.10	5	0.02	down
3	1	10/26/93	0.00	7	0.00	none
3	1	11/2/93	0.02	7	0.00	up
3	1	11/9/93	0.00	7	0.00	none
3	1	11/16/93	0.02	7	0.00	down
3	1	11/30/93	0.00	14	0.00	none
3	1	12/16/93	0.00	16	0.00	none
3	1	12/30/93	0.00	14	0.00	none
3	1	1/15/94	0.00	16	0.00	none
4	1	8/31/93	4.49	13	0.35	up
4	1	9/7/93	0.35	7	0.05	down
4	1	9/16/93	0.00	9	0.00	none
5	1	8/31/93	2.73	13	0.21	down
5	1	9/7/93	2.21	7	0.32	up
5	1	9/16/93	9.71	9	1.08	down
5	1	9/21/93	9.79	5	1.96	up
5	1	9/28/93	0.00	7	0.00	none
5	1	10/5/93	0.05	7	0.01	up
5	1	10/14/93	0.00	9	0.00	none
5	1	10/19/93	0.07	5	0.01	down
5	1	10/26/93	0.00	7	0.00	none
5	1	11/2/93	0.00	7	0.00	none
5	1	11/9/93	0.00	7	0.00	none
5	1	11/16/93	0.03	7	0.00	up
5	1	11/30/93	0.02	14	0.00	down
5	1	12/16/93	0.00	16	0.00	none
5	1	12/30/93	0.00	14	0.00	none
5	1	1/15/94	0.04	16	0.00	up
6	1	8/31/93	2.37	14	0.17	down
6	1	9/7/93	11.76	7	1.68	down
7	1	8/31/93	18.70	14	1.34	down
7	1	9/7/93	3.55	7	0.51	down

Fish Number	Site	Date	Distance Moved (km)	Days Since Last Location	Movement Rate (km/day)	Direction
7	1	9/16/93	3.73	9	0.41	down
7	1	9/21/93	18.54	5	3.71	down
7	1	9/28/93	0.02	7	0.00	up
7	1	10/5/93	0.00	7	0.00	none
7	1	10/14/93	0.00	9	0.00	none
7	1	10/19/93	0.03	5	0.01	up
7	1	10/26/93	2.13	7	0.30	down
7	1	11/2/93	0.16	7	0.02	down
7	1	11/9/93	2.79	7	0.40	down
7	1	11/16/93	3.71	7	0.53	down
7	1	11/30/93	1.17	14	0.08	down
7	1	12/16/93	2.91	16	0.18	up
7	1	12/30/93	0.62	14	0.04	up
7	1	1/15/94	1.29	16	0.08	up
8	1	8/31/93	0.26	13	0.02	down
8	1	9/7/93	0.07	7	0.01	up
8	1	9/16/93	0.71	9	0.08	down
8	1	9/21/93	14.53	5	2.91	up
8	1	9/28/93	13.73	7	1.96	down
8	1	10/5/93	0.86	7	0.12	down
8	1	10/14/93	0.14	9	0.02	up
8	1	10/19/93	0.18	5	0.04	down
8	1	10/26/93	0.05	7	0.01	up
8	1	11/2/93	0.05	7	0.01	down
8	1	11/9/93	0.68	7	0.10	down
8	1	11/16/93	0.35	7	0.05	down
8	1	11/30/93	1.99	14	0.14	up
8	1	12/16/93	0.06	16	0.00	down
8	1	12/30/93	0.07	14	0.00	up
8	1	1/15/94	0.07	16	0.00	up
9	1	8/31/93	22.23	13	1.71	down
9	1	9/7/93	0.00	7	0.00	none
9	1	9/16/93	0.23	9	0.03	down
9	1	9/21/93	0.13	5	0.03	up
9	1	9/28/93	7.75	7	1.11	down
9	1	10/5/93	7.60	7	1.09	up
9	1	10/14/93	0.12	9	0.01	up
9	1	10/19/93	0.05	5	0.01	down
9	1	10/26/93	0.13	7	0.02	down
9	1	11/2/93	0.11	7	0.02	up
9	1	11/9/93	0.00	7	0.00	none
9	1	11/16/93	0.00	7	0.00	none
9	1	11/30/93	0.00	14	0.00	none
