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AN ABSTRACT OF THE THESIS OF

Ralph Tatsuo Lampman for the degree of Master of Science in Fisheries Science presented on November 22, 2011.

Title: Passage, Migration Behavior, and Autoecology of Adult Pacific Lamprey at Winchester Dam and within the North Umpqua River Basin, Oregon, USA

Abstract approved: ____

Carl B. Schreck

The extensive reduction in adult Pacific lamprey (*Entosphenus tridentatus*) counts at many hydroelectric dams in the northwestern USA signals a substantial decline in lamprey numbers across the entire region in the past 40 to 50 years. Among the many potential causes of this decline, obstruction of migration routes has likely played a substantial role. Within the North Umpqua River basin in southwest Oregon, USA, I focused on the following three research goals: 1) to describe the passage efficiency and migration routes of adult Pacific lamprey at Winchester Dam; 2) to evaluate the seasonal movement patterns of adult Pacific lamprey and their use of holding habitat at Winchester Dam in relation to temperature conditions; and 3) to portray the diversity of upstream migratory behaviors of adult Pacific lamprey and the environmental factors that influence these behaviors. This radio telemetry study was conducted between March 2009 and August 2011 with a combination of fixed stations and manual tracking.

Passage efficiency was low in both years (8% and 19%, respectively), and all tagged lamprey that successfully passed the dam used routes other than the fish ladder. Lamprey that migrated early within the run and those with relatively small tags had

higher passage rates and traveled further than the other groups of lamprey. Lamprey released above of the dam or those that passed the dam on their own distributed themselves widely in the upstream environment, suggesting that the dam deterred their upstream migration. Using mark-recapture data for the two years, the adult Pacific lamprey population upstream of Winchester Dam was estimated at 960 (95% C.I. [188, 4760]) in 2009 and 556 (95% C.I. [110, 2798]) in 2010, which was considerably lower than historical counts at the dam (between 14,532-46,785 in 1965-1971).

Most tagged lamprey that did not pass the dam remained at the base of the dam at the end of the summer migration (63% in 2009 and 67% in 2010). Types of habitat most frequently used by lamprey downstream from the dam included the dam surface (wooden structures with crevices), interface zones between fast and slow water, and highway bridge pilings. The lamprey movement changed considerably between August and September, and the frequency of movements decreased sharply during this period. Tagged lamprey were detected using thermal refuges immediately downstream of the dam that were 0.4 to 2.8 C° colder than the mean river temperature at the dam, and this temperature differential increased as the season progressed. Lamprey may be seeking overwintering habitat associated with hyporheic exchange flows at the dam towards the end of the summer season after their display of heightened activity early in the summer.

Ninety-five percent of the overall upstream migration took place during the first spring/summer period, and only small-scale upstream movements were observed during the winter and second spring/summer (4% and 1%, respectively). The rate of upstream migration (median) was the fastest during the initial migration phase and was 1.9 km/day (ranging from 0.3 to 11.0 km/day) for tagged lamprey released above Winchester Dam.

During winter, 71% of the lamprey remained in the same location where they initiated holding. Multiple regression analysis indicated that the total upstream distance traveled by individual lamprey was most strongly related to presence/absence of Winchester Dam, relative tag size, and water temperature and photoperiod conditions at release. The presence of Winchester Dam, large relative tag size, and high water temperature / short photoperiod conditions at release significantly reduced upstream migration distance.

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Passage, Migration Behavior, and Autoecology of Adult Pacific Lamprey at Winchester Dam and within the North Umpqua River Basin, Oregon, USA

by

Ralph Tatsuo Lampman

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APPROVED:

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Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Ralph Tatsuo Lampman, Author

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"The last word in ignorance is the man who says of an animal or plant: 'What good is it?' If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering."

From “Round River” by Aldo Leopold

CONTRIBUTION OF AUTHORS

Dr. Carl B. Schreck (U.S. Geological Survey / Oregon Cooperative Fish and Wildlife Research Unit / Oregon State University) contributed to the study design, data analysis, and editing of all sections of this manuscript. Mr. Sam Moyers (Oregon Department of Fish and Wildlife, Roseburg Office) contributed to the study design, data collection, data analysis, and editing of all sections of this manuscript. Mr. Fabian Carr (Oregon Department of Fish and Wildlife, Roseburg Office) assisted with lamprey collection and provided the logistical support and advice at Winchester Dam. Mr. Reed Janke (Oregon State University, undergraduate student at the time) assisted with data collection of all sections of this manuscript.

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PASSAGE, MIGRATION BEHAVIOR, AND AUTOECOLOGY OF ADULT PACIFIC LAMPREY AT WINCHESTER DAM AND WITHIN THE NORTH UMPQUA RIVER BASIN, OREGON, USA

CHAPTER 1: GENERAL INTRODUCTION

Project Overview

Native Americans of the northwestern USA have depended on Pacific lamprey (*Entosphenus tridentatus*) as a key food source and medicine for over 10,000 years, and many stories and legends passed down from generation to generation portray lamprey as a crucial cultural icon (Close et al. 2002; NUYWT 2008). In recent years, the extensive reduction in adult Pacific lamprey (*Entosphenus tridentatus*) counts at many hydroelectric dams in the northwestern USA has signified a substantial decline in their numbers across the entire region (Moser and Close 2003). The causes for this decline are most likely multifaceted, and many of the causes responsible for the decline in Pacific salmon populations could also be affecting Pacific lamprey considering their analogous life histories, habitat requirements, and population collapse (Brumo 2006). Impaired freshwater habitat for rearing and spawning, poor water quality, dewatering of streams, increases in predatory invasive species, climate change, overharvesting of marine fish stocks, and changes in ocean conditions are all possible causes of lamprey decline (Close et al. 2002; Nawa 2003; ODFW 2006). Among these many causes, obstruction of migration routes may have played a substantial role (Beamish and Northcote 1989; Moursund 2001; Moser et al. 2002b).

There are several reasons why dams and other human-made obstacles are specifically problematic to Pacific lamprey. Most fishways at dams have high water velocities (>2 m/s) and were originally designed to provide passage for anadromous salmonids (*Salmonidae spp.*), a group of fish that are known for their superb swimming capabilities (Mesa et al. 2003; Keefer et al. 2010). Lampreys' swimming motion (anguilliform) is significantly less efficient than the burst-and-glide swimming motion displayed by salmonid species (subcarangiform) (Mesa et al. 2003). Furthermore, lamprey lack swim bladders that are essential in maintaining neutral buoyancy; hence, to maintain position, lamprey have to swim constantly or hold fast (Hardisty and Potter 1971). Several studies on sea lamprey, *Petromyzon marinus*, also report that lamprey are weak swimmers compared to most teleosts (Beamish 1974; Hanson 1980; McCauley 1996).

When navigating through swift current velocities, adult Pacific lamprey make use of their suctorial disc to grasp onto surfaces and rest between periods of burst swimming (Kemp et al. 2009). When current velocities are greater than 0.6 m/s, this saltatory mode of movement becomes most evident (W. Daigle, University of Idaho, unpublished data). Right-angle corners in high velocity conditions often prevent lamprey from staying attached as they move around such sharp corners (Moser et al. 2002a). However, when these sharp corners are rounded off at fishway entrances and at bulkheads downstream of fishway entrances, higher passage success has typically been achieved. Preferred surfaces for lamprey to cling to include polished metal, glass, and roughened concrete in addition to natural, coarse substrate.

Winchester Dam on the lower North Umpqua River is one of the few facilities in the northwestern North America that has maintained long-term, continuous fish counts for adult Pacific lamprey dating back to 1965. Although the decline in Pacific lamprey numbers since the 1970s seems apparent from this historical data, there is uncertainty as to what proportion of the run is using alternate passage routes both historically and currently. Improved understanding of dam passage and associated migration routes selected by Pacific lamprey could provide crucial information necessary to improve lamprey passage locally at Winchester Dam as well as at other dam facilities. The seasonal movement and associated holding behavior of adult Pacific lamprey at dams are also important topics that have not been fully addressed in past studies. Finally, enhanced knowledge of seasonal migration behavior and the environmental factors that affect migration would help managers predict annual run timing and target passage improvement efforts during the most critical periods of the lamprey run.

My primary research goal was three-fold: 1) to describe the passage efficiency and migration routes of adult Pacific lamprey at Winchester Dam; 2) to evaluate the seasonal movement patterns of adult Pacific lamprey and their use of holding habitat at Winchester Dam in relation to temperature; and 3) to portray the diversity of upstream migratory behaviors of adult Pacific lamprey (including upstream migration, holding, and spawning) and the environmental factors that influence these behaviors.

Related Studies

To date, several radio telemetry studies on Pacific lamprey have been conducted in the northwestern USA. A study in the John Day River (Robinson and Bayer 2005) confirmed that the lamprey upstream movement was exclusively at night and that the fish moved at a rate of 11.1 ± 6.3 km/day (standard error). A median of 87% of their upstream migration was completed by September at which time they stayed completely stationary in a single position, overwintering in lateral margins of riffles and glides for six months before the final spawning migration. A study in the Willamette River demonstrated that 84 % of the detected tagged lamprey stayed in the mainstem river channel, while others moved to major tributaries (Clemens et al. 2006).

Studies from the Columbia River (Moser 2002a; Cummings 2007) found that passage success at major dams ranged from 35% to 82% annually and the median passage times ranged from 1 to 11 days. The effects of radio tagging on lamprey were also analyzed in depth, and the relative size of surgically implanted transmitters was negatively correlated with dam passage (Moser et al. 2007). Keefer et al. (2009) suggested that upstream movements of Pacific lamprey were associated with increases in river temperature, which coincided with decreasing river discharge. McCovey Jr. et al. (2007) reaffirmed this relationship between migration timing and temperature and discharge in a Klamath River study.

Life History

The Pacific lamprey (*Entosphenus tridentatus*), is an endemic, anadromous fish distributed in rivers and streams from Baja California, Mexico along the Pacific Rim including Alaska to eastern Honshu Island, Japan (Ruiz-Campos and Gonzalez-Guzman 1996; Yamazaki et al. 2005). Pacific lamprey adults are parasitic and feed on a diversity of marine and anadromous fish (Beamish 1980), such as Pacific salmon (*Oncorhyncus* species), Pacific hake (*Merluccius productus*), sharks (superorder *Selachimorpha*), flatfish (*Atheresthes* species), rockfish (*Sebastes* species), as well as marine mammals (Pike 1951) including whale (*Cetacea*) species. The parasitic adults are thought to remain in the marine environment for 2-3 years before they embark on a migration to freshwater spawning habitats (Beamish 1980). Pacific lamprey have been captured in ocean depths ranging from 0 to 1100 m, and at locations as far as 100 km offshore off the west coast in ocean haul nets (Orlov et al. 2008; Kan 1975). Over 80% of the captures, however, were made in water shallower than 500 m (Orlov et al. 2008). Diurnal vertical migration, showing more frequent catch in the epipelagic zone at nighttime, was also reported.

Adults return to freshwater between spring and summer to commence upstream anadromous migration and stop feeding during this freshwater phase (Beamish 1980). Spawning takes place the following spring, almost a year later, in tributary streams. The larval lamprey (ammocoetes) burrow into the stream sediments soon after hatching and exhibit a largely sedentary lifestyle for the next 4-6 years as filter feeders (Beamish and Levings 1991). After this period of freshwater residence, the juvenile lamprey metamorphose into macrophthalmia (equivalent to salmonid smolts) with newly developed oral disc and eyes and migrate to the sea between winter and spring.

