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MOVEMENTS AND BEHAVIOR OF LARGEMOUTH BASS (Micropterus salmoides)
AND STEELHEAD (Salmo gairdneri) DETERMINED BY RADIO TELEMETRY

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TABLE OF CONTENTS

PREFACE	ii
ACKNOWLEDGEMENTS	iii
PART I RADIO-TRACKING FRESHWATER FISH	1
INTRODUCTION	2
EQUIPMENT	5
METHODS OF TRACKING	13
ATTACHING RADIO TRANSMITTERS	26
SUMMARY	35
REFERENCES	38
PART II HOME RANGE MOVEMENTS AND HABITAT USE OF LARGEMOUTH BASS IN MARY LAKE, NORTHCENTRAL MINNESOTA	40
INTRODUCTION	41
STUDY AREA	44
MATERIALS AND METHODS	44
RESULTS	49
DISCUSSION	62
SUMMARY	66
REFERENCES	68
PART III MOVEMENTS AND BEHAVIOR OF STEELHEAD IN WESTERN LAKE SUPERIOR	71
INTRODUCTION	72
STUDY AREA	74
METHODS	80
RESULTS AND DISCUSSION	82
FALL MOVEMENTS	82
PRESPAWNING BEHAVIOR	105
THE SPAWNING RUN	137
DISPERSAL AND SUMMER MOVEMENTS	162
THE EFFECTS OF CAPTURE AND TAGGING	175
SUMMARY	185
REFERENCES	191

PREFACE

The organization of this thesis reflects the development of underwater radio tracking methodology for monitoring movements of freshwater fish. Equipment and techniques developed during this research are described in Part I and represent a cooperative effort between the author and the University of Minnesota's Cedar Creek engineering staff. In 1970, the equipment and techniques were tested and perfected during a study of largemouth bass movements in Mary Lake. The bass project provided an ideal situation to test the system. Since Mary Lake was small and the bass exhibited localized movements, the fish could be found easily; consequently, the performance of the system could be continually analyzed and problems could be quickly solved. The home range movements of the bass are described in Part II. After establishing the reliability and usefulness of the system, a much more difficult project was attempted. In 1971, a program was initiated to study the movements and behavior of steelhead in western Lake Superior. Results of this project (1971-1974) are presented in Part III.

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PART I

RADIO-TRACKING FRESHWATER FISH

Introduction

Aquatic animal tracking had its origins in the late 1950's (Trefethen, 1956; Trefethen, et al., 1957; and Johnson, 1960). Initially, ultrasonic transmitters in the 30-300 KHz frequency range were developed because low frequency, long wave signals travel well through water and are minimally affected by the ionic concentration of water. Ultrasonic tracking has been widely used since 1970. The history and development of ultrasonic tracking equipment has been recorded in the Underwater Telemetry Newsletter published by the Fisheries Research Board of Canada (St. Andrews, N.B.) edited by Aivars B. Stasko (1971-1975). About the same time that aquatic ecologists were developing ultrasonic transmitters, terrestrial ecologists were developing radio transmitters in the 27-300 MHz range as described by Slater (1963, 1965) and Brander and Cochran (1971).

In 1969 the University of Minnesota's Cedar Creek Bioelectronics Laboratory began radio tracking carp and northern pike in a stream (unpublished data) using an automatic tracking facility (Cochran, et al., 1965). Since then we have tracked largemouth bass in a northern Minnesota lake (1970), steelhead in Lake Superior (1971-1974), and yellow perch in the thermal plume from a power plant (1975). It is clear that an ecologist can now choose to track aquatic animals with either radio or ultrasonic equipment depending on the requirements of the project.

Underwater radio telemetry has many important features. The first is that the equipment is relatively inexpensive. Transmitter parts cost about \$16 (U.S.) and receiver components about \$125 (U.S.). A yagi antenna, which gives the best range, can be purchased for \$35 (U.S.). Although transmitters cost more than simple marking tags, the cost-information ratio decreases rapidly as greater quantities of data are collected and becomes lower than similar mark-recapture studies.

Second, radio transmitters can be designed with low current drain to give long life. For example, a transmitter with a 0.5 ma current drain and powered by a 42 milliampere-day (Mallory, RM 1) battery will transmit about 3 months.

Another important feature is that radio-tagged animals can be tracked by several remote and mobile methods. Since ultrasonic signals are highly attenuated in air, they must be detected with a receiver connected by a cable to a stationary submerged hydrophone or a hydrophone suspended from a boat. Attenuation of radio signals, on the other hand, is much less in air than in water and therefore, transmitters can be monitored by mobile antennas from shore, boat or airplane.

Since radio transmitters use crystals to minimize frequency changes, many individuals can be distinguished at the same location and time because each tag transmits on a different frequency. Although ultrasonic transmitters can be built using crystals for frequency control, cost and bulk have usually precluded their use. Consequently, ultrasonic telemetry must use elaborate decoding

techniques to identify individuals; however, the number of tags that can be identified at one time is generally less than with radio telemetry (30-100). Radio signals are only slightly affected by turbulent water, aquatic vegetation or a thermocline. These factors have been reported to interfere with and reduce the range of ultrasonic signals (Schiefer and Power, 1972; Ziebell, 1973).

Finally, radio telemetry is versatile. The same receivers and antennas can be used to monitor both aquatic and terrestrial animals. Thus, if an institution cannot afford to have both an ultrasonic and a radio tracking system, the latter will suffice for terrestrial work and many aquatic projects.

Although there are many advantages, there are also limitations for underwater radio telemetry. The radio signal attenuates with increasing salinity and depth. This limits radio tracking to freshwater species or to marine animals that surface periodically. Ultrasonic transmitters, on the other hand, are well suited for tracking animals in salt water or deep water. Powerlines, unshielded ignition systems, citizen's band radio, large metal objects, terrestrial vegetation and terrain may interfere with radio signals; however an experienced tracker can usually surmount such difficulties.

This paper describes the application of radio tracking technique to aquatic animals. Terrestrial radio tracking literature is summarized and the equipment and methods that have been used to track freshwater fish are described. It is hoped that this

information will aid fisheries biologists, who may not be familiar with the wildlife literature, to establish aquatic radio tracking programs with a minimum of literature search.

Equipment

The basic transmitter circuit (Fig. 1) is similar to that described by Cochran and Lord (1963), but most of the components are different (Table 1). The original design was for a continuous-wave ("whistling") signal. We added capacitor (C_3) and resistor (R_2) which cause the transmitter to emit a pulsing signal. Continuous-wave signals were easier to distinguish from background noise than pulsing-signals and therefore, were detected at greater distances. It was also easier to detect animal activity with continuous-wave signals because animal movements caused the frequency and output of the transmitter (antenna orientation) to vary slightly so that a wavering signal was produced (Cochran and Lord, 1963; Marshall and Kupa, 1963). Signal or activity patterns can be recorded on strip charts (Gilmer, et al. 1971; Siniff, et al., 1971) or 16 mm film (Cochran, et al., 1965).

Pulsing-signals reduced the power consumption and therefore increased transmitter life. The pulse width (on-time) of our transmitters was .02 - .025 seconds and the pulse rate was set between 60 and 120 pulses per minute. The duty cycle or the ratio of on-time to total time was $3\% \pm 1\%$. Physiological and environmental information may be coded by a pulsing-signal. For example, we decoded temperature data from a recently developed temperature radio transmitter (unpublished data) by measuring the period between pulses.

FIGURE 1. Transmitter circuit diagram and component arrangement.

Table 1. Aquatic radio transmitter components (53 MHz).

	<u>Component</u>	<u>Comments</u>
Crystal	Holder type HC18/U, (International Crystal Co., 10 North Lee, Oklahoma City, Oklahoma 73102	determines the operating frequency of the transmitter
Transistor	Amperex A415	provides feedback to sustain the oscillation
Capacitor C ₁	0.01 μ f ceramic 10 volt	(bypass capacitor) eliminates the influence of the battery and the leads on transmitter operation
Capacitor C ₂	10 - 35 pf, silver mica: CDE CD6 Series	(final tuning capacitor) restricts the oscillator to operate on the correct overtone of the crystal. Use the <u>least capacitance</u> (critical step) which initiates pulsing with the antenna under water.
Capacitor C ₃	2 - 10 μ f, Sprague 162D series	controls pulse width and rate along with R ₂
Resistor R ₁	.3 to .8 ma at 56 K Ω to 20 K Ω , 100 K Ω typical; 1/8 or 1/10 watt	(current drain resistor) is selected to give the desired current drain
Resistor R ₂	1 K Ω to 2.2 K Ω , 2.2 K Ω typical; 1/8 or 1/10 watt	controls pulse width and timing along with C ₃
Coil	Belden #32 enameled wire	20 turns on 3 mm form for C ₂ between 15 and 35 pf
Whip Antenna	.5 mm stainless steel wire in teflon tubing	length depends on fish length
Attachment Wire	Teflon coated electrical wire (26 gauge)	provides a ground plane for the antenna
Battery	certified mercury cell (1.4 volt) or 2.8 v lithium cell (Power Conversion, Inc.)	

Transmitters were powered by 1.4 volt mercury cells or 2.8 volt lithium batteries used singly or in series for more power. The types of mercury batteries available and their usefulness for biotelemetry have been described by Kuechle (1967). We used certified mercury cells for greater reliability because they are manufactured to rigid specifications and are inspected at each stage of construction. Most sizes had to be ordered specially, but the costs for sizes other than RM-1 and RM-640 were prohibitive unless ordered in large quantities.

Lithium batteries are a recent development and show much promise for underwater telemetry. They have half the weight in water and twice the voltage of an equivalent sized mercury cell. Compared to mercury cells with the same Mah rating, lithium batteries have 2.5 times greater volume; however, because of the higher voltage of lithium cells, smaller cells can be used to produce the same power at a lower current drain. Lithium batteries also have better cold temperature performance.

The approximate transmitter life under ideal conditions was computed by dividing the manufacturer's milliamper-hour (Mah) rating for a battery (q.v. Kuechle, 1967) by the average current drain of the transmitter.¹ For most of our steelhead and largemouth bass tracking we used certified Mallory RM-1 mercury cells with a 1000 Mah capacity rating. Average current drain was usually between 0.5 ma and 0.7 ma. The expected and observed transmitter life was between 60 and 83 days. Our smallest transmitters for perch had a

¹ $\frac{\text{Mah battery rating}}{\text{average current drain}} = \text{expected life in hours}$

160 Mah (Mallory RM-675) battery and a 0.2 ma current drain. Actual transmitter life was 30 ± 5 days.

The size of the underwater transmitter was determined largely by the size of the battery. Battery life in turn depended on its dimensions and weight. Transmitter range was increased in a non-linear manner by increasing the current drain but this produced an almost linear decrease in battery life. Therefore, the desired transmitter size, life and range were matched to each other and the demands of the project.

Transmitter components, without the battery, weighed 2.5 gm. With a 2.0 gm RM-675 battery, a package was made suitable for 300 gm yellow perch. This package weighed 3.3 gm in water (6.5 gm dry) and measured 30 mm X 10 mm X 5 mm. By using miniature components, the transmitter could be made smaller, but at greatly increased cost. In water, the transmitter (Scotchcast epoxy encapsuled) weight with a mercury cell was 50-60% of the dry weight whereas it was 40% with a lithium battery. Steelhead transmitters (RM-1 battery) had a dry weight of 26 gm and weighed about 15.6 gm in water. Dimensions were 17 mm in diameter and 40 mm long. I feel that the transmitter weight in water should not exceed 1-1.25% of the fish's weight out of water. With a package weight below this amount, a fish regains his equilibrium within minutes after tagging and total habituation time is kept to a minimum.

Transmitters were encapsulated in Scotchcast #5 electrical resin (3M Co.). This two-part epoxy was found to be very durable and was compatible with transmitter components. Hardening time

was reduced by heating the resin (A) to 60°C before the hardener (B) was added. Transmitters were potted in molds made by pouring a silicone rubber compound (RTV-30, General Electric) into a box around a smooth dummy transmitter or by carving hardened RTV-30 with a scalpel. Scotchcast was poured over the components in the mold and heat was applied briefly to eliminate air bubbles. After removing the transmitter, excess epoxy was taken off with an electric hand grinder. Marine boat epoxy was painted over the transmitter to cover any bare spots and to coat an identification label.

Although there are a number of theoretical papers concerning the transmission of radio waves in water, the practical application of these findings to fish tracking is limited. Marshall (1960) reported that "a transmitter (150 MHz) with antenna was tried underwater and the distance of reception was cut down to a few inches". Our success with underwater radio transmitters is partly due to tuning (capacitor C_2) the transmitter with the antenna underwater. The smallest capacitance which initiated pulsing is chosen. This results in the transmitter working well in water but poorly in air. We also connect a capacitance wire to the battery which provides a ground plane for the dipole antenna. The capacitance wire is also used in attaching the transmitter.

Saran and Held (1960) found that the field strength received at a submerged dipole antenna was attenuated exponentially with increasing depth. Our calculations show that a signal transmitted by a submerged dipole antenna will also be attenuated exponentially with increasing depth. Attenuation tests (Fig. 2) were conducted

FIGURE 2. Attenuation of radio signals with increasing depth in lakes with different conductivities. Curves marked with dots and squares are from Lake Superior (80 $\mu\text{mho/cm}$) and triangles are from Lake Bemidji (300 $\mu\text{mho/cm}$).

on two lakes that are representative of the low conductivity water in eastern Minnesota and moderate conductivity water of central Minnesota. Transmitter range was determined by ear for each depth with the transmitter antenna horizontal and pointed at the receiver. Range was 35-45% less when the transmitter antenna was broadside to the receiver. Preliminary tests with a signal strength meter indicated that the transmitter transmission pattern is probably elliptical. The range at each depth was expressed as a percentage of the surface or maximum range. In Lake Superior we lost 50% of the range at 8 m depth but received the signal down to 50 m. In Lake Bemidji, 50% of the signal was lost at 4 m. The shapes of the curves (Fig. 2) suggest that underwater radio signals are attenuated exponentially with depth. They also indicate that attenuation is greater in water of higher conductivity. The top curve has an exponential shape but does not start at 0 meters because of a probable surface range error. Our tracking observations indicated that a thermocline or ice had little effect on the signal.

We chose 53 MHz as our operating frequency because this frequency travels through water better than higher v.h.f. signals. Calculations indicated that the advantages of lower v.h.f signals were offset by the need for a bulkier receiving antenna and because the transmitting antenna would be a smaller fraction of the wave length.

Radio receivers for animal tracking can be purchased from commercial sources (BIAC, 1967). The Cedar Creek Bioelectronics Laboratory of the University of Minnesota designed and constructed

our receivers (Kuechle, et al., 1971). They were portable, hand held units (13 cm x 18 cm x 13 cm) with detachable loop antenna, and jack for connecting other antenna systems (eg. yagi). Parts for the receiver cost about \$125 (U.S.). The receiver was essentially an automobile "radio" which was modified for tracking purposes. The frequency range was 52.5 to 53.5 MHz. Different transmitter frequencies were used for each animal and up to 30 individuals (33 KHz apart) were distinguished, provided the animals were not close together.

Our newest receiver (unpublished) has channel selecting tuning and can distinguish up to 100 different transmitter frequencies spaced 10 KHz apart. The new receiver is a double conversion using a frequency synthesizer for tuning. It has a 1.2 KHz i.f. band width and uses a b.f.o. to detect continuous wave and pulsing signals. The noise figure is about 4 d.b.

Methods of Tracking

Underwater radio transmitters were monitored from shore, by boat or airplane. Most tracking involved plotting the animal's location on a map from compass bearings, visual bearings or a combination of the two. Compass bearings were taken on the transmitter direction from locations that were recognizable on a map or in some cases (eg. airplane, boat) from an unknown location (the animal's) to landmarks. The compass bearings were plotted on a map and the point where the lines intersected was the animal's calculated position. Visual bearings on the transmitter direction

were used when the observer was close to the animal and when the animal was near good landmarks. In addition, line of sight and compass bearings were used together with grid systems established around largemouth bass home ranges. Markers were placed at 6 m (20') intervals on shore and 15 m (50') offshore.

Shore tracking was done with a portable hand held unit, a semi-permanent tower, or a mobile unit. The advantages of shore tracking were that it could be done during stormy weather or at night and it did not disturb the fish. Our portable receiver was attached to a diamond-shaped, bi-directional loop antenna (Fig. 3). For this equipment a minimum or null signal occurred when the plane of the antenna was perpendicular to the transmitter direction, and a maximum signal occurred when the sides of the loop were pointed at the transmitter. Since the null gave a clearer direction than the maximum signal, the null was generally used for taking bearings (Cochran and Lord, 1963). An animal was located by moving to places which provided bearings that intersected as close to 90° as possible. Maximum working range of our underwater transmitter monitored by a loop antenna was .8 - 1.2 km.

A temporary tower was useful for projects on small lakes, on aquatic animals with small home ranges, and on specific areas of a lake or river such as near a thermal effluent or dam (Fig. 3). Temporary towers have been described by Marshall and Kupa (1963), Houseknecht (1970), and Brander and Cochran (1971). We used a 1 m long, 4 cm (1 1/2 inch) diameter pipe welded to a metal plate as

Figure 3. Radio tracking receiver and antennas.

- 3a. A radio receiver with channel selecting tuning, headset and a hand-held loop antenna.
- 3b. A semi-permanent tower with yagi antenna and compass dish, which is indicated by an arrow.

the base. On the opposite end of the short pipe, a compass disk was attached. A yagi antenna was mounted with the elements vertical on a 6 m long, 3 cm (1 1/4 inch) diameter pipe which was inserted into the base pipe. The tower was guyed with wires to a slip-ring located on the mast below the yagi antenna. A pointer was attached to the mast just above the base pipe and in the same direction as the antenna reception so that bearings could be read on the compass rose. The azimuth to the transmitter was determined by finding the mid-point between the two null points (Marshall and Kupa, 1963). We found that the range of the yagi antenna was up to 3 times greater than the loop antenna. Temporary towers can be used in pairs and fixes taken simultaneously with the aid of two-way radio communication. A modification which uses the temporary tower is to connect the receiver to a strip chart or tape recorder (Gilmer, et al., 1971; Siniff, et al., 1971) so that presence of a signal, activity, temperature or pressure is recorded.

A mobile tracking unit was valuable for scouting along rivers or around a lake with good access (Fig. 4). Verts (1963) described a mobile tracking unit with a loop antenna. Marshall and Kupa (1963a) described a mobile unit with a tip-up yagi antenna which gave greater range. The design of a mobile tracking unit depends on antenna size, type of vehicle, overhead obstructions, and the number of locations used in tracking.

Along Lake Superior we were faced with many stops which made a tip-up or telescopic mount too time consuming. Since a 53 MHz yagi antenna is large, overhead obstructions presented problems.

Figure 4. Radio tracking antenna systems.

- 4a. Mobile tracking vehicle with a yagi antenna and antenna rotors.
- 4b. A yagi antenna mounted on a boat.
- 4c. A loop antenna attached to an airplane wing strut by hose clamps.

The tracking vehicle was a van with a television tripod mast-mount bolted to a plywood sheet attached to car-top carriers. Two television antenna rotors were used: one was attached to a 1 meter mast and the other to the antenna beam. When traveling, the antenna was carried with the elements horizontal. While monitoring fish, one rotor turned the yagi to vertical and the other rotated the antenna. Rotors were powered by a 12 v to 110 v power converter. The range of the mobile unit was 2-3 times a loop antenna.

A boat with a yagi was the best way to search a small area thoroughly. We mounted the yagi on a 4 m telescopic mast in a 5.5 m long boat (Fig. 4). The boat-mounted yagi, like the mobile unit, was primarily used to initially locate signals. Once the signal was localized, a loop antenna was used. When a fish was close to shore, we obtained two bearings that intersected at 90° with one of the bearings aligned with a landmark. When a fish was far from shore, we approached the fish until the signal became loud and omni-directional. This indicated that we were within 20 m of the fish. The location was determined by taking compass bearings on landmarks or measuring two adjacent horizontal angles between three landmarks on shore with a navy Mark II sextant (McCleave and Horrall, 1970). Sextant bearings were obtained more quickly than compass bearings, were less affected by rough water or metal and were very accurate ($\pm 0.5^\circ$). Angles were set on a three-arm protractor and aligned with landmarks on an aerial map. The origin of the angle marked the calculated location of the fish.

Airplane tracking was useful on large lakes ($>125 - 250 \text{ km}^2$) and for nomadic species. Loop antennas were insulated from and bolted to pieces of aluminum (75 mm x 300 mm x 3 mm) bent in a 45° angle. The aluminum brackets were attached to airplane struts by hose clamps and the antennas were mounted under each wing perpendicular to each other. A switch allowed the tracker to listen to both antennas at the same time, which gave wide reception, or to each separately to determine signal direction. A plane with the ignition noise suppressed must be used. Noise inside the airplane was reduced by padded stereophonic headsets that fit tightly around the ears.

After the animal was initially located, the aircraft was flown in circles of decreasing circumference and the receiver volume and sensitivity were reduced until the signal was received only over a small area. An alternative method was to listen for the maximum signal and then a decrease as the airplane passed over the fish. Compass bearings were taken on landmarks from the fish's location. Maximum transmitter range was slightly better at higher altitudes but locations were determined more accurately at lower altitudes. Average ranges from various altitudes expressed as a per cent of maximum range were as follows: 150 m altitude, 60%; 300 m, 75%; 450 m, 75%; 600 m, 93%; and 750 m, 100%. Transmitter locations were determined as accurately as 100 m radius providing that good landmarks were near (1 - 3 km).

A disadvantage of airplane tracking was that the speeds flown ($>96 \text{ km/hr}$) allowed only a short time to listen for individual

transmitters. Furthermore, the high airplane cost limited tracking to periods when many fish were radio tagged or to occasional searches for missing fish.

Tests were conducted on the accuracy of yagi and loop antennas. Two 6 m high temporary towers were located near the thermal discharge of a power plant. The receiving end of the yagi was oriented 90° - 180° from the plant for tracking and accuracy tests. Transmitters were placed in the water near locations recognizable on an aerial photograph. Bearings on each location were close together (S.E. $< .45^{\circ}$) with 2.0° to 5.0° difference between the highest and lowest bearings (Table 2). One wild bearing was excluded because it was over 4.5° from the next closest reading. The mean bearing error for each distance ranged from $.25^{\circ}$ to 6.25° ; however, tower errors were systematic. Towers were corrected to within $\pm 3^{\circ}$ by adding 3.0° to tower #2 and subtracting 2.0° from tower #1. Distance errors using the correction factors were less than 5 m at 100 m and 43 m at 800 m. From a van-mounted yagi, the mean bearing error was approximately 14 m from 200 m and about 28 m from 400 m. These results compared closely with yagi accuracy tests conducted by Marshall (1962, 1963) in a wooded area and on grasslands by Slade et al. (1965).

Loop antennas were very accurate at close ranges and were useful in recovering transmitters. Cochran and Lord (1963) found that they could locate an animal with a loop antenna to within a 10 ft (3 m) radius (no distance specified). Verts (1963) reported

Table 2. Accuracy of Yagi Antennas.