9	1	12/16/93	0.00	16	0.00	none
9	1	12/30/93	0.00	14	0.00	none
9	1	1/15/94	0.00	16	0.00	none
10	1	10/14/93	0.67	9	0.07	down
10	1	10/19/93	0.05	5	0.01	down
10	1	10/26/93	0.72	7	0.10	up
10	1	11/2/93	0.26	7	0.04	up
10	1	11/9/93	0.03	7	0.00	down
10	1	11/16/93	1.97	7	0.28	down
10	1	11/30/93	1.46	14	0.10	up
10	1	12/16/93	0.70	16	0.04	up
10	1	12/30/93	0.02	14	0.00	up
10	1	1/15/94	0.02	16	0.00	up
11	1	10/5/93	0.05	7	0.01	up

Fish Number	Site	Date	Distance Moved (km)	Days Since Last Location	Movement Rate (km/day)	Direction
11	1	10/14/93	6.55	9	0.73	up
11	1	10/19/93	0.00	5	0.00	none
11	1	10/26/93	6.58	7	0.94	down
11	1	11/2/93	6.55	7	0.94	up
11	1	11/9/93	0.03	7	0.00	up
11	1	11/16/93	0.00	7	0.00	none
11	1	11/30/93	0.00	14	0.00	none
11	1	12/16/93	0.03	16	0.00	up
11	1	12/30/93	0.04	14	0.00	down
11	1	1/15/94	0.03	16	0.00	up
12	1	9/7/93	4.41	20	0.22	up
12	1	9/16/93	5.91	9	0.66	up
13	1	10/14/93	4.80	9	0.53	down
13	1	10/19/93	0.02	5	0.00	down
13	1	10/26/93	4.86	7	0.69	up
13	1	11/2/93	1.17	7	0.17	up
13	1	11/9/93	1.16	7	0.17	down
13	1	11/16/93	0.00	7	0.00	none
13	1	11/30/93	0.05	14	0.00	down
13	1	12/16/93	6.18	16	0.39	up
13	1	12/30/93	5.95	14	0.42	up
13	1	1/15/94	0.09	16	0.01	up
14	2	8/31/93	0.10	11	0.01	down
14	2	9/7/93	0.14	7	0.02	down
14	2	9/16/93	4.87	9	0.54	down
14	2	9/21/93	1.24	5	0.25	up
14	2	9/28/93	0.02	7	0.00	up
14	2	10/5/93	0.04	7	0.01	down
14	2	10/14/93	0.05	9	0.01	up
14	2	10/19/93	0.00	5	0.00	none
14	2	10/26/93	0.04	7	0.01	down
14	2	11/2/93	0.08	7	0.01	up
14	2	11/9/93	0.05	7	0.01	down
14	2	11/16/93	0.18	7	0.03	up
14	2	11/30/93	4.13	14	0.29	down
14	2	12/16/93	0.00	16	0.00	none
14	2	12/30/93	0.98	14	0.07	down
14	2	1/15/94	0.54	16	0.03	up
15	2	8/31/93	0.01	11	0.00	none
15	2	9/7/93	1.04	7	0.15	down
15	2	9/16/93	2.58	9	0.29	down
15	2	9/21/93	0.00	5	0.00	none
15	2	9/28/93	0.14	7	0.02	up
15	2	10/5/93	0.07	7	0.01	down
15	2	10/14/93	0.00	9	0.00	none
15	2	10/19/93	0.06	5	0.01	down
15	2	10/26/93	0.00	7	0.00	none
15	2	11/2/93	3.89	7	0.56	down
15	2	11/9/93	1.05	7	0.15	down
15	2	11/16/93	0.92	7	0.13	down
15	2	11/30/93	0.00	14	0.00	none
15	2	12/16/93	1.18	16	0.07	down
15	2	12/30/93	0.02	14	0.00	up
15	2	1/15/94	0.00	16	0.00	none
16	2	8/31/93	N/A	N/A	N/A	prey
17	2	8/31/93	0.00	11	0.00	none
17	2	9/7/93	0.10	7	0.01	down

Fish Number	Site	Date	Distance Moved (km)	Days Since Last Location	Movement Rate (km/day)	Direction