Ecological Roles

Pacific lamprey, an ancient species that arose at least 350 million years ago (Gess et al. 2006), is ecologically important to the northwestern North America for many reasons. Due to their semelparous life history, spawned-out lamprey provide marine-derived nutrients to the freshwater environment particularly during a period when other anadromous inputs are low. Numerous marine and freshwater species, including sharks (superorder *Selachimorpha*) and sturgeons (*Acipenser* species), use lamprey as an important food source (Semakula and Larkin 1968; Galbreath 1979), and lamprey may act as a predation buffer for both juvenile and adult Pacific salmon (Close et al. 2002). It was estimated that 96% of feeding observations of California sea lion (*Zalophus californianus*) in spring were of Pacific lamprey off the coast near the Klamath River estuary in California (Bowlby 1981). Similarly, a gastrointestinal tract study conducted in the lower Rogue River reported that lamprey were the principal prey for California sea lions, occuring in 93% of the samples (Roffe and Mate 1984).

The lamprey's functional role as a benthic filter feeder during their larval stage is also essential in facilitating healthy nutrient recycling within streams and is vital in converting unused nutrients into usable forms for other organisms (Merritt et al. 1984; Moore and Mallatt 1980). Pacific lamprey are also invaluable to Native Americans of the northwestern USA and are an important cultural icon (Close et al. 2002). Indigenous peoples from across the region, including interior Columbia and Snake rivers, have gathered lamprey for subsistence, religious, and medicinal purposes for many generations.

Study Location

The North Umpqua River is a tributary of the Umpqua River in southwest Oregon, USA, with a total drainage area of 3,554 km^2. The study area includes the stretch of river from its mouth to Soda Springs Dam (river km 113) including all its tributaries. The river originates from Maidu Lake at an elevation of 1,830 m in the High Cascade Mountain Range approximately 110 km east of Roseburg. It follows a serpentine course through steep canyons westward along the southern side of the Calapooya Mountains. The approximately 170 km-long mainstem river drains a scenic and rugged area of the Cascade Range southwest of Eugene, and combines with the South Umpqua River to form the mainstem Umpqua River at elevation 244 m about 11 km northwest of Roseburg, Oregon. The North Umpqua basin (3554 km^2) contains twelve smaller watersheds (mean size = 296 km^2) and has a total of approximately 570 km of anadromous stream habitat. On the North Umpqua River, anadromous fish passage extends to near Toketee Falls, where historically impassable natural barriers (121 km) and presently the 35-m high Soda Springs Dam (113 km) block all anadromous fish migrations (Lauman et al. 1972).

The west side of the subbasin falls under the Umpqua Interior Foothills ecoregion, a complex of foothills and narrow valleys containing fluvial terraces and floodplains with hot and dry summers. Oregon white oak woodland, Douglas-fir, grand fir, ponderosa pine, madrone, tanoak, and chinkapin represent the main overstory vegetation. The east side of the subbasin falls under the Western Cascades Lowlands and Valleys ecoregion, a network of steep ridges and narrow valleys on the lower slopes of the Cascade Mountains with mild, wet climate. Forests are dominated by western hemlock and Douglas-fir, with western red cedar, bigleaf maple, and red alder.

Because the North Umpqua River begins farther inland and flows for a substantial distance at a higher elevation than most other Oregon coastal rivers, it historically had cooler water and larger summer water flows than these other rivers. Over 20% of the North Umpqua River basin lies above 1,700 m elevation, which brings about plentiful snowpack melt that supplies strong flows lasting through the summer. The snowpack melts into deep, porous pumice soil in the upper reaches, giving rise to the unique “emerald” green color of the North Umpqua River pools. Due to these factors the North Umpqua River contained a large and diverse salmonid population. However, beginning in the mid-1950s, summer water temperatures and the frequency of winter flooding increased in the North Umpqua River basin due to changes that have been attributed to clear-cut logging in many of its tributaries (Hostetler 1991).

The naturally silted, lower gradient stream reaches of the Umpqua River and its tributaries historically provided ideal habitat for Pacific lamprey, which local native tribes consumed smoked or dried (A. Amoroso, the Cow Creek Band of Umpqua Tribe of Indians, pers. comm. 2011). Today, the upper part of the project area is primarily federally-owned forest lands, whereas the lower part is mostly privately-owned and managed for both forestry and agriculture (Umpqua Basin Explorer, available at: http://oregonexplorer.info/umpqua/). Historical anthropogenic impacts on the stream ecosystem within the basin consist of timber harvest (clear-cutting) and associated activities (road building, log drives, etc.), dam constructions, hatchery operations, grazing, and introduction of non-indigenous species.

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CHAPTER 2: PASSAGE AND AUTOECOLOGY OF ADULT PACIFIC LAMPREY AT WINCHESTER DAM IN THE NORTH UMPQUA RIVER, OREGON, USA: IMPLICATIONS FOR POPULATION STATUS

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Abstract

The passage efficiency and migration routes of adult Pacific lamprey, *Entosphenus tridentatus*, at Winchester Dam on the North Umpqua River were examined using radio telemetry in 2009 and 2010. Passage efficiency was low in both years (8% and 19%, respectively), and all tagged lamprey that successfully passed the dam used routes other than the fish ladder. The migration timing within the run and relative tag size affected passage efficiency, and these two factors combined with the presence of the dam appeared to impose a synergistic effect on the overall lamprey upstream migration. Among the three groups of lamprey, the early run group that were exposed to lower water temperatures (14-20 C°) had the highest passage efficiency (33%), followed by the middle run (12%) and late run (0%) groups that were both exposed to higher water temperatures (>20 C°). Lamprey with smaller tags had the highest passage efficiency (33%), followed by lamprey with the medium (18%) and large (6%) tags. Lamprey released above the dam or those that passed the dam on their own distributed themselves widely in the upstream environment, suggesting that the dam deterred their upstream migration. Using mark-recapture data for the two years, the adult Pacific lamprey population upstream of Winchester Dam was estimated at 960 (95% C.I. [188, 4760]) in 2009 and 556 (95% C.I. [110, 2798]) in 2010, which was considerably lower than the historical counts at the dam (between 14,532-46,785 in 1965-1971).

Introduction

The Pacific lamprey (*Entosphenus tridentatus*) is among the earliest known fish species, dating back 360 million years in fossil record and has inhabited the streams, rivers and coastal waters of the Pacific Rim relatively unchanged from its primordial form (Gess et al. 2006). Recent data from counts of migrating individuals at many hydroelectric dams in the northwestern USA show that populations have diminished dramatically in the last few decades (Kostow 2002). There is evidence that poor passage at dams may have played a substantial role in this decline (Beamish and Northcote 1989, Moursund 2001, Moser and Close 2003).

Most fishways at dams have high water velocities (>2 m/s) and were originally designed to provide passage for anadromous salmonids (*Salmonidae spp.*), a group of fish with superb swimming capabilities (Mesa et al. 2003). Several studies on sea lamprey, *Petromyzon marinus*, show that lamprey are weak swimmers compared to most teleosts (Beamish 1974; Hanson 1980; McCauley 1996). Right angles in high velocity segments of the fish ladder often prevent lamprey from staying attached as they move around such sharp corners using their suctorial disc. Moser et al. (2002b) found that only about 50% of the adult Pacific lamprey passed the lowermost mainstem dam on the Columbia River in contrast to the 90% and higher passage efficiency demonstrated by Pacific salmonids (*Oncorhynchus* spp.). Further upstream at McNary Dam (Columbia River) and Ice Harbor Dam (Snake River), the passage efficiency for lamprey was estimated to be about 60% (Cummings 2007).

Constructed in 1907, Winchester Dam on the North Umpqua River (Oregon, USA) is one of the few dams in the Pacific Northwest that has maintained a continuous historical record of the adult Pacific lamprey counts since 1965. Records indicate that the number of Pacific lamprey have declined sharply since the early 1970s (Figure 2.1). However, lamprey numbers in recent years are perhaps not as low as the fish count data indicates because lamprey are potentially capable of avoiding the counting stations by passing through the small openings on the dam surface. The dam surface is not completely water-tight because of its rock-filled timber crib design. There are also picketed leads and diffuser gratings that have 2.5 cm or larger gaps inside the fish ladder, and according to Moser et al. (2008) most adult Pacific lamprey can squeeze through an opening of this size. The magnitude of the decline may be much less than what is suggested by the fish counts if considerably more lamprey are using these alternate routes for dam passage in recent years. Identifying the extent to which lamprey may use these alternate routes for passage, therefore, is essential for assessing the true annual passage rates as well as for population estimation.

The primary goal of this study was to evaluate the passage efficiency and migration routes for the adult Pacific lamprey at Winchester Dam. Based on our results, we estimated the number of adult lamprey upstream and downstream of the dam. Radio telemetry was used to monitor the behavior of adult Pacific lamprey captured at Winchester Dam in 2009 and 2010. The migration behavior of fish released below the dam were compared with those that were released above the dam to evaluate dam effects. Other biotic and abiotic factors that impact the upstream migration were also examined.

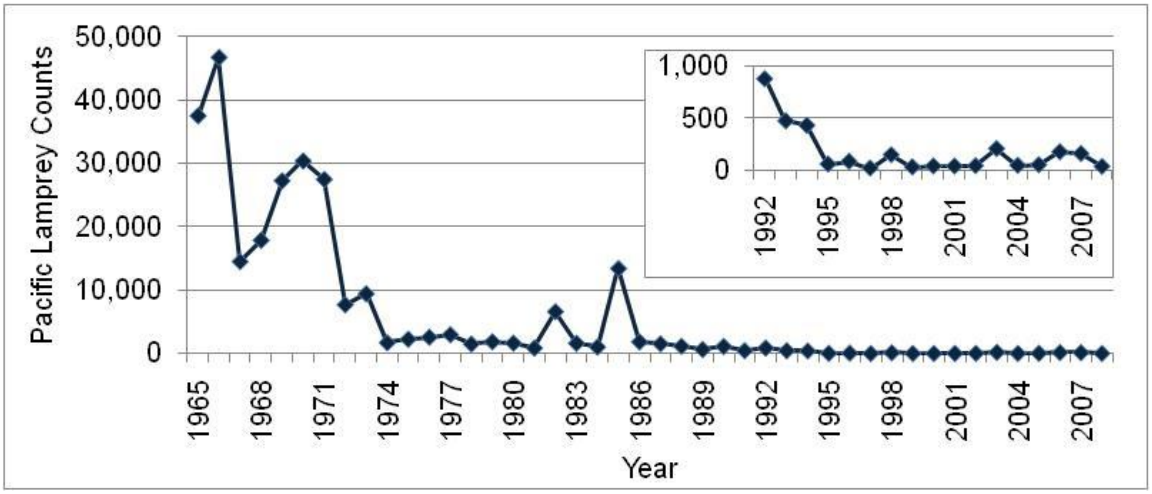

Figure 2.1. Counts of adult Pacific lamprey at Winchester Dam, Oregon, between 1965 and 2008 (data provided by Oregon Department of Fish and Wildlife). The embedded graph displays the Pacific lamprey counts from 1992 through 2008 using a finer scale.