Distance m	Tower	Trials	Bearing range in degrees	Mean bearing error in degrees*	S.E. in degrees	Mean bearing error in m*
138	1	10	5.0	6.25	.45	16.0
275	1	10	4.0	.25	.38	2.0
338	2	10	3.0	2.85	.37	16.5
438	2	10	2.5	3.55	.22	27.0
438	1	10	2.0	1.70	.23	10.5
450	2	9	4.0	1.11	.27	3.0
463	1	10	5.0	1.90	.29	16.0
575	2	10	4.0	5.35	.34	52.0
738	2	10	4.0	3.05	.40	35.0

* without correction factors for the systematic errors: tower #1, -2° ;
tower #2, $+3^{\circ}$

that triangulations from his truck mounted loop antenna were ± 25 ft (7.6 m) at 1/4 mile (400 m) and about ± 25 yards (23 m) at 1/2 mile (800 m).

Most locations recorded in our studies were made with a hand-held receiver and loop antenna from distances less than 100 m. Accuracy tests on transmitters submerged in an aquatic grid system suggested that maximum triangulation errors were about ± 1.5 m from 15 m, ± 3 m from 30 m and ± 6 m from 60 m. Further tests on the accuracy of a portable loop antenna were conducted on a football field (Table 3) with easily computable bearings to a transmitter submerged in water in a plastic container. Test bearings were taken with a Silva Ranger compass. The mean bearing error ranged from .3 m (5-15 m class) to 4.81 m (76-92 m class). However, at very close ranges the signal was so strong that the exact direction was difficult to determine or the directivity of the loop antenna was reversed. Antenna reversal occurs theoretically at a distance equal to 1/4 wave length which is 1.4 m at 53 MHz (Cochran, 1967). We have detected antenna reversal starting at 4.6 m and becoming complete at 2.7 m for 53 MHz. Consequently, the smallest distance class in the accuracy study was 5-15 m which reduced wild fixes and better approximated field tracking conditions.

Theoretical triangulation error was determined by plotting the mean and maximum degree errors from points representing distance classes on two lines intersecting at right angles. Right angles were chosen because the highest accuracy for triangulation occurs when the bearing lines intersect at 90° on the perpendicular

Table 3. Accuracy of loop antenna.

Distance class meters	Number of trials	Mean distance of trials	Mean bearing error in degrees	S.E. in degrees	Mean bearing error in meters	S.E. meters	Triangulation theoretical error			
							<u>maximum</u>		<u>mean</u>	
							°	m	°	m
5 - 15	16	8.8	1.92	.382	.30	.06	+5	2.1	+2	.79
16 - 30	13	25.6	2.62	.311	1.26	.14	+4	3.2	+2.5	1.82
31 - 45	10	41.1	3.89	.564	3.01	.46	+6	7.5	+4.0	4.39
46 - 60	8	55.2	3.07	.735	3.14	.63	+5.5	9.1	+3.0	4.66
61 - 75	7	68.3	2.17	.654	2.64	.80	+5	10.4	+2.0	3.78
76 - 92	13	86.3	2.94	.412	4.81	.60	+4.5	10.7	+3.0	6.49

bisector between two tracking stations (Tester, 1971; Heezen and Tester, 1967). A tracker moves in the field to obtain bearings intersecting near 90°. The calculated maximum triangulation error ranged from 2.1 m (5-15 m class) to 10.7 m (76-92 m class) and the calculated mean triangulation error ranged from .79 m to 6.49 m. Discussions of factors causing errors in radio-location data can be found in Tester, 1971; Marshall, 1962, 1963; and Slade et al., 1965.

Attaching Radio Transmitters

Attachment methods depend on the morphology and behavior of the species, the nature of the aquatic ecosystem and the type of project. Radio transmitters can be attached externally on the back or internally in the body cavity or stomach. External attachment is quicker and easier than implanting and can be used for spawning and feeding fish. The disadvantages of external attachment are that transmitter movement can erode larger holes in the skin around the attachment wires. This could lead to fungal infection. External transmitters increase the drag on the fish and can become snagged in vegetation.

Internal transmitters are less subject to wear, drag and snagging. Since an implanted transmitter is below a fish's center of gravity, a heavier package can be used internally without creating balance problems rather than a dorsal-mounted external package. Disadvantages of internal transmitters are that they should not be implanted when the body cavity is filled with eggs

nor can they be retained long in the stomachs of many species. Surgical implantation takes longer than external attachment or stomach insertion. Surgery also increases the chance of infection. The time necessary for a fish to recover from surgical implantation is much greater than for external attachment or stomach insertion. However, implantation is well suited for long term tracking and physiological telemetry.

I attached radio transmitters by a sub-dorsal fin mount, a mid-dorsal saddle mount and implantation. The length of the whip antenna varied with the length of the fish, and was determined before the transmitter was tuned. In general, I feel that an external antenna should not extend beyond the caudal fin nor an internal whip antenna beyond the anal fin.

The sub-dorsal fin mount (Fig. 5) was best suited for fish with long dorsal fins (eg. Centrarchidae, Percidae, etc.) and little space for an external saddle transmitter without excising part of the dorsal fin. Two teflon coated electrical wires (ground plane) extended from the transmitter. Either a surgical needle or a hypodermic needle was used to thread the teflon coated wires through the supporting tissue under the dorsal fin. The transmitter was snugged to the fish and on the opposite side of the body a soft plastic washer was slid over the wires and against the fish. Overhand knots prevented the wire from slipping through the washer.

Most salmonids were tagged with a mid-dorsal saddle mounted transmitter (Fig. 6). A saddle for 1.5 - 5.0 kg fish was made

Figure 5. Attaching a radio transmitter along side of the dorsal fin.

5a. Threading an attachment wire through a hypodermic needle under the dorsal fin.

5b. Dorsal view of a transmitter and soft plastic "washer".

5c. A 340 gm radio tagged perch.

Figure 6. Attaching a saddle-mounted radio transmitter to a steelhead.

- 6a. A surgical needle was used to thread the attachment wire through the fish and saddle.
- 6b. Dorsal view of a saddle-mounted radio transmitter on a 1.7 kg steelhead. The wire on the left is the attachment or ground plane wire and the antenna is to its right.
- 6c. A 60 cm long radio tagged steelhead swimming upstream.

from soft (1 mm) plastic measuring 16 mm x 45 mm which was bent in a U-shape by heat or a sharp crease. After two pair of small holes were made on top of the saddle for tying it to the transmitter, the transmitter and saddle were potted together in epoxy. In the field the saddle was trimmed and fitted in front of the dorsal fin. A long surgical needle was used to thread the teflon coated ground plane wire through one side of the saddle, under the skin and connective tissue of the back, and through a hole in the other side of the saddle. The saddle was drawn snug on the fish's back and two overhand knots were tied on the wire. A whip antenna trailed along the fish's body.

I have also experimented with surgically implanting underwater radio transmitters (Fig. 7). Tests indicated that very little (<10%) of the radio signal was absorbed by the fish's body. Transmitter antennas were made from flexible braided wire (.5 mm, Twist-o-flex) encased in teflon tubing. The fish was placed in a tilted V-shaped trough with its head immersed in water containing an anesthetic (MS-222) but its body out of water. A small longitudinal incision was made behind the pectoral fins. The transmitter antenna was tied by thread to a small (#1) knitting needle which was used to tunnel under the skin. As the needle was pulled through the tunnel and out a hole near the anal fin, the antenna followed into the tunnel. After the transmitter was inserted into the body cavity, sutures were taken around the base of the antenna to keep the transmitter from shifting in the body cavity. This method was tried on 3 fish but none lived longer than 2 weeks.

Figure 7. Implanting a radio transmitter with a flexible whip antenna.

- 7a. An internal transmitter with flexible whip antenna.
- 7b. Making a tunnel under the skin for the whip antenna. The antenna is connected to the tunneling tool by a thread and follows the tool into the tunnel.
- 7c. Implanting the transmitter into the body cavity behind the pectoral fins.

Since there was no infection, inflammation or injury from the transmitters, we felt the causes of death were related to poor initial physical condition. Incisions appeared to heal slowly in fish so that non-absorbable suture should be used. Radio transmitters with loop antennas can be implanted easier than whip antennas (R.W. Larimore, Illinois Natural History Survey); however, the range of the loop antenna is shorter and the signal more directional.

Radio transmitters can be implanted into the stomachs of fish. The National Marine Fisheries Service in Seattle, Washington inserted radio tags through the mouth into the stomachs of spawning salmon (G. Monan and G. Esterberg, pers. comm.). A whip antenna extended through the esophagus and was attached to the roof of the mouth with a plastic barb. Since the antenna was short, the range was less than from an external transmitter.

Summary

Freshwater fish were tracked by radio, telemetry which was well suited for use in turbulent and shallow freshwater. Radio signals attenuated exponentially with increasing salinity and depth. The signal was not affected greatly by aquatic vegetation, ice or a thermocline. Fish were tracked from shore with a hand-held loop antenna or with yagi antennas mounted on temporary towers and trucks. They were also tracked by loop antennas mounted on an airplane and a yagi antenna attached to a boat. Many individuals were distinguished and tracked at the same time because each

transmitter broadcasted on a different frequency between 52.5 to 53.5 MHz. Because of a low current drain, transmitters operated for long periods ranging from 30 $\pm$ 5 days for small fish (yellow perch) to several months for larger fish.

Transmitter parts cost about \$16 (U.S.). The pulse rate was set between 60 and 120 pulses per minute. Pulse width (on-time) was .02-.025 seconds and the duty cycle (on-time:total time) was 3% $\pm$ 1%. Whip antennas of varying lengths were constructed from .5 mm stainless steel wire. Transmitters were powered by certified mercury cells (1.4 v) or lithium batteries (2.8 v) used singly or in series for more power. The battery was the largest component and was chosen to fit fish size, and transmitter range and life requirements. I feel that the transmitter weight should not exceed 1-1.25% of the fish's weight out of water. Mallory RM-675 batteries were used on yellow perch transmitters, which measured 30 mm X 10 mm X 5 mm and weighed 3.3 gm in water (6.5 gm dry). Steelhead transmitters (Mallory RM-1) weighed 15.6 gm in water (26.0 gm dry) and measured 17 mm diameter X 40 mm. Scotchcast #5 electrical resin (3M Co.) was used to cover the components. Transmitters were attached along side the dorsal fin or on the back with a saddle mount and internally in the body cavity.

An automobile "radio" was modified into a portable tracking receiver with detachable loop antenna and jack for connecting other antenna systems. Parts for the receiver cost about \$125 (U.S.). A more complex, channel selector receiver is now available and can distinguish up to 100 different transmitter frequencies spaced 10 KHz apart.

Maximum signal ranges in water of 80-300 $\mu\text{mho/cm}$ conductivity were: loop antenna, .8-1.2 km; yagi, 2.4-3.6 km; and loop on airplane, 4.5 km. Mean bearing error for a loop antenna was $\pm 3.0^\circ$ at 5-15 m to $\pm 4.8^\circ$ at 76-92m. Yagi antenna bearings were accurate to $\pm 3.0^\circ$ or $\pm 5^\circ$ at 100 m to $\pm 43^\circ$ at 800 m.

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PART II

HOME RANGE MOVEMENTS AND HABITAT USE OF
LARGEMOUTH BASS IN MARY LAKE

INTRODUCTION

With the exception of migrations and occasional wanderings, most vertebrates confine their movements and activities to specific areas. The area over which an animal normally travels has been defined as its home range (Burt, 1943; Hayne, 1949). Home range movements are influenced by habitat, season and social interactions (Tester and Siniff, 1973). If an animal excludes other animals from all or part of its home range, then the defended area is usually referred to as a territory.

The home range concept has important management implications. Knowledge of a species' movements in relation to its habitat may reveal environmental requirements. Consequently, population densities may be greatly influenced by managing these requirements. Information on home range patterns aid population censuses by indicating the best times and places to sample and by yielding information on the assumptions used in population estimates. Since small, localized populations can be depleted by generous harvest quotas, home range data are useful in establishing non-harvest areas and harvest quotas.

Studies have shown that stream fishes have home pools or areas. Gerking (1953) discussed the concept of home range and presented evidence that stream fishes live in restricted areas from 30-120 m long¹. Gunning and Shoop (1963) observed that sampling shortly after marking yielded convincing data on the occupancy of home range by sunfish but the data were less

¹ All data presented have been converted to metric.

convincing several months after release. They presumed that the diminishing recaptures were due to natural mortality not emigration. Gunning (1965) demonstrated that fin clips and metal tags did not alter the frequency of localized recaptures in the presence or absence of a barrier to emigration. Furthermore, Larimore (1952) observed that some displaced smallmouth bass returned to their home pools.

The literature contains conflicting reports on largemouth bass (Micropterus salmoides) movements in lakes. Ball (1944) tagged 52 largemouth bass in a 4.0 ha, 17 m deep Michigan lake with a narrow littoral zone. From multiple recaptures on seven fish he concluded that the bass "roved over the entire lake and showed no tendency to remain in one location". Dequine and Hall (1950) tagged 1,616 largemouth bass during the winter in six connected Florida lakes but were unable to determine a migration pattern. From 308 angling returns over a period of 30 weeks, they found that 39.6% were caught within 2.59 km² of the release site and 84.1% within 8.0 km (sic) of release. There was some movement between closely connected lakes and the maximum distance traveled was 20.1 km. Moody (1960) tagged largemouth bass in Lake George which is a wide area of the St. Johns River, Florida. He concluded that Lake George contained a resident population with restricted ranges, and a mobile population which moved through the St. Johns River.

If an animal has a preference for a specific area, then a displaced animal might try to return to the area. Parker and

Hasler (1959) displaced largemouth bass in Wisconsin lakes. They found that the "percentage of fish returning to the capture site was usually unaltered by season, size of individuals and multiple recapture". Homing increased with time between release and recapture. They suggest that "part of the population returns to the capture site, but the remaining fish wander about randomly".

Lewis and Flickinger (1967) believed that largemouth bass had home ranges in a shallow ($\bar{z} = 1.8$ m), 3.4 ha Illinois farm pond. The pond was electrofished weekly from May to October with a 230 volt, 180 cycle a. c. generator. They observed that 59% of the recaptures were within 30 m, 83% within 61 m and 96% within 91 m of the original capture site.

Mark-recapture studies often have an insufficient number of recaptures on individuals to determine movement patterns. Furthermore, the extensive effort or methods needed to get sufficient recaptures often has an influence on an animal's movements.

To resolve the conflict on whether largemouth bass wander randomly or restrict their movements to specific areas, I decided during the summer of 1970 to monitor ~~their~~ movements using radio telemetry. Underwater radio tracking provided a method to study animal movements whereby the investigator has a minimal influence on an animal's movement and yet collects large amounts of information. This project also confirmed the feasibility and value of using radio telemetry to study fishery problems.

STUDY AREA

The study was conducted in Mary Lake located within Itasca State Park in northcentral Minnesota. Mary Lake is 22.6 ha in area and has a 7.5 ha littoral zone. The elliptical basin has a length of 852 m, a mean breadth of 265 m and a maximum depth of 12.5 m. There is a small outlet from the north end which flows into Lake Itasca and a small inlet at the south end but neither permitted fish migration. The lake becomes thermally stratified in summer.

There were extensive areas of sedge (Carex spp.) in the south and northwest ends of the lake. Most of the shoreline was lined with emergent vegetation consisting of bulrush (Scirpus spp.), cattail (Typha latifolia), reed (Phragmites communis), and arrowhead (Sagittaria spp.). Water lilies (Nymphaea odorata and Nuphar variegatum) were scattered in patches along the shoreline. Submergent vegetation, growing to 4-5 m depths included pondweeds (Potamogeton crispus, P. amplifolius and P. praelongus), coontail (Ceratophyllum demersum), water milfoil (Myriophyllum spp.), muskgrass (Chara spp.) and spikerush (Eleocharis acicularis). Fishes inhabiting Mary Lake are listed in Table 1.

MATERIALS AND METHODS

Radio tracking equipment was designed and constructed by the Cedar Creek Bioelectronics Laboratory of the University of Minnesota. The radio receiver used an automobile "radio" as the nucleus and tuner (Kuechle et al., 1971). An r.f. preamp and

Table 1. Fishes of Mary Lake

Common shiner	<u>Notropis cornutus frontalis</u>
Blackchin shiner	<u>N. heterodon</u>
Mimic shiner	<u>N. volucellus</u>
Blacknose shiner	<u>N. heterolepis</u>
Bluntnose minnow	<u>Pimephales notatus</u>
Mudminnow	<u>Umbra limi</u>
Northern pike	<u>Esox lucius</u>
Killifish	<u>Fundulus diaphanus menona</u>
Yellow perch	<u>Perca flavescens</u>
Johnny darter	<u>Etheostoma nigrum</u>
Iowa darter	<u>E. exile</u>
Largemouth bass	<u>Micropterus salmoides</u>
Pumpkinseed	<u>Lepomis gibbosus</u>
Bluegill	<u>L. macrochirus</u>
Rock bass	<u>Ambloplites rupestris</u>
Black crappie	<u>Pomoxis nigromaculatus</u>
Stickleback	<u>Eucalia inconstans</u>
White sucker*	<u>Catostomus commersoni</u>
Brown bullhead*	<u>Ictalurus melas</u>

from Underhill and Dobie

* Additional species trapped during this study.

converter enabled the automobile "radio" to receive 53 MHz signals. Signals were received by a diamond-shaped, bi-directional loop antenna mounted on the receiver.

Transmitters were modified for underwater use from the circuit described by Cochran and Lord (1963). A 30 cm whip antenna was attached to the transmitter. The mass of the transmitter in water was 14-15 gm, expected transmitter life was 60-90 days and maximum range using a loop receiving antenna was .8-1.2 km. Total cost was \$30 per transmitter.

Transmitters were attached to fishes' backs beside the dorsal fin. A surgical needle was used to pass a teflon-coated wire connected to the transmitter underneath the dorsal fin's supporting tissue. On the opposite side of the fish a plastic washer was placed over the wire and against the fish. Overhand knots prevented the wire from pulling through the washer and fish.

Largemouth bass were caught by angling or trap nets and all except a Lake Itasca fish were released at their capture sites. Trapping was conducted from 1 July to 14 July. Bass were sexed using the method reported by McComish (1968). Grid systems were established around each bass' home area by placing markers on shore at 6 m (20 ft) intervals and stakes and floats at 30 m (100 ft) and 61 m (200 ft) from shore. Radio locations were determined by triangulation using compass bearings from known locations or line of sight to shore markers. Data were converted from the small grids to an X-Y coordinate system encompassing the entire lake.

Computer programs described by Siniff and Tester (1965) and Siniff (1966) were used to determine home range parameters and construct map overlays. I analyzed movement data following the concept of maximum and utilized home range of Odum and Kuenzler (1955). They determined maximum home range size by a modification of Mohr's (1947) "minimum area method." Mohr (1947) connected the outlying animal locations on a map. Unfortunately, not everyone would construct the same polygon given the same data. Odum and Kuenzler (1955) connected the extreme outermost locations forming the smallest convex polygon which contained all the location points. Only one polygon fits this description. If a polygon side cut across land, I used the shoreline as the boundary. "Minimum area" or polygon methods are underestimates for mark-recapture data because an animal probably covers some area beyond the outermost trap. Since telemetry provides a larger number of locations, "minimum area" methods delimit an area that approaches the maximum area covered by an individual.

Odum and Kuenzler (1955) recognized the need to measure the proportion of the maximum area that is utilized. Gilmer (1971) determined the "primary" home range size by connecting the outermost locations after excluding peripheral points greater than a designated distance from an adjacent point recorded on a different day. I measured the utilized or primary home range by a grid-square method (Siniff and Tester, 1965; Rongstad and Tester, 1969). The computer program partitioned the rectangular coordinate system of the lake containing the bass locations into 5 m squares. I chose 5 m squares because my mean location error

was less than 5 m. To calculate utilized area the computer summed the areas of the squares which contained locations. Since the whole area of a square is added even though only a single location may occur in a corner, the area is slightly biased. However, an advantage of this method is that intensity of use is printed as the number of locations per square.

For constructing map overlays, the computer assumed that squares without fixes are part of a block of intensively used squares provided that not more than X empty squares separated two horizontally or vertically adjacent fixes. The number of empty squares included (X) was chosen arbitrarily to be 4.

Other home range parameters were determined by the following methods. Geometric centers of activity were calculated by averaging the X coordinate values for all locations and then the Y values (Hayne, 1949). Activity radii or distances from the center of activity to each location were measured (Dice and Clark, 1953). All locations except for an excursion around the lake by bass #3 were used to determine geometric centers of activity and activity radii. The frequency distribution of activity radii from the geometric center was compiled as described by Tester and Siniff (1965) and Ables (1969). Home range length and width was measured by Gilmer's (1971) method. The shapes of home ranges were described by an "index of linearity" which was calculated by the ratio of home range length to width (Ables, 1969). An "observation-area" curve or cumulative increase in maximum home range area with time was drawn to determine whether home range

size was stable or increasing (Odum and Kuenzler, 1955; Ables, 1969). Odum and Kuenzler (1955) recommended that home range size be determined at the point on the "observation-area" curve beyond which each additional observation will produce less than one percent increase in area. If the curve does not level-off, then not enough observations have been made to determine home range size.

RESULTS

Tracking data

Four largemouth bass weighing 1.4 to 1.6 kg were tracked between 26 June and 31 August 1970 and 18-20 September 1970. Bass #1 and #3 were believed to be males and #2 and #4 females. The period of tracking ranged from 25 to 87 days ($\bar{X} = 59.5$) and the number of days tracked ranged from 19 to 56 ($\bar{X} = 38.2$). The total number of radio locations was 434 ($\bar{X} = 108.5$).

Figure 1 shows home range maps for three bass. Maximum home ranges are delimited by the convex polygons and the utilized or primary areas are indicated by the shaded grid-squares. The shaded areas encompass 90.0% of the total fixes or a mean of 83.8% fixes for individual home ranges. Table 2 summarizes home range parameters. Data from the first three days were excluded for bass #3 because it is not known whether the bass was captured during an excursion or whether the long movement was caused by handling.

Locations with respect to depth contours and the intensity

FIGURE 1. Summer home ranges of three largemouth bass in Mary Lake. Convex polygons enclose the maximum home range. Shaded grid-squares represent the primary or utilized range.

Table 2. Size estimates of largemouth bass summer home ranges.

	1	2	3	4	
Beginning of tracking	26 June	1 July	9 July	31 July	
End of tracking	20 Sept.	25 July	20 Sept.	20 Sept.	
Number of locations	185	28	150	65	
Number of days tracked	56	19	49	29	
Period of tracking (days)	87	25	74	52	
Maximum home range area	1.17	.275	1.41	none	hectares
(Convex polygon method)	11,696	2,752	14,116	--	m ²
Utilized or primary H.R.	.35	.04	.26	none	hectares
	3,541	441	2,598	--	m ²
Length	192	110	173*	--	m
			447	--	m
Width	94	47	52*	--	m
			59	--	m
Index of linearity $L \div W$	2.04	2.34	3.33*	--	

*First three days excluded.

of habitat use are illustrated in Figures 2 and 3. The bottom contours within the bass home ranges were plotted from the 1964 lake survey map prepared by the Minnesota Conservation Department and test soundings made during this study. Approximately 409 of 434 locations or 94.2% were from depths shallower than 3 m (10 ft). Since bass were moving between shore and 3 m, shapes of the maximum home ranges tended to be linear. This is indicated by indexes of linearity greater than 2.0 (Ables, 1969).

