A Description of the Migratory Behavior of Steelhead (*Oncorhynchus mykiss*) in the Pere Marquette River, Michigan

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A DESCRIPTION OF THE MIGRATORY BEHAVIOR OF STEELHEAD

(Oncorhynchus mykiss) IN THE PERE MARQUETTE RIVER, MICHIGAN.

FINAL REPORT
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BY

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ABSTRACT

Radio-telemetry studies indicate that a pumped source fish passage built around a pulsed-DC electrical sea lamprey barrier was effective at passing at least 67% of tagged adult steelhead on the Pere Marquette River, MI. Steelhead were captured using trap nets and hook-and-line fishing in 2000 and 2001. Most (87) were captured at the mouth of the river, approximately 20 km downstream of the barrier, while additional fish (26) were captured directly below the barrier. A total of 113 fish were tagged by either surgical or gastric implantation, and their movements were monitored as they approached and ascended the fish ladder. An estimated 68% of fish tagged at the mouth of the river were successful at traveling upstream to the barrier. Fish tagged at the mouth of the river moved upstream faster in 2001 than in 2000, taking a mean time of 76.8 hours to reach the barrier. Once arriving at the barrier, fish were present for a mean time of 184.4 hours before ascending the ladder.

Fish that ascended the ladder were twice as active in seeking passage as those that did not ascend the ladder. Successful fish moved from one antenna to another a mean of 7.1 times per hour. All fish that entered the ladder eventually ascended, and navigated the channel quickly (mean 0.58 hours). Most passage through the ladder was during daylight hours for tagged and untagged fish.
INTRODUCTION

The Pere Marquette River is one of the last free flowing coastal streams in Michigan. It is a state “Natural River” and a national “wild and scenic” river, and is highly regarded by anglers for its resident and anadromous fish populations. The river experiences a naturally-reproducing run of steelhead (*Oncorhynchus mykiss*), and like many Great Lakes tributaries, has been colonized by sea lamprey (*Petromyzon marinus*). As part of the effort to control sea lamprey, an electrical barrier was installed on the Pere Marquette to prevent their passage to upstream spawning habitat. A pumped-source fish passage built around the barrier is designed to facilitate the upstream migration of steelhead.

Electrical barriers have been used successfully for completely blocking spawning migrations of sea lamprey (Swink 1999), as well as guiding adult chinook salmon (*O. tshawytscha*) into a channel where they could be trapped (Palmisano and Burger 1988). However, little is known about the behavior of steelhead as they encounter an electrical barrier, or the efficiency of this unique design of fish passage. More common fish passage scenarios, such as hydroelectric dams with pool and fall fish ladders, have been studied extensively in recent years and passage rates in excess of 90% are common (Bjorn et al. 2000, Gowans et al. 1999). An understanding of steelhead behavior near all migration barriers is critical to the viability of the population, as well as upstream fisheries.

This two-year study was designed to determine the effects of an electrical lamprey barrier on the migratory behavior of steelhead in the Pere Marquette River, MI. The objectives were to 1) describe the timing of migration, 2) determine the proportion of fish
that succeed in bypassing the weir, 3) measure the rate of ascent from the mouth of the
Pere Marquette River to the electrical lamprey barrier, 4) measure the amount of time
required by fish to bypass the electric barrier, and 5) measure the time required by fish to
reach spawning habitat after passing the barrier.
STUDY SITE

The Pere Marquette River is located along the eastern shoreline of Lake Michigan in west central Michigan (Figure 1). The watershed encompasses an area of 1956 km$^2$ and contains 612 lineal kilometers of streams. From the headwaters near Chase to Pere Marquette Lake in Ludington, the Pere Marquette River courses a distance of about 154 km (MDNR/IFR 1998). The historic mean discharge in the spring (February - April) is 914 cfs (USGS 1998). In 2000, the mean discharge in spring was 671 cfs, and in 2001 it was 1040 cfs.