Methods

Study Area

The study was conducted at Winchester Dam, which is located at river km 11.2 on the North Umpqua River in southwest Oregon, USA (Figure 2.2). Water discharge at the dam typically ranges from 30 m^3/s during the summer low-flow period (July-September) to 180 m^3/s during the winter-spring high-flow period (December-February), with an average annual flow of 105 m^3/s. To make comparisons between the lamprey released downstream and upstream of the dam, the study area also included the mainstem river and all of its tributaries within the North Umpqua Basin below Soda Springs Dam (3,520 km^2). Anadromous species, including Pacific salmonids (*Oncorhynchus* spp.) and Pacific lamprey, migrate roughly 179 km from the ocean along the Umpqua River to reach the mouth of the North Umpqua River. The basin (3,520 km^2) holds roughly 110 km of anadromous fish habitat in the mainstem river and 450 km in all of its tributaries

(Umpqua Basin Explorer, available at: http://oregonexplorer.info/umpqua/). The historical extent of Pacific salmon and Pacific lamprey distribution is considered to be comparable in many basins within the Northwestern USA (Scott and Crossman 1973; Simpson and Wallace 1978; Moyle 2002).

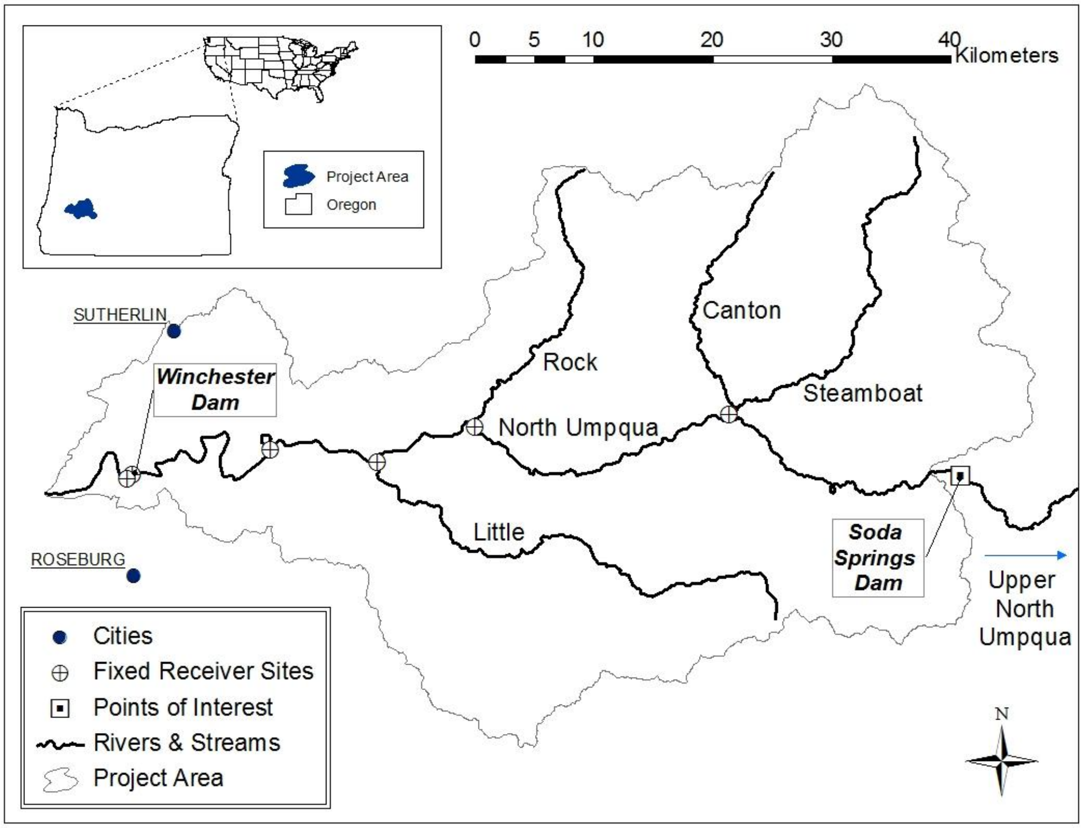

Figure 2.2. Map of North Umpqua River below Soda Springs Dam, including major tributaries. Locations of fixed receiver sites and Soda Springs Dam are identified. Soda Springs Dam has been the upper extent of the anadromous fish habitat, but new fish ladders will enable anadromous fish to use the upper North Umpqua watershed starting in 2012.

The North Umpqua River originates from Maidu Lake at an elevation of 1,824 m on the western slope of central Cascade Mountains and joins the South Umpqua River northwest of Roseburg, Oregon, at an elevation of 110 m. Over 20% of the subbasin lies above 1,700 m elevation, which supplies strong, cool flows from the snowmelt runoff that last through the summer.

Sampling and Tagging

In 2009 and 2010, adult Pacific lamprey were collected from May–September during their upriver migration at Winchester Dam (collection started in March, but none were captured until May). Adults were captured either inside the fish ladder or immediately downstream of the dam using dip nets, an assortment of traps, or by hand (see Appendix A for details). Traps were designed to capture adult Pacific lamprey of all sizes. In an effort to minimize capturing lamprey that had already selected passage routes at the dam, traps were placed in a wide variety of locations on both banks and within 2 km downstream of the dam to diversify the sample. However, a large portion of the sample was from the mid to lower fish ladder of Winchester Dam (74%). Hence, many of our tagged fish already had some experience with the ladder. This likely did not affect our results as the fish were free to enter the ladder again if there was a preference, and given the low passage estimates for fish at the counting window, we suspect that these fish would have likely looked for alternative places to approach the dam. Those observed in the upper portion of the fish ladder were allowed to continue through the ladder.

Following the surgical techniques described by Moser et al. (2002a) and the training and practice provided by lamprey telemetry experts, lamprey were surgically implanted with radio tags. To ensure that the tags represented less than 8% of the fish's cross-sectional area, only lamprey that met the minimum mid-girth criteria of 102 mm were surgically implanted with the Lotek NTC-6-2 nano tags (4.3 g in air, 9x30 mm) in 2009. In 2010, two additional types of tags were deployed: Lotek NTC-3-2 nano tags

(1.1 g, 6x16 mm) and MST-820T temperature sensor tags (2.2 g, 8x22 mm). The minimum girth threshold was reduced to 73 mm and 90 mm, respectively, for these two smaller tags, using the same 8% criterion. All of the tagged lamprey had a tag/lamprey weight ratio lower than 1.2%.

Captured lamprey were either handled immediately or held in perforated flow-through containers (30 – 70 L) in the river for 1 – 48 hours before the surgery. Lamprey were individually placed in 15 L water with 70 mg/L tricaine methanesulfonate (MS-222, Argent Chemical Laboratories, Redmond, WA) and 70 mg/L bicarbonate buffer and anesthetized for approximately 4 minutes in a darkened container (to minimize stress). They were measured to the nearest millimeter and weighed to the nearest gram in water. A fish was then positioned in a PVC cradle with their gill openings submerged in a solution containing 45 mg/L buffered MS-222. Mid-girth (girth at base of first dorsal fin) and dorsal fin interval (interval between first and second dorsal fins) were measured to the closest mm. Dorsal fin interval was measured in both years to gauge the level of sexual maturity as suggested by Clemens et al. (2009). Sex (male, female, unknown), color (four categories), ventral firmness (soft, hard), and genital papilla size (large, medium, small) were also documented at this time.

A 1-2 cm incision was made in the ventral body wall below the anterior base of the first dorsal fin. The transmitter’s antenna was positioned using a 14 gauge catheter needle inserted through the initial incision and pushed through the lateral body wall until it was in line with the posterior end of the first dorsal fin. The transmitter was then gently inserted into the body cavity, and the incision was closed using braided synthetic absorbable sutures in a simple, interrupted suture pattern. In addition, each tagged lamprey was given an intra-muscular injection of oxytetracycline (11 mg/kg) as a precautionary measure. During high temperature conditions (> 20° C), ice packs were utilized to reduce the water temperature throughout the entire process (before anesthesia and post surgery) to reduce physiological stress. Tagged lamprey were held in an aerated recovery bucket for at least 1-3 hours to monitor their conditions before release; all recovered from the anesthetic within 10 minutes.

Radio Tags and Monitoring of Location

The objective in both years was to tag individuals throughout the run. The peak of the run has been observed primarily between late June and early July based on the previous 10 years (1999-2008) of records of lamprey run timing at the fish ladder. Seventeen lamprey in 2009 and 45 lamprey in 2010 were implanted with a radio transmitter. Seven additional radio-tagged lamprey from 2009 were analyzed separately because they were captured just below the dam during a dewatering event late in the migration season (1 September, 2009) when most other lamprey had already stopped moving.

Tagged fish were released in different locations to better understand the potential impact of the dam on migration behavior. In 2009, 15 radio-tagged lamprey were released 0.9 km downstream of Winchester Dam while two were released 2.5 km and 23.9 km upstream of the dam, respectively (Figure 2.3). In 2010, 31 radio-tagged lamprey were released 0.9 km downstream of the dam while 14 were released 2.5 km upstream of the dam past the reservoir. All tagged lamprey were released in slow water to minimize post-release stress, and timing of release was primarily during the day around noon.

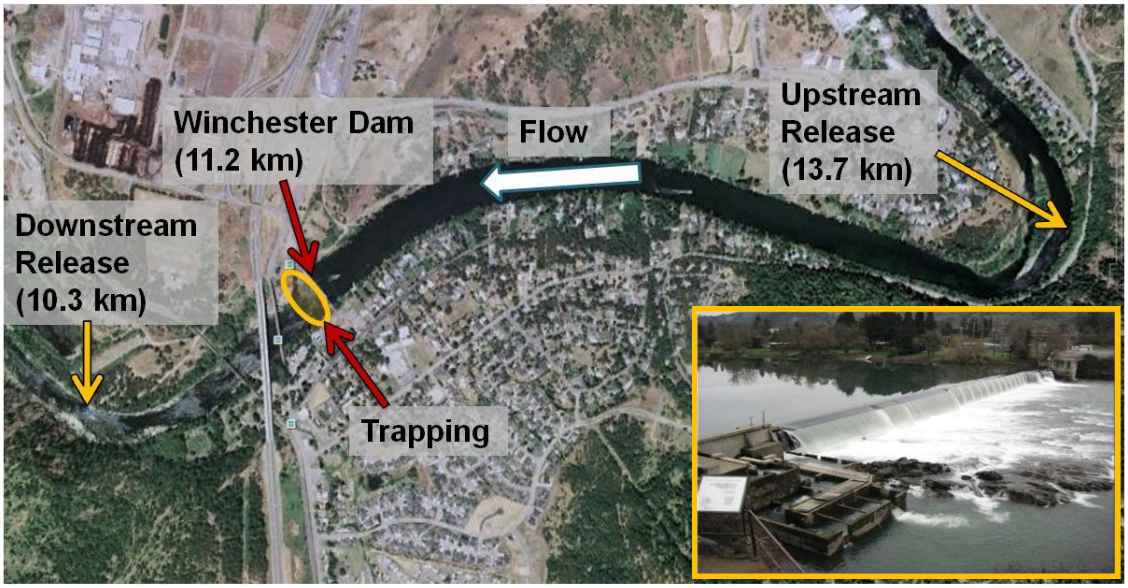

Figure 2.3. Aerial map of North Umpqua River near Winchester Dam (see embedded photo) at river km 11.2. The trapping location as well as the primary release locations downstream and upstream of the dam are shown with arrow pointers.

Radio-tagged lamprey were tracked using manual tracking and fixed receiver sites. Manual tracking involved mainly vehicle tracking using the extensive road networks in the basin, but when the tagged lamprey were detected, more precise locations (< 15 m) were found by on-foot mobile tracking using triangulation when feasible. Tracking by rafts was also used in mid-summer in both years to cover a portion of the river that was otherwise hard to access. Fixed sites were established at Winchester Dam and directly above major tributary junctions [Little River (river km 46.7), Rock Creek (river km 57.5), and Steamboat Creek (river km 84.9)]. All fixed sites had a minimum of two aerial antennas to detect both lamprey presence and direction of movement. In 2010, additional fixed sites were established downstream (river km 10.6) and upstream (river km 33.2) of the dam starting in September to detect small scale movements, including fallbacks.