Bass tended to spend the afternoon in very shallow water (.6 m). For example, bass #1 moved between 0800-1000 C.S.T. to resting areas averaging .5 m deep and 4 m from shore. This corresponds to the timing (0900-1300 E.S.T.) of the lowest oxygen consumption determined in the laboratory by Clausen (1936). None of the other bass showed as pronounced a periodicity in behavior as bass #1. With the possible exception of mid-afternoon (1400-1700 C.S.T.), frequent bass activity, as determined by the varying intensity of the radio signal, was observed during all hours. Irregular sampling prevented a more comprehensive determination of activity patterns.

Largemouth bass made occasional excursions. Figure 4 shows an excursion by bass #3 around Mary Lake. The total distance traveled in seven days was 1600 m if the shoreline was followed or 1160 m if the fish moved in straight lines between radio locations. The rate of movement was between 165.7 m per day and 228.6 m per day. Since some of the locations during the excursion were about 3 m deep, the 3 m (10 ft) contour interval

FIGURE 2. Summer home range and intensity of habitat use for two largemouth bass. Maximum range is enclosed by convex polygons. Intensity of use is illustrated by the number of locations per grid-square. The point of capture is indicated by C and R designates mid-day resting areas.

FIGURE 3. Summer home range and intensity of habitat use for largemouth bass #3. Maximum range is enclosed by a convex polygon and intensity of habitat use is illustrated by the number of locations per grid-square. C indicates point of capture.

FIGURE 4. Excursion of largemouth bass #3 around Mary Lake. C indicates point of capture and H indicates the primary range.

probably describes the actual path best. This represents a distance of 1320 m at 188.6 m per day. The fish returned to its primary range and apparently remained there the rest of the summer. Bass #3 also made a similar movement three days after release. It moved 324 m to the center of its primary range. This fish was probably captured during an excursion. However, the fish could have been returning late from a spawning area or the movement could have been influenced by handling and tagging. Bass #1 and #2 made excursions as long as 110 m and 70 m respectively.

An experiment was conducted to test whether a bass caught in another lake and transplanted to Mary Lake would exhibit:

- 1) movement confined to a small area similar to the Mary Lake bass or
- 2) movement over a large area.

Figure 5 shows the movements of a 1.4 kg bass caught in Lake Itasca and transplanted to Mary Lake. The movements covered a large portion of the littoral zone of the northern half of the lake and the longest time spent in a small (.4 ha) area was five days. This area coincided with part of bass #3's primary range. On 3 August both bass #3 and #4 were within 6 m of each other. From locations taken at 15 minute intervals, it appeared that bass #4 moved around bass #3 while the latter remained relatively stationary. Bass #4 stayed in the south end of bass #3's primary range from 3-8 August. During this same period bass #3 remained in the north end of its primary and secondary range. No similar radio locations were made that would confirm whether this was an agonistic encounter. However, there appeared to be little home range overlap between large

FIGURE 5. Movements of a Lake Itasca largemouth bass transplanted into Mary Lake. R indicates the release point and I indicates the area of interaction with Mary Lake bass #3.

Mary Lake bass. The only other large bass observed was a 1 kg bass which was trapped between home ranges #1 and #3.

The mobility of bass is described by Figure 6 which shows how the percentage of activity radii was distributed with distance from the geometric centers of activity. This is a cumulative histogram for the three Mary Lake bass. The mean distance from the geometric centers was 32.1 m. Activity radii or locations were distributed from the geometric centers of activity as follows: 54.4% within 25 m, 86.9% within 50 m, 92.5% within 75 m and 95.0% within 100 m.

Figure 7 is a modification of the "observation-area curve" containing the cumulative weekly maximum home range size. Summer home range areas of the Mary Lake bass began to level off after 2-5 weeks of radio tracking and 15-145 radio locations. However, bass #1 and #3 had further increases in home range area after 6 and 8 weeks of radio tracking, respectively. Bass #1 shifted its home range to deeper water about 15 August. The shallow areas that bass #1 occupied in July had become overgrown with vegetation and smelled of H_2S . After I returned to the study area during 18-20 September, bass #3 was found 40-80 m from its primary summer range. Since the primary range was not excessively vegetated, it is not known if this movement represented a fall shift or break-up of the home range. No late summer shift was observed in the home range of bass #2 because of a premature transmitter failure.

Transmitter effect

I found no instances where the transmitters influenced the

FIGURE 7. The cumulative weekly maximum home range areas or "observation area" curves for three largemouth bass.

results obtained. The radio transmitters did not cause mortality or fungal infection nor prevent fast escape, feeding and long movements. There was no mortality during the radio tracking period; however, one transmitter quit after 25 days. On at least eight occasions, I was able to observe bass #1, #3 and #4. There was no fungal growth at the attachment location but bass #3 had some fungus on the right eye which may have been caused by handling. Transmitters wore some scales off but no open wound was visible. Some weeds were observed on the transmitter but no changes in behavior were noticed. Bass continued to inhabit the weediest parts of the lake. For example, I was never able to observe bass #2 because it escaped under the sedge mat or dense bottom vegetation before I could spot it. When startled, bass darted for deeper water or cover without any sign of being hindered by a transmitter. On four other occasions I observed radio tagged bass breaking the surface, which I believe was feeding behavior. This behavior occurred from 0700-0930 hr (C.S.T.) except for one time at 1630 hr. The best evidence that radio transmitters did not inhibit feeding came from angling. Bass #1 was hooked at 1900 hr on 29 August but was lost at the boat. Attempts to recover the other bass by angling also failed. Radio tracking revealed that poor casting near the fish spooked them. Lastly, radio transmitters did not prevent long movements. For example, the following is the number of movements greater than 50 m: bass #1, 4; #2, 2; #3, 5; and #4, 7. The longest movements were: #1, 110 m; #2, 70 m; #3, 1600 m and 305 m; and #4, 286 m and 283 m.

After radio tagging and release, bass swam to the bottom and hid their heads in weeds. They initially had a tendency to tip towards the transmitter side which resulted in increased fin movements for compensation. All bass moved from the release area in less than 24 hr. No extensive data collection was made during this compensation period. Gallepp and Magnuson (1972) found that bluegills compensated in less than 24 hr for weights with a mass in water equal to about 2% of the fish's mass (out of water). I tagged bass with transmitters weighing in water about 1% of the fish's mass.

DISCUSSION

Individual largemouth bass utilized specific areas in Mary Lake during the summer of 1970. Maximum ranges were about .3 to 1.4 ha and the primary or utilized areas were about .04 to .35 ha. Most radio locations (67.9% to 92.4%) were confined to a block of adjacent grid squares represented by the shaded areas in Figure 1. The distribution of fish locations from the geometric centers of activity compared very closely to the recapture distance from the original point of capture reported by Lewis and Flickinger (1967). They found among 96 recaptures that 59% were recaptured within 30 m, 83% within 61 m and 96% within 91 m of the original capture point. I found that 54.4% of the activity radii or locations were within 25 m of the geometric centers; 86.9% within 50 m, 92.5% within 75 m and 95.0% within 100 m.

Largemouth bass appeared to have preferences or attractions

for these small areas. First, the fact that bass #3 returned to its primary range after an excursion around the lake suggests that this area had special significance to the fish. Other shorter excursions also resulted in bass returning to their primary ranges. Secondly, bass #4, which was transplanted to Mary Lake from Lake Itasca, exhibited an entirely different movement pattern than the Mary Lake bass. Possibly, this bass could not find an area to establish a home range or it was searching for "home" which lay north of Mary Creek. Observations by other workers suggest that bass are attracted to specific areas. Parker and Hasler (1959) found that 27.7% to 46.1% of their displaced largemouth bass returned to the original capture area. After bass overwintered in deeper water, Lewis and Flickinger (1967) observed that a large percentage of bass returned to the same segment of shoreline previously occupied.

My observations on largemouth bass home ranges and those of Lewis and Flickinger (1967) differ from other workers. Ball (1944) reported that bass roved over the entire lake. Lewis and Flickinger (1967) attributed the difference to density of large fish. The 4.0 ha lake that Ball (1944) studied had a population of only 219 bass over 15 cm, whereas Lewis and Flickinger (1967) found 644 bass over 23 cm in their 3.4 ha pond. However, the density of bass appeared to be low in Mary Lake and therefore, crowding did not seem to be completely responsible for restricting bass to small areas. Perhaps the main reason Ball's (1944) conclusion differs is that he had very few recaptures. The greatest number of recaptures was four and only five of seven

fish were caught more than once. Ball (1944) also trapped over a longer period; ice out to freeze up. Dequine and Hall (1950) and Moody (1960) found long movements of bass. This can probably be explained by a difference in habitat and geographic area. They tagged Florida largemouth bass in shallow lakes connected by rivers whereas Lewis and Flickinger (1967) and I studied bass in small northern lakes. However, Moody (1960) did find evidence that some bass had restricted ranges. Parker and Hasler (1967) suggested that the fish that failed to home wander about randomly. They tracked some displaced bass with floats. Bass moved randomly from the center of the lake to shore but some homed by searching the shoreline. It is not known whether Wisconsin lakes have a sub-population that prefers to wander or whether the sub-population preferred specific areas but were unable to find "home". It is possible that I did not observe random movement because only a small proportion of the population demonstrates such movement and my sample size may have been too small to include such individuals.

Largemouth bass made occasional excursions. Lewis and Flickinger (1967) found two fish that made excursions and returned to the area of repeated capture. This was typical of most excursions in my study. However, they also observed two individuals that moved long distances and showed a preference for a new area. Bass #3 also moved to a new area three days after tagging. These fish may have been captured during an excursion from the home range or the movements could have been induced by

handling. Lewis and Flickinger (1967) found that 18% of the total recaptures were across a cove or across the lake. They measured straight-line distances because they did not capture a bass along a probable shoreline route. Since their pond was shallow, bass could have traveled across the pond. However, they were not likely to capture a fish along a probable shoreline route by electrofishing once a week. I radio tracked bass #3 on an excursion around the lake and back to its primary range. Since all home ranges contained a large population of small sunfish, food was probably not the main reason for the excursion. The reason for excursions is open for speculation.

Many fisherman believe that largemouth bass spend the hottest part of the day in deep water and feed in the shallows during the morning and evening. The large percent (94.2%) of locations less than 3 m deep indicated that this was not true in Mary Lake. In fact, bass tended to spend mid-day in about .6 m of water near shore. There may be several reasons for this apparent discrepancy. Since there was much vegetation for concealment, bass were not forced to deep water as they might be in a clearer, less productive lake. Secondly, shallow water temperature in Mary Lake does not exceed the avoidance temperature of largemouth bass. Coutant (1974) found that wild largemouth bass in Tennessee have a final preferendum near 27°C. This temperature coincided with the optimum temperature for growth that he determined in the laboratory. Coutant (1974) found that ultrasonic tagged largemouth bass preferred the warm shallow water in March but remained in deeper

water in July as the surface temperatures exceeded 26°C. The littoral zone in northern Minnesota lakes seldom exceeds 27°C. Furthermore, many reports of deep water bass come from southern U. S. (Underwood, 1973). Besides warm lake temperatures, there may be behavioral differences in southern largemouth bass varieties.

SUMMARY

Four largemouth bass were radio tracked in Mary Lake during the summer of 1970. The three Mary Lake bass had preferences for specific areas. Maximum home range size ranged from .3 to 1.4 ha and primary or utilized ranges were about .04 to .35 ha. Activity radii or locations were distributed from the geometric centers of activity as follows: 54.4% were within 25 m, 86.9% within 50 m, 92.5% within 75 m and 95.0% within 100 m. Since most (94.2%) bass locations were between shore and 3 m deep, home range shapes tended to be linear. Indices of linearity range from 2.04-3.33.

Bass #1 shifted its summer home range to deeper water after 15 August. I feel this change occurred because the primary range became overgrown with vegetation and smelled of H₂S. Bass #3 may have shifted its home range during September.

Bass also made excursions from their primary ranges and returned. Bass #3 swam around the lake which was a distance of 1320 m in seven days or 188.6 m per day.

A fourth bass was transplanted to Mary Lake from Lake Itasca. This bass wandered around the north half of Mary Lake and did not

establish a home range.

Since the observation intervals were irregular, the activity patterns were not precisely determined. However, radio tagged bass were observed surface feeding on three occasions between 0700-0930 C.S.T. and once at 1630 hr. Bass #1 often moved between 0800-1000 C.S.T. to resting areas averaging .5 m deep and 4 m from shore. Bass spent the afternoon in shallow water (.6 m) and the least amount of movement occurred from 1400-1700 C.S.T.

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PART III

MOVEMENTS AND BEHAVIOR OF STEELHEAD IN
WESTERN LAKE SUPERIOR

INTRODUCTION

The native range of rainbow trout (Salmo gairdneri Richardson) after the last glacial period was primarily the Pacific Ocean and coastal drainage of North America from Alaska southward to Mexico; however, rainbow trout have now been introduced into waters on all continents except Antarctica (MacCrimmon, 1971). MacCrimmon and Gots (1972) reported that rainbow trout were first introduced into Lake Superior from McCloud River stock by Ontario in 1883. By 1900 more than one million McCloud River rainbows and steelhead trout had been planted into Lake Superior tributaries of Minnesota, Wisconsin and Michigan. Rainbow trout were considered common in western Lake Superior by 1902 and in the entire lake by 1920.

In addition to McCloud River and steelhead trout, other varieties such as Kamloops, Madison, Donaldson, etc. have been introduced. Valadykov (1963) believes all local North American rainbow trout forms belong to one species. Shapovalov and Taft (1954) report that the term "steelhead" does not refer to a distinct species or subspecies but designates "any species of trout that has been in salt water." However, popular usage has limited "steelhead" to ocean migratory rainbow trout rather than marine cutthroat, brook or brown trout.

Anglers refer to the large, silver rainbow trout that migrate up Lake Superior tributaries as "steelhead." I shall follow this usage for the following reasons: 1) Pacific steelhead and Lake Superior steelhead are considered the same species; 2) the

behavior and life history patterns of Lake Superior steelhead are similar to west coast steelhead as determined by my study and those of others (Niemuth, 1970; Kwain, 1971; Dodge and MacCrimmon, 1971; and Hassinger et. al., 1974); 3) rainbows are more or less migratory and inland stock rainbows can acquire a steelhead-like migratory behavior when allowed to migrate to the ocean (Shapavalov, 1951; MacKay, 1963) or Great Lakes; and 4) despite its lack of salinity, Lake Superior resembles a small sea because of its currents, tide, great area and depth.

Steelhead trout have a wide variety of life history patterns. They may spend a portion of a year to four years in their natal stream before migrating to the ocean or the Great Lakes. Downstream migration is triggered by physiological and external changes called smolting. It is believed that salmonids become imprinted on stream odor shortly before or during downstream migration (Madison et. al., 1973). After a pelagic existence of one to four years, steelhead return to spawn in the stream in which they were imprinted.

Steelhead may enter west coast streams any month under high water conditions but typically migrate in two seasonal runs. Shapovalov and Taft (1954) define a fall-run fish as one "which enters a stream at any time from the late summer through the following spring and will spawn sometime during that same period." A spring-run fish is one that "enters a stream in the spring or early summer, but which will not spawn until the following fall, winter or spring." Smith (1960) and Withler (1966) use the terms

"winter-steelhead" and "summer-steelhead" instead of fall-run and spring-run, respectively. These terms describe whether fish are "overwintering" or "summering-over" in the stream. Winter-steelhead have well developed gonads and spawn within three or four months of entering the stream (Smith, 1960). Summer-steelhead have slightly developed gonads and spawn after 9-12 months in the stream.

Along western Lake Superior steelhead enter streams mainly from April through May and September through October. I will follow popular usage and refer to these as fall-runs and spring-runs. To avoid confusion I will refer to west coast runs as winter-steelhead and summer-steelhead. I will present data that show that Lake Superior fall-runs and spring-runs are similar to winter-steelhead but summer-steelhead are rare in Lake Superior.

A radio tracking project was conducted from 1971-74 to broaden understanding of the movements and behavior of rainbow trout in western Lake Superior. Data will be presented in the following sequence: fall movements, pre-spawning run, spawning run, and dispersal and summer movements.

STUDY AREA

Lake Superior is not only the largest body of fresh-water in the world but one of the deepest. It is 579 km long, with a maximum width of 257 km and an area of about 82,800 km² (Schwartz and Thiel, 1963). Maximum depth is 397 m. The study area (Fig. 1) was limited for airplane tracking to the extreme western

FIGURE 1. Maps showing the relationship of the study area (below) to Lake Superior (upper insert).

arm of Lake Superior and tributary streams from Duluth, Minnesota ($46^{\circ}50'N$, $92^{\circ}11'W$) northeast (90 km) along Minnesota's "North Shore" to Silver Bay, southeast (45 km) to the Apostle Islands of Wisconsin and southwest (95 km) along Wisconsin's "South Shore" to Duluth. The shoreline consists of a steep rocky North Shore, a 16 km sand bar between the cities of Duluth and Superior (Wisconsin), and a red clay South Shore. In two kilometers, the bottom drops off sharply to over 90 m deep on the North Shore and drops slowly to about 18 m on the South Shore. Maximum depth within this area was over 200 m. All fish were captured in the vicinity of French and Knife Rivers and most of the tracking was along Minnesota's North Shore.

Minnesota's North Shore extends for 238 km to Ontario, Canada. A 32 km wide belt of Keweenaw Age lava flows and intrusive rocks slope down to Lake Superior (Schwartz and Thiel, 1963). Within the rugged terrain, 59 streams arise with 213 km of water accessible to steelhead (Hassinger et. al., 1974). Most of the steelhead water, which is contained in 21 streams, is located within the study area. The headwaters of most streams are at elevations 200 to 350 m above Lake Superior (183 m a.s.l.). Since the last 125 m of descent occurs in the lower 5 km, high falls and steep cascades restrict migrating steelhead to the lower stream (Hassinger et. al., 1974). Almost half (28/59, 47.4%) of the streams have less than .16 km of steelhead water. Boulders, rubble and gravel line the stream bottom.

Stream flow, which depends primarily on surface runoff, is

highly variable. Smith and Moyle (1944) cite several rivers with minimum flows as low as $.06 \text{ m}^3/\text{sec}$ and maximum flows greater than $34 \text{ m}^3/\text{sec}$. Melt-water and high precipitation produce peak flows in April and May. In summer, water flows are extremely low and sand bars from east winds almost completely block most streams. Heavy rain again produces some peak flows during late August through October. Streams can ice over as early as mid-October and stream flow becomes extremely low from November to March.

Major North Shore streams are described by Smith and Moyle (1944). The two main streams in the study are French and Knife Rivers. French River drains 80 km^2 in St. Louis County (T.51N, T.52N and R.12, R.13) with the mouth located about 9 km NE of Duluth. It has a length of 19 km of which .3 km is accessible to steelhead (Hassinger, et. al., 1974). The Minnesota Department of Natural Resources maintains a weir about 60 m from Lake Superior. To reach the weir, steelhead leave the lagoon and swim over a small rock slide. Most steelhead are taken into the fish hatchery for egg collecting. Above the weir a series of pools lead to a 5 m high concrete dam which was designed for water storage and imprinting of smolts. An Alaskan Step-pass Fishway makes it possible for steelhead to pass over the dam but a waterfall located just above Interstate Highway #61 is a complete barrier. Smith and Moyle (1944) report that the water is moderately hard with a total alkalinity from 52.5 to 77.5 ppm and a pH about 7.6.

Knife River has the largest amount of water (112.6 km)

accessible to steelhead and the largest steelhead runs on the North Shore (Hassinger, et. al., 1974). Nine tributaries enter Knife River and the total drainage area encompasses 233 km². The headwaters are located 10 km NW of Two Harbors in Lake County. Rock outcrops force the river to flow southwestward and parallel to Lake Superior for over 12 km. The river meets Stony Point Ridge, which is a massive lava flow, and makes a hairpin turn to Lake Superior (Schwartz and Thiel, 1963). Most water is diverted from the hairpin turn and the two channels meet above Interstate 61. The mouth of Knife River lies 10.5 km NE of French River and 6.4 km NE of Sucker River. A 200 m long, 50 m wide and 1.5 m deep lagoon drowns the river mouth.

Two waterfalls and many rapids line the river. The lower falls, which is about 5 m high and 40 m wide, lies 1.3 km upstream from Lake Superior. An 8 m high and 30 m wide upper falls lies 4 km from the mouth. Step-pockets, which were blasted by the Minnesota D.N.R., allow steelhead to pass.

Steep red clay banks and rock outcrops surround the river channel. The banks are covered mostly by aspen (Populus tremuloides) and birch (Betula papyrifera) with an understory of balsam fir (Abies balsamea) and hazel (Corylus sp.). Between the morainic hills are swamps and springs which augment stream flow. The lowland areas are covered with cedar (Thuja occidentalis).

The water of Knife River is moderately hard with a total alkalinity from 47.5 to 70.0 ppm and a median pH of 7.5 (Smith and Moyle, 1944). Stream flow near the mouth is as low as

1.4 m³/sec during early summer.

Chemical and physical characteristics of western Lake Superior are described in a series of papers by the School of Public Health, University of Minnesota (1956-61). Lake Superior has an orthograde oxygen curve with dissolved oxygen near saturation at all depths. Chemical concentrations are uniform in the upper 60 m indicating strong mixing during circulation. Carbonate hardness varies from 44.2-45.0 mg/l and the pH ranges from 7.2 to 7.9. Total phosphorus is very low (.24-.48 ug/l) suggesting that it is a limiting factor in productivity. Secchi disc transparency ranges from 1-2 m near the South Shore to 17 m near Grand Marais. The lake begins to stratify in mid-June and becomes isothermal again after mid-November (Sydor, 1974). During August the thermocline may lie between 12 and 18 m. Surface temperatures usually are below 16°C and the hypolimnion remains between 4°C and 8°C.

Surface waters in Lake Superior tend to circulate in a counterclockwise cyclonic pattern (Ruschmeyer, et. al., 1958; Baumgartner, et. al., 1971). Strong sinking occurs along the south shore and Canadian north shore and an easterly drift with upwelling is common along the Minnesota shore. A southwesterly current from Grand Marais diverges near Silver Bay with one component flowing southeasterly to the main lake (Baumgartner, et. al., 1971) and the other component continuing southwesterly to Duluth and along Minnesota Point (Sydor, 1974). The southwesterly along shore current has an average speed of 9 cm/sec in

the Lester River area (Sydor, 1974). Within the western arm, drift bottle experiments, dynamic (temperature) heights calculations and transparency data indicate that a counterclockwise eddy exists from July to September (Ruschmeyer, et. al., 1958). However, reversals of the pattern occur (Ruschmeyer, et. al., 1958) but the counterclockwise pattern probably is restored by 1-2 days of easterly winds (Baumgartner, et. al., 1971). Between Two Harbors and French River a current cuts across the arm to Port Wing and along the south shore to the Apostle Islands. Sydor (1974) used ERTS satellite photographs of red clay turbidity to determine current patterns near Duluth-Superior. During summer, eddies form off Minnesota Point that flow towards Lester River with east winds and away with west winds. A complex pattern exists in open water over 5 km from Minnesota Point, Wisconsin and Minnesota. Sometimes the currents move northeast toward the open lake. East of the Superior port entrance the currents flow along the south shore. During spring and fall, the currents tend to sweep counterclockwise around the southern tip of the lake. After the ice forms, the winter currents near Duluth diminish to less than 1 cm/sec (Maanum, 1974).