The electrical sea lamprey barrier is located at the Custer Road Bridge, about 2 km south of Custer, MI, and approximately 20 km upstream of the river mouth. There is no documented spawning habitat available to sea lamprey downstream of the barrier (Koon Personal Communication). A pulsed-DC electrical barrier (Smith-Root, Inc., Vancouver, Washington) was first used at the site in 1989. It was successful at blocking sea lamprey but did not allow the upstream passage of non-target species (Rozich, Personal Communication). The current barrier was completed in 1999, and has been modified with state-of-the-art pulsators and electronics, as well as a pumped-source pool-and-weir fish ladder. The fish ladder is constructed with walls of corrugated steel sheet piling, and is 4’ wide and about 64’ in length. Removable weirs separate 3 pools. Because the electrical barrier does not create an impoundment, water must be pumped into the fish ladder. One pump delivers water to a false weir at the top of the channel at 12 cfs, creating a 8-12” head over the removable weirs, and a larger pump is used to create an attracting flow (25 cfs) closer to the entrance of the ladder. Upon entering the
Figure 1. Location of the Pere Marquette River in Michigan.
passage, fish must navigate the series of four weirs before being returned to the river upstream of the barrier via a 12” PVC tube. In 2001, a net was placed over the exit end of the tube to allow observers to count and examine passing fish.

The barrier was in operation from 21 March-30 June 2000 and 5 April-30 June 2001. The normal operating procedure for the electrical barrier is to run continuously for the duration of the sea lamprey spawning migration. However, this protocol was not followed during part of the 2000 field season. A damaged pump prevented the circulation of water through the fish ladder from 31 March to 8 April, so the electrical field was turned off between the hours of 10:00 and 16:00 to allow fish passage. Several radio-tagged fish passed over the electrical barrier during this time, thereby compromising the design of the study. Additionally, at the conclusion of the 2000 field season, stray voltage from the barrier was discovered near the entrance to the fish ladder. It is believed that this condition may have existed throughout the period of operation and was corrected for the 2001 field season.

The area of study (Figure 2) extended from the mouth of the Pere Marquette River upstream to Bowman Bridge (48 km). Much of the river within this area has a stream gradient of less than 1 meter per kilometer and is characterized by slow runs and deep pools. Generally, streams best suited for trout reproduction have a gradient ranging from 1.9-13 meters per kilometer (Hay-Chmielewski et al. 1985). In the Pere Marquette, much of this higher quality spawning habitat occurs upstream of Bowman Bridge. Therefore, it is likely that fish that were successful in passing through the fish ladder would continue their migration upstream past Bowman Bridge.
Figure 2. Area of study on the Pere Marquette River, MI.
METHODS

I captured steelhead in trap nets and by hook and line fishing. Trap nets were fished near the mouth of the Pere Marquette River, and hook and line fishing was conducted near the mouth, as well as directly below the barrier. The nets were fished at all times for approximately 25 days each year, and were checked daily for the presence of steelhead. In order to minimize mortality, only those fish measuring 50 cm or more in length, migrating upstream, and appearing in good physical condition were selected for the study. I implanted digitally encoded radio transmitters (Lotek Engineering, Inc., Model MCFT-7A; 16 x 83 mm, 12.8g in water) into 113 steelhead (56 in 2000 and 57 in 2001). The fish were anesthetized in a 15-gallon tank of tricaine methane sulfonate (MS-222), outfitted with a transmitter and an external T-type tag (Floy Tag Co.), and transferred to a recovery tub prior to being released at the point of capture. Fish caught in the trap nets were released approximately 200 m upstream of the nets in order to minimize recapture. In 2000, I surgically implanted radio transmitters using methods similar to Hart and Summerfelt (1975). The entire procedure, from induction of anesthesia to release took approximately 15 minutes to complete. In response to concerns that the surgical procedure might alter behavior, I used an alternative implant method, gastric insertion, in 2001. I surgically implanted transmitters into the peritoneal cavity of 24 fish, and non-surgically inserted transmitters into the stomach of 33 fish. Gastric implants were executed by inserting the transmitter through the esophagus and into the stomach of an anesthetized fish. The antenna extended out the fish’s mouth, and was bent to trail along the fish’s side.
**Monitoring movement**