To document specific migration routes at Winchester Dam, we set up a receiver station on each side of the river. The station on the north bank was comprised of one aerial antenna for general detection and a minimum of three underwater antennas covering the fish ladder for more precise detection. The station on the south bank of the dam had two aerial antennas, which were located 40 m upstream and downstream of the dam, for general detection. Minimum detection distances of each antenna was confirmed by tests with active radio tags in water. Tagged lamprey within 100-150 m from the dam (both upstream and downstream) were generally detected by these two stations.

Data Analysis

All recorded locations from manual tracking and fixed sites were entered into and processed in ArcGIS 10 and Google Earth 6. After cross examinations with the fixed site data, each lamprey location was given a start and an end date, from which the duration of stay (in days) for each location was calculated. River habitat was divided into 0.5 km segments using the split function in ArcGIS 10, and each lamprey location was assigned to the closest 0.5 river km for the calculation of migration distance.

Statistical analyses were performed using R statistical software (R Development Core Team 2011). Variables were analyzed for normality of distribution using normal probability plots and Shapiro-Wilk normality test. Variables with normal distributions were analyzed using means, and a two-sample t-test was conducted for any comparisons. Variables with skewed distributions were analyzed using medians, and a Wilcoxon two-sample test was conducted for comparison. A significance level of p-value = 0.05 was used for all statistical analyses performed in this study.

Dam Passage

The passage efficiency, timing, and locality of passage were evaluated in relation to tag size and run timing of the lamprey. Evidence suggests that there are three distinct phases in the spawning migration of Pacific lamprey (Beamish 1980; Robinson and Bayer 2009; Clemens et al. 2010), and we used terminology from Clemens et al. (2010) to refer to these three phases. The initial migration phase (May-September) is generally characterized by the active upstream migration during the summer. The pre-spawning holding phase (October-February) is a period of prolonged holding and metabolic depression during the winter. The final migration phase (March-July) is characterized by the enhanced level of activity associated with the spawning migration and movement to spawning habitat in the spring. Tags from 2009 and 2010 were included in the initial migration phase analysis. Only tags from 2009 were included in the analysis for the pre-spawning holding and spawning migration phases because of limitations in the research timeframe.

Results

Lamprey Run Timing

We captured and measured 131 adult Pacific lamprey in 2009 and 77 in 2010. Eighty-eight additional adults captured in 2009 during a reservoir dewatering event for dam maintenance were excluded from this dataset because they were captured late in the initial migration phase (1 September, 2009) when most other lamprey had already stopped moving. The run timing of the adult lamprey at Winchester Dam in 2009 and 2010 was similar to the general run timing displayed by the previous 10 years of records, with the 50th percentile capture dates falling on July 6 and July 11, respectively. Based on the multimodal distribution of the capture data and the associated breakpoints, tagged lamprey captured before July 1 were classified as the "early run," those captured between July 1 and July 15 were classified as the "middle run," and those captured after July 16 were classified as the "late run" (Figure 2.4). The early run group made up 29.2 % and 15.6 %, the middle group made up 25.0 and 53.3 %, and the late group made up 45.8 and 31.1 % of the whole sample in 2009 and 2010, respectively.

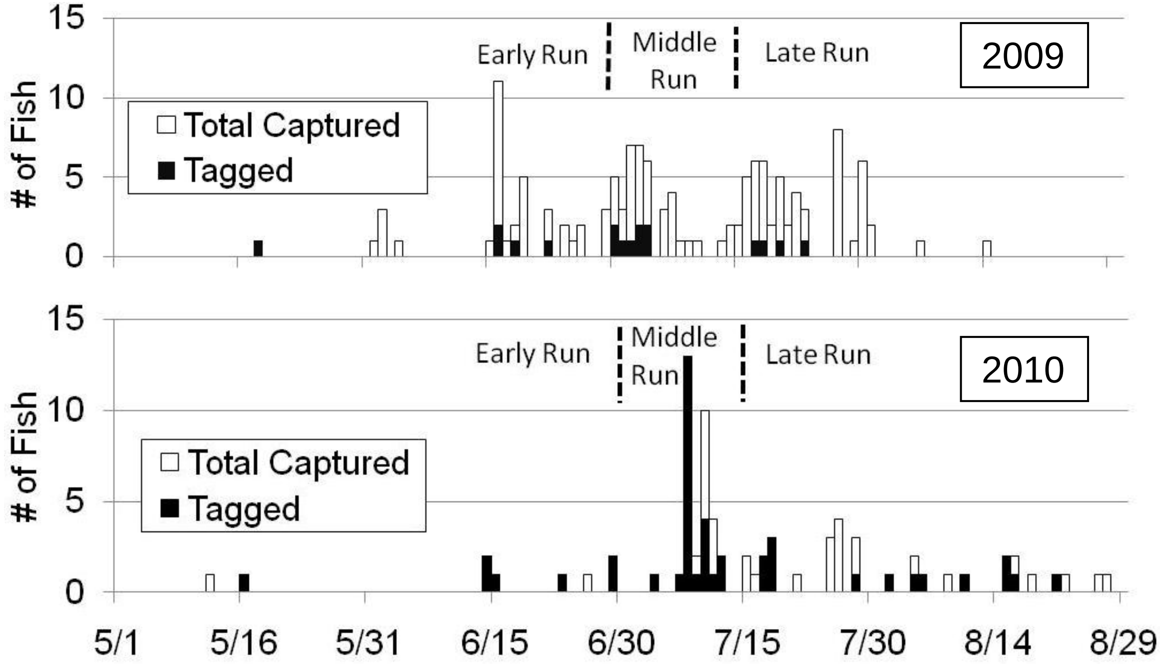

Figure 2.4. Number of adult Pacific lamprey captured in 2009 (n = 131) and 2010 (n = 77). The filled bars display the number of lamprey that were tagged. For analysis we divided the run into three segments: early, middle, and late run.

For all the body measurements obtained (length, weight, condition factor, girth and dorsal fin interval; Table 2.1), there was no significant difference between data for the two years (df = 196, t = 1.808, p-value = 0.072 for dorsal fin interval; t < |-0.789|, p-value > 0.431 for all others). One sexually mature fish was captured on 12 May, 2010, which had the shortest body length (420 mm) and dorsal fin interval (0 mm), and the highest condition factor (0.407) among all the sampled lamprey from both years. All other captured lamprey displayed no signs of sexual maturity (e.g. small dorsal fin interval, stunted body length, pseudo-anal fin, distended abdomen) and appeared to be in their first spring/summer migration.

Because only larger lamprey (the upper 13% percentile) were tagged in 2009, tagged fish in 2009 were significantly larger in length, weight, and mid-girth compared to the overall sample (df > 31, t > |10.846|, p-value < 0.0001; Table 2.1, Figure 2.4). In contrast, there was no significant difference between the tagged lamprey and the overall sample in 2010 for all measurements (df = 110, t < 1.927, p-value > 0.056; Table 2.1, Figure 2.5).

Table 2.1. Summary of the morphology data for the tagged lamprey and overall sample in 2009 and 2010. Lamprey captured during a dewatering event between 31 August, 2009, and 2 September, 2009, are excluded from this summary data.

	Overall Sample (N=131)					Tagged Lamprey (N=17)				
2009	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)
Mean	561.2	296.2	0.166	93.7	19.3	604.2	387.9	0.176	104.94	21.8
Standard Error	2.7	4.6	0.001	0.6	0.4	4.3	4.4	0.003	0.7	1.1
Minimum	485	176	0.134	77	5	575	363	0.154	102	15
Maximum	644	436	0.204	113	33	644	436	0.203	113	33

	Overall Sample (N=77)					Tagged Lamprey (N=45)				
2010	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)
Mean	565.7	301.6	0.167	93.7	18.0	579.1	323.7	0.166	96.3	18.6
Standard Error	5.1	7.4	0.004	1.0	0.6	5.4	8.5	0.002	1.1	0.7
Minimum	415	202	0.132	79	0	511	228	0.133	83	8
Maximum	643	464	0.407	112	27	643	464	0.202	112	27

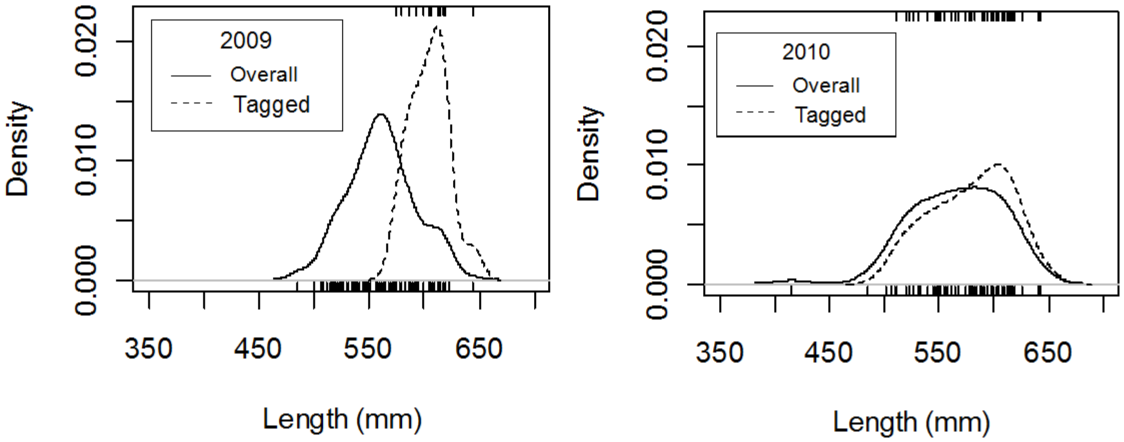

Figure 2.5. Probability density plots of the lamprey body length for the overall sample and tagged lamprey in 2009 and 2010. Individual data points are denoted by rug representations (1-d plot); the bottom rug represents the overall sample data points and the top rug represents the tagged lamprey data points.

Dam Passage

The majority of the tagged lamprey released 0.9 km downstream of the dam returned to the dam by the end of initial migration phase (80.0% in 2009 and 87.1% in 2010) (Table 2.2). In 2009, one tagged lamprey returned to the dam for the first time during the final migration phase, increasing the overall return rate to 86.7%. The return time varied considerably, ranging from 9 hours to 9 months; a large portion returned on the very first night after their release in 2009 and 2010 (38.5% and 40.7%, respectively). The median return time was 2.4 days in 2009 and 4.4 days in 2010. All of the returning lamprey were first detected at the dam between 22:46 and 1:55 at night.

The passage efficiency (the number passing divided by the number returning to the dam) for tagged lamprey was low in both years (8.3% in 2009 and 18.5% in 2010). Most of the passage events took place between late June and early July during the evening hours (between 22:00 and 3:00), but there were also some delayed passage in mid-August and mid-September during the morning hours (between 6:00 and 8:00)

(Table 2.3). Those that passed earlier in June and July spent 3-12 days at the dam prior to passage, whereas the two fish that passed later in August and September spent considerably longer time at the dam (26 and 71 days, respectively). The fixed receiver data indicated that all dam passage events were directly over or through the dam wall itself, and none of them passed through the fish ladder. Passage in 2009 was closer to the north bank side, whereas in 2010 lamprey passed closer to the south bank side (earlier passage near the center and later passage further south).

Table 2.2. Summary of the tagged lamprey by release location, year, and run timing. Run timing depicts the migration timing of individual fish within the run.