METHODS

Steelhead were captured in the weir at French River. At Knife River steelhead were electrofished at the lower falls during the spring using a 300 watt a-c Honda generator and 2 m electrodes. The electrofishing unit was attached to a boat and

the lagoon of Knife River was fished during the fall. A d-c converter was sometimes used with the Honda generator. Since the power of the generator was low, most steelhead were barely stunned. A hoop net with two 15 m long leads was used in Knife River lagoon during the fall of 1973. During the summer of 1972, two 60 m long, 114 mm stretch mesh gill nets were set at the surface to 5 m deep from 10 m to 800 m offshore between French and Sucker Rivers.

Trapped fish were anesthetized in a 1:10,000 tricaine methanesulfonate (M.S. 222) solution. Atkin's tags were attached to 147 steelhead by monofilament line under the anterior supporting tissue of the dorsal fin. Radio transmitters with the mid-dorsal saddle mount as previously described were attached to 104 fish weighing 1.5 kg or more. In addition to weight, total length, fork length and standard length were taken. Sexes were determined according to methods described by Niemuth (1970). Ovaries were taken from angler caught fall-run fish and weighed fresh. Stomach samples were collected from fish caught by trolling on Lake Superior in the summer and preserved in 10% formalin. Contents were expressed as percentage of total volume.

Field work was conducted between the following dates: 6 May to 24 October 1971; 30 April to 31 December 1972; 25 April to 31 December 1973; and 28 April to 5 June 1974. Attempts were made to locate each fish at least once a day except in December.

During December, the river mouths and lagoons from Lester to Knife Rivers were monitored every 7 to 10 days for returning radio tagged steelhead.

RESULTS AND DISCUSSION

Fall Movements

Fall-run steelhead entered North Shore streams as early as mid-August and as late as mid-November; however, most entered streams in September and October. Fall angling was much more variable than spring fishing but sometimes almost as good. The Minnesota Department of Natural Resources has been seeking ways to establish a strong fall fishery. One goal of this project was to describe fall behavior and find an explanation for fall runs. Some of the hypotheses held by fishermen and biologists for the fall run were as follows: 1) fall-run steelhead were a fall spawning strain of rainbow trout; 2) steelhead wandered into rivers because they have a natural tendency to orient (positive rheotaxis) into river currents, especially during high water; 3) fall-run steelhead were early spring arrivals that overwinter in the streams; 4) fall-run steelhead were early spring arrivals that sought to overwinter but could not because of unfavorable conditions; and 5) fall-run steelhead were making a migration at the same time of the year that their ancestors made on the West Coast.

In order to determine whether the fall run was made by fall spawning fish, I examined the spawning times reported for other

areas, stocking records for fall spawning strains, status of fall strains in the Great Lakes and gonad development. Rainbow trout have variable spawning times in North America. In its native McCloud River (California) rainbow trout spawned from February to April (Agersborg, 1937). Both winter and summer steelhead usually spawned during March and April in British Columbia (Withler, 1966). However, Shapovalov and Taft (1954) reported that summer-steelhead, which did not occur in most California streams, spawned in November and December and winter-steelhead spawned during winter and spring. As rainbow trout were introduced into other areas of North America, it became apparent that they spawned during different times at hatcheries in different locations. Many of these hatcheries had spring water with little seasonal temperature variation which permitted trout to spawn over a broad time period. Agersborg (1937) reported the following spawning times: New Hampshire, November-June; Wytheville, Va., November-February; Colorado, May-July; Neosho, Mo., 1 November-1 March; Manchester, Iowa, 15 November-15 March; Montana, 15 April-1 June; and Pittsford, Vt., November-December and April-June. Fish culturists recognized spawning variability and artificially selected for fall-spawning rainbows (Toney and Bowen, 1968). The advantage of fall brood stock was that the fry had more time to grow before stocking than spring fry.

To estimate the extent of fall spawning in North Shore streams, I searched for stocking records of a fall spawning strain. Minnesota acquired a Missouri fall spawning rainbow in

the 1930's (Eddy and Underhill, 1974). They were stocked mainly in inland waters but possibly some reached Lake Superior. In 1959 the Manchester, Iowa federal hatchery shipped 1,776,000 eyed eggs from fall spawners to the Duluth Hatchery, Minnesota (N. Hines, pers. comm.). Minnesota D.N.R. records did not indicate the strain but showed large rainbow fry plants in numerous North Shore streams in June 1959 (S. Daley, pers. comm.). Between 1960 and 1967 the Lanesboro, Minnesota hatchery received at least 1,050,000 eyed eggs from the Manchester fall strain (N. Hines, pers. comm.). About 576 yearlings that were probably Manchester rainbows were stocked in French River during 1968. In addition, Minnesota acquired the Madison fall strain from Wisconsin and has used them for inland stocking. The Madison strain was introduced into North Shore streams during the spring of 1973 but small numbers could have been introduced earlier. In conclusion, large numbers of fall spawning rainbows have been introduced into North Shore streams and possibly could be responsible for the fall run.

Since fall spawners have been stocked along the North Shore, I inquired about the status of fall strains in the Great Lakes to determine if they run and spawn in the fall. Mr. Russell Daly (pers. comm.) of the Wisconsin D.N.R. wrote, "We regularly encounter gravid and egg running rainbows during our (Lake Michigan) salmon harvest operations in November. Until we started stocking fall spawning rainbows our rainbow fishery was confined March through June; now we have a fall fishery on fall spawners beginning in late September through November." Most Lake

Michigan tributaries in Wisconsin were of poor quality for spawning so hatchery fish were used to perpetuate the runs. Mr. Clarence Taube (pers. comm.) of the Michigan D.N.R. has observed fall-run rainbow trout on redds in the Platte River, a tributary of Lake Michigan. During the fall of 1971, he examined the spawning conditions of rainbows at the Platte River weir:

16 October, no ripe fish in 26; 9 November, 9 ripe males and no ripe females in 101 additional fish; and 23 November, 6 ripe males and 2 ripe females in 55. The sex ratio was approximately 1:1.

A different view of fall-run rainbows in Lake Michigan was expressed by Vernon Bennett (pers. comm.) who was the biologist in charge of Michigan's domestic Salmonid Brood Stock program. Michigan's management program was based on planting wild progeny from spawning spring-run rainbows which ascend the Little Manistee River. During October and November 1973, Michigan trapped 1,899 rainbows and held 1,478. He estimated that 950 females were handled but only 2 were ripe when released. Most fall-run males had sperm production. Bennett wrote, "However, it is my opinion that these 'wild' fall running fish are not true fall spawners, but instead they are early spring spawners which descend the streams during February and March...It has been my observation (outlined below) that fall spawning domestic hatchery rainbows will revert to the spring spawning pattern when released into a natural environment:"

1. Fall spawning domestic brood stock which were clipped and released into Lake Michigan by the state of Wisconsin ran the Little Manistee River and were spawned in March of 1972.

2. Fall spawning brood stock retired from Harrietta [Hatchery] and placed into impoundments have been recaptured while on a 'spring spawning run' into small tributaries.
3. In the spring of 1970, over 20,000 yearling domestic rainbows escaped from a rearing station on an access river to Lake Michigan. In the spring of 1972, the run on this river evidenced a significant visual increase even though the spring run of 1972 was down on other rivers.

Further clues on whether North Shore fall-runs were domestic fall spawners was provided by the success of fall spawning strains recently planted into Lake Superior by Michigan and Wisconsin. Mr. James Peck (pers. comm.) of the Michigan D.N.R. reported that they have seen ripe fall-run rainbows but did not know when egg deposition occurred. He believed that the ripe fish were domestic strain rainbows. Wisconsin stocked over 500,000 fall-spawning rainbows between 1966 and 1973. No evidence has been found of fall rainbows successfully spawning in the fall (Neimuth, 1970; B. Belonger and B. Swanson, pers. comm.). Returns have been small and it was believed that some may have reverted to spring spawning.

Thus, in areas that were more suitable for fall runs than the North Shore, there was confusion over whether fall-running fish were domestic fall spawners or early native arrivals. Since a fall trout season was recommended as early as 1945, fall migrations in Wisconsin's Brule River were believed to have started during the early 1940's or before (Niemuth, 1970). This was before extensive stocking of fall strains. However, most must spawn in December or later because only a small percentage of

females were ripe in November. There was also evidence that fall spawners reverted to spring spawning on Lake Michigan and the South Shore of Lake Superior.

Analysis of gonad development provided information on fall spawning during the North Shore fall run. Some anglers reported fall-run steelhead "full of eggs". However, neither Dr. Hollie Collins (pers. comm.) of the University of Minnesota at Duluth nor myself have found ripe females. I have examined the ovaries of over 75 fall fish and obtained ovary weights from 27 trout. These ovaries weighed less than 6.0% of the fish body weight whereas ovaries of ripe spring spawning steelhead weighed 9-14% of the body weight (Fig. 2).

I have found several ripe fall-run males in October. Eight ripe or nearly ripe males were trapped in French River and 5 were known to be Minnesota stocked Kamloops or Wisconsin stocked fall-spawners. No ripe males were captured at Knife River. The presence of ripe males did not prove fall spawning because males could be ripe over a long period of time. Agersborg (1937), for example, reported on a male that started spawning in November and continued to spawn as late as March. I believe that most reports of ripe fall-run female steelhead were actually female coho salmon (Oncorhynchus kisutch). During the first two years of this study, I observed that most fishermen could not readily distinguish the newly introduced coho from steelhead.

Although fall-spawning rainbow trout have been introduced into North Shore streams, fall spawning appeared to be rare and

FIGURE 2. Comparison of ovary weight:body weight ratios of fall-run and spring-run steelhead.

not the motivation for most fall-run fish. Some females were ripe in Lake Michigan during the fall; however, there was evidence that some fall-spawners reverted to spring spawners. Selection pressure would be great against a self-perpetuating fall-spawning population on the North Shore because of sand bars blocking river mouths, erratic stream flow, and early river freeze-over. The ovaries of all fall-run females examined were slightly developed and spawning was not likely until late winter or spring.

The second fall-run hypothesis was that rainbows wandered into rivers because they have a natural tendency to orient into currents, especially during high water. Some fish, which were trapped and released near French River, wandered into other rivers. For example, two (16.7%) of the radio tagged fish and four (14.8%) of the Atkin's tagged trout were caught in a different river during the fall (Table 1). No other French River fish were radio tracked into other rivers. Most radio and Atkin's tagged fish (74.4%, 29/39) were released directly off French River and the rest were released either 2.4 km SW (Talmadge River) or 3.5 km NE (Bluebird Landing) of French River. The release site did not appear to greatly influence the straying. From French River, two fish strayed into Knife River and one strayed into each of the Stewart, Sucker and Lester Rivers. One fish, which was released at Bluebird Landing, was caught .5 km NE in Sucker River. However, no Knife River fish were caught or tracked into other rivers.

Table 1. Movements of fall-run steelhead released near French River or in Knife River lagoon.

	Number of Fish	Fish Caught in Another River in the Fall		Fish Returning to Same River in the Fall		Fish Moving Upstream in the Fall		Fish Returning to Same River in the Spring		Fish Returning to a Different River in the Spring	
		No.	%	No.	%*	No.	%*	No.	%*	No.	%*
<u>French River</u>											
1971-1973											
No. radioed	12	2	2/12 16.7%	1	1/10 10.0%	--	--	0	0	1	1/10 10.0%
No. Atkin's	27	4	4/27 14.8%	3	3/23 13.0%	--	--	2	2/23 8.7%	0	0
Total Tagged	39	6	6/39 15.4%	4	4/33 12.1%	--	--	2	2/33 6.1%	1	1/33 3.0%
<u>Knife River</u>											
1972-1973											
No. radioed	29	0	0	1	1/27 3.7%	2	2/28 7.1%	3	3/26 11.5%	0	0
No. Atkin's	18	0	0	--	--	--	--	3	3/18 16.7%	0	0
Total Tagged	47	0	0	--	--	--	--	6	6/44 13.6%	0	0

*Percentages based on the number of fish available after anglers' catches were subtracted.

On the other hand, the movements of some fall-run steelhead did not indicate random wandering but orientation toward a specific stream, possibly the "home stream." A 1.4 km (green) female (#350, Fig. 3) was much more persistent than any other fish in returning to the stream where tagged. On 15 September 1973, the fish was captured in French River, Atkin's tagged and released off the river. After 36 days, she returned to French River. The steelhead was radio tagged and released off Talmadge River. For the next 19 days, she moved between Lester and Knife Rivers. The fish was radio tracked into French River lagoon at 2400 C.S.T. on 13 November 1973. On the next day the D.N.R. caught the fish, still green, while seining for coho. After spending a week in the lagoon, she left as the river iced over and was not found again. There was light rain preceding all three times that the steelhead entered the river. Since she returned to French River both as an Atkin's tagged fish and later as a radio tagged fish, she was counted in both categories in Table 1.

Other rainbows also returned to the river where tagged. The percentage of fish, which were not caught elsewhere by anglers, that returned in the fall was: 10.0% (1/10) radio tagged, French River; 13.0% (3/23) Atkin's tagged, French River; and 3.7% (1/27) radio tagged, Knife River (Table 1). Several (Fig. 4, 5, 6) Knife River fish showed movements away from and back to the stream where tagged even though they did not re-enter.

Thus, in the fall some steelhead probably just wandered into the rivers during high water. This idea was supported by 6

2

FIGURE 3. Movements and return of a fall-run female steelhead (#350) to French River. The fish was first trapped and tagged on 15 September 1973. It was re-trapped and radio tagged on 21 October. After release at Talmadge River, the fish returned to French River at 2400 C.S.T. on 13 November 1973. Light rain preceded all three movements into French River. (Numbers indicate dates.)

FIGURE 4. Movements of a fall-run steelhead (#273) tagged in Knife River and tracked from 26 October 1972 to 17 November 1972. No evidence that the fish re-entered the river in the fall.

FIGURE 5. Movements of a fall-run steelhead (#263) near Knife River from 19 October 1972 to 18 November 1972. No evidence that the fish re-entered the river in the fall but it was caught upstream during the first large spring run.

FIGURE 6. Movements of a fall-run steelhead (#271) tagged in Knife River. No evidence that the fish re-entered the river in the fall.

French River fish caught in other rivers and several radio tagged fish that traveled long distances from the capture site. No fall-run fish from Knife River were found in another river. However, since some rainbows re-entered the same stream or re-turned to the vicinity, this suggested that some fish have been searching and selected a specific stream, presumably the "home stream."

The third and fourth hypotheses stated that fall-run steelhead were early spring arrivals but differed in whether or not steelhead overwintered in North Shore streams. Gonad analysis suggested that fall-run fish would not be ready to spawn until winter or spring. Niemuth (1970) reported that the Brule River on Wisconsin's South Shore had a large fall run but a small spring run. Furthermore, fall-run rainbows overwintered in the Brule River and spawned between late March and the middle of May.

Since Knife River was the largest North Shore stream and had the best fall run, it was the stream most likely to have an overwintering population. For instance, anglers reported catching steelhead in the fall well above the upper falls of the river. Dr. Hollie Collins (pers. comm.) also caught steelhead over 15 km up Knife River. Consequently, I radio tagged 29 steelhead from Knife River and released them again into the lagoon to determine the distance of upstream migration and whether overwintering would occur. Only two (7.1%) radio tagged fish migrated upstream from the lagoon (Table 1). One was caught .7 km upstream. The radio signal from the other was located 9 September

1973 in a deep pool about 2.7 km upstream. Initially, the steelhead left the river two days after tagging and was re-discovered 43 days later. It may have returned during one of two large rainfalls which occurred before the fish was re-discovered: 2.49 cm during the day before (9-26) and .91 cm six days before (9-21). However, the radio location remained stationary and neither the transmitter nor fish were recovered. There were no fall returns on Knife River Atkin's tagged fish, which also suggested that few moved upstream.

Since we electrofished after a rain, it could be argued that many steelhead moved upstream earlier and even jumped the lower falls. However, because of the lag time, water levels were usually still high when we collected. Also, there were previously radio tagged fish in the lagoon that failed to move upstream during rainfall. Consequently, many rainfalls probably brought steelhead into the lagoon but few were sufficient to allow long upstream migration. Since few radio tagged fish moved upstream, this suggested that only a small percentage of all steelhead that entered the river became potentially available to anglers at the lower falls.

Because of the weir on French River, it was not possible to say how far steelhead would have moved upstream on their own or how long they would have stayed. Therefore, the percentage of upstream migrants was left blank in Table 1. However, most (83%, 5/6) stray French River rainbows were caught in lagoons but one was caught .6 km upstream in the Sucker River.

Overwintering appeared to be rare because most (96.6%, 28/29) steelhead left Knife River shortly after release and only one was known to have returned in the fall (Table 1). The number of nights spent in the river by radio tagged fish ranged from 0 to 5 but most (60.7%, 17/28) left during the first night. A radio tagged rainbow from French River moved into Knife River lagoon and spent 7 nights before getting caught. The short stay after release was believed to reflect poor stream conditions rather than capture method or tagging effects. Three trapped fish spent 0, 0, and 5 nights after release, a pattern similar to that of the electro-fished steelhead. Radio tagging probably did not cause the fish to leave the river because spring radio tagged fish, which had better stream conditions, moved upstream after release. Since no Atkin's tagged fish were caught upstream in the fall, this also suggested dispersal from the stream.

Steelhead appeared to leave the lagoon during the night. Only two (7.1%, 2/28) were known to leave during the day. Unfortunately, the period between radio locations was too long and at irregular times so that the exact time of dispersal was not determined. The period between radio locations during which a fish dispersed is represented by a horizontal bar in Figure (7). Sunrise and sunset are indicated by a thin vertical line.

Since most steelhead did not travel far upstream but left the river without returning in the fall, they had to re-enter the rivers in the spring to spawn. All steelhead tagged at Knife River were believed to be native fish. Three (11.5%, 3/26)

FIGURE 7. The period between radio locations during which individual steelhead left Knife River in the fall and the relationship of this period to sunrise and sunset. The left end of the bar represents the last fix before dispersal and the first fix after dispersal is indicated by the right end of the bar.

of the fall radio tagged fish that were not caught by anglers and three (16.7%, 3/18) of the uncaught Atkin's tagged rainbows definitely returned to Knife River in the spring to spawn. No fish were reported in other rivers. Only tags turned in or radio transmitters located were counted as returns in Table 1 and Fig. 8. Two ripe radio tagged fish were caught below the lower falls during the largest spring run (16-19 April) of 1973. During this same period there was an unconfirmed report of an angler releasing a radio tagged fish and an observation by Richard Hassinger (Minn. D.N.R.) of a radio tagged steelhead jumping the lower falls. On 11 May 1973, a signal from a fall 1972 transmitter was located .6 km upstream. The transmitter and some decayed flesh were recovered on 19 May 1973. This fish probably came in with the first run, possibly spawned and then died. The Cedar Creek engineers concluded the transmitter was in good condition and the warm water reactivated the battery. One Atkin's tagged steelhead was caught 1.0 km upstream on 11 May 1973. In addition, two Atkin's tagged fish were caught a day apart (12, 13 May 1973) in the same pool about 9.0 km upstream. Both were males and appeared to be downstream migrants. There were also unconfirmed reports on 17 May 1973 of a yellow tagged fish on the Little Knife near the Shilon Road (4.0 km) and one on the West Branch of the Knife near Co. Rd. #9 (12.0 km).

Tag returns at French River also showed that some fall-run fish returned in the following spring to spawn (Table 1). For example, two Atkin's tagged fish (8.7%, 2/23) returned in the

FIGURE 8. Locations of anglers' catches and recoveries of dead fish from tagged fall-run steelhead. #353 and #269 were fall recoveries and the rest were from the spring. Waterfalls are indicated by S.

spring of 1972. Both were Kamloop rainbows that were stocked in French River as yearlings in 1969. The male, which was almost ripe on 22 October 1971, was caught by angling in French River lagoon on 23 April 1972. On 27 October 1971, the female was green when tagged but was ripe when trapped in French River on 14 June 1972. Since there was ice on the western arm of Lake Superior until 10 June 1972, many fish were late in running. On the other hand, no radio tagged fish returned to French River but a radio signal (10.0%, 1/10) was located in Knife River lagoon (21 May 1974). Neither the transmitter nor fish were recovered. Since this fish was not located in Knife River from 26 October 1973 to 15 December 1973, it seemed possible that the rainbow entered Knife River during spring and died. The warm water may have re-activated this transmitter too.

The last hypothesis was that fall-run steelhead on the North Shore were making a migration at the same time of the year that their ancestors made on the Pacific Coast. It is commonly believed that geographic races exist that are characterized by distinct migration times which are heritable (Smith, 1960; Mills, 1971). However, studies on the heritability of upstream migration timing have produced conflicting results (Mills, 1971). Steelhead on some of the better Great Lakes streams have migration times similar to West Coast streams (Shapovalov and Taft, 1954; Withler, 1966). Bothwell's creek, located along north-eastern Lake Huron, had a low gradient (6.5 m/km) and warm temperatures at the stream mouth (1-4°C) during mid-November to

December (Dodge and MacCrimmon, 1971). Steelhead ascended from 29 October to 15 May and had two peaks; late December and from 16 February to early April. This corresponded with the 1 November to 30 April dates for winter steelhead in British Columbia reported by Withler (1966). Spawning was first observed in Bothwell's creek on 27 December and spent fish moved downstream between 31 January and 13 February. The last spawning was observed on 26 April and spent fish from the second peak moved downstream during late April and early May.

On Wisconsin's Brule River which flowed into the western arm of Lake Superior, most steelhead ascended between late August and the middle of November (Niemuth, 1970). Unlike North Shore streams, the low gradient (1.7 m/km) and depth allowed fish to overwinter. Only a small spring run occurred during the spawning period from late March into May.

The basic timing of migration for North Shore steelhead was probably similar to Bothwell's creek and the Brule River but stream conditions limited the spawning run to April and May. Actual migration times corresponded with winter steelhead runs on Cheakamus River, B. C. (Withler, 1966). Due to delayed freshets winter steelhead were unable to run until April and May. In order to run in the fall, North Shore steelhead had to ascend during a heavy freshet sometime after the summer sand bar was removed from the mouth but before freeze-over which occurred as early as 17 October in 1973. Since fall freshets were sporadic and pools too shallow for overwintering, steelhead were forced to

run in the spring. Fall-run steelhead on the North Shore tried to ascend the river a few months before being ready to spawn which was also consistent with Withler's (1966) description of winter steelhead.