17	2	9/16/93	1.30	9	0.14	down
17	2	9/21/93	0.07	5	0.01	up
17	2	9/28/93	7.60	7	1.09	up
17	2	10/5/93	0.14	7	0.02	down
17	2	10/14/93	10.26	9	1.14	down
17	2	10/19/93	0.06	5	0.01	up
18	2	8/31/93	0.04	10	0.00	up
18	2	9/7/93	0.16	7	0.02	down
18	2	9/16/93	3.37	9	0.37	down
18	2	9/21/93	0.02	5	0.00	down
18	2	9/28/93	0.02	7	0.00	down
18	2	10/5/93	0.00	7	0.00	none
18	2	10/14/93	0.02	9	0.00	down
18	2	10/19/93	0.03	5	0.01	up
18	2	10/26/93	2.71	7	0.39	up
18	2	11/2/93	2.59	7	0.37	up
18	2	11/9/93	1.97	7	0.28	down
18	2	11/16/93	0.05	7	0.01	down
18	2	11/30/93	1.40	14	0.10	up
18	2	12/16/93	8.32	16	0.52	up
18	2	12/30/93	0.19	14	0.01	down
18	2	1/15/94	0.55	16	0.03	down
19	2	8/31/93	0.02	10	0.00	up
19	2	9/7/93	2.93	7	0.42	down
19	2	9/16/93	2.05	9	0.23	down
19	2	9/21/93	0.03	5	0.01	up
19	2	9/28/93	0.00	7	0.00	none
19	2	10/5/93	0.12	7	0.02	up
19	2	10/14/93	0.12	9	0.01	down
19	2	10/19/93	0.04	5	0.01	down
19	2	10/26/93	0.21	7	0.03	up
19	2	11/2/93	0.16	7	0.02	down
19	2	11/9/93	1.02	7	0.15	up
19	2	11/16/93	0.22	7	0.03	up
19	2	11/30/93	3.70	14	0.26	down
19	2	12/16/93	2.62	16	0.16	down
19	2	12/30/93	0.08	14	0.01	down
19	2	1/15/94	0.03	16	0.00	down
20	2	8/31/93	0.00	10	0.00	none
20	2	9/7/93	17.07	7	2.44	up
20	2	9/16/93	20.42	9	2.27	down
21	2	11/16/93	0.03	7	0.00	down
21	2	11/30/93	1.53	14	0.11	up
21	2	12/16/93	7.68	16	0.48	up
21	2	12/30/93	0.78	14	0.06	up
21	2	1/15/94	0.89	16	0.06	up
22	2	8/31/93	0.18	11	0.02	up
22	2	9/7/93	0.37	7	0.05	down
22	2	9/16/93	0.15	9	0.02	up
22	2	9/21/93	0.00	5	0.00	none
22	2	9/28/93	0.09	7	0.01	down
22	2	10/5/93	0.12	7	0.02	up
22	2	10/14/93	0.00	9	0.00	none
22	2	10/19/93	0.04	5	0.01	up
22	2	10/26/93	0.03	7	0.00	down
22	2	11/2/93	0.00	7	0.00	none
22	2	11/9/93	0.00	7	0.00	none

Fish Number	Site	Date	Distance Moved (km)	Days Since Last Location	Movement Rate (km/day)	Direction
22	2	11/16/93	0.00	7	0.00	none
22	2	11/30/93	0.02	14	0.00	up
22	2	12/16/93	0.00	16	0.00	none
22	2	12/30/93	0.02	14	0.00	down
22	2	1/15/94	0.00	16	0.00	none
23	2	9/16/93	17.53	27	0.65	up
24	3	8/31/93	0.43	8	0.05	up
25	3	8/31/93	0.21	8	0.03	down
25	3	9/7/93	0.31	7	0.04	up
25	3	9/16/93	4.12	9	0.46	down
25	3	10/5/93	72.75	19	3.83	down
25	3	10/14/93	0.04	9	0.00	down
25	3	10/19/93	0.04	5	0.01	up
25	3	10/26/93	0.00	7	0.00	none