Lamprey Released Upstream of the Dam

Year	Run timing	No. of tagged Lamprey
2009	Late	2
2010	Early	2
2010	Middle	9
2010	Late	3

Lamprey Released Downstream of the Dam

Year	Run timing	No. of tagged Lamprey	No. that returned to the dam	Median return time (days)	No. that passed the dam
2009	Early	7	7	0.5	1
2009	Middle	6	4	8.5	0
2009	Late	2	2	5.4	0
2010	Early	5	5	8.6	3
2010	Middle	15	14	1.0	2
2010	Late	11	8	2.5	0

Table 2.3. Summary of all passage events at Winchester Dam by individual tagged lamprey (n=1 in 2009 and n=5 in 2010). Run timing depicts the migration timing of individual fish within the run. “Temp. (C°)” represents the water temperature during the passage time. “Delay Time” is the time interval between the fish’s first arrival at the dam and dam passage. All passage was over or through the crib structure.

Year	Run timing	Tag size	Passage date	Passage time	Temp. (C°)	Delay Time (days)	Passage Route (on crib structure)
2009	Early	Large	6/29/2009	2:22	20.7	12.1	north bank side
2010	Early	Medium	6/28/2010	22:49	20.8	4.0	center-south bank side
2010	Early	Small	7/5/2010	2:59	18.9	10.2	center-south bank side
2010	Early	Small	7/10/2010	23:30	22.8	3.0	center-south bank side
2010	Middle	Medium	8/16/2010	7:29	22.2	26.3	south bank side
2010	Middle	Medium	9/19/2010	6:11	16.8	70.8	south bank side

There was a considerable difference in the distances travelled by the fish released below the dam and those released above the dam (W = 205.5, p-value = 0.0056). Of the fish released below the dam (n = 46), 84.8% (n = 39) moved the 0.9 km back to the dam during the initial migration phase, and 15.4% (n = 6) migrated beyond it. Tagged lamprey released above the dam distributed themselves widely in the upstream environment in both years as did those that successfully passed the dam in 2010 (Figure 2.6). Although untagged adult Pacific lamprey have been observed and captured just downstream of Soda Springs Dam at river km 113 on the mainstem North Umpqua River, none of the tagged lamprey from this study traveled that far. All of the tagged lamprey appeared to remain solely in the North Umpqua River, and even during the final migration phase, none were detected moving into tributary streams.

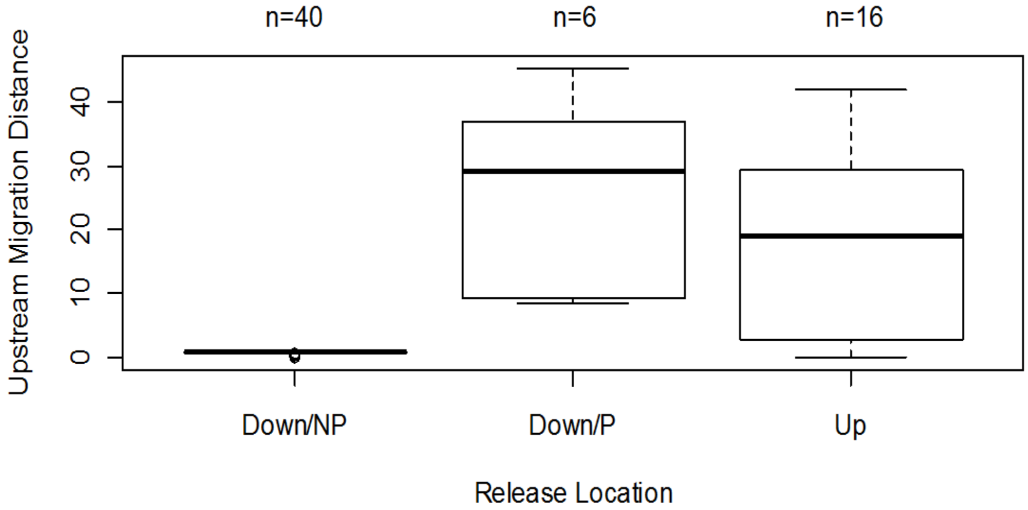

Figure 2.6. Boxplots displaying the total upstream migration distance traveled by tagged lamprey in 2009 and 2010 by the end of the initial migration phase. The tagged lamprey were separated into three categories: 1) released below Winchester Dam and did not subsequently pass the dam (Down/NP), 2) released below Winchester Dam and subsequently passed the dam (Down/P) and 3) released above Winchester Dam. Zero km is the release location.

There was also a considerable variation in the maximum upstream migration distance depending on the migration timing of the individual tagged lamprey within the run (Figure 2.7). Overall, the early run fish traveled farther compared to the middle and late run fish (W=199, p-value=0.0146), and this difference in migration distance was most significant for the downstream release group (W=308.5, p-value=0.0022). The early run group had the highest passage efficiency (33%), followed by the middle run (12%) and late run (0%) groups.

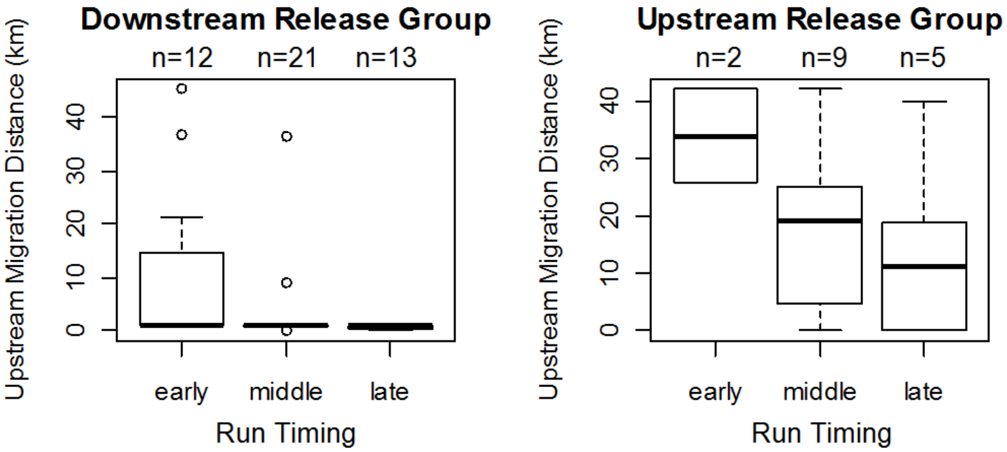

Figure 2.7. Boxplots displaying the total upstream migration distance traveled by the tagged lamprey in 2009 and 2010 by the end of the initial migration season according to the migration timing of the individual fish within the run. Downstream release and upstream release groups were examined separately. Zero km is the release location.

In 2010, we had the opportunity to examine the effects of using smaller sized radio tags on the lamprey migration behavior. Although the difference was only suggestive due to the small sample size for the smaller tag category, we observed an incremental decline in the average upstream migration distance travelled by the lamprey with medium and large tags was (W=175, p-value=0.0855) (Figure 2.8). However, tag size effects were not observed for the upstream release group. Lamprey with smaller tags had the highest passage efficiency (33%), followed by lamprey with the medium (18%) and large (6%) tags.

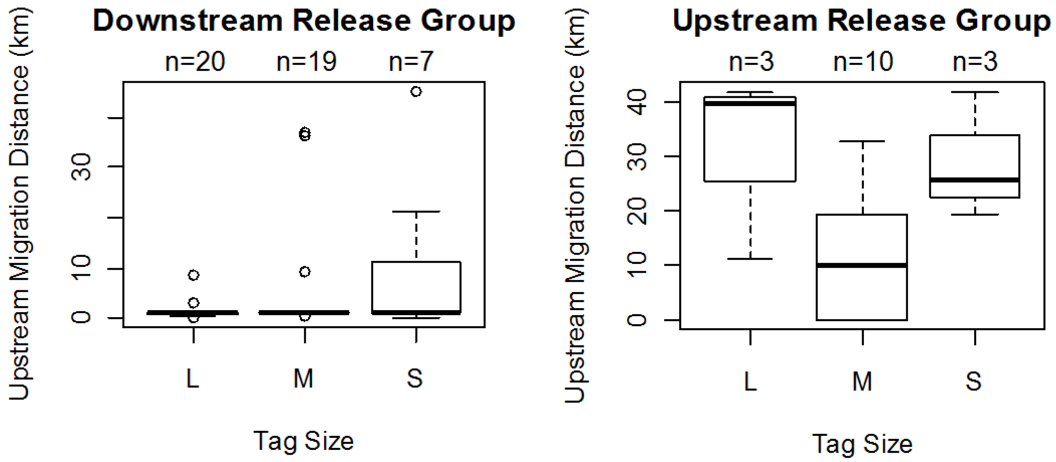

Figure 2.8. Total upstream migration distance traveled by the end of the initial migration season by individual lamprey tagged with large (L), medium (M), and small (S) transmitters. Downstream release and upstream release groups were examined separately. Zero km is the release location.

Because the size of tag surgically implanted into each individual lamprey were determined based on the lamprey girth size, the size categories of tags (large, medium, and small) also reflected the lamprey size categories. Therefore, it is unclear whether the tag size or the lamprey body size influenced upstream migration. The effect of tag/lamprey cross-sectional area ratio on the upstream migration distance of individual tagged lamprey was analyzed, and we found a strong negative correlation (r = -0.353, df = 60, t = -2.93, p-value = 0.0024; Figure 2.9). The correlation between lamprey size (girth) and the upstream migration distance, on the other hand, was not significant (r = -0.099, df = 60, t = -0.77, p-value = 0.4445), suggesting that the relative tag size, rather than the lamprey body size, played a significant role in influencing their upstream migration. Furthermore, among the lamprey released below Winchester Dam, the mean tag/lamprey cross-sectional area ratio of lamprey that passed the dam was consistently lower than that of lamprey that only approached the dam (7.0% and 7.4% for large tags, 6.1% and 6.7% for medium tags, and 4.4% and 4.9% for small tags, respectively).

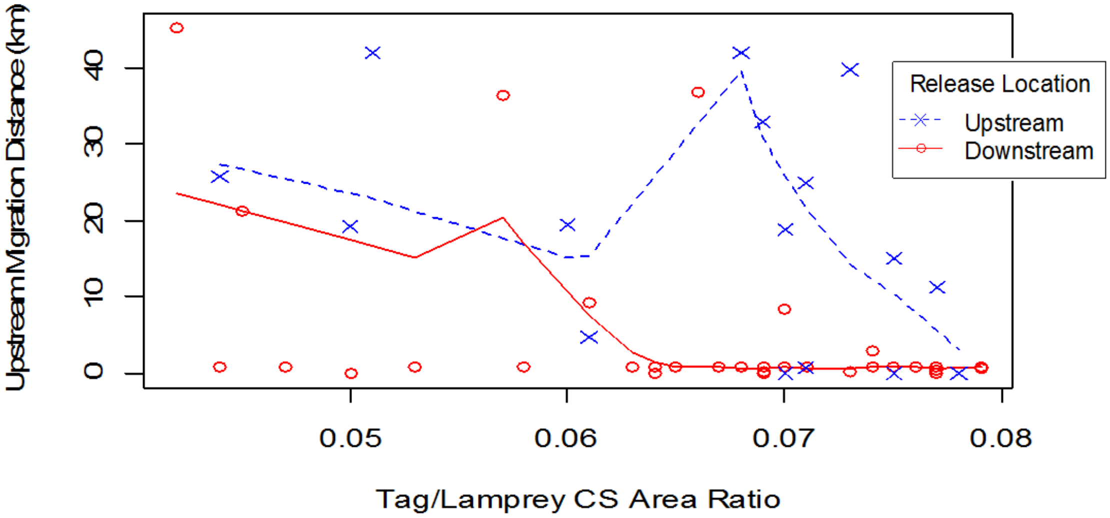

Figure 2.9. Scatter plot of the total upstream migration distance traveled by individual lamprey by the end of the initial migration season vs. the tag/lamprey cross-sectional (cs) area ratio (tag cs area divided by lamprey cs area). Lowess smoothing lines are drawn separately for the upstream and downstream release groups.