I monitored movements of the radio-tagged steelhead from the time of tag implantation until the end of the upstream spawning run. I used Lotek SRX-400 receivers at two fixed (base) stations, and one portable station to monitor fish movement. A portable receiver along with a boat-mounted Yagi antenna (Lindsay, Lindsay, Ontario) were used from Custer downstream to Pere Marquette Lake to locate radio-tagged fish, and to ensure that the radio transmitters were functioning prior to implantation. The primary base station was located at the barrier site in Custer. This site was equipped with a recording receiver, and a Digital Spectrum Processor (DSP-500) equipped with a fast antenna switching option. The DSP-500 is a digital coprocessor that provides frequency discrimination using real-time analysis. This allowed for simultaneous scanning of multiple antennas and frequencies. The receiver logged all data into memory, and was downloaded daily. I used seven antennas at this station in order to detect the movement of fish near the barrier (Figure 3). One aerial Yagi antenna was mounted approximately 70 m downstream of the barrier (A1), and another aerial Yagi was located 30-m upstream (A7) of the barrier. These two antennas were used to detect the direction of travel, along with the times of arrival and departure in the reception area. Three submerged antennas (A2, A3, and A4) were placed across the face of the barrier, another was placed at the mouth of the fish passage (A5), and one more was installed within the ladder (A6). The submerged antennas allowed the monitoring of fish as they encountered and attempted to negotiate the barrier and the fish passage structure. I constructed submerged antennas using RG-58 coaxial cable, and left approximately 20 cm of center wire exposed at the end. A calibration of the SRX/DSP unit was performed in order to determine the
Figure 3. Antenna arrangement at the electrical barrier site in Custer, MI.
reception area of the seven antennas. The aerial antennas were positioned at a 45° angle to the riverbank (directed away from the barrier) to achieve greater range, and to avoid possible overlap with underwater antennas. Areas of overlap in the underwater reception cells ensured that a fish could not swim between antennas without being detected (Figure 3). The second base station was located about 2 km upstream of Bowman’s Bridge. The station was equipped with a recording receiver (SRX-400) housed in an environmental chamber. An LA51 solar panel along with a 12-volt deep-cycle battery and photovoltaic charge controller (Kyocera, Arvada, CO) were used to supply power at this remote site. Two aerial Yagi antennas were mounted approximately 80 m apart to detect direction of movement, and the date and time of arrival and departure of tagged fish.

**Data analysis**

I divided the study site into three river sections for data analysis. Section A was the stretch of river from Pere Marquette Lake upstream to the detection limit of A1 at the electrical barrier (20 km). Fish tagged in the vicinity of the barrier were not included in the analysis of section A. Timing of migration and arrival at Custer were determined by dates and times of capture and first detection at the barrier, respectively. The detection zone of the telemetry equipment located at the barrier served as Section B. The time elapsed between first detection at the barrier and last detection on the upstream antenna was used to determine time of passage. Conversely, downstream time of passage was calculated as the fish moved downstream through the array. Fish tagged at the barrier were included in downstream time of passage as well as percent passage, but were excluded from upstream time of passage. A fish was considered to have passed the barrier when it moved upstream of antenna seven, was captured upstream, recorded on
the Bowman Bridge receiver or, in the case of radio failure, when the barrier attendant observed the fish in the capture net on the upstream tube. Activity levels of tagged fish in the vicinity of the barrier were determined by dividing the number of times a fish switched from one antenna to another by the total time spent at the barrier before ascending or before swimming downstream and not returning. Fish tagged at the barrier were not included in this analysis of activity. Detailed analysis of movement downstream and through the barrier was carried out only for the 2001 field season. Barrier operations, broken antenna moorings, and a non-functioning antenna (A2) in 2000 made further analysis impractical. Section C extended from the upstream detection limit of A7 to Bowman Bridge, which covers a river distance of approximately 28 km. All radio-tagged fish that ascended the fish ladder and continued their migration upstream to Bowman Bridge were included in the analysis of this section.