In summary, most fall-run rainbows on the North Shore were migrating at a time similar to Pacific Coast fish but were forced to return in the spring to spawn. Gonad weight indicated that fall migrants would not have been ready to spawn until winter or spring. Some fish (15.4%) from French River wandered into other rivers or traveled long distances in the fall. However, many returned to the river in which they were tagged in the fall and in the spring: 12.1% to French River in fall, 6.1% French River, spring; and 13.6% Knife River, spring. This suggested that many steelhead had selected a specific stream in the fall. Only a small percentage (7.1%) of steelhead moved upstream from Knife River lagoon. Most (96.6%) left Knife River within 5 days after tagging and only one (3.7%) returned in the fall. Since most left the river where tagged and at least 6.1% and 13.6% returned in the spring to French and Knife Rivers, respectively, overwintering was believed to be small in North Shore streams. Consequently, instead of separate fall and spring populations, there was one large population that ascended and spawned in the spring. From Michigan and Wisconsin stocking results, I believe that future fall-spawning strain planting along the North Shore probably will increase the numbers returning in the fall but most will be forced to make a spring spawning run.

Prespawning Behavior

Studies on salmonid prespawning behavior have focused primarily on mechanisms guiding mature adults to the home stream, recognition of the home stream and environmental factors that trigger the run. I concentrated on home stream recognition and the influence of environmental factors on the run. Although data on the return from the high seas to the home stream are inadequate, the number of hypotheses explaining the mechanism of return is numerous. Harden Jones (1970) believes that "the return of mature salmon from the North Pacific to the coastal waters can be accounted for by drift, by random or systematic search, by orientation to water currents at a rheocline, or by orientation to celestial clues: All appear to fit the facts so far as they are known." Whatever the mechanisms are that bring salmonids to the coast, they must search until they recognize an area of coastal water or river. Recognition of the home stream has been shown to depend on olfactory (Hasler, 1966; Harden Jones, 1970) and visual cues (LaBar, 1971; McCleave and LaBar, 1972; and Harden Jones, 1970).

Studies on home stream recognition have found that rainbow trout can have a high fidelity of homing to the natal stream. Lindsey et. al. (1959) observed at Loon Lake, B.C. that 94% of the spawners had returned to the stream where they were fin clipped when young. Furthermore, almost all repeat spawners (99.6%) returned to the stream where they had spawned previously. Shapovalov and Taft (1954) found that homing of steelhead marked

as smolts in Waddell Creek, California was 98.1% and only 1.9% strayed 7.6 km away to Scott Creek. Homing of hatchery reared steelhead stocked in Scott Creek was 97.1% and straying to Waddell Creek was only 2.9%.

Since spawning steelhead were in short supply at the French River hatchery, I decided to initiate some displacement and homing experiments with mature brown trout (Salmo trutta) in the fall of 1971 to learn the percentage of homing, the search pattern and length of time needed to return, the fate of non-homing fish and environmental conditions during the second run. Brown trout were chosen because they were native fish, were not being stripped at the hatchery, and have been reported to have homing behavior similar to steelhead (Harden Jones, 1970).

Displacement experiments have several shortcomings. The natal stream is often unknown but it is generally assumed that the stream where the fish is captured before displacement is the home stream. Consequently, homing has been broadly defined (Gerking, 1959) and accepted (Harden Jones, 1970) as "the return to a place formerly occupied instead of going to other equally probable places." Unfortunately, the natal stream was unknown for most salmonids that I displaced. Secondly, in order to compare homing to straying, recapture methods and effort should be the same. Since a fish found the home stream once, some learning probably occurred so that subsequent displacement may not reflect the initial search for the home stream. Moreover, if fish arrive offshore well in advance of the spawning run like fall-run

steelhead, they have probably become very familiar with a large area. I was not able to conduct long distance displacements as planned because of a shortage of trout and too small a boat (5.5 m). Therefore, the distances that I displaced fish were likely within an area recognized by many fish as suggested by some of the fall steelhead movements (Fig. 3). Lastly, handling, tagging and sensory deprivation may cause abnormal behavior in displacement experiments.

Four early running brown trout were displaced on different days between 11 September and 26 September 1971. Two green Atkin's tagged females and a green radio tagged female were released 1.6 km off French River. None homed but one of the Atkin's tagged trout was caught in Sucker River and the radio tagged fish was caught at the mouth of the Brule River, Wisconsin. Since radio contact was lost, the fish may have traveled across the western arm instead of following the shoreline. The time between release and capture was 10 days and the minimum distance was 27.4 km. A ripe radio tagged male was released off Talmadge River on 26 September 1971 to see if it could be attracted into that river. The trout initially moved 1.4 km SW of Talmadge River and during the night moved NE to French River. After spending the next day (27 September) off French River, the fish moved during the night to Sucker River where it was caught. In summary, no early running brown trout homed but 3 strayed.

Brown trout from a large run on 26-27 September were divided into 4 groups of nearly equal mean weight (1.4 - 1.5 kg) but

unequal sex ratios for a displacement experiment. The weather during the run was overcast and misty with light onshore winds (7.4 and 4.7 km/hr). Rain fell (.38 cm) early on 27 September. Three groups of 4 Atkin's tagged and 1 radio tagged trout were transported in covered tubs via an indirect route and released 1.6 km off Talmadge, French and Sucker Rivers. In addition, the Minnesota D.N.R. released 12 Atkin's tagged trout in Knife River below the lower falls (1.3 km upstream) to supplement the spawning population and angler catches. The percentage of homing was computed two ways because a fish was considered to have homed if it was recaptured at French River weir or if it just entered the lagoon. Table 2 summarizes the results.

Two radio tagged trout returned to the lagoon but left after two days. It was not known if they spawned in the lagoon. The male was found dead the next day after leaving and the female was presumed dead 11 days later. Mortality of brown trout during the spawning run was high because of poor physical condition and the high incidence of furunculosis (Niemuth, 1967). The most outstanding result was that 5 of 12 fish quickly backed downstream at Knife River. One strayed to Sucker River and four were captured at French River. Another was caught at the mouth of French River 42 days after displacement but it was not known if or where the fish spawned.

The overall percentage of homing was at least 45.2% returning to the lagoon with 35.5% recaptured at the weir. The total straying (12.9%) was three from the first displacement group and

Table 2. Homing and straying in brown trout.

Release Site	Date	No. Released	Number Homing				Percent Homing		Straying		Rivers strayed to
			Atkins weir	radio weir	Atkins lagoon	radio lagoon	weir	lagoon	No.	%	
French R. 1.6 km S.E.	9/11/71- 9/13/71	3	0	0	0	0	0	0	2	66.7	Sucker R. Brule R. (Wisc.)
Talmdage R. mouth	9/26/71	1	0	0	0	0	0	0	1	100.0	Sucker R.
French R. 1.6 km S.E.	9/29/71	5	2	1	0	0	60.0	60.0	0	0.0	
Talmdage R. 1.6 km S.E.	9/29/71	5	1	0	0	1	20.0	40.0	0	0.0	
Sucker R. 1.6 km S.E.	9/29/71	5	3	0	0	1	60.0	80.0	0	0.0	
Knife R. 1.0 km upstream	9/28/71	<u>12</u>	<u>4</u>	<u>--</u>	<u>1</u>	<u>--</u>	<u>33.3</u>	<u>41.7</u>	<u>1</u>	<u>8.3</u>	Sucker R.
Totals		31	10	1	1	2	35.5	45.2	4	12.9	

only one from the later groups. Straying was probably much greater than this because it had to be determined from angler returns; hence, straying was not comparable to homing. Almost all (92.8%, 13/14) homing fish returned 3 or 4 days after displacement. It rained during the nights of 30 September - 1 October (.71 cm) and 1 October - 2 October (1.04 cm). Six (42.8%, 6/14) returned on 1 October and seven (50.5%, 7/14) on 2 October. All (4) fish homing from Knife River returned on 2 October. Since the timing was similar, most fish probably arrived prior to 1 October or 2 October and awaited rain and increasing stream flow. There was no significant difference in the proportion of fish homing to the weir based on sex ($\chi^2 = .102$, $p = .75$), displacement location ($\chi^2 = 1.303$, $p = .75$) or tagging method ($\chi^2 = .399$, $p \sim .5$). However, since the number of fish returning was small, some expected frequencies were less than 5 which biases the χ^2 test. Homing of cutthroat trout (Salmo clarki) in Yellowstone Lake also was not significantly different between sexes (LaBar, 1971) or open water and shoreline displacements within 22 km (McCleave and LaBar, 1972).

The olfactory pits of 3 Atkin's tagged brown trout were plugged with vaseline coated cotton similar to the method described by Wisby and Hasler (1954). They were displaced 1.6 km off French River to see if trout could home without olfaction; none returned. Unfortunately, only one brown trout was displaced in subsequent years because few were captured at French River. Fall weir counts were as follows: 1971, 51; 1972, 7; 1973, 3.

The extreme fluctuations probably reflect the difficulties that fall-running fish have migrating up North Shore streams. Favorable stream conditions and reproduction may have occurred in 1966 and 1967 resulting in good runs during 1971. Records were not available to confirm this.

On 13 September 1972, a 1.6 kg female brown trout was trapped in French River following 1.8 cm of rain and light on-shore winds. The fish was radio tagged and displaced 2.0 km off French River (Fig. 9). Fixes were taken by sextant every 15 to 20 minutes as she traveled almost straight to the mouth of French River and was probably following the current. Within 30 m of the river, the trout turned and headed 2.4 km SW to Talmadge River. However, during the night she traveled 9.7 km NE to Stony Point and remained there from 16 to 19 September. The weather during this period was partly cloudy, sunny and only two light rain showers fell. On 20 September a thunderstorm and heavy rain (4.8 cm) occurred between 0400 and 0900 C.S.T. During this time the trout swam from Stony Point and up French River. Since it rained during both runs, this is good evidence that rain and the subsequent increase in stream flow is a stimulus for upstream migration. The large discharge should increase both the strength and effective area of an olfactory sign.

In summary, the overall percentage of brown trout homing was at least 45.2% returning to the lagoon and 35.5% to the weir.

FIGURE 9. Homing movements of a female brown trout displaced 1.75 km off French River. Both migrations up French River occurred during rain storms.

Some trout recognized that they were displaced into the wrong stream and they returned home. The proportion of fish homing was similar based on sex, displacement location and tagging method. Most fish returned on the same days and rain proved to be an important factor inducing upstream migration. Those fish that did not return may have: 1) initially strayed into French River while searching for the natal stream; 2) died due to poor condition and high incidence of furunculosis; 3) strayed into another stream but were not caught by angling; 4) spawned in French River lagoon; 5) returned late but were barred by unfavorable stream conditions; and 6) imprinted poorly when young and could not repeat their choice.

Some information on salmonid home stream recognition was obtained from three different species of salmonids radio tagged before they made their spawning run. A male coho salmon (Oncorhynchus kisutch) was electrofished in Knife River lagoon on 26 September 1972 and radio tagged. Coho have been reported to have similar homing ability to steelhead (Shapovalov and Taft, 1954). This fish had been stocked at French River in 1970. During the night of 26 September, the coho left Knife River and headed SW. Figure 10 shows that most activity was concentrated in the vicinity of French River except for a brief trip to Stony Point. After the signal was stationary for 4 days, we found the transmitter in the lake with the antenna tied in a loop but no fish. This indicated that a fisherman had caught the fish but had thrown the transmitter back. It appears that the fish had

FIGURE 10. The apparent rejection of Knife River by a spawning male coho salmon and the return to the vicinity of the stream where it was stocked. On 26 September 1972, the fish was radio tagged in Knife River. After leaving the river, it was caught near French River about 12 October.

entered Knife River as part of the search for the home stream but recognized that it was the wrong stream. Since activity was concentrated around French River, the fish possibly recognized French River as the home stream and may have moved upstream if it had not been caught. The largest rainfall between release and capture was .48 cm on 28 September and .74 cm on 10 October.

A ripe female steelhead (#300) was also caught before it had chosen a spawning stream. On 31 May 1973, the fish was trapped in French River. After radio tagging, the fish was returned to the trap to recover from the anesthetic. However, the trout found its way out of the trap and we later observed the fish downstream, active and in excellent condition. Instead of reascending the river, she left at 2200 C.S.T. Figure 11 shows that she moved SW from French River and made several passes by Talmadge River, which had a sand bar completely blocking the mouth. On 3 June rain fell (.58 cm) and the bar opened slightly. A light rain fell again from 2100-2400 C.S.T. on 4 June. At 2300 C.S.T. on 4 June the fish entered Talmadge River and spawned 2 days later. The stream depth near the mouth was only 10 to 20 cm.

These data illustrate several points. First, the fish entered another stream prior to entering the spawning stream. This may have been part of the initial search for the home stream. Moreover, because of the late date, the steelhead may have become impatient waiting to ascend the Talmadge River and explored another stream. However, this conflicts with Hartman's

FIGURE 11. The apparent rejection of French River by a female steelhead (#300) and the subsequent spawning in Talmadge River. After rain washed open the sand bar blocking the Talmadge River, the fish made a spawning run.

and Raleigh's (1964) observations that sockeye salmon (Oncorhynchus nerka) in Karluk Lake, Alaska failed to seek another spawning stream when the home stream was blocked. Sockeye, which were repeatedly displaced to the lake, returned an average of 11 times before disappearing and they were not observed at other rivers. It is possible that this behavior was an artifact from handling and radio tagging. But, some stripped steelhead that were radioed and Atkin's tagged returned upstream after release in French River lagoon. Lastly, it illustrates the importance of rain in permitting and releasing the spawning run.

A green female brown trout was also tracked prior to the spawning run. She was trapped in the lagoon of Knife River on 23 September 1973 and radio tagged. A light rain fell during the night the fish was trapped and .91 cm fell the previous night. Knife River was low because it had been 20 days since a heavy rain (2.51 cm) had fallen. The brown left the lagoon during the night after radio tagging. Figure 12 shows that the fish traveled to the mouth of the Sucker River. Rain fell on 25 September (.43 cm) and 26 September (2.48 cm). Instead of entering Sucker River, the trout headed towards Knife River. By the time the fish entered Knife River on 30 September, the water level was low. Again the trout left Knife River and traveled SW to French River. Unfortunately, the transmitter failed and it was not known if the fish returned to Knife River. Although there was sufficient water for a fish to ascend Knife River, this suggests that falling water levels inhibit a spawning

FIGURE 12. The failure to make a spawning run in Knife River by a female brown trout, which entered the river twice, during adequate but falling water levels.

run. The spawning urge also may not have been fully developed because rain did not stimulate a quick return to the river. Furthermore, it may indicate the difficulty that fall-running steelhead have finding good stream conditions, especially since fall steelhead may not be as strongly motivated to run as a fish that has to spawn. Evidence that radio tagging did not cause the fish to leave Knife River was suggested by an Atkin's tagged brown trout trapped in Knife River on 31 August 1973 but caught 10 September 1973 in Sucker River. It is apparently common for salmonids to enter another river while searching for the home stream.

Since salmonids may enter another stream before selecting a spawning stream, I decided to test whether displaced steelhead would recognize that they are in the wrong stream. I hypothesized that some steelhead would home because 4 of 12 displaced brown trout rejected Knife River in 1971 and returned to French River. I expected about the same percent homing as observed in brown trout (35.5-45.2%).

Steelhead chosen for displacement were new arrivals and in different stages of sexual development: 10 green females, 5 ripe females, 2 green males and 3 ripe males. The lack of fin clips and hatchery growth rings on scales suggested that most were native fish. None were stripped at the hatchery. I displaced 10 radio tagged steelhead each to Lester and Knife River lagoons. The lagoons lie about 10 km SW and 10 km NE of French River respectively. Fish were transported by truck in covered

tubs and released between 0730 and 1730 C.S.T. on the following dates: 1, 6, 8, 16, 22, 30 May 1974. On each date the same numbers were released at both rivers within 1 to 5 1/2 hours. The sizes were similar (mean: 2.1 kg, 61.0 cm; 2.2 kg, 61.2 cm) and the sex ratios were the same except for the last date (1 male vs. 1 female). More females were displaced than males (15:5) because males were in short supply at the hatchery.

The most surprising result was that no steelhead returned to French River (Table 3). A run was defined as leaving the lagoon and traveling upstream through fast water or if spawning activity was observed. At Knife River 9 of 10 trout ran up that river. It was not known what river one fish ran up because the radio signal was lost near Duluth. This fish traveled 27.3 km SW of Knife River in 44 hours (.62 km/hr). During various observation periods, the average speed traveled was: .58 km/hr, 1830-1230 C.S.T., 23 May 74; 1.18 km/hr, 1230-1555; 1.43 km/hr, 1555-1810; and .48 km/hr, 1810-1425, 24 May. Another trout left Knife River after release and spent at least 8 hours of the next day (2 May) within 800 m on either side of French River. Two days after release (3 May) the fish returned to spawn in Knife River.

Only 3 of 10 displaced steelhead ran up Lester River but 7 trout ran up 5 other streams including 3 fish traveling 20 km to Knife River. No data were obtained from one fish. A steelhead ran up Lester River and was presumed to have spawned during a 6 day stay. However, this fish also made a run, according to

Table 3. The rivers "run" by steelhead trapped and radio tagged at French River and released in two groups of ten fish into the lagoons of Lester and Knife Rivers.

RIVER "RUN"	RELEASED	
	LESTER RIVER	KNIFE RIVER
Lester	3	0
Knife	3	9
Talmdage	1	0
French	0	0
Sucker	1	0
Stewart	0	0
Silver	0	0
Encampment	1	0
Other	1	0
Unknown	<u>1</u>	<u>1</u>
Total	11*	10

*One fish migrated up two rivers.

my definition, up the Encampment River which is 45 km NE of Lester River. Consequently, both runs were counted and the "river run" column adds up to 11 in Table 3.

From Lester River, 8 fish traveled NE and 7 passed by French River. Most apparently spent less than four hours off French River. One trout spent at least 7 1/2 hours within 100 m of French River before migrating up Knife River. Two fish probably spawned close to French River. A female swam from Lester River almost to Sucker River but backtracked to spawn in a very small, intermittent stream .8 km SW of French River. Another female spent 6 days at the entrance to a small boat harbor 100 m NE of French River and 40 m SW of Schmidt Creek. Although the fish was not observed, its localized movements suggested spawning. The bottom near the breakwater consisted of small rock comparable to a spawning stream. An intermittent stream flowed through the harbor but its discharge was very small.

Many factors may have contributed to the absence of homing among displaced steelhead: 1) steelhead may have initially wandered into French River while searching for the natal stream; 2) some may have returned if they had not been caught by anglers; 3) favorable stream conditions may have outweighed imprinting and induced a run in a different river; 4) returning adults may have had difficulty distinguishing the natal stream because North Shore streams are very close together ($\bar{x} = 4.0$ km) and have similar water characteristics; and 5) imprinting may have failed to occur.

Steelhead may have initially wandered into French River while searching for their home stream. Data have been presented which show that some steelhead, brown trout and coho entered another stream prior to the spawning stream. Since French River weir was close (60 m) to Lake Superior, steelhead might have backed downstream if they had not been trapped. Many of the fish could have been destined for Knife River because of the large amount of reproduction there compared to all other streams. However, if most fish were reared in Knife River, the number of displaced fish running the Knife from the Lester (3/10) and Knife River (9/10) displacement groups should have been more similar.

The results could have been an artifact of angling. Since 6 trout (30.0%) were caught before spawning, they might have returned. But, 2 of the 6 had already bypassed French River in favor of the stream caught. Even if the other 4 had returned, the amount of homing is smaller than expected.

It is possible that favorable environmental conditions can outweigh imprinting and induce steelhead to run up other rivers. This would be most likely if fish were ready to spawn when displaced; however, most were not ripe (60.0%, 12/20). Other displacement studies have found homing using salmonids with similar sexual development (Hasler, 1966; Harden Jones, 1970; LaBar, 1971; McCleave and LaBar, 1972). Moreover, Hartman and Raleigh (1964) found that sockeye salmon did not seek alternative spawning streams as spawning condition advanced but continued to

try to ascend the home stream. Since steelhead were displaced between freshets except for one occasion, stream conditions were good but not exceptional. The following is the amount and number of days since rain for each displacement: .64 cm, 4 days; 1.07 cm, 4 days; 1.07 cm, 6 days; .81 cm, 2 days; .91 cm, 1 day; and 1.57 cm, 0 day. Since Lester River is smaller and shallower than Knife River and has a 4 m falls that is only surmounted by fish during a freshet, the greater number of displaced trout running up Knife River compared to Lester River could have been due to better stream conditions. Thus, the idea that Lake Superior steelhead can be induced during good environmental conditions to spawn in another stream deserves more study. A management implication is that spawning steelhead could be used to establish a new population in a stream following removal of a barrier.

Returning adults may have difficulty distinguishing the natal stream because North Shore streams are very close together. The mean distance between designated steelhead streams is about 4.0 km. Since many streams have similar watersheds and basins, their odors may be markedly similar. The uniqueness of stream odors may be further complicated by the numerous intermittent streams. For example, I have presented evidence that a displaced radio tagged steelhead spawned in a small intermittent stream only .8 km from French River. I suspect that many North Shore steelhead may appear to stray but actually are imprinted on a region rather than a particular stream.

Lastly, imprinting may have failed to occur in many individuals. Imprinting has been defined by Madison et. al. (1973) as "the process of learning the odors of the home stream (perhaps irreversibly) during some 'critical' or 'sensitive' period in the early life of the salmon, and the retention of this information without re-exposure" until the spawning run. Straying in rainbow trout appears to be more common in the Great Lakes than reported for the West Coast (Shapovalov and Taft, 1954; Lindsey et. al., 1959). The greatest percentage of homing was reported by Hassinger et. al. (1974). They fin clipped 4637 native juvenile steelhead in two adjacent Minnesota tributaries into Lake Superior. As spawning adults, 18 (75%) fish returned to Kimball Creek and 6 (25%) strayed into adjacent streams. They also found 6 (85.7%) trout returning to Kadunce Creek and 1 (14.3%) straying. Furthermore, most repeat spawners (6) returned to the stream of previous spawning but some (2) returned to a different stream. On the other hand, I had only one tag return (#23979) from a repeat spawner and this was over 416 km from French River in the Little Garlic River, Michigan. Since Hassinger's et. al. (1974) calculations included different capture methods and effort, I excluded all other sources of tag returns except trapping from their data. As a result, steelhead homing and imprinting appeared stronger because 18 (85.7%) fish returned to Kimball and only 3 (14.3%) strayed into the adjacent (1.6 km) Kadunce Creek. On the Kadunce 6 (100%) returned and none strayed to the Kimball.

Other studies have found a high incidence of straying.

Wisconsin's D.N.R. has observed small returns on hatchery reared rainbows and it is believed that a high degree of wandering is one explanation (King and Swanson, 1973). They released 12,086 dart tagged rainbows from 1969 to 1972 into Sioux River, Brule River and Lake Superior at Bark Point and Houghton Point. By 31 January 1973 there were 476 tag returns and 84 (17.6%) were from outside Wisconsin's waters. Straying was observed as follows: Michigan, 55; Minnesota, 10; Ontario, 15; Lake Huron, 3; and Lake Michigan, 1 (King and Swanson, 1973). Similarly, Michigan's D.N.R. planted 102,054 two and three year old rainbow trout of three stocks at 29 locations in the Great Lakes (Hansen and Stauffer, 1971). They found that 54% of the lake-planted fish and 45% of the stream-planted fish strayed. There was also evidence that straying was common in coho salmon. Michigan stocked 192,400 coho in the Huron River of Lake Superior in 1965 (Peck, 1970). Most smolts left the river within a week. Adult coho strayed extensively in the fall of 1967. Stray coho were found in 33 of 120 Michigan streams on Lake Superior and as far away from the Huron River as 300 km. Young coho were later found in 16 of 20 streams surveyed and were probably present in many more streams. Peck (1970) believed that the reproduction and 4% return at Huron River indicated that a sizeable proportion had strayed.