The total upstream migration distance was not significantly different between male and female lamprey (df = 41, t = 0.4569, p-value = 0.6502). However, 31% of the tagged lamprey's sex was unidentifiable.

Population Estimate

Of the six lamprey that passed Winchester Dam, none appeared to use the fish ladder. If this is representative of the entire population, then the fish ladder counts of Pacific lamprey would need to be multiplied by at least a factor of seven (based on lack of passage with six lamprey) to provide an estimate of the actual population size above the dam. Furthermore, if we use 18.5% as our estimated dam passage efficiency (from 2010 results), the estimated number of adult Pacific lamprey below the dam is projected to be approximately 38 times higher than the number suggested by the fish ladder counts.

The number of adult Pacific lamprey below Winchester Dam was estimated from mark-recapture data. The recapture rate was 2.56% (1 out of 39 returning tagged lamprey was recaptured). Assuming a binomial distribution, the 95% confidence interval is estimated to be between 0.51% and 12.91%. These statistics place the lamprey population estimate below Winchester Dam at 5,109 (95% C.I. [1015, 25727]) in 2009 and 3,003 (95% C.I. [596, 15122]) in 2010. Using our estimated dam passage efficiency of 18.5%, the number of Pacific lamprey upstream of the dam is estimated to be 960 (95% C.I. [188, 4760]) in 2009 and 556 (95% C.I. [110, 2798]) in 2010.

Discussion

Lamprey Run Timing

The majority of the lamprey were captured between the months of June and July, which coincides with the general timing for high and rising water temperatures and low and decreasing discharge levels. If lamprey rely on either of these two variables as physiological cues for upstream migration activity, as suggested by Keefer et al. (2009), the slightly delayed run in 2010 may be a result of the lower water temperature and higher discharge level experienced during the early summer in 2010 compared to 2009. The mean daily water temperature in June was 17.9 C° in 2009 compared to 15.8 C° in 2010, and the mean discharge in June was 57.5 m^3/s in 2009 compared to 144.6 m^3/s in 2010.

Spawning activities immediately downstream of Winchester dam were also observed much later in 2010 compared to 2009; several lamprey were observed spawning on May 28 in 2009, whereas spawning was not detected until mid-June in 2010. The synchronized shifting as well as the slight temporal overlap in the run timing of the initial migration and the final migration from the previous year's cohort is an interesting phenomenon, leading us to speculate that pheromones from the spawned out lamprey could also be acting as migration cues for the new migrants. Robinson et al. (2009) confirmed that adult Pacific lamprey are indeed capable of sensing two types of unique lamprey bile acids [a component of the migratory pheromone and sex pheromone for sea lamprey (*Petromyzon marinus*)] during the vast majority of their yearlong spawning migration. Fine and Sorensen (2010) recently reported that larval lamprey are capable of emitting this migratory pheromone in discernible quantities to guide the newly arriving adult lamprey, but spawned-out lamprey could also potentially contribute olfactory cues.

Dam Passage

Compared to the passage efficiency at other mainstem dams in the northwestern USA (50~80%) (Moser et al. 2002b; Cummings 2007), the rates of passage at Winchester Dam (8.3% in 2009 and 18.5% in 2010) were low. This low passage efficiency, however, may be related to other endogenous and exogenous causes to lamprey besides the structural impact of the dam itself.

We discovered that the tag size appeared to play an essential part in their passage efficiency. Lamprey tagged with the smallest tags (1.1 g, 6x16 mm) displayed the highest passage rate (33.3%), followed by those lamprey with the medium tags (2.2 g, 8x22 mm) and large tags (4.3 g, 9x30 mm) (17.6% and 6.7% respectively). In addition, there was a strong negative correlation between the tag/lamprey area ratio and their upstream migration distance. Close et al. (2003) demonstrated that Pacific lamprey implanted with tags up to 7.4 g (or 2.5% body weight) showed minimal short-term and virtually no long-term negative effects based on swimming performance and physiological effects. Although the tag/lamprey weight ratio remained low in our study (< 1.2% body weight), it is possible that the cross-sectional area of the larger tags within the visceral cavity may have negatively affected lamprey's passage success as reported by Moser et al. (2007).

Migration timing of individual fish within the run also had a large impact on passage efficiency in both years. The passage efficiency was highest in the early run (33.3%), followed by the middle run (11.8%); none of the lamprey in the late run passed the dam. Moreover, all of the tagged lamprey in the early run group successfully returned back to the dam, whereas 14.3% of the middle run group and 23.1% of the late run group never returned to the dam after their release.

The biological mechanism behind the effects of the migration timing on dam passage is unknown. We hypothesize that warm water experienced later during the initial migration phase may have affected lamprey movement. The maximum upstream migration distance traveled by the tagged lamprey in 2010 was strongly inversely correlated with the mean water temperature experienced on the release date ($r = -0.454$, $df = 43$, p-value = 0.0009). Our results also indicated that the mean water temperature during the release date was significantly lower for the early run group (mean = 17.4 ± 0.5 C°) compared to the middle (mean = 22.0 ± 0.1 C°) and late run (mean = 22.0 ± 0.2 C°) groups in both years (± represents standard error). Therefore, high water temperatures (> 22 C°) experienced later in the summer may have significantly impacted the swimming performance by lamprey.

Meeuwig et al. (2005) indicated that Pacific lamprey larvae reared in 22 C° water had the lowest rates of survival and growth compared to those reared in 10-18 C° water. Moreover, the proportion of larvae born with abnormalities was highest for larvae reared in 22 C° water. Although 22 C° water appears to be physiologically stressful for lamprey, as many as 42% of the captured lamprey in this study were trapped when the daily mean water temperature was over 22 C°, indicating that a large portion of the lamprey run continued to move upstream to approach the dam during this warmer period. We speculate that lamprey may be moving upstream in search of cooler water to evade the rising water temperature. The thermal conditions that larval lamprey experience are directly tied to the thermal conditions in which the adults spawn. Larval lamprey are considered weak swimmers that generally cannot migrate a substantial distance upstream to seek thermal refuges, so they will likely be exposed to thermal conditions that are as warm or warmer than what the adults experience at the spawning grounds in late spring / early summer.

Although water temperature on the release date was strongly inversely correlated with the discharge level ($r = -0.850$, $df = 60$, $p\text{-value} < 0.0001$), we focused our analysis on the temperature conditions because low discharge is unlikely to impose any type of physiological stress to the lamprey. For instance, if the low level of discharge (most lamprey moved upstream during this condition) were physiologically stressful to lamprey, they would be motivated to migrate downstream instead of upstream, but that is contrary to the trend we observed in this study. On the other hand, lamprey exposed to high temperature conditions could easily avert these conditions by migrating upstream to access the generally, colder upper river conditions.

Despite the negative impacts associated with the temperature and relative tag size, tagged lamprey released above the dam displayed significantly longer upstream migrations compared to the downstream release group. Therefore, we suspect that there were synergistic effects from multiple factors, such as the passage obstacle, water temperature, and relative tag size, which jointly influenced the passage efficiency and upstream migration of the tagged lamprey. For instance, the impact of tag size in the early run lamprey was completely absent, but in the middle run lamprey, incremental negative impacts of tag size were observed. However, for the late run lamprey, we suspect that the impact of tag size was indiscernible because the migration was already suppressed due to late run timing. Similarly, the migration timing within the run influenced both upstream and downstream release groups, but the impact appeared to be much more pronounced for the downstream release group compared to the upstream release group (Figure 2.6). We also observed differential threshold levels for the tag/lamprey cross-sectional area ratio depending on their release location (0.06 for downstream release and 0.075 for upstream release; Figure 2.8), suggesting that the effect of relative tag size is greater for fish that must navigate the dam.

Johnson (1994) indicated that the maximum yearly water temperature at Winchester Dam has increased significantly between the years of 1946 and 1993, equating to a 0.53 C° increase in temperature every 10 years based on the positive linear trend line (r = 0.46, p-value = 0.001). More importantly, the July and August maximum monthly water temperatures, during which many Pacific lamprey actively migrate upstream, exhibit an even stronger warming trend from 1946 to 1968, equating to a 0.75 C° increase in temperature every 10 years based on the positive linear trend lines (r =

0.60, p-value = 0.0008 and r = 0.75, p-value = 0.00004, respectively). This could easily cause physiological difficulties if Pacific lamprey are evolutionarily adapted to making the upstream migration during these particular summer months. For example, Pacific lamprey may rely partially on photoperiod length as clues for upstream migration. Although the longest photoperiod is always on summer solstice around 21 June every year, the water temperature during this time period has been increasing significantly, potentially placing the lamprey in an environment outside of their optimal temperature range (Meeuwig et al. 2005).

Although Pacific lamprey may be able to adjust their run timing based on temperature , the seasonal window that the water temperature stays between 15 C and 21 C (preferred temperature range illustrated by Keefer et al. 2009) during the spring/summer season can be extremely short at Winchester Dam (42 days in 2009 and only 19 days in 2010). Thus, the warming trend in the past half century at Winchester Dam may have negatively impacted the dam passage of Pacific lamprey, and if this warming trends continue through global climate change or other means, this could further hinder dam passage and upstream migration.

Reservoir water above Winchester Dam was drained in 2009 during the low flow period in early September to repair and fill enlarged holes on the face of the dam. During the very first day of dewatering, over 250 adult lamprey were observed retreating from inside one of these enlarged openings. From the second and third day of the operation, 160 more adult lamprey were captured from the lower fish ladder and bedrock spaces below the dam. These observations confirmed the fact that many of the untagged lamprey also halted their migration at the base of the dam. The fact that such a large number of adult lamprey held at the dam towards the end of the initial migration period points to the possibility that some lamprey may be deliberately using the dam as overwintering holding habitat and are less motivated to pass the dam (see Chapter 3).

Population Estimate

Our research showed that the count data at Winchester Dam underestimated the Pacific lamprey numbers that actually migrated past the dam by at least a factor of seven. Population estimates of adult lamprey upstream of Winchester Dam using mark-recapture also indicated that lamprey abundance (556 in 2009 and 960 in 2010) was much higher than the fish counts reported at the ladder (26 in 2009 and 31 in 2010). The adjusted numbers, however, were still considerably low when compared to the historical count data from the late 1960s and early 1970s (14,532~46,785). Moreover, these calculations were made with the assumption that capturing and marking did not affect the probability of recapture. The estimates will be lower if any of the tagged lamprey become wary or shy of the trapping efforts after their first capture. Furthermore, the extent to which lamprey used alternate routes in the late 1960s and early 1970s is completely unknown, and the lamprey numbers in this period could have been even higher than what the fish count records indicate, if some of them were also using alternate routes.

Conclusion

While the impacts from Winchester Dam in association with the rising temperature may have played a sizeable role in the decline of the Pacific lamprey above the dam, a variety of other potential causes could also be partially or totally responsible for their decline, including poor water quality, dewatering activities during low flow conditions, invasive predators (e.g. smallmouth bass and striped bass), stream and floodplain degradation, reduction in estuarine habitat, and ocean conditions.