For all statistical analysis, I first tested for equality of variance. If variance was equal, I used a pooled t-test, and if variances were unequal, I used Satterthwaite’s approximation. All statistical tests were performed using $\alpha=0.05$. 
RESULTS

Timing of migration

Steelhead were captured in the trap nets from 3 March to 28 March, 2000, with many of the fish being caught during the week of 18 March to 24 March (Figure 4). All fish were captured when water temperature was 3°C or warmer, and 65% of the fish were captured when water temperature was at least 7°C. Radio-tagged steelhead arrived at the Custer reception area (Section B) from 1 March to 15 April, and most of the arrivals occurred over a one-week period from 22 March to 30 March.

In the 2001 field season, I captured steelhead in trap nets from 14 March to 16 April (nets were not fished from 20 March to 1 April), and all fish were caught when water temperature exceeded 2.5°C (Figure 5). However, 72% of the fish were captured when the water temperature was 7°C or warmer. The daily catch was quite stable with the exception of 20 fish being captured on 8 April. It was during this and the next two days that the majority of the tagged fish arrived at the Custer barrier site.

Water temperature and discharge were very different between the 2000 and 2001 study periods (Figures 4 and 5). In 2000, water temperature fluctuated greatly, but warmed much earlier than in 2001. The temperature was consistently above 4°C after 4 March 2000, whereas the river did not reach these temperatures until 30 March in 2001. The river did, however, reach a higher water temperature during the capture portion of the 2001 field season (11.2°C) than it did in 2000 (9.5°C). Discharge steadily decreased throughout the 2000 study period, but increased during the 2001 season. In 2000, discharge was highest on 1 March (1176 cfs) and rapidly fell until 8 March. It then
Figure 4. Daily catch of steelhead in fyke nets at the Twin Bridges in Ludington, and daily arrival of tagged steelhead, water temperature, and discharge at the Custer station, Spring 2000.
Figure 5. Daily catch of steelhead in fyke nets at the Twin Bridges in Ludington, and daily arrival of tagged steelhead, water temperature, and discharge at the Custer station, Spring 2001.
remained between 567 cfs and 767 cfs through the rest of the field season. Conversely, discharge in 2001 was generally increasing, and reached its maximum (2170 cfs) at the end of the capture period. The minimum discharge was 767 cfs.

**Percent passage**

In the spring 2000, I implanted radio transmitters into 44 steelhead at Ludington. Twenty-seven (61%) were detected at the Custer receiver. Five of these fish passed through the section before the barrier began operation (21 March). I tagged twelve more steelhead directly below the barrier. Three of these fish moved downstream and remained stationary. Thirty-one tagged fish were actively seeking passage around the barrier at some time during the study period. Seventeen of these steelhead were able to pass upstream of the barrier during the period when the grid was de-energized. Only 1 (3%) fish ascended the ladder when the barrier was fully operational. Of the fish tagged in Ludington that never reached Custer, two were recaptured in other rivers. One by an angler in the Sable River, a Lake Michigan tributary whose mouth is about 9.5 km north of the Pere Marquette River, and the other at the Little Manistee River egg collection weir (MDNR), approximately 34 km north. I found nine fish that were never detected at the barrier, and failed to locate six other fish after tag implantation.