25	3	11/2/93	2.44	7	0.35	up
25	3	11/9/93	5.23	7	0.75	up
25	3	11/16/93	0.31	7	0.04	up
25	3	11/30/93	2.69	14	0.19	up
25	3	12/16/93	4.18	16	0.26	down
25	3	12/30/93	0.20	14	0.01	down
25	3	1/15/94	0.54	16	0.03	up
26	3	8/31/93	0.66	8	0.08	down
26	3	9/7/93	3.25	7	0.46	up
26	3	9/16/93	40.07	9	4.45	down
26	3	9/21/93	7.77	5	1.55	down
26	3	9/28/93	7.29	7	1.04	down
26	3	10/5/93	21.10	7	3.01	down
26	3	10/14/93	3.27	9	0.36	down
26	3	10/19/93	0.17	5	0.03	up
26	3	10/26/93	0.11	7	0.02	up
26	3	11/2/93	0.23	7	0.03	down
26	3	11/9/93	0.03	7	0.00	down
26	3	11/16/93	0.03	7	0.00	up
26	3	11/30/93	0.00	14	0.00	none
26	3	12/16/93	0.00	16	0.00	none
26	3	12/30/93	0.00	14	0.00	none
26	3	1/15/94	0.00	16	0.00	none
27	3	8/31/93	29.13	8	3.64	down
27	3	9/16/93	30.27	16	1.89	down
27	3	9/21/93	13.02	5	2.60	down
27	3	9/28/93	13.54	7	1.93	up
27	3	10/5/93	20.62	7	2.95	down
27	3	10/14/93	0.06	9	0.01	down
27	3	10/19/93	0.00	5	0.00	none
27	3	10/26/93	4.31	7	0.62	down
27	3	11/2/93	1.75	7	0.25	up
27	3	11/9/93	2.33	7	0.33	up
27	3	11/16/93	0.03	7	0.00	up
27	3	11/30/93	0.12	14	0.01	up
27	3	12/16/93	0.05	16	0.00	up
27	3	12/30/93	0.18	14	0.01	up
27	3	1/15/94	0.00	16	0.00	none
28	4	8/31/93	0.00	7	0.00	none
28	4	9/7/93	0.00	7	0.00	none
28	4	9/16/93	0.42	9	0.05	down
28	4	10/5/93	17.51	19	0.92	up
28	4	10/14/93	1.20	9	0.13	down

Fish Number	Site	Date	Distance Moved (km)	Days Since Last Location	Movement Rate (km/day)	Direction
28	4	10/26/93	0.48	12	0.04	up
28	4	11/2/93	13.75	7	1.96	down
28	4	11/9/93	0.00	7	0.00	none
28	4	11/16/93	0.00	7	0.00	none
28	4	11/30/93	0.00	14	0.00	none
28	4	12/16/93	0.00	16	0.00	none
28	4	12/30/93	0.00	14	0.00	none
28	4	1/15/94	0.00	16	0.00	none
29	4	8/31/93	0.00	7	0.00	none
29	4	9/7/93	0.00	7	0.00	none
29	4	9/16/93	0.00	9	0.00	none
29	4	9/21/93	29.30	5	5.86	up
29	4	9/28/93	28.74	7	4.11	down
29	4	10/5/93	22.63	7	3.23	down
29	4	10/14/93	33.65	9	3.74	down
29	4	10/19/93	14.11	5	2.82	down
29	4	10/26/93	7.27	7	1.04	up
29	4	11/2/93	1.54	7	0.22	down
29	4	11/9/93	0.82	7	0.12	up
29	4	11/16/93	0.44	7	0.06	up
29	4	11/30/93	9.02	14	0.64	up
29	4	12/16/93	2.95	16	0.18	up
29	4	12/30/93	3.25	14	0.23	down
29	4	1/15/94	2.42	16	0.15	up
30	4	8/31/93	0.10	7	0.01	up
30	4	9/7/93	2.04	7	0.29	down
30	4	9/16/93	15.95	9	1.77	down
30	4	9/21/93	2.47	5	0.49	down
30	4	9/28/93	1.47	7	0.21	down