Since there is a large amount of straying in Great Lakes salmonids, several factors may be interfering with imprinting.

First, floods may wash juveniles out of the stream before imprinting and increase the amount of straying. Madison et. al. (1974) deduced from the literature that in coho salmon the "sensitive period" occurs within two months before or after smolting. Their experimental data suggested that the period from one to two weeks after the onset of smolting behavior was critical for imprinting to morpholine, an artificial odor which was neutral to non-imprinted fish. However, imprinting in Atlantic salmon may depend on the release environment's condition (e.g., water level, etc.) rather than developmental age or post-smolting age (Madison et. al., 1973). Floods are common in the spring and fall on North Shore streams because the rocky terrain has a small water storage capacity. Furthermore, the current velocity can be very fast because of the high stream gradients. Rearing areas on most streams (72.9%) are within .8 km of Lake Superior. If fish are reared, stocked or forced by lack of food to venture near the river mouth, a flood could force them out before they have reached the "sensitive period."

Poor imprinting may also be caused by hatchery-rearing, stocking location and stocking timing. Most steelhead used in the displacement experiment were believed to be native fish but some may have been only one generation removed from hatchery-rearing. There may be little selection pressure for a good imprinting mechanism in domesticated broodstock. Consequently, some hatchery fish may make a spawning run up any stream if environmental conditions are favorable.

Stocking location may influence the amount of straying.

Wisconsin's D.N.R. released rainbows directly into Lake Superior to avoid competition with native trout in streams and reduce early angling pressure. They found that lake-stocking provided the same creel returns as stream-stocking if the initial three month creel returns from the stream were discounted (King, 1972). Moreover, Michigan's D.N.R. found that straying was greater in lake-planted (54%) than stream-planted (45%) steelhead but straying was large in both groups. Theoretically, lake-stocked fish will stray more because they may not imprint to a particular stream or they may move away from the stocking location and imprint later on water from another stream. Wagner (1969) believed that imprinting occurred continuously during downstream migration. He stated that the amount of time spent in an area and/or the necessary distance traveled to imprint is unknown but straying may increase as these factors decrease.

The timing of stocking may influence the amount of straying. King and Swanson (1973) found that straying in Lake Superior was greater among rainbows released late (July) than those released early (April). Wagner (1974) found that parr-smolt transformation and migratory behavior in steelhead were controlled by photoperiod but temperature influenced the length of the migratory period. When the temperature cycle lagged behind the photoperiod (water cooler than normal), the migratory period was extended. If the temperature cycle was ahead of photoperiod (water warmer than normal), the migratory period was shorter

than when both cycles were in phase. Wagner (1968) suggested that fish released prior to the parr-smolt transformation into water where they are subjected to food shortage or physical stress, may deplete their energy reserves to the point of interfering with smolting. It also seems likely that fish released after parr-smolt transformation may not imprint if they are stocked in Lake Superior or forced out of the stream by flood, low water or competition. Since Michigan stocked two and three year old steelhead, many fish could have spent the "sensitive period" in the hatchery before stocking.

The second aspect of prespawning behavior that I examined was on the environmental factors that initiated upstream migration. Weather data were compared to the daily weir counts at French River. Since the weir counts were the most accurate in the spring of 1973 and 1974, data were examined only from these years. Because of failures in temperature recording equipment, minimum water temperatures were used to investigate possible relationships with weir counts. Minimum temperatures usually occurred between 0500 and 1000 C.S.T. Water level was recorded with a staff guage at a point below the weir near the north bank. The location had the same minimum depth as the weir entrance but was accessible during all stream levels.

All other environmental data were obtained from local climatological data collected by the U.S. weather station (NOAA) at the Duluth International Airport. The airport is located about 20 km from the headwaters, 25 km from the mouth of French

River and 252 m above Lake Superior. Weather data were analyzed only between the dates the first fish and last fish were trapped. Steelhead usually entered the trap during the night or early morning. Since the trap was emptied between 0800 and 0900 C.S.T., weather data were compiled for the period 0900 to 0859 C.S.T.

Weir counts have several weaknesses according to Banks (1969). The period when fish are allowed to collect in the trap may not reflect the migrating period adequately. Some fish may have more difficulty than others in finding the trap entrance and the attractiveness of the trap also varies with different water levels. Furthermore, trap location affects the pattern and timing of migration. Lastly, fish may pass over the weir during floods.

The springs of 1973 and 1974 were very different. Ice melted from the rivers early in 1973. On Knife River steelhead began running about 15 March instead of the first week in April; the peak runs were 15-17 April (R. Lakso, Minnesota D.N.R., pers. comm.). The first steelhead was trapped on 7 April 1973 at French River and the runs lasted for 63 days. I believe the spring of 1974 was more typical since steelhead were first trapped on 26 April and the runs lasted 36 days.

The number of fish per day entering the trap was statistically examined to determine if they were random events. Expected frequencies of days with X fish were calculated by the binomial distribution and compared to the observed data by the chi-square test. Results indicated that in 1973 the runs were significantly

different from random at the .10 probability level; thus, the interpretation is uncertain. However, runs were definitely non-random in 1974 ($\chi^2 = 30.1$, $p < .001$).

Weather data were grouped according to good runs, no runs and average runs to determine if the mean environmental parameters were significantly different by single factor analysis of variance. A good run was defined as at least three fish and an average run as 1-2 fish. The only significantly different results were in 1973 for rainfall and stream level (Table 4). In addition, 1974 data were grouped into 0, 1-4, and ≥ 5 fish but the analysis of variance results were not significantly different either.

Interactions of environmental factors and their influence on the number of steelhead trapped were analyzed by χ^2 tests. The null hypothesis was that the number of fish trapped under each environmental condition was the same. However, since the number of days occurring with each condition differed, the expected number of fish per cell would not be equal. Therefore, the expected number of fish per cell was computed by multiplying the proportion of days of each condition times the total number of fish.

Each environmental parameter was grouped into dichotomous types of days: rainy vs. dry, high vs. low (≤ 24 cm) stream level, onshore vs. offshore winds, and rising vs. falling barometric pressure. First, the number of fish trapped during eight possible combinations of rainy-dry, high-low stream level,

Table 4. Analysis of variance of environmental parameters during good and poor runs.

	1973		1974	
	F	F _{.05}	F	F _{.05}
rainfall	3.35*	3.15	1.75	3.29
water level	4.10*	3.24	2.31	3.33
water temperature	1.44	3.23	2.39	3.29
cloud cover	1.10	3.15	.65	3.29
barometric pressure	.08	3.15	.16	3.29

*Significant at .05 level.

and onshore-offshore winds were examined by the χ^2 test. These factors were examined as a group because of significant analysis of variance F tests and reports of their influence on fish runs by other investigators (Banks, 1969). Then environmental parameters were tested in pairs and singly. Table 5 summarizes the results.

Data analysis did not reveal a key environmental factor associated with the runs but suggested that the interaction of a few environmental factors may be important; furthermore, each environmental factor appeared to vary in importance between each year and both years combined. For example, significantly greater numbers of fish were trapped under rainy plus either high stream levels and onshore winds (1974) or low stream levels and offshore winds (combined years). However, significantly fewer fish than expected were trapped during dry days with low stream levels and offshore winds for both 1974 and the combined data.

Chi-squared tests of environmental factors by pairs indicated that significantly different fish runs occurred in both years and the combined data only for stream level and resultant wind direction. High stream level plus either onshore (1974 and combined) or offshore winds (1973) were associated with greater than expected runs. Significantly larger runs also occurred during high stream levels and rainy days (1973 and combined) and significantly fewer fish during low water and dry days. However, no significant differences in the number of fish trapped were found in 1974 for stream level and rainfall. Rainfall and wind

Table 5. χ^2 test analysis of the number of steelhead trapped during various environmental conditions.

Condition	1973		1974		Combined	
	χ^2	$\alpha.05$	χ^2	$\alpha.05$	χ^2	$\alpha.05$
Rainfall, stream level and wind direction	--	-- ^a	20.50*	14.07	30.18*	14.07
Rainfall and stream level	12.50*	7.82	3.39	7.82	18.55*	7.82
Rainfall and wind direction	8.73*	7.82	10.19*	7.82	6.54	7.82
Stream level and wind direction	18.38*	7.82	10.48*	7.82	16.34*	7.82
Stream level	10.59*	3.84	1.11	3.84	16.07*	3.84
Rainfall ≥ trace	4.16*	3.84	.49	3.84	1.06	3.84
≥ .025 cm	6.48*	3.84	.004	3.84	3.63	3.84
≥ .13 cm	8.31*	3.84	.43	3.84	1.97	3.84
≥ .25 cm	.35	3.84	5.30*	3.84	2.48	3.84
Wind direction	.18	3.84	9.64*	3.84	2.19	3.84
Barometric pressure	.91	3.84	2.00	3.84	.28	3.84

*Significant at .05 level.

^aExpected frequencies < 3.

direction were tested together also and the most pronounced pattern was that fewer fish ran during dry days with either an onshore (1973) or offshore (1974) wind but the combined data had no significant differences.

Single environmental factors were examined by the χ^2 test and analysis of variance. No factor had significant differences for both years and the combined data. Only high stream level (1973 and combined), onshore winds (1974) and rainy days had significantly greater numbers of fish than expected. Significantly larger runs occurred during days with trace, $\geq .025$ cm and $\geq .13$ cm of rain in 1973 but only occurred with rainfall $\geq .25$ cm in 1974. No differences in number of fish trapped were found with cloud cover, water temperature and barometric pressure.

In summary, interactions of rainfall, stream level and wind direction were associated with significant differences in the number of fish trapped. Rainfall and stream level seemed most important. Dry days with low stream levels and either onshore or offshore winds resulted in significantly fewer fish. Rainy days usually with high stream levels and either onshore or offshore winds were associated with significantly larger runs. Banks (1969) reviewed the literature and concluded that the rate of water discharge is an important, if not dominant, stimulus to the upstream migration of salmonids but other environmental factors modify this effect depending on location, season, species, etc. The mean stream levels for days when no steel-head ran were 22.1 cm and 23.35 cm in 1973 and 1974 respectively.

When the mean stream levels were 31.8 cm and 29.7 cm, the best runs occurred.

Differences in the effects of rainfall probably depend on soil moisture and thus the amount of runoff. In 1974 significantly larger runs only occurred when rainfall was $\geq .25$ cm. Whereas in 1973 they only occurred $\leq .25$ cm. This suggests that rainfall greater than this amount in 1973 may have produced runoff and increased stream turbidity. Radio tagged steelhead were observed to leave streams during high turbidity and to avoid turbidity plumes in Lake Superior.

Resultant wind direction seemed to vary in its effects when analyzed with either rainfall or stream level. However, when analyzed alone, onshore winds were associated with a significantly greater number of fish ($\chi^2 = 9.6$, $p < .05$) in 1974. Huntsman (1939) believed that northwesterly and northerly onshore winds concentrated Atlantic salmon against the coast and brought them into the estuary mouth. Onshore winds may keep steelhead closer to shore so that they may respond quicker to rainfall, increases in stream flow or other factors.

Analysis of variance suggested that steelhead were not responding strongly to any particular water temperatures. Steelhead may migrate as soon as the ice melts. A generalization that I have drawn from the data is that when minimum water temperatures were 6-9°C, steelhead usually ran but above or below this range runs were irregular. Rising stream levels may induce early arrivers to run when the temperature is low or late

arrivers when the temperature is above 9°C.

Barometric pressure is often regarded by anglers as important in determining whether a steelhead will migrate upstream or will take a bait. Analysis of variance showed no difference in barometric pressure readings between good, average and no runs. In addition, χ^2 tests indicated no difference in the total numbers of steelhead trapped during rising and falling barometric pressures. Peterson (1972) believed that barometric pressure was associated with fall spawning rainbow trout in Wyoming leaving the hatchery pond and entering a spawning trap. Increased fish activity occurred with falling pressure and decreased activity occurred with increasing pressure. He divided the trapping days into nine possible combinations of stable or changing pressure and changing trap counts. Combinations of pressure up--fish down and pressure down--fish up accounted for 72% of the days. I found that these combinations occurred only 36.6% of the time and therefore were not more frequent than other combinations.

The Spawning Run

Spawning run data will be discussed according to upstream movements, spawning behavior and downstream movements. A total of 32 adult steelhead were radio tracked in Knife River between 1 May and 12 June during the springs of 1971 to 1974. Steelhead were tracked during all stages of the run except for the very earliest. In streams 170 km NE of Knife River, Hassinger et. al. (1974) found that the first entry of steelhead varied from

16 April to 4 May but over 50% of the run occurred by 20 May and 80% occurred by 30 May. In 1972, 6 steelhead were tagged during the peak run which was delayed until 8-9 May because of ice on Lake Superior. During 1973, on the other hand, 8 fish were tagged on 9-10 May but this was near the end of the run due to an early spring. The peak was about 17-18 April 1973. In 1974, fish were tracked from just after the peak run (26-29 April) until the last run (3 June). Most (65.6%, 21/32) tagged steelhead were upstream migrants but 11 were spent emigrants. In Knife River, from 1971-1973, steelhead were captured by electrofishing in the lagoon or below the lower falls. All (13) steelhead tracked in Knife River during 1974 were displaced from French River (home stream recognition experiment) to the lagoons of Knife River (10) and Lester River (3).

Radio tracking upstream migrants provided information on activity periods, rates of movement, maximum distance traveled, and behavior during various stream flows. Steelhead appeared to enter rivers more frequently (5) during the night and early morning than late morning or afternoon (1). Although entry times were determined for only 6 radio tagged steelhead, these data were supported by 2 radio tagged brown trout that homed during the night. Furthermore, weir counts of salmonids at French River were higher in the morning than late afternoon. However, even though the weir was located 60 m from the mouth, there could be a long lag time for some fish between entry and leaving the lagoon towards the trap. Three radio tagged steelhead

entered Talmadge and French Rivers during the night and early morning. During the spring run at Talmadge River, fish #300 (Fig. 11) entered at 2300 C.S.T. and steelhead #402 entered sometime between 0600-0900 C.S.T. A fall-run steelhead was radio tracked into French River at 2400 C.S.T. Since the entrances to both rivers were shallow (< 30 cm), the risk of being detected by a predator was much greater if they entered during the day than night. The entrance to Knife River, on the other hand, was usually deep enough (> 1 m) to permit fish to enter any time without being spotted. For example, one fish (#416), which was released at Lester River, entered Knife River sometime between 0930 and 1500 C.S.T. However, two other radio tagged fish entered Knife River during the night or early morning. Steelhead #434, which was released at Lester River, entered shortly before 0900 C.S.T. and fish #404 re-entered between 1950 and 0500. After a freshet, steelhead may enter a stream during the day more frequently because of decreased water transparency; but I did not have a chance to observe this.

The activity pattern of upstream migration was not readily discernible because of irregular observation periods. Steelhead have been reported to move upstream mainly in the daytime (Chapman, 1941; Shapovalov and Taft, 1954; Banks, 1969). Since these observations were from counts at weirs or fish ladders, daylight may have been important in finding the ladder or weir entrance.

My observations indicated that steelhead moved not only

during the daytime but also at night if there were no obstacles. The maximum rate of movement for most (13/16, 81.2%) upstream migrants occurred during the daytime (Table 6). Unfortunately, these data are biased slightly toward larger daytime rates: first, observation periods were shorter in the daytime than night because many stretches of the river were inaccessible for tracking in the dark; and secondly, many observation intervals overlapped sunrise and sunset. Three (18.8%) steelhead (#408, 410, 422), on the other hand, had their maximum rate of movement at night and traveled distances of 965 m to 2253 m. Areas in which steelhead moved during the night were those without rock slides or those with deep, slower channels. For instance, I observed the most night movement in the lower section of the river between the mouth and lower falls (1.29 km). Many fish that were moving during the night were found below falls or rock slides early in the morning. This suggests that the falls may have blocked night migration and that daylight may be necessary to surmount the falls. Evidence for the importance of daylight in surmounting falls was provided by 5 radio tagged fish which passed over the 5 m high lower falls of Knife River. Four definitely went over during the day and one may have gone over after sunrise because it was just at the top of the falls at 0800 C.S.T. These results agree with Stuart's (1962) observation that the jumping behavior of Atlantic salmon and brown trout ceased at night fall. Since steelhead jump falls during the daylight, this suggests that vision is important in judging the situation and timing the jump.

Table 6. Movements of upstream migrants.

Animal code	Sex	Dates tracked in river		Farthest upstream distance km	Maximum Upstream Rate				Total Upstream Rate			Fate	
					Time		Distance m	Rate cm/sec	Minutes	Distance			Rate cm/sec
					C.S.T.					m	cm/sec		
201	F	5/9/72	5/19/72	3.86	1015	1700	483	1.99	5880	2796	.79	disp.	
203	M	5/9/72	5/19/72	8.20	1515	1545	60	3.34	6275	8640	1.21	disp.	
205	F	5/9/72	5/20/72	6.44	0845	0920	152	7.25	11520	5149	.75	disp.	
207	F	5/9/72	5/20/72	1.29	--	--	--	--	--	--	--	disp.	
209	M	5/9/72	5/12/72	3.70	1015	1650	644	2.72	--	--	--	caught	
211	F	5/9/72	5/10/72	1.29	--	--	--	--	--	--	--	caught	
307	F	5/10/73	5/21/73	1.29	0645	1850	322	1.26	5400	1030	.32	disp.	
315	F	5/10/73	5/18/73	1.06	1100	1445	804	5.97	225	804	5.97	disp.	
404	F	5/1/74	5/7/74	1.29	0805	1555	161	.57	3380	664	.33	poached	
406	M	5/1/74	5/7/74	1.29	1015	1700	402	1.66	7350	985	.22	caught	
408	F	5/6/74	5/18/74	2.90	2030	0650	965	2.60	16655	3049	.31	predation	
410	M	5/6/74	5/18/74	4.00	1830	0630	2253	5.22	3500	3745	1.79	disp.	
416	F	5/12/74	5/18/74	1.40	1500	2000	644	3.58	5075	1498	.49	--	
422	F	5/8/74	5/11/74	1.30	2100	0510	1126	3.83	490	1126	3.83	disp.	
424	F	5/16/74	5/22/74	2.25	0900	2000	804	2.04	7780	1302	.28	disp.	
426	F	5/16/74	5/24/74	3.54	0945	1500	804	4.27	5790	3768	1.09	caught	
434	F	5/28/74	5/29/74	1.29	1040	1450	603	4.03	350	844	4.03	disp.	
436	M	5/30/74	6/2/74	.97	0730	1845	563	1.39	3180	834	.44	died	
Mean				2.63				3.23			1.46		

Another explanation for daytime movement may be that because good cover is scarce in some stream sections, upstream movement during the daylight may be a better defense against predation than resting in a semi-conspicuous place or near other fish.

The rates of upstream movement for each fish have been summarized as the total upstream rate and the maximum observed rate (Table 6). Total upstream rate was calculated by dividing the distance from the release site to the redd or the farthest upstream location by the elapsed time. Elapsed time was measured from the onset of movement to avoid any bias caused by inactivity due to handling and tagging. Total upstream rates ranged from .22 cm/sec to 5.97 cm/sec. Mean total rate was 1.46 cm/sec. Since fish were usually far apart causing the time between observations to be irregular or long, it was difficult to get an estimate of the mean rate of movement exclusively for active periods. Because the maximum observed rate may include some period of inactivity, this rate probably reflects the typical active migration rate rather than a biological maximum rate. The maximum observed rate of movement ranged from .57 cm/sec to 7.25 cm/sec and the mean maximum rate was 3.23 cm/sec. These rates compared very closely to those determined by Niemuth (1967) for fall-running brown trout in the Brule River, Wisconsin. Trout were tagged near the mouth and retrapped 39-47 km upstream. The slowest total upstream rate was .54 cm/sec (.47 km/day) and the fastest total rate, from an angler caught fish, was 7.47 cm/sec (6.44 km/day). For the two upstream weirs, the mean total rate

was 1.36 cm/sec (1.17 km/day) and 1.24 cm/sec (1.06 km/day).

These rates are slower than those reported for salmonids in other locations.

Mills (1971) reported the average rate of upstream travel for Atlantic salmon ascending the Indalsälven in Sweden as 11.6 cm/sec to 23.2 cm/sec (10-20 km/day). Furthermore, Gard (1973) found that the apparent rate of travel varied greatly among sockeye salmon in the Karluk River, Alaska. Rates varied from .46 cm/sec (.40 km/day) to 19.6 cm/sec (16.9 km/day). The slower rates in Knife River were probably because of the shallow water, steep gradient and the short distance to suitable spawning areas.

Upstream migration was influenced by water level and turbidity. Figure 13 shows the farthest distances migrated upstream for each tagged fish and not only includes redds but locations where fish were captured before spawning. The longest distance migrated upstream by a radio tagged fish (#203) was 8.2 km and the mean for all fish (18) was 2.63 km. However, anglers catch fish over 16 km upstream. These fish are probably early migrants which have the highest water levels and therefore, can travel the farthest. For example, two fall Atkin's tagged steelhead were captured a day apart (12-13 May 1973) in the same pool 10.4 km upstream. Both were spent and could have migrated upstream during the first big run (16-19 April) when other fall tagged fish were caught. Under low water conditions, many radio tagged steelhead did not pass over the lower falls. For example, I found that 8 radio tagged

FIGURE 13. The farthest upstream locations of spring-run steelhead on the Knife River which includes redds and points of angler's catches. This excludes locations where fish were captured on their downstream migration. (Waterfalls are indicated by SS.)

upstream migrants did not go over the falls and 6 fish probably spawned downstream from the falls (Fig. 14). During the same period many untagged fish were observed in these areas also. Steelhead #404 was observed spawning below the lower step-pocket with 3 other fish on 6-7 May 1974. Unfortunately, this radio tagged fish and another disappeared from the no-fishing zone three hours later suggesting they had been poached. Most fish approached the falls before going downstream to spawn. Steelhead #307 made at least three approaches to the step-pockets before spawning downstream. It therefore appears to me that those steelhead that migrate just after the ice goes out probably migrate the furthest upstream. Most fish, on the other hand, that migrate with freshets during the last week of April or first two weeks of May probably do not migrate much farther upstream than the most distant location I observed. By the time they travel 5-6 km upstream, the water level usually has dropped greatly. Most fish that migrate after the third week of May probably spawn below the lower falls.

Flood conditions and high turbidity impeded upstream migration. Fish either stopped moving or came downstream. For example, steelhead #416 took refuge behind a log jam underneath the Interstate highway #61 bridge. During the same flood (11-14 May 1974), another steelhead (#408) came down the main branch of Knife River about 800 m to the same log jam. For 4 days, the main branch of the Knife above the Interstate highway was a continuous, swift rapids over 1 km long. On 15 May 1974, steelhead #408 chose to travel up the SW branch of Knife River (Fig. 14). This branch

FIGURE 14. The locations of redds used by radio tagged steelhead in Knife River. Circles indicate definite spawning sites. Since some steelhead exhibited localized movement for a day or more followed by rapid downstream migration, these areas are considered as probable redds and are marked by triangles.

was usually shallow but the flood made it deep with a moderate current. Instead of rejoining the main channel further upstream, she spawned in the Little Knife River. This strongly suggests that environmental conditions influenced the spawning area rather than homing to a specific tributary. Floods also caused some fish to leave the river. Two fish (#410, #422) never returned. Rapidly rising water levels may stimulate some steelhead on redds to finish spawning and disperse quickly or these fish could enter other rivers to complete spawning. Other fish may be weak and are carried out of the river.