In 2001, I radio-tagged 43 steelhead at Ludington. Thirty-two (74% total, 69% surgical, 78% gastric) fish were detected at Custer. Of the 32 tagged fish that arrived at Custer, nine passed before the barrier began operation (5 April). I tagged an additional 14 steelhead, one of which remained stationary after release (and presumably died or expelled its transmitter), just below the barrier. Thirty-six fish were assumed healthy and actively seeking passage around the barrier. At least twenty-four (67%) of these fish
were able to ascend the ladder. The successful passage of 19 of these fish was recorded on the Custer receiver, and five were accounted for by other means. Two of the 5 successful fish were detected at Custer and at Bowman Bridge, but the Custer receiver did not detect their passage through the fishway. Another of the five fish was captured by an angler upstream of Custer, and its transmitter was nonresponsive. Barrier personnel handled and recorded floy tag numbers from one steelhead with an unresponsive transmitter, and one that had regurgitated its transmitter. The twelve fish that did not ascend the ladder were either located downstream (7 fish), or were not relocated (5 fish). Of the eleven fish tagged in Ludington that never reached the barrier at Custer, three were never located. One was recaptured by an angler in Cooper Creek, a small tributary to Lake Michigan, the mouth of which is about 28 km north of the Pere Marquette, and another was caught by a charter boat in August, about 31 km offshore from Frankfort, MI. Six of the tags remained stationary, and did not reach Custer through the end of the study period.

Males and females were equally successful at ascending the fish ladder (males=69% passage, females=65% passage), and there is no significant difference (t=1.83, df=31, P=0.08) between the size of fish that ascended the fish ladder (3.4 kg, SE=0.18) and those that did not (3.9 kg, SE=0.35). Additionally, there is no significant difference between percent passage of gastrically tagged fish (74% passage) and surgically tagged fish (54% passage) (Fishers Exact Test, P=0.14).

Of the fish that were tagged immediately downstream of the weir, 85% succeeded in passing through the fishway and 57% of the fish that were tagged at Ludington were
successful. These proportions were not significantly different (Fisher’s Exact Test, 
p=0.086).

Rate of ascent to Custer

The mean (median in parentheses) time from tag implantation in Ludington to first 
detection at the Custer receiver station in 2000 was 151.2 hours (103.2 hours) (n=27, SE=26.4 
h, range 24-456 h). Steelhead that were radio-tagged in Ludington in 2001 were detected at 
the Custer station in a mean time of 76.8 hours (38.4 hours)(n=29, SE=21.6 h, range=16.8- 
604.8 h), which is significantly faster than in 2000 (t=2.31, df=54, P=0.02). There is no 
significant difference in time of passage between surgically and gastrically implanted fish 
(t=0.62, df=20, P=0.54).

Rate of bypassing weir

In 2001, tagged and untagged fish exhibited similar patterns in their timing of 
migration through the fish ladder (Figure 6 and 7), suggesting normal behavior of radio-
tagged fish. The first radio-tagged fish entered and ascended the ladder on 10 April when 
the water temperature was 9.5°C (Figure 7). Most fish, both tagged and untagged, moved 
upstream through the ladder when water temperature was above 9°C, and remained stable 
or was on the increase. Eighteen tagged fish ascended the ladder upon first entry, while 
three ascended on their second entry into the passage. Detailed movements were not 
available for three fish due to tag loss or failure.

The first approach to the electrical barrier was not focused on any one area of the 
stream, but there was a slightly greater likelihood of fish approaching on the north side of 
the channel (Figure 8). Activity of tagged fish in the vicinity of the barrier ranged from 
0.3-21.5 antenna switches per hour (sph), and although not statistically significant (t=--
1.21, df=16, P=0.24), fish that passed the barrier (7.1 sph) were, on average, twice as active as those fish that did not pass (3.5 sph). Gastrically tagged fish and surgically tagged fish were equally as active in their search for passage (t=1.73, df=15, P=0.10).

Tagged fish arrived at the Custer station at all times of the day, with 62% arriving during daylight hours and 38% arriving in the dark (Figure 9). Approximately 58% of the 24-hour period at this time of year was daylight. Most (88%) tagged fish that passed through the barrier section before the barrier was operating (5 April) moved in the dark (Figure 10). Most (86%) tagged fish that ascended the ladder during weir operation moved during daylight hours.