30	4	10/5/93	27.24	7	3.89	down
30	4	10/14/93	4.51	9	0.50	down
30	4	10/19/93	0.26	5	0.05	down
30	4	10/26/93	0.02	7	0.00	up
30	4	11/2/93	0.16	7	0.02	up
30	4	11/9/93	5.34	7	0.76	up
30	4	11/16/93	4.00	7	0.57	up
30	4	11/30/93	0.16	14	0.01	up
30	4	12/16/93	0.02	16	0.00	down
30	4	12/30/93	0.10	14	0.01	up
30	4	1/15/94	0.02	16	0.00	down
31	4	8/31/93	0.03	7	0.00	down
31	4	9/7/93	0.03	7	0.00	up
31	4	9/16/93	7.98	9	0.89	up
31	4	9/21/93	15.83	5	3.17	down
31	4	9/28/93	0.73	7	0.10	down
31	4	10/5/93	5.46	7	0.78	down
31	4	10/14/93	7.85	9	0.87	down
31	4	10/19/93	29.19	5	5.84	down
31	4	10/26/93	4.85	7	0.69	down
31	4	11/2/93	0.18	7	0.03	up
31	4	11/9/93	3.84	7	0.55	up
31	4	11/16/93	12.03	7	1.72	up
31	4	11/30/93	4.60	14	0.33	up
31	4	12/16/93	5.01	16	0.31	up
31	4	12/30/93	5.75	14	0.41	up
31	4	1/15/94	0.42	16	0.03	down
32	4	8/31/93	0.00	7	0.00	none

Fish Number	Site	Date	Distance Moved (km)	Days Since Last Location	Movement Rate (km/day)	Direction
32	4	9/7/93	2.45	7	0.35	up
32	4	9/16/93	2.43	9	0.27	down
32	4	9/21/93	19.46	5	3.89	down
32	4	9/28/93	2.63	7	0.38	down
32	4	10/5/93	20.36	7	2.91	down
32	4	10/14/93	8.34	9	0.93	down
32	4	10/19/93	0.08	5	0.02	up
32	4	10/26/93	0.10	7	0.01	up
32	4	11/2/93	8.12	7	1.16	up
32	4	11/9/93	1.66	7	0.24	up
32	4	11/16/93	3.11	7	0.44	up
32	4	11/30/93	0.87	14	0.06	up
32	4	12/16/93	7.02	16	0.44	up
32	4	12/30/93	3.06	14	0.22	up
32	4	1/15/94	0.06	16	0.00	up
33	4	8/31/93	0.00	7	0.00	none
33	4	9/7/93	0.88	7	0.13	down
33	4	9/16/93	17.93	9	1.99	down
33	4	9/21/93	3.02	5	0.60	down
33	4	9/28/93	0.53	7	0.08	down
33	4	10/5/93	0.83	7	0.12	up
33	4	10/14/93	0.00	9	0.00	none
33	4	10/26/93	0.00	12	0.00	none
33	4	11/2/93	0.06	7	0.01	up
33	4	11/9/93	0.03	7	0.00	down
33	4	11/16/93	0.00	7	0.00	none
33	4	11/30/93	0.00	14	0.00	none
33	4	12/16/93	0.00	16	0.00	none
33	4	12/30/93	0.03	14	0.00	down
33	4	1/15/94	0.00	16	0.00	none
34	4	8/31/93	0.02	7	0.00	down
34	4	9/7/93	0.07	7	0.01	up
34	4	9/16/93	19.52	9	2.17	down
34	4	9/21/93	1.23	5	0.25	down
34	4	9/28/93	0.16	7	0.02	up
34	4	10/5/93	1.82	7	0.26	down
34	4	10/14/93	1.27	9	0.14	down
34	4	10/19/93	22.35	5	4.47	down
34	4	11/2/93	2.43	14	0.17	up
34	4	11/9/93	7.54	7	1.08	up
34	4	11/16/93	2.85	7	0.41	up
34	4	11/30/93	0.11	14	0.01	down
34	4	12/16/93	5.07	16	0.32	up
34	4	12/30/93	0.00	14	0.00	none
34	4	1/15/94	0.02	16	0.00	down