According to a U.S. Geological Survey report on water quality and algal conditions in North Umpqua Basin by Anderson and Carpenter (1998), the impacts of the hydroloelectric projects in the upper reaches coupled with the effects of basin-wide forestry have “induced a fundamental shift in the river’s food web, from a detritus-based system to a system with a higher emphasis on algal production” (pp 1-2). For Pacific lamprey larvae that depend on organic detritus as their primary food source (Sutton and Bowen 1994; Graham and Brun 2006), this fundamental shift in the food web may be detrimental to the juvenile survival. The increase in smallmouth bass (*Micropterus dolomieu*) populations in the 1970s (Simon and Markle 1999) may also have played a large role in the lamprey juvenile survival as well. It is unlikely that only one of these factors is solely responsible for the decline of the local Pacific lamprey numbers and future conservation efforts will need to evaluate these numerous threats and their synergistic effects on the completion of their life cycle to achieve effective population recovery.

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CHAPTER 3: SPATIOTEMPORAL MOVEMENT AND BEHAVIORAL THERMOREGULATION IN ADULT PACIFIC LAMPREY AT WINCHESTER DAM IN THE NORTH UMPQUA RIVER, OREGON, USA

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Abstract

Seasonal movement patterns of adult Pacific lamprey, *Entosphenus tridentatus*, at Winchester Dam on the North Umpqua River were examined using radio telemetry in 2009 and 2010. Passage efficiency was low in both years (8% and 19%, respectively), and most tagged lamprey that did not pass the dam (63% and 67%, respectively) remained and held at the base of the dam at the end of their summer migration. Types of habitat most frequently used by lamprey downstream of the dam included the dam surface, interface zones between fast and slow water, and highway bridge pilings. The timber crib structural design of Winchester Dam offers unique interstitial spaces, and Pacific lamprey may be accessing these small openings not only for passage but also for holding habitat. Our study indicated that the movement behavior changed considerably between August and September, and the frequency of movements decreased sharply during this period. A general shift in the holding locations at the dam was also observed around this period; detections in the fish ladder decreased steadily since August, and lamprey using the dam surface increased and remained high throughout the winter season. Tagged lamprey were detected using coldwater thermal refuges immediately downstream of the dam that were 0.4 to 2.8 C° colder than the mean river temperature at the dam, and this temperature gap increased as the season progressed. After their display of heightened activity in the early to mid summer, we speculate that lamprey may be seeking overwintering habitat associated with hyporheic exchange flows at the dam towards the end of the summer season.

Introduction

Lampreys (*Petromyzontidae*), a family of jawless fish that represents one of the most ancient vertebrates, are well known for their slender, eel-like appearance, which sets them apart from most other species of true fish. Using their jawless mouth that functions like a suction cup, some anadromous lampreys can climb steep surfaces that are impassable to other fish species (Kemp et al. 2009; Clemens et al. 2010). Pacific lamprey (*Entosphenus tridentatus*), a native anadromous species distributed in rivers and streams along the Pacific Rim from Baja California, Mexico, to eastern Honshu Island, Japan (Ruiz-Campos and Gonzalez-Guzman 1996, Yamazaki et al. 2005), uses their superior climbing abilities to surmount > 1.7 m wetted, vertical surfaces as well as 12 m high natural waterfalls (Clemens et al. 2010). Despite their large body size (~65cm), adult Pacific lamprey are also capable of squeezing through small openings the size of 2.2 cm (Moser et al. 2008).

Winchester Dam on the North Umpqua River (Oregon, USA), originally built in 1890, is a 5 m high dam constructed from rock-filled timber cribs. Because the dam surface is not watertight, lamprey are potentially capable of circumventing the counting stations by passing through the small openings in the dam surface. There are also picketed leads and diffuser gratings that have 2.5 cm or larger gaps inside the fish ladder. Passage may not be the only reason that lamprey would use these types of small openings. For Pacific lamprey that hold for an extensive period during the winter (approximately 6 months) (Clemens et al. 2010; Robinson and Bayer 2005), these small openings may provide ideal overwintering habitat that protect them from potential predators.

In this study, the seasonal movements of adult Pacific lamprey released below the dam were monitored extensively using radio telemetry in 2009 and 2010. Because of the unique, interstitial spaces available at Winchester Dam inside the timber cribs and bedrock/boulder surfaces immediately below the dam, we assessed their use of these spaces for temporal holding and potential long-term overwintering. In particular, we assessed the time they spend holding and repositioning in the various sections of the dam. We evaluated the multitude of behaviors expressed by adult Pacific lamprey at the dam and used this information to assess whether the adults are approaching the dam mainly to move further upstream in the river or to take advantage of the holding habitat made available by the dam.

Lautz et al. (2010) and Sawyer et al. (2009) suggested that geomorphic features, such as log dams and beaver dams, could greatly enhance hyporheic exchange because of the prominent shifts in lateral and vertical hydraulic gradient. Hyporheic exchange flow can greatly influence the temperature regimes of the surface flow and often buffers the temperature by storing and releasing heat over a range of time scales (Burkholder et al. 2008). In essence, it tends to reduce the temperature extremes and lowers temperature when the surface flow is warm and raises temperature when the surface flow is cold. To evaluate whether lamprey are keying into this type of hyporheic exchange flow at Winchester Dam, temperature sensor tags that monitor the internal fish temperature were deployed in 2010. The hourly body temperatures of the lamprey were compared with the hourly mean river temperatures to assess whether the tagged lamprey displayed behavioral thermoregulation that may be tied to the local hyporheic exchange flow.

Methods

Study Area

The study was conducted at Winchester Dam, which is located at river km 11.2 on the North Umpqua River in southwest Oregon. Water discharge at the dam typically ranges from 30 m^3/s during the summer low flow period (July-September) to 180 m^3/s during the winter-spring high flow period (December-February), with an average annual flow of 105 m^3/s. Anadromous species, including Pacific salmonids (*Oncorhynchus*spp.) and Pacific lamprey, migrate roughly 190 km from the ocean along the Umpqua River to reach Winchester Dam on the North Umpqua River.

The North Umpqua River originates from Maidu Lake at an elevation of 1,824 m on the western slope of central Cascade Mountains and joins the South Umpqua River northwest of Roseburg, Oregon, at an elevation of 110 m. Over 20% of the subbasin lies above 1,700 m elevation, which supplies strong, cool flows from the snowmelt runoff that last through the summer. Furthermore, the flow is augmented by large-volume groundwater systems stemming from the upper reaches (Wallick et al. 2010).

Sampling and Tagging

In 2009 and 2010, returning adult Pacific lamprey were collected from May–September during their upstream migration at Winchester Dam (collection started in March, but none were captured until May). Adults were captured either inside the fish ladder (74%) or immediately downstream of the dam (26%), using dip nets, an assortment of traps, or by hand. Traps were designed to capture adult Pacific lamprey of all sizes. For more details on lamprey capture methodology, see Appendix A.

Captured lamprey were handled immediately or held in a flow-through container (30 – 70 L) in the river for 2 – 48 hours before surgically implanting radio tags. Lamprey were individually anesthetized with MS-222, measured, and surgically implanted with radio transmitter tags following the surgical techniques described by Moser et al. (2002a) and the training and practice provided by lamprey telemetry experts. For more details on tag implantation, see Chapter 2.

Dorsal fin interval (interval between first and second dorsal fins) was measured in both years to gauge the level of sexual maturity as suggested by Clemens et al. (2009). Sex was identified during tag implementation for 52.9 % of the fish in 2009 and 77.8 % of the fish in 2010. Females made up 66.7 % and 61.8 % of the sample, respectively. The identification of female fish was easier than male fish because their gonads occupy a much larger space within the body cavity even at the early maturation stage. Hence, a larger portion of the fish for which we were not able to identify sex could have been male fish. To account for the biological diversity expressed by the wide variety of lamprey coloration, the color of the fish on the ventral surface was classified into four categories: "black," "gold/silver, light spottings," "gold/silver, heavy spottings," and "white." Ventral firmness (soft, firm) and genital papilla size (large, medium, small) were also documented at this time.

To ensure that the tags represented less than 8% of the fish’s cross-sectional area, only lamprey that met the minimum mid-girth criteria of 102 mm were surgically implanted with the Lotek NTC-6-2 nano tags (4.3 g, 9x30 mm) in 2009. Pacific lamprey captured at Winchester Dam on the North Umpqua River were significantly smaller in length, weight, and girth compared to those captured at Bonneville Dam on the Columbia River (mean percentage difference of 16.5%, 43.5%, and 15.3%, respectively, from the 2009 capture data; data for Pacific lamprey measurements from the Columbia River were provided by M. Moser, NOAA Fisheries). As a result, we employed two types of smaller tags in 2010: Lotek NTC-3-2 nano tags (1.1 g, 6x16 mm) and MST-820T temperature sensor tags (2.2 g, 8x22 mm). These smaller tags enabled us to include smaller lamprey in the sample to better represent the overall run. The minimum girth threshold was reduced to 73 mm and 90 mm, respectively, for these two smaller tags, using the same 8% area ratio criterion. All of the tagged lamprey had a tag/lamprey weight ratio lower than 1.2%. All tagged lamprey were released in slow water to minimize post-release stress, and timing of release was primarily during the day around noon.

Radio Tags and Monitoring of Location

The objective in both years was to tag individuals throughout the run. The peak of the run has been observed primarily between June and July based on the previous 10 years (1999-2008) of records of lamprey run timing at the fish ladder. In 2009 and 2010, 15 and 31 radio-tagged lamprey were released 0.9 km downstream of Winchester Dam, respectively. Seven additional lamprey, captured during a two-week-long reservoir water dewatering event for dam maintenance on 1 September, 2009, were also radio-tagged; 4 were released immediately upstream of the dam in the dewatered reservoir water, and the remaining 3 were released immediately downstream of the dam. Among the 31 tagged lamprey in 2010, 5 were implanted with large tags (NTC-6-2), 19 with medium tags (MST-820T), and 7 with small tags (NTC-3-2).

Radio-tagged lamprey were tracked using manual tracking and fixed sites. Manual tracking involved mainly vehicle tracking using the extensive road networks in the basin, but when the tagged lamprey were detected, more precise locations (< 15 m) were found by on-foot mobile tracking using triangulation when feasible. All fixed sites had a minimum of two aerial antennas to detect both lamprey presence and direction of movement.

To detect the specific lamprey locations and migration routes at Winchester Dam, we set up a receiver station on each side of the river (Figure 3.1). The station on the north bank was comprised of one aerial antenna for general detection (represented by I in Figure 3.1) and a minimum of three underwater antennas covering the fish ladder for more precise detection (represented by 1-3 and a-c in Figure 3.1; a-c were only used in 2009). The station on the south bank had two aerial antennas, which were located 40 m downstream and upstream of the dam for general detection (represented by II and III in Figure 3.1, respectively). Detection distances of antennas were confirmed by tests with active radio tags in water. Tagged lamprey within 100-150 m from the dam (both upstream and downstream) were generally detected by these two stations. In 2010, two additional fixed sites were set up downstream (river km 10.6) and upstream (river km 33.2) of the dam starting in September to detect small-scale movements including fallbacks.