The time it took for the tagged steelhead to pass through the weir site (Section B) in 2000 depended on the operation of the barrier. The fish that arrived before the barrier was turned on (21 March) passed through the section relatively quickly, with a mean time of 1 hour (n=4, SE=0.35 h, range=0.43 to 2 h). Once the barrier was operating, only one steelhead was able to successfully navigate its way through the fish passage and around the barrier, and it did not pass until 511.2 hours after its arrival at the barrier. Many of the steelhead passed through the section from 31 March to 8 April, when the electrical field was turned off between 10:00 and 16:00 to allow fish passage. The mean time of passage during this period was 105 hours (136 hours)(n=11, SE=20.2 h, range=1 to 171 h).

In 2001, fish that arrived before the barrier was energized passed through the section quickly, with a mean time of 0.78 hours (n=9, SE=0.43 h, range=0.17-4 h). Steelhead that arrived after 5 April were present for a mean of 184.4 hours (108 hours)(n=10, SE=55.2 h, range=28.8-576 h) before ascending the ladder. Upon entering
Figure 6. Number of untagged fish ascending the fish ladder in Custer, MI, Spring 2001
Figure 7. Number of tagged steelhead passing through the fish ladder, water temperature, and discharge at the Custer station, Spring 2001
Figure 8. Location of first approach to the electrical barrier based on antenna location, Spring, 2001
Figure 9. Number of fish and time of arrival at the Custer, MI barrier, Spring, 2001.
Figure 10. Number of tagged steelhead passing the barrier at Custer before (barrier off) and during (barrier on) weir operation, Spring 2001.
the fish ladder, fish were able to navigate their way through the structure (entrance to return tube) in a mean time of 0.62 hours (0.58 hours) (n=15, SE=0.08 h, range=0.08-1.05 h). A total of three tagged fish (12.5%) fell back through the electrical field before ascending the ladder for a second, and in one case, third time.

**Rate of ascent to spawning site**

The Bowman Bridge base station was inoperable for most of the 2000 field season due to malfunctioning equipment. Only one fish was recorded at this site. The fish traveled from Custer to Bowman in 120 hours. In 2001, tagged fish arrived at Bowman Bridge in a mean of 84 hours (median = 48 hours)(n=6, SE=28.8 h, range=38.4-228 h) after passing the electric barrier.

Fish moving downstream over the weir during normal operation in 2000 took a mean time of 7.3 hours (7 hours) (n=7, SE=2.1 h, range=2.2 to 17.1 h). In 2001, steelhead that moved downstream after the spawning period passed through the barrier in a mean time of 37 hours (23.5 hours) (n=5, SE=14.1 h, range=2.6-87 h). All of these fish passed through the electric field.
DISCUSSION

Adult steelhead entered the Pere Marquette River nearly two weeks earlier in 2000 than in 2001. In both years, fish appeared to be triggered to migrate when water temperature was steady or increasing, with the peak of activity occurring when water temperatures exceeded 7°C. Differences between years are most likely the result of between year variation in stream temperature and discharge. Additionally, most of the upstream migration during both years occurred within the last two weeks of March and the first two weeks of April, which is typical according to previous studies on the Pere Marquette River (Workman 2001).

Some steelhead left the Pere Marquette River after being tagged in both years of the study, which may occur when tagging anadromous species near the mouth of a river (Eiler 1990, Webb 1990). The steelhead in the present study may have been homing to a geographical area rather than specifically to the Pere Marquette, which may occur when streams are close together and similar in chemical and physical condition (Biette et al. 1980).