Most steelhead migrate up the main branch of the Knife. As the water level returned to normal (17 May 1974), two other radio tagged steelhead (#424, #426) also migrated up the SW branch. While I was tracking these fish, I observed many other steelhead in the Little Knife River. It is possible that some signal indicated to these fish that many other fish had taken this route. Therefore, these fish chose the SW branch over better water conditions in the main channel. Nordeng (1971) suggested that conspecific odors of juveniles may aid home stream recognition by adults. It seems possible that the signal detected by these fish may have been a pheromone or odor from migrating adults. Another possibility is sound from other migrants passing over rocks.

Since male steelhead begin migrating upstream before females, I will begin my discussion of spawning behavior with the arrival of males. The role of male steelhead in spawning has been largely neglected by many investigators. My observations suggest

that many males have chosen pools or areas in pools before most females arrive. Furthermore, a male will intercept a female as she enters the pool and will try to induce her to spawn there. If this fails, he will try to follow her upstream. This behavior was best observed while tracking female #426 but it was also observed tracking other females (#408, #424). As radio tagged female #426 entered Little Knife River, she was met by about a 2.25 kg (estimated) male. Since the male had torn caudal and dorsal fins, bare spots under the tail, and a large fungal patch around the adipose fin area, he probably had been in the stream for some time. The male periodically nudged the underside of the female with his snout and moved beside her. These advances probably were to induce her to select a redd in his pool. She almost continually scraped the gravel with the bottom of her tail. Scraping probably provided her with information on the suitability of the gravel for nest digging and helped prepare her for spawning. During a 2 1/2 hour period, she turned on her side and flexed her body briefly at three different locations. After rejecting the first pool, she moved into the next pool and the male followed. I suspended observations at 1830 C.S.T. and found her the next day at 1100 C.S.T. about 600 m upstream. She was attended by a small (1 kg) male. The first male may have had neither the motivation to leave his area of the river nor the strength left to follow her upstream and confront other aggressive males. I definitely believe he could not have passed through a pool 400 m upstream which was occupied by a large (3 kg), aggressive male. In two

hours, I watched female #426 travel through 4 pools and 4 riffles. She spent 15-30 minutes scraping above each riffle with her tail but did no redd digging. Scraping probably causes most sores and worn fins common in downstream migrants. The small male exhibited nudging behavior similar to the first fish and followed her through all 4 pools. During 20-21 May 1974, I watched her dig redds and spawn in a pool 150 m farther upstream. She spawned with a different (1.5 kg) male with a scarred cheek. The second male was in the pool below and every time he entered the spawning pool, he was chased downstream. On 20 May 1974, I observed similar downstream chases. A 3.5 kg untagged female was spawning with the previously mentioned 3 kg male above a rock slide at the downstream end of the largest pool on the Little Knife. Another (2.5 kg) male tried to enter the pool but was repeatedly chased downstream. Because of the large size of the fish, the vigorous splashing and dislodging of rocks could be heard for 100 m as described by Shapovalov and Taft (1954). The large male also had forced at least another pair of steelhead upstream in the pool.

The aggressive behavior of males probably reduces the interference by other males with nest digging and spawning and permits the most competitive males, which presumably have the best genotypes, to do the most spawning (Alcock, 1974). It is believed that males spawn with more than one female (Shapovalov and Taft, 1954). Those males that migrate at the optimum time and have the most strength left from the arduous journey presumably have the best genotype and will contribute most to the next generation.

Weaker and later running males find fewer females and poorer water conditions to reproduce. It is not known if the most aggressive males have defended prime spawning riffles before females arrive. Some studies report remarkable tolerance of adjacent spawning pairs. Niemuth (1970) reported a hundred or more spawning rainbows in good stretches of the Brule River with little antagonism. They used what he termed "community redds." Likewise, Orcutt et. al. (1968) observed that spawning proceeded without evident interference even though redds sometimes were as little as 1.2 m apart. My observations, on the other hand, indicated that spawning pairs usually occupied the prime areas at slightly different times because the most aggressive male kept the other pairs away until his spawning was completed.

The spawning behavior of North Shore steelhead was similar to the spawning activities described by Needham and Taft (1934) and Shapovalov and Taft (1954) for West Coast steelhead and for inland rainbow trout described by Hartman (1970). Females chose redd sites usually above riffles. The female turned on her side, flexed her body vigorously several times and dislodged gravel for a redd. Before digging, I noticed that females point their heads towards the bottom, often touching the gravel with their snout. Since females tend to float to the surface while flexing, the nose-touching probably keeps the first movements next to the gravel. Nose-touching may cause many of the scarred snouts common on downstream female migrants. Hartman (1970) found that nest digging activity was primarily nocturnal during the first part of

the season but occurred around the clock during the middle of the season. I found nest digging activity common from after sunrise to about 2200 but I did not make nest digging observations at night. Before spawning, Hartman (1970) observed that rainbows dug about 5 times per 10 minute period but after spawning about 15 times in 10 minutes. The number of body flexures per dig was about 5-6 and increased to about 9 after spawning. I found that the mean number of flexures per dig was 5.39 for 17 steelhead.

Egg deposition and fertilization last only a few seconds (Shapovalov and Taft, 1954); consequently, I observed deposition only by two radio tagged females (#426, #104) and three untagged females. The male and female positioned themselves side by side over the redd. Hartman (1970) observed that as the female pulled her anal fin erect, she inserted the fin between the stones in the redd which anchored her spawning posture. The eggs and milt were extruded into the redd while the male and female arched their backs and quivered. Females occasionally gulped at the surface during and after spawning. After spawning, females proceeded upstream and dug another redd which also covered the first redd with gravel. Needham and Taft (1934) believed that one female dug 6 or 7 redds in line with the current to complete spawning. None of the fish that I observed appeared to dig more than 2 or 3 redds above the same riffle. In Idaho streams, the intervals between spawning acts by a single female ranged from 2 to 10 minutes or longer (Orcutt et. al., 1968). Spawning acts by these North Shore steelhead were at least 15 minutes to perhaps hours apart.

Radio tagged female steelhead spent from less than a day to 7 days near the spawning area with a mean time of 3.11 days (Table 7).

The time spent near a redd was determined for only one male and was 1.5 days. Shapovalov and Taft (1954) reported that a female, which was not ready for artificial spawning, completed spawning within 12 hours in a pen but they believed spawning often takes a week or more. Perhaps the earliest running fish spend more than a week on redds; however, water conditions often do not allow most North Shore steelhead to spend more than four days. Needham and Taft (1934) reported that a female apparently continued and completed spawning after dark. It was common for radio tagged steelhead to finish spawning and begin downstream migration after dark.

The locations of spawning sites in Knife River are shown in Figure 14. Spawning activity was not visible in all cases but I labeled some sites as probable redds because of localized movement for a day or more followed by rapid downstream migration. Steelhead chose sites with gravel ranging from less than 1 cm to about 13 cm in size. This was similar to Orcutt's et. al. (1968) findings that about 70% of the spawning gravel in Idaho streams was 13 mm to 102 mm. Orcutt et. al. (1968) reported that the shallowest redd was 21 cm and some were over 1.5 m deep. I never observed any deeper than 1 m but steelhead #300 (Fig. 11) spawned in water less than 16 cm deep. Most radio tagged steelhead spawned in water between 23 and 61 cm with a mean depth of 31.9 cm. Their backs were often out of the water and they could be approached

Table 7. Movements of downstream migrants.

Animal Code	Sex	No. days in river	No. days near redd	Spawn act.	Maximum Downstream Rate			Total Downstream Rate			Fate
					Time C.S.T.	Distance m	Rate cm/sec	Minutes	Distance m	Rate cm/sec	
103	F	--	--	--	0945 1930	804	2.56	4140	1287	.31	disp.
201	F	10	4	++	1530 0630	1931	3.59	2160	3862	2.98	disp.
203	M	12	1.5	++	1530 1245	4827	6.32	5040	8260	2.72	disp.
205	F	11	2	++	1600 1400	6436	8.14	1320	6436	8.14	disp.
207	F	11	6	+	1245 1830	483	2.34	996	5760	.29	disp.
215	M	--	--	--	1800 1940	161	2.69	2880	1287	.75	disp.
307	F	11	4	+	2000 0645	1126	2.91	1305	1287	1.65	disp.
315	F	8	7	+	2000 0530	965	2.83	570	965	2.83	disp.
406	M			+	1435 0940	1126	1.64	--	--	--	caught
408	F	12	1	++	1900 0835	2253	4.62	2253	815	4.62	predation
410	M	--	--	+	1630 0815	4042	7.11	945	4022	7.11	disp.
422	F			0	1630 0530	965	2.07	3350	1201	.60	disp.
424	F	6	.5	+	1930 0635	665	5.66	665	2253	5.66	disp.
426	F	9	2	++	1845 1400	644	.93	2280	765	.44	caught
434	F	--	--	0	1450 1725	804	8.14	320	1287	6.72	disp.
Mean		10.0	3.11				4.10			3.20	

readily to within 4 m (Fig. 15).

Radio tracking downstream migrants provided information on rates of movement, total time spent in the spawning stream, behavior with respect to water conditions and the percent of spawning run survivors. Downstream migration data are summarized in Table 7. Once downstream migration was initiated, movement was often continuous throughout the night and day. Although rates between individuals were variable, the mean maximum migration rates (4.10 cm/sec) and mean total migration rates (3.20 cm/sec) were similar. Maximum rates ranged from .93 cm/sec to 8.14 cm/sec and total rates ranged from .29 cm/sec to 8.14 cm/sec. The mean total downstream rate was over twice as fast as the mean total upstream rate. Furthermore, three steelhead (#203, 205, 410) traveled over 4 km downstream in less than 24 hours.

Downstream female migrants spent from 6 to 12 days in Knife River (Table 7) whereas the one male that was followed through both upstream and downstream trips spent 12 days. I assumed for computations that fish collected below the lower falls had come up the river during the night or early morning before capture. This assumption was consistent with radio tracking data and the existing high water levels. The mean residence time in the river for females was 9.75 days and was 10.0 days for both sexes combined. These data compare closely to the times between upstream marking and downstream retrapping observed by Hassinger et. al. (1974). They found that the length of stay ranged from a few hours to 38 days with a mean of 10.5 days. The earliest running fish, which

Figure 15. Spawning behavior of steelhead.

- 15a. Radio tagged female #426 scraping and digging a redd in the Little Knife River.
- 15b. A pair of steelhead spawning on a redd in the Little Knife River. The female is on the right.

are predominantly males and a few green females, probably spend times much longer than I observed. Late running fish probably spend the shortest times in the river. For example, female #300 spent only 2 days in Talmadge River during very low water early in June. Furthermore, steelhead #434 spent less than a day in Knife River, but no spawning activity was observed. Since this fish probably rejected the river, I did not use her time in calculating the residence time for spawning.

Some unusual observations on downstream migrations and water conditions were made in 1972. The peak run was delayed until 8-9 May because of ice on Lake Superior. During 19-20 May, the bulk of this run including 4 radio tagged fish migrated downstream. In spite of the ice on Lake Superior, the stream had rapidly become warm and low. Either these individuals were at the same stage of spawning development when they migrated upstream or they timed their spawning with some environmental factors such as dropping water levels. Moreover, the farther upstream the radio tagged fish traveled, the less time was spent on redds which resulted in downstream migration about the same time: 1.29 km, 6 days; 3.86 km, 4 days; 6.44 km, 2 days; and 8.20 km, 1.5 days. For all radio tagged fish, no pattern appeared between distance migrated upstream and time spent on the redd. When these fish reached the lake, the ice mass held up dispersal. Three steelhead (#201, 205, 207) stayed in the warm river plume just off the ice pack and one (#203) dispersed quickly. The temperature difference between river and lake was about 8°C. After 4 to 5 days, fish #201 and

#207 dispersed but steelhead #205 re-entered the lagoon and presumably died. Many steelhead that ran after the peak run were entrapped in very warm ($> 17^{\circ}\text{C}$) and low water. As a result, fishermen became alarmed at the unusual number of dead or badly fungused fish in many North Shore streams.

In addition to spawning run behavior, radio tracking provided information on mortality and dispersal of adult steelhead. All 20 fish, which were displaced to the lagoons of Lester and Knife Rivers, had not spawned. Table 8 summarizes the fate of the fish or reason for terminating tracking. Mortality on this spawning group was at least 55%. Anglers caught at least 5 fish (25%) before spawning and at least 2 (10%) after spawning. Another (5%) steelhead (#404) was presumed to have been poached because it disappeared abruptly from the no-fishing zone below the lower falls of the Knife River where it was spawning. Only one (5%) fish was believed to have died before spawning and it was a very late (30 May) running male (#436) that became inactive after a .97 km trip up Knife River. After spawning, at least two (10%) steelhead died of natural causes. Steelhead #408, for instance, spawned in the Little Knife River (Fig. 14) and was found dead 2.25 km downstream (Fig. 16). At 0820 C.S.T. on 18 May 1974 the fish was still active but it was found dead along the bank at 1300 C.S.T. Since the eyes and gills were torn out, I believe that the fish was too weak to escape sea gulls. The external appearance was similar to many downstream migrants: a hole had been worn behind the pelvic girdle; the fork was worn off the caudal fin and the tail was

Table 8. Angling and spawning mortality of steelhead displaced to Lester and Knife Rivers.

	Before spawning		After spawning		Total	
	No.	%	No.	%	No.	%
Caught	5	25.0	2	10.0	7	35.0
Poached	1	5.0	0	0	1	5.0
Died	1	5.0	0	5.0	2	10.0
Predation	0	0	1	5.0	1	5.0
						55.0 mortality
Dispersed	--	--	5	25.0	5	25.0
Unknown	4	20.0	--	--	4	20.0
					20	100.0

FIGURE 16. Locations of anglers' catches and recoveries of dead fish during the spring.

badly scraped. Scraping behavior undoubtedly caused much of this wear. Another steelhead (#418) was presumed to be dead in a section of the river (1.9 km) where we could not recover the transmitter. Since this fish spent 6 days near a boat harbor and possibly 7 days in Knife River before being discovered, it had probably spawned. This mortality could have been influenced by the warm conditions existing late in the season (29 May). Since the fates of 4 fish were not known (20%), the actual angling mortality could have been higher than 35%. Five steelhead (25%) were known to have survived spawning and dispersed. This figure probably is a good estimate of the mortality that anglers, steep gradients and waterfalls inflict on migrating steelhead. I computed the approximate percentage of steelhead dispersing from the Kimball and Kadunce Rivers by dividing Hassinger's et. al. (1974) downstream weir counts by their upstream counts. These results compared closely to the percentage of radio tagged fish dispersing: 1962, 44.7%; 1963, 32.9%; 1964, 36.4%; 1965, 5.6%; and the total, 31.9%. Similarly, on the River Meig, Mills (1971) reported that the mean survival of downstream migrant Atlantic salmon at two traps was 14% (10.2%-24.6%) and 26% (20%-36%). Since the demands of a spawning migration are great, salmonids must use large amounts of energy reserves which weakens them critically. Mills (1971) reported that the typical weight losses of 31% to 44% for Atlantic salmon leave them close to the loss causing physiological death. North Shore steelhead also lose considerable weight as indicated by 9.4% to 14% decreases in condition factors (C) determined by Hassinger et. al. (1974).

Dispersal and Summer Movements

The distribution of salmonids in the ocean was unknown until recently but the movement patterns are still subject to speculation. Hasler (1966, 1971) reported that prior to World War II it was generally believed that salmonids remained on the continental shelves of the ocean. After World War II, the Japanese fishing fleet was forced to go far to sea because they no longer had access to the Russian coast. They caught large quantities of salmonids which created a problem because the origin of the salmon they were catching was unknown. In 1953, an international agreement limited the Japanese fishing to west of 175°W longitude and also established a cooperative research program between Japan, Canada and the United States to determine the distribution of salmonid stocks. Research disclosed that Pacific salmon are found over most of the northern Pacific Ocean and Bering Sea; in addition, Atlantic salmon from North America and northern Europe were found as far as Greenland (Hasler, 1971). When this project began, it was widely believed that steelhead remained close to shore or shoals in the Great Lakes (Daly, 1968; Hansen and Stauffer, 1971). It became apparent during this research that this may not be the case. Therefore, it is also important for each state or province on Lake Superior to know where their stocks are being harvested. Because of the lack of information on steelhead movements in the Lake, almost all management efforts have been limited to the stream life. An attempt was made to gather information on movement patterns in the Lake by radio tracking downstream migrants and fish stripped

at French River fish hatchery. It was hoped that these fish would retrace their migration route or reveal summer open water movement patterns. Data on lake movements are presented under dispersal patterns, summer distribution, vertical distribution and diet.

Dispersal of post-spawning steelhead was probably predominantly SE or offshore, with a current and sometimes for long distances. For Lester, French and Talmadge Rivers combined, the direction of dispersal was determined for 16 radio tagged fish: SW, 2; NE, 5; and SE or offshore, 9. Dispersal direction was tested for uniform distribution and was not significantly different ($\chi^2 = 4.63$, $p \approx .10$). At Knife River, the dispersal direction was determined for 13 fish and there was a highly significant ($\chi^2 = 36.0$, $p < .001$) tendency towards offshore dispersal: SW, 2; NE, 1; and SE, 10. For all rivers combined, the results indicated offshore dispersal ($\chi^2 = 13.7$, $p \approx .001$).

The pattern of dispersal also appeared to be influenced by the shoreline and water current. Steelhead that dispersed NE or SW followed the shoreline for 3 km to 45 km. The movement was usually within 50 m of shore and was often just beyond the area where wave action had sorted out the smaller rocks. Radio signals were lost in the vicinity of large rocky points and areas where currents moved away from shore. I believe these steelhead followed the points outward and caught the current. For example, steelhead #306 (Fig. 17) dispersed on 2 July 1973 NE from French River along the shore to Stony Point. Upon reaching Stony Point, the fish followed the rocks outward at depths exceeding 20 m and then

FIGURE 17. Alongshore dispersal after spawning by three steelhead followed by offshore movements in the vicinity of rocky points. (Top left, #317; bottom left, #306; right, #216.)

returned to the surface. Since the wind was from the west (resultant direction, 270°) with gusts up to 45 km/hour (mean, 14.1 km/hr), the steelhead headed offshore with the wind. We drifted in the boat at the same rate as the fish but rough weather forced us to break radio contact over 3.0 km off Knife River. I believe steelhead #216 and #317 dispersed in the same manner (Fig. 17). Both were tracked to Two Harbors where there are three points similar to Stony Point. Radio contact was lost during the night and intensive search could not re-establish contact in the following weeks. During the night they left, the resultant wind directions were offshore (#216, 10° - 20° ; #317, 310° - 270°). In a similar manner, two fall steelhead (#359, #363) traveled NE along the shore and disappeared in the Two Harbors area. The winds were offshore during the nights they left (#359, 250° ; #363, 250°). Studies on the current patterns indicate that currents cut across the lake to Port Wing, Wisconsin from the Knife River-Two Harbors area (Ruschmeyer and Olson, 1958), but the offshore currents are less pronounced in the French River-Duluth area (Sydor, 1974). The pronounced offshore current in the Knife River-Two Harbors area may be the reason why Knife River fish disperse immediately offshore whereas no directional tendency was found for steelhead from rivers closer to Duluth.

Post-spawning steelhead may disperse long distances. For example, an Atkin's tagged steelhead (#23949) from French River was caught in a Minnesota D.N.R. assessment net at Grand Portage, Minnesota. Since the straight line distance was 205 km and the

elapsed time was 130 days, the average rate of travel was at least 1.58 km/day. A steelhead (#23979) tagged during the spawning run at French River was caught 329 days later in the Little Garlic River at Marquette, Michigan. Since the shortest route possible was 416 km, the average rate was at least 1.26 km/day. The longest post-spawning dispersal by a radio tagged steelhead (#400) was 45 km from Lester to Encampment River. Almost all post-spawning tag returns were from nearby rivers during the spawning period. The lack of returns after the spawning season was probably due to the:

- 1) small number of fish tagged; 2) low angling activity on the lake;
- 3) high post-spawning mortality; and 4) offshore summer movement.

Data on the summer distribution of steelhead from radio tracking, gill netting, trolling and other studies suggest that steelhead do not remain along shore. Hansen and Stauffer (1971) reported that Michigan tagged rainbow trout were taken as incidental catches by the commercial fishing industry within 19.2 km of shore at depths of 2-18 m. They stated that this may indicate the major fishing locations but "it also means that many rainbow trout inhabit shoal water in the Great Lakes." Since the bottom drops off rapidly along the North Shore, almost all shoal water is within .4 km or less from shore. However, only one radio tagged fish that dispersed was found alongshore again. Steelhead #215 left Knife River on 19 May 1972 and was believed to have dispersed SE or offshore. After 103 days, the signal was detected alongshore about 4.8 km NE of Knife River. The fish was alive and was tracked for 5 more days before the signal was lost.

It was not likely that post-spawning radio tagged steelhead spent much time close to shore because of our intensive search efforts. We covered an area about 3 km wide from Duluth to Encampment River about twice a week with a boat mounted yagi antenna. On the other days, searches were conducted from shore with a van mounted yagi antenna and by airplane tracking, which extended the surveillance to Silver Bay. However, if post-spawning mortality was high, then the number of fish and the amount of time spent offshore would be less than it appeared. Unfortunately, no radio tagged fish were detected more than 4.0 km offshore. This was probably mostly due to the limited amount of time spent searching offshore because of the small boat and rough weather.

Since the lack of alongshore radio locations could have been due in part to post-spawning mortality, an effort was made to capture steelhead during the summer for radio tracking. Two 60 m long, 114 mm stretch mesh gill nets were set almost every day from 24 July 1972 to 17 September 1972. Nets fished the surface to 5 m deep and were set from 10 to 800 m offshore between French and Sucker Rivers. No steelhead were caught but other salmonids were caught in small numbers. The catch per net per night was: brown trout, .09; coho salmon, .22; and lake trout, .61. These data indicate that steelhead were not concentrated alongshore. Since the population density of lake trout is probably the highest in Lake Superior, it was not surprising that more lake trout were caught than the other species; however, brown trout and coho have the smallest densities. Perhaps, the main reason the other

salmonids were caught but not steelhead is that they are fall spawners and therefore, had moved closer to shore for spawning purposes.

Additional evidence that steelhead are not concentrated alongshore in the summer is provided by Wisconsin and Minnesota D.N.R. assessment netting data. From 1970-1973, Wisconsin sampled 20-28 locations yearly from Superior, Wisconsin to the Michigan-Wisconsin border and around the Apostle Islands (King and Swanson, 1973). Most stations (23/28) were within 4.0 km of land. A 1097 m long gang of nets was used ranging from 3.8 cm to 17.8 cm stretch mesh in intervals of 12.7 mm. Nets were set on the bottom in 4.0 m to 110 m of water for periods of 24 hours at each location. A yearly average of 3477 fish were taken but only one was a steelhead. Minnesota D.N.R. assessment data (1967-1971) also suggested that steelhead were not concentrated alongshore. The distance from shore was not listed for most catches (80%) but 13 (10.3%) were caught 6.4 km to 8.0 km offshore and 11 (8.7%) were caught within 2.0 km of shore. Since the purpose of the netting was to census lake trout, most effort was probably concentrated within 2.5 km of shore.