The percentage of radio-tagged steelhead reaching the barrier site in Custer after being surgically implanted in Ludington was comparable between years, and similar to earlier studies (57% in 1997, 63% in 1998)(Workman 2001). Movement rates, activity levels at the barrier, and percent passage did not differ between surgically implanted steelhead and gastrically implanted steelhead. However, the faster, less invasive method of gastric implant may be practically significant, and would be recommended for future research.
At least 67% of radio-tagged steelhead ascended the fish passage during the 2001 field season. While this percentage falls short of the proposed goal (70%), it should be considered a minimum estimate of passage. It is known that 24 fish ascended the fish ladder, but it is also known that there was a certain degree of equipment failure. The Custer receiver contained incomplete records of two radio-tagged fish that are known to have passed the weir. These fish were detected on the Bowman Bridge receiver and their passage could have been missed during the process of downloading data from the Custer receiver. Two radios failed after implantation (one was handled by barrier personnel and one was captured upstream by an angler), and one fish regurgitated a radio before ascending and being captured in the upstream net. Of the 24 fish that were confirmed moving upstream through the ladder, only 14 were handled by barrier personnel. Because three tagged fish were never located after implantation, and the fate of seven more is unclear, it is possible that one or more of these fish might have passed the barrier undetected.

Radio-tagged steelhead traveled faster through all three sections in 2001 than in 2000. Fish most likely moved faster due to the difference in water temperature between years, which has been found to be the dominant factor in triggering upstream migration in Pere Marquette River steelhead (Workman et al., submitted). In 2000, a larger number of fish were tagged when water temperature was below 7°C. In 2001, many steelhead were tagged when water temperature exceeded 9.5°C, and based on previous studies it is clear that the propensity to migrate increases dramatically with increasing water temperatures (Workman et al., submitted).
Faster movement rates through section B in 2001, which includes the fish passage, are most likely the result of the improved barrier operations (correcting stray voltage problems near the entrance of the fish ladder). While fish were able to find passage around the barrier in 2001, the effect of the delay on individual steelhead is unclear. Bjornn et al. (1998) found that chinook salmon that took extended periods of time (twice the median) to ascend ladders on the Snake River were less likely to reach spawning areas. Fish in the Snake River, however, must travel much greater distances than steelhead in the Pere Marquette. Furthermore, mean delays were shorter than those reported in similar studies of salmonids by Gowans (1999) (14.8 days) and by Laine (1995) (14 days), but median delay was longer than that reported by Bjornn et al. (1998) (0.25-0.86 days).

Passage times through section C are difficult to compare between years due to the small sample sizes. If tagged fish did, indeed, move faster in 2001, the difference may again be explained by Workman’s temperature based model. Alternatively, salmonids have also been found to migrate faster once ascending a dam to compensate for the delay incurred below the dam (Bjornn et al. 1998). A larger sample would be necessary to evaluate this in the present study.

The fish ladder was an effective passage for steelhead around the barrier once the fish located its entrance, and fish moved through the ladder relatively quickly upon entrance. However, fish were quite active in seeking passage before finally entering the ladder. It is clear that the process of finding the entrance to the ladder, rather than the process of ascending the ladder, led to the increased time spent by fish in the area downstream of the barrier during barrier operation. It has previously been suggested that
fish must become acquainted with the entrance to a fish ladder before actually ascending (Laine 1995).

Tagged steelhead mainly ascended the ladder during daylight hours, supporting the idea that salmonids may rely heavily upon light to navigate such obstacles (Banks, 1969). Fish ladder data also confirms this for untagged fish, as nearly 70% passed in daylight. Similar diel patterns have been observed in chinook salmon (Bjornn et al. 1998), Atlantic salmon (*Salmo salar*) (Gowans 1999), and steelhead (Chapman 1941, Sapak 2001 Personal Communication) migrating through fish ladders.

Passage times of tagged steelhead migrating downstream through the barrier was longer, in both years of the study, than before the operation of the barrier (11 minutes) (Workman 2001). This may be caused by stray voltage on the upstream side of the barrier. Stray voltage on the upstream side may also be blamed for the 12% fallback rate. Rather than being released upstream of the electrical field, some fish falling from the return tube were dropped directly into stray voltage, and subsequently washed back downstream.