Trolling catches suggest that steelhead may move offshore in the summer. We caught over 26 steelhead in over 700 man hours of trolling and 5 were caught 6.4 to 8.0 km offshore. Less than 100 man hours were spent over 4.0 km offshore. Similarly, Kernen (1970) reported that two charter boats which were fishing for lake trout in Lake Michigan caught 28 steelhead from 4.8 km to 6.4 km

offshore between the surface and 7.6 m deep. Since most of their lines were deep, this suggested that large numbers of steelhead ranged offshore.

The hypothesis that Lake Superior steelhead may move offshore in the summer is also supported by Pacific Ocean research. Recently, Sutherland (1973) compiled the catch data of Canadian, Japanese and United States research vessels for 1953 to 1967 and deduced steelhead distribution. He concluded that steelhead ranged virtually throughout the entire North Pacific Ocean, north of lat. 42°N . However, they were not uniformly distributed because of definite seasonal shifts of abundance. Steelhead ranged extensively in the summer. During late summer, fall and early winter, abundance shifted southward and eastward as spawning fish returned to the coast. After the spawning season, abundance shifted northward and westward in late winter and early spring. Catches were made where surface water temperatures ranged from 5° to 14.9°C but most (61%) catches were in 8° to 11.4°C surface water.

Records of long steelhead movements in Lake Superior suggest that some may have been made across the Lake. First, steelhead are capable of covering long distances in a short time. For example, steelhead #432 was tracked 27.3 km along the shore in 44 hours (.62 km/hr) at rates up to 1.43 km/hr. Sutherland (1973) reported a steelhead tagged in the North Pacific that traveled at a minimum speed of 19.8 km/day (.82 km/hr) between captures and covered 2,963 km. At these rates steelhead could potentially make

long periodic inshore and offshore movements. In the Great Lakes, steelhead also traveled long distances from tagging sites. For example, fall radio tagged steelhead from French and Knife Rivers were received at Silver Bay, Minnesota (#250, 67.2 km) and near Split Rock, Minnesota (#251, 416 km). Since two large peninsulas lie between French River and Marquette, Michigan, steelhead #23979 could have cut across open water instead of following the shoreline around the bays. Although the shoreline distance is 694 km, the fish would have only had to average 2.1 km/day which seems within the cruising speed of steelhead. Wisconsin D.N.R. found that 84 (17.6%) of 476 tag returns from stocked rainbow trout were from outside Wisconsin waters: Michigan, 55; Minnesota, 10; Ontario, 15; Lake Huron, 3; and Lake Michigan, 1 (King, 1972). Returns from Ontario and the other Great Lakes suggests that these steelhead may have crossed open water rather than followed the shore. Hansen and Stauffer (1971) reported that migrations over 160 km were common among rainbows stocked by Michigan and 11 fish were recaptured over 800 km from the release site. They also indicated that the prevailing direction of movement appeared to be down the lakes.

The vertical distribution of steelhead in Lake Superior and the Pacific Ocean is not well known. Salmon are assumed to live near the surface. For example, Harden Jones (1970) reported that Pacific salmon lead a "pelagic life most probably in the surface 50 to 60 m." Royce et. al. (1968), on the other hand, believed that salmon migrate mostly in the upper 10 m but a few salmon,

which were mostly chum salmon, were netted at 30 m to 70 m depths. Japanese scientists, according to Hasler (1971), caught salmon in gill nets principally in the upper 20 m except under isothermal conditions in spring when they were found as deep as 40 m. Salmon have also been reported to swim near the surface during the night and at sunrise but swim deeper during the day (Hasler, 1971). The vertical distribution data for steelhead was recently compiled from the Japanese, Canadian and United States research vessels (1953-1967). Sutherland (1973) reported that over 85% of the catch was in the upper 7 m of nets but significant numbers were caught between 15 and 23 m. Since most gill nets were set within 10 m of the surface, the true distribution may not be known.

In the Great Lakes, Hansen and Stauffer (1971) reported that during 1955-1959 tagged rainbow trout were taken as incidental catches by the commercial fishing industry between 2 and 18 m deep. Furthermore, almost all steelhead that we caught trolling in Lake Superior were in the upper 5 m. Radio tagged steelhead that were tracked over .5 km from shore were always in the upper 5 m as estimated by signal strength except for one occasion. For instance, steelhead #306 was located with a Vexilar Sonagraf (model 155) about 24 m to 27 m deep off Stony Point on 2 July 1973 (Fig. 18). We made two passes over the signal but did not detect the fish. On the third pass, we decided to mark the location on the chart with a vertical line. At the same time that we marked the spot on the tape, a fish signature appeared on the tape. It seems very likely that this was the radio tagged fish because:

FIGURE 18. Echolocation trace of a radio tagged steelhead off Stony Point. Three passes were made over the radio location before a signature was recorded. The fourth run is a bottom profile from the fish's location to shore.

1) the density of fish usually observed with the echo locator was low so that the probability of marking the radio location and a wrong fish simultaneously is very low; and 2) the signal range was about 150 m which is about the expected range at those depths. No other radio tagged steelhead were detected with the echo locator usually because they were too shallow to be included in the ultrasonic cone produced by the transducer. In conclusion, steelhead have been detected as deep as 27 m but the amount of time or frequency that they spend at the surface compared to other depths is not known.

Analysis of stomach contents from steelhead ($n = 23$) caught during the summer by trolling suggests that they do considerable surface feeding. All fish were collected by surface trolling which biases the samples towards those individuals that feed on the surface; however, this bias may not be great because the probability of catching a steelhead near the surface is much greater than catching one deeper than 5 m. Those steelhead deeper than 5 m could perhaps be satiated from surface feeding. Figure 19 shows that in July, August and September steelhead fed primarily on terrestrial insects and smelt. Ants (Hymenoptera) accounted for 29.4% by volume of stomach contents and were most abundant (36.5%) in July. Lady bird beetles (Coleoptera), on the other hand, were most abundant in September (58.7%) but composed 21.2% of the total samples. The only other common invertebrates were Lepidopterans which composed 12.0% of the total diet. These three invertebrate groups composed 62.6% of the diet, smelt (Osmerus mordax) accounted

FIGURE 19. Organisms in the diet of steelhead captured by trolling in the summer on Lake Superior expressed as a percentage of total food volume. N = 23.

for 23.1% and all other species represented only 7.0% of the total diet. Steelhead fishermen have learned that a good method to catch steelhead is to look for wind rows or "slicks" of insects and debris and troll through them. On windy days, the "slicks" are churned up and steelhead may be feeding at a wider range of depths. Consequently, the amount of feeding at various depths awaits an extensive study of vertical distribution and diet.

Effects of capture and tagging

In this section the effects of capture and tagging methods on behavior will be considered. Very little work has been done on the effect of capture on specific aspects of fish behavior but there have been some studies on capture induced stress and mortality. Bouck and Ball (1966) found that mortality among small rainbow trout (20 cm) held for ten days after capture was as follows: angling, 87%; electrofishing, 5%; and seining, 5%. All angled fish were played until exhaustion which placed a similar stress on all members of this group and simulated many fishermen's technique. Fish which were bleeding after angling were eliminated from the survival study. They concluded that the high angling mortality was caused by in vivo coagulation of blood which induced a condition of progressive shock. My observations on steelhead caught by trolling were similar to theirs. In spite of considerable care, I managed to transport only three steelhead alive to a holding tank. They were much more lethargic in the tank than fish caught in the weir or by electrofishing. Two died in less than 24

hours and one was radio tagged and released. After about 11 days, the radio tagged fish (#217) died and this may have been from progressive shock.

Electrofished trout had about the same variation in blood characteristics as seined fish and less than angled trout (Bouck and Ball, 1966). On the other hand, they also found that electrofished trout were extremely excitable in the tanks and showed little interest in food. Electrofishing could cause radio tagged fish to move more than radio tagged fish captured by other methods; however, it was not apparent in this study. In addition, mortality in trout due to electrofishing has been reported by Hauck (1947) and Pratt (1954). Mortality on steelhead that were electrofished and radio tagged was believed to be low: 1) the electrofishing unit only slightly stunned most fish and only a small percentage were captured; 2) fish were held in a live box and were not tagged unless they regained their equilibrium. Only four (7.8%) of 51 electrofished fall-run trout failed to regain equilibrium. These were fish that had hit the electrodes and autopsy showed that they had broken vertebrae or hemorrhages. 3) all radio tagged fish were believed to be alive after one day, the period in which Pugh (1961) concluded most mortality would occur. Only one fish (#353) was presumed dead but this was 43 days after tagging and neither the fish nor transmitter were recovered. 4) all radio tagged steelhead except one caught by an angler were able to leave Knife River and some moved long distances (33 km). Electrofishing was not believed to have caused the

fish to leave the river because this behavior was exhibited also by radio tagged fish caught in traps. Other observations on electrofished trout suggest that they were not harmed because at least seven were caught six months later and spring electrofished trout were able to hurdle the falls on Knife River and spawn.

Trapping is the capture method least likely to physically harm the fish; however, this does not mean that it does not induce stress. Some trout captured in the fyke-net were missing scales and had torn fins suggesting that they may have fought the trap.

Another factor which may have influenced fish behavior was stripping at the hatchery. Stripping leaves more eggs in the coelom than natural spawning and is also accompanied by blood (Shapovalov and Taft, 1954). Consequently, some stripped steelhead returned to French River or entered other rivers to complete spawning. Stripping may also cause delayed mortality. Hatchery stripped steelhead were a convenient source but they were used mainly to study dispersal direction. It was believed that stripping would not alter this direction.

Data were collected from confinement studies and field situations to assess the possible effects of transmitters on fish behavior. First, tests were conducted in a tank to determine the optimum package mass that a fish could carry. Since some fish had to be released shortly after tagging, I wanted the habituation period as short as possible. It was found that if the package mass in water was less than 1-1.25% of the fish's mass out of

water, steelhead were able to balance transmitters almost immediately after tagging or recovering from an anesthetic. This meant that our standard transmitter, which weighed about 16 gm in water and contained a Mallory RM-1 battery, should only be used on fish weighing over 1.5 kg. Smaller fish were tagged with transmitters containing lighter batteries.

Since the transmitter wet weight/dry body weight ratio used in this study was over 50% less than the dummy weight/body weight ratio used by Gallepp and Magnuson (1972) in studying induced negative buoyancy in bluegills, I feel that steelhead adjusted as quickly as bluegills to the added mass. They found that weighted bluegills sank to the bottom immediately after handling and used the tank bottom for support. Radio tagged steelhead, on the other hand, initially sank but were swimming from one end of the tank to the other within minutes after release. The median number of fin beats made by a bluegill in midwater approximately doubled after treatment but decreased to pretreatment rates after 3 to 24 hours. The number of fin beats also increased for radio tagged steelhead; moreover, steelhead extended their pectoral fins fully and used them as stabilizers. Gallepp and Magnuson (1972) found that bluegills, which are physoclists, secreted gas into the gas bladder and compensated for increased negative buoyancy. At depths of .5 m they were able to reach hydrostatic equilibrium in 300 minutes; however, greater depths will require longer times. After radio tagging, many steelhead swam with their heads at the surface of the tank and their body angled slightly (20°) downward. They

appeared to "gulp" at the surface and were apparently filling their gas bladders. Since the pectoral fins of many physostomes are smaller than those of physoclists and ventrally located, they are less efficient in producing a continuous upward force; consequently, physostomes react to negative buoyancy by tilting upwards and swimming with the caudal fin (Gallepp and Magnuson, 1972).

Some steelhead were held in a pool on French River for observations on transmitter induced mortality, fungal infection, wear and abnormal behavior. Two groups of one radio tagged and four Atkin's tagged fish were released at different times (24 May 1971 and 24 May 1972) and held for 10 days. All fish were stripped at the hatchery as were most steelhead tagged at French River. Since one Atkin's tagged fish died during the first day (1972), it may not have recovered from stripping. Another Atkin's tagged trout was found dead after eight days of confinement in 1971 but neither radio tagged fish died. Since the water became warm ($> 16^{\circ}\text{C}$), most fish developed fungus and were therefore released after 10 days. Observations on these fish and other tagged fish that remained in the river indicated that the transmitter attachment site was less prone to fungal infection than other areas of the fish. The caudal fin and tail seemed to be the first area affected and was probably caused by bottom scrapping. Fungus appeared next on the paired fins and with less frequency on the snout. Only after other areas of the body were infected did fungus appear around the attachment site. Transmitter saddles

that conformed to the shape of the fish's back caused little wear. Figure 20 shows the attachment site on a brown trout after 3 weeks. Saddles wore off some of the scales but no cuts were observed in any fish. Movement of saddles enlarged the attachment holes in the skin but not in the tissue. No inflammation of the tissue was noticed. Unfortunately, I was not able to observe transmitter wear from fish tagged longer than a month but reports from anglers indicated that the transmitter did not harm the fish or cause infection. Lastly, confined steelhead did not exhibit any tendency to scrape or shake off the transmitter.

Field tracking data suggest that radio transmitters did not noticeably influence reproductive behavior, migration, angling vulnerability and long term survival. At least 18 radio tagged steelhead were observed nest digging or spawning. Their behavior was not noticeably different than untagged spawners. The number of flexures per digging bout was recorded for three digs from each of 10 untagged steelhead and seven radio tagged fish. The mean flexures per dig was not significantly different ($T = .598$, $p \geq .7$) for untagged fish (5.47) and radio tagged fish (5.28). Males showed no aversion to radio tagged females.

Migration did not appear to be affected by transmitters. Radio tagged steelhead were able to jump over both the lower and upper falls of Knife River during high water. In Lake Superior, radio tagged steelhead were observed moving at rates over 1.0 km/hr and one (#432) averaged .62 km/hr for 27.3 km. Transmitters did not prevent steelhead from traveling long distances: 67.2 km,

Figure 20. The transmitter attachment site on a free-ranging brown trout after three weeks. Some scales were worn off but there were no cuts or inflammation of the tissue.

#205; 45 km, #400; and 33 km, #251. However, two Atkin's tags were returned from distances considerably greater (205 km, 416 km) but the rest were from distances less than 30 km.

Angling returns and long term survival data suggest that transmitters did not adversely affect the fish (Table 9). From 1971-1974 there was no significant difference ($\chi^2 = 2.5$, $p > .1$) in angling mortality between radio and Atkin's tagged fish. Although the returns were low, there did not seem to be a significant difference in long term (≥ 4.25 months) survival either ($\chi^2 = .94$, $p > .2$). There is possible bias in these data because anglers may be more likely to return radio transmitters than Atkin's tags. However, this bias may be partly compensated by cooperative anglers who released radio tagged fish. This was known to happen at least four times.

Since the transmitter package mass and attachment method were designed to be compensated for by steelhead within minutes after tagging, transmitters appeared to have minimal effects on steelhead behavior. Direct observation and radio tracking data indicated that reproductive behavior, migration, angling vulnerability, long term survival, and fungal infection were not greatly different from non-radio tagged steelhead.

Table 9. Angling returns and survival of tagged steelhead.

A. Angling returns on tagged steelhead 1971-1974

	<u>Caught</u>	<u>Percent</u>	<u>Not Caught</u>	<u>Total Tagged</u>
Radio	16	17.0	78	94
Atkin's	13	9.1	130	143
Totals	29	12.2	208	237

$$\chi^2 = 2.5 \quad .20 > p > .1 \quad 1.64 < 2.5 < 2.71$$

B. Survival (≥ 4.25 months) and recovery by angling, gill nets and traps.

	<u>Recovered</u>	<u>Percent</u>	<u>Not Recovered</u>	<u>Total</u>
Radio	3	3.2	91	94
Atkin's	7	4.9	136	143
Totals	10	4.2	227	237

$$\chi^2 = .94 \quad .5 > p > .2$$

$$.455 < .94 < 1.64$$

SUMMARY

From 1971 to 1974, 104 adult steelhead trout were radio tracked in western Lake Superior and tributaries between 25 April and 31 December. Fall-run steelhead from Knife River had ovary weight:body weight ratios less than 6.0% indicating that they would not have spawned in the fall. Most (96.6%, 28/29) radio tagged fall-run steelhead left Knife River lagoon within five days after release and only one was known to have returned in the fall. At French River, only 12.1% (4/33) of the radio and Atkin's tagged fish, which were released mostly (74.4%) at the mouth of French River, returned in the fall. In addition, no Knife River fish but 15.4% (6/39) of the French River fish were found in other rivers. Only two (7.1%, 2/28) fall-run radio tagged steelhead from Knife River migrated upstream through fast water. However, in the spring 6.1% (2/33) and 13.6% (6/44) of the steelhead not caught in the fall returned to the same rivers, French and Knife Rivers, respectively. Only one fish was found in a different river in the spring. Since fall rains were sporadic, most steelhead did not encounter good stream conditions to migrate upstream. Furthermore, most North Shore streams do not have pools deep enough for steelhead to overwinter. Consequently, fall-run steelhead were forced to make a spawning run in the spring. Since a high proportion (8:1) of the steelhead returned to the same rivers in the spring, this suggests that they had selected a specific stream in the fall.

In addition to steelhead, pre-spawning behavior was monitored

in brown trout and coho salmon because they were sometimes more available than steelhead and they have been reported to have similar homing behavior. The total homing percentages for brown trout to French River was 45.2% to the lagoon and 35.5% to the weir. There were no significant differences in the proportion of brown trout homing to the weir based on sex, displacement location or tagging method. Almost all (92.5%, 13/14) homing trout returned three or four days after displacement during rain storms and high water.

During spawning runs some salmonids were observed to leave one river following tagging or release and to enter another river. Moreover, five of twelve Atkin's tagged brown trout displaced to Knife River from French River backed downstream and entered the Sucker (1) and French Rivers (4). These observations prompted a displacement experiment to see if steelhead would reject another stream and home to French River. Radio tagged steelhead were displaced in two groups of ten to Lester and Knife River lagoons. These lagoons were about 10 km SW and 10 km NE of French River, respectively. No steelhead returned to French River. At Knife River, 9 of 10 trout migrated up that river and the river chosen by one fish was unknown. Only 3 of 10 displaced steelhead ran up Lester River but seven trout ran up five other streams including three fish traveling 20 km to Knife River. Many factors may have contributed to the absence of homing among displaced steelhead:

- 1) steelhead may have initially wandered into French River while searching for the natal stream;
- 2) some possibly may have returned

if they had not been caught by anglers; 3) favorable stream conditions may have outweighed imprinting and induced a run in a different river; 4) imprinting may have failed; and 5) returning adults may have difficulty distinguishing the natal stream because North Shore streams are very close together ($\bar{X} = 4.0$ km) and have similar water characteristics. Therefore, steelhead may be imprinted to a region of the North Shore rather than a specific stream.

From this displacement experiment, radio tracking provided information on mortality and dispersal of adult steelhead during the spawning run. Total mortality was at least 55% (11). Anglers caught at least five fish (25%) before spawning and at least two (10%) after spawning. One (5%) was poached from a no fishing zone where it was spawning. Only one (5%) fish, which was very late in running (30 May), died before spawning. After spawning, at least two (10%) steelhead died of natural causes. One of these was apparently killed by sea gulls. Since the fates of four radio tagged fish (20%) were not known, angling mortality could have been higher than 35%. Only five steelhead (25%) were known to have survived spawning and dispersed.

Weir counts at French River were analyzed with respect to environmental factors present during the runs. No key environmental factor was found to be associated with the runs but interactions of several factors appeared to be important. Dry days with low stream levels and either onshore or offshore winds resulted in significantly fewer fish. Rainy days with high stream levels and

3

either onshore or offshore winds were associated with significantly larger runs. When minimum water temperatures were 6-9°C, some steelhead usually run but above or below this range runs were irregular. No significant differences in runs were found between rising and falling barometric pressure.

During the springs of 1971-1974, a total of 32 adult steelhead were radio tracked in Knife River. Steelhead appeared to enter the rivers more frequently (5) during the night and early morning than late morning or afternoon (1). They appeared to move upstream not only during the daytime but also at night if there were no obstacles. Many fish that were moving during the night were found below falls or rock slides early in the morning. Evidence for the importance of daylight in surmounting falls was provided by five radio tagged fish which passed over the 5 m high lower falls of Knife River just at sunrise or during the day. Total upstream rates of movement ranged from .22 cm/sec to 5.97 cm/sec. Mean total rate was 1.46 cm/sec. The maximum observed rates of movement ranged from .57 cm/sec to 7.25 cm/sec and the mean maximum rate was 3.23 cm/sec.

Stream level influenced upstream migration. The longest distance migrated up Knife River by a radio tagged steelhead was 8.2 km and the mean for all fish (18) was 2.63 km. Anglers catch steelhead as far upstream as 16 km. These are probably fish that migrate shortly after the ice goes out with high water. For example, two fall Atkin's tagged fish, which most likely migrated during the first big run, were caught 10.4 km upstream. Most fish,

on the other hand, that migrate with freshets between 21 April and 15 May probably do not migrate much farther upstream than the most distant radio location I observed. After the third week of May, most fish encounter low stream levels and probably spawn below the lower falls (1.3 km). During this period, eight radio tagged upstream migrants did not go over the falls and six fish spawned downstream from the falls. Many untagged fish were also observed spawning downstream from the falls.

Flood and turbidity caused fish to stop moving, move downstream or leave the river. One radio tagged fish switched from the turbulent main channel of Knife River to the slower moving SW branch. As the water level returned to normal, two other radio tagged steelhead also migrated up the SW branch. Many other steelhead were observed along this route. This suggests that some signal indicated to these fish that many fish had taken this alternative route rather than the main channel with its apparently better conditions.

Radio tagged downstream female migrants spent from 6 to 12 days in Knife River whereas the one male that was followed through both upstream and downstream trips spent 12 days. Once downstream migration was initiated, movement was often continuous throughout the night and day. Although rates between individuals were variable, the mean maximum downstream rate (4.10 cm/sec) and mean total downstream rate (3.20 cm/sec) were similar. Maximum rates ranged from .93 cm/sec to 8.14 cm/sec and total rates ranged from .29 cm/sec to 8.14 cm/sec. The mean total downstream rate

was over twice as fast as the mean total upstream rate.

After spawning, most steelhead (19/29, 65.5%) dispersed almost immediately offshore (SE). Those that dispersed NE or SE followed the shoreline for 3 km to 45 km. Alongshore dispersal switched to offshore movement in the vicinity of rocky points and areas where currents moved away from shore.

Most post-spawning tag returns were within 30 km of the spawning stream. However, Atkin's tagged steelhead were captured as far away as Grand Portage, Minnesota (205 km) and Marquette, Michigan (416 km). A radio tagged steelhead was captured 45 km from the spawning stream.

Radio tracking, gill netting and trolling suggest that steelhead are not concentrated alongshore or on shoals in the summer but may range far offshore. Steelhead are believed to swim near the surface but a radio tagged steelhead was detected with an echolocator between 25 m and 27 m deep.

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