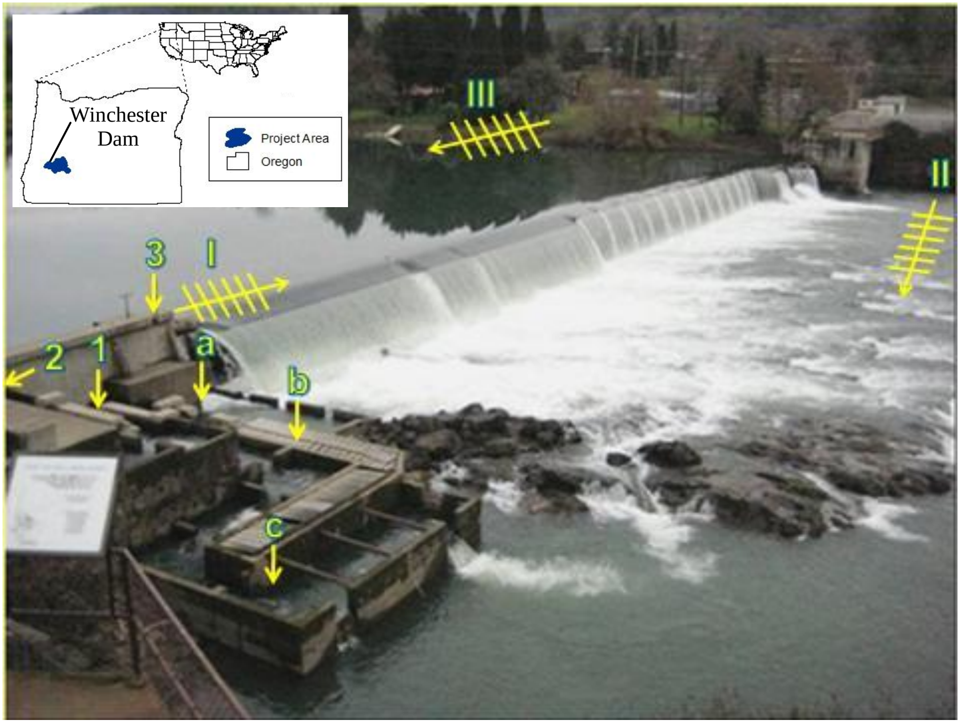

Figure 3.1. Photo of Winchester Dam with an embedded location map of the North Umpqua River basin in Oregon. The locations of the three aerial antennas are shown by the crossed arrow symbols and labeled as I, II, and III. The underwater antenna locations are exhibited by the straight arrows and labeled as 1, 2, 3, a, b, and c. The width of the channel (the waterfall portion) is approximately 125 m.

Data Analysis

All recorded lamprey locations from manual tracking and fixed sites were entered into and processed in ArcGIS 10 and Google Earth 6. After cross examinations with the fixed site data, each lamprey location was given a start and an end date, from which the duration of stay (in days) for each location was calculated. Statistical analyses were performed using R statistical software (R Development Core Team 2011). Variables were analyzed for normality of distribution using normal probability plots and Shapiro-Wilk normality test. Variables with normal distributions were analyzed using means, and a two-sample t-test was conducted for any comparisons. Variables with skewed distributions were analyzed using medians, and a Wilcoxon two-sample test was conducted for comparison. A significance level of p-value = 0.05 was used for all statistical analyses performed in this study.

Seasonal Movement

The temporal and spatial use of Winchester Dam was evaluated using a combination of data from manual tracking and fixed sites. Evidence suggests that there are three distinct phases in the Pacific lamprey spawning migration (Beamish 1980; Robinson and Bayer 2005; Clemens et al. 2010). The summer/fall season (May-October) is generally characterized by active upstream migration. The winter season (November-February) is a period of prolonged holding and metabolic depression . The spring season (March-July of the second year) is characterized by the enhanced level of activity associated with the final migration and movement to spawning habitat. To account for the distinct temporal patterns in the use of the dam, we categorized the data into these three phases and analyzed them separately. Tags from 2009 and 2010 were included in the summer/fall season analysis. Only tags from 2009 were included in the analysis for the winter/spring season.

Because evidence suggest that adult Pacific lamprey are predominantly nocturnal (Moser 2002a; Robinson and Bayer 2005), we analyzed lamprey behavior in both daytime (7:00~19:00) and nighttime (19:00~7:00) settings. Manual tracking was conducted during the daytime, so locations identified in this process represented the "daytime" locations of lamprey. Manual tracking data that described the specific geographic locations of individuals at the dam were evaluated to identify the spatial, temporal trends in daytime use. We partitioned the dam into five sections (fish ladder, dam surface, southeast bank, bedrock riffle, and side channel) to summarize the daytime holding habitat. We used the spatial join feature in ArcGIS 10 to link the lamprey location data and the five partitioned areas.

Many of the tagged lamprey displayed diel behavior, repeatedly entering and exiting out of the dam detection zone during the crepuscular period. Using fixed station data, we identified the general location of these approaches and withdrawals for each of the radio-tagged lamprey and categorized them as either "fish ladder," "dam surface," or "southeast bank." We examined the trends associated with the entry and exit locations as well as the daily timing (hour of the day), duration, and interval of each entry and exit. Underwater antenna detections of lamprey from the fish ladder side were also evaluated to describe the more specific locations of lamprey within the fish ladder side. Capture location data provided additional insights to supplement the results.

Behavioral Thermoregulation

Temperature sensor tags were implanted into 19 lamprey that were released 0.9 km downstream of the dam in 2010. The internal temperature of the tagged lamprey were monitored continuously once they migrated upstream and remained within the dam detection zone beginning on 9 July, 2010, until 28 October, 2010. Seventeen lamprey provided data for this analysis (two tagged lamprey never returned to the dam). The temperature sensor tags were programmed to shift into a reduced burst rate (1 burst per hour; originally 1 burst per 10 seconds) between late September and early October to extend battery life. As a result, the number of temperature readings was considerably less for the month of October compared to the earlier months; only 1.7% of the mean monthly readings for July through September were detected in October.

We used hourly river water temperature data provided by the Winchester Water Treatment Plant (City of Roseburg) located 35 m downstream of Winchester Dam to compare with the hourly body temperature of the lamprey. The temperature of water withdrawn from this deep, swift segment of the river at a depth of 3.7 m was used to represent the river water temperature immediately below the dam. Temperature readings by the temperature sensor tags were monitored prior to release for quality control to ensure that the readings were accurate and reliable. Absolute temperature differences among lamprey body temperatures and river temperature as well as patterns in temperature fluctuations were monitored to evaluate the presence or absence of behavioral thermoregulation and the potential use of hyporheic exchange flows.

Results

Lamprey Sampling

We captured and measured 219 adult Pacific lamprey in 2009 and 77 in 2010. An additional 88 adults from 2009 were captured in late summer during a two-week long reservoir dewatering event for dam maintenance. Among these 88 adults, 27 were selectively measured on 1 September, 2010 (i.e. only large ones were measured). As a result, these 27 lamprey were not included in the summary calculations in Table 3.1 because they do not adequately represent the overall run. One sexually mature fish was captured on 12 May, 2010, which had the shortest body length (420 mm) and dorsal fin interval (0 mm), and the highest condition factor (0.407) among all the sampled lamprey from both years. All other captured lamprey displayed no signs of sexual maturity (e.g. small dorsal fin interval, stunted body length, pseudo-anal fin, distended abdomen) and appeared to be in their initial migration phase.

Table 3.1. Summary of the morphology data for the tagged lamprey and overall sample in 2009 and 2010. Lamprey captured on 1 September, 2009, are excluded from this summary data because of the size-selective nature in which we chose the lamprey we measured (only large lamprey were measured).

	Overall Sample (N=192)					Tagged Lamprey (N=24)				
2009	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)
Mean	549.3	279.3	0.167	91.5	18.0	602.8	384.0	0.176	104.7	21.0
Standard Error	2.7	4.3	0.001	0.6	0.4	3.4	3.6	0.002	0.5	0.9
Minimum	444	131	0.125	66	3	574	356	0.154	102	14
Maximum	644	455	0.210	113	33	644	436	0.203	113	33

	Overall Sample (N=77)					Tagged Lamprey (N=45)				
2010	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)	Length (mm)	Weight (g)	Condition Factor (g/mm^3)	Mid-Girth (mm)	Dorsal Gap (mm)
Mean	565.7	301.6	0.167	93.7	18.0	579.1	323.7	0.166	96.3	18.6
Standard Error	5.1	7.4	0.004	1.0	0.6	5.4	8.5	0.002	1.1	0.7
Minimum	415	202	0.132	79	0	511	228	0.133	83	8
Maximum	643	464	0.407	112	27	643	464	0.202	112	27

The proportions of the four categories of ventral surface lamprey color were very similar for the overall sample in 2009 and 2010 as well as for the 2010 tagged lamprey (df = 1, x-squred < 1.37, p-value > 0.242 with continuity correction). However, the tagged lamprey in 2009 had a significantly lower proportion of the black category (58% decrease; df = 1, x-squared = 7.01, p-value = 0.008 with continuity correction) and a higher proportion for the other three categories (33~71% increase) compared to the overall sample in 2009 (Figure 3.2). Because the tagged lamprey in 2009 were significantly larger in size compared to the overall sample, this suggests that the black lamprey may be smaller in size.

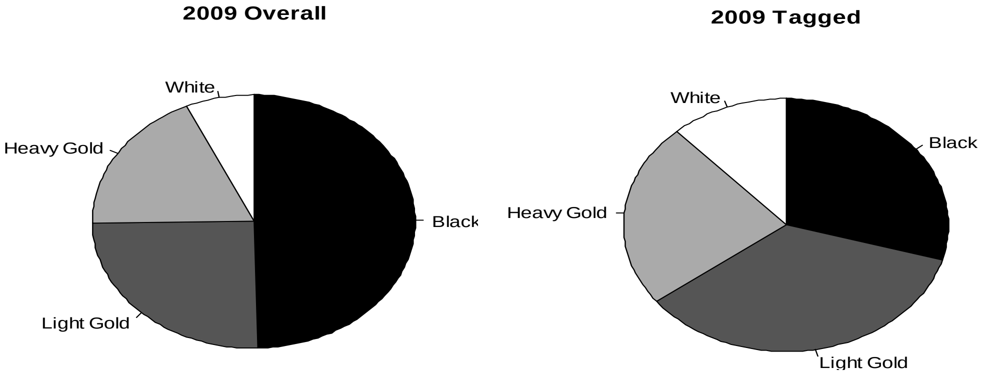

Figure 3.2. Proportion of colors in the lamprey ventral surface for the overall and tagged sample in 2009. [Heavy Gold = gold/silver heavy spottings, Light Gold = gold/silver light spottings]

Spatiotemporal Movement

The majority of the tagged lamprey released 0.9 km downstream of the dam returned to the dam (86.7% in 2009 and 87.1% in 2010). The median return time was 2.4 days in 2009 and 4.4 days in 2010. The passage efficiency for the tagged lamprey was low in both years (8.3% in 2009 and 18.5% in 2010). Those that passed earlier in June and July spent only 3-12 days at the dam prior to passage, whereas the two lamprey that passed later in August and September spent a considerably longer time at the dam (26 and 71 days, respectively). All passage events by the tagged lamprey were identified as passage over or through the dam wall, and none of them were detected passing through the fish ladder.

In both years, lamprey were detected more frequently and with a stronger signal (indication of range) during nighttime at the dam. The proportion of detections and the mean signal strength were higher particularly between 22:00 and 8:00 during the early and mid summer (Figure 3.3). This pattern was observed clearly between the months of June and August, but after September the stronger detections were observed predominantly during the morning hours (3:00 to 8:00). This indicated that at least some lamprey were displaying distinct, circadian movement behavior; during the daytime, these fish used holding locations that were not detectable by the fixed site at Winchester Dam. Although it is possible that some lamprey may have been moving to the dam at night and away from the dam during daylight hours, we suspect that most of them remained at the dam during daylight hours, but were hidden in places that were much harder to detect by the fixed station antennas. This was based on the fact that very few lamprey were detected downstream of the dam from manual tracking during the daylight hours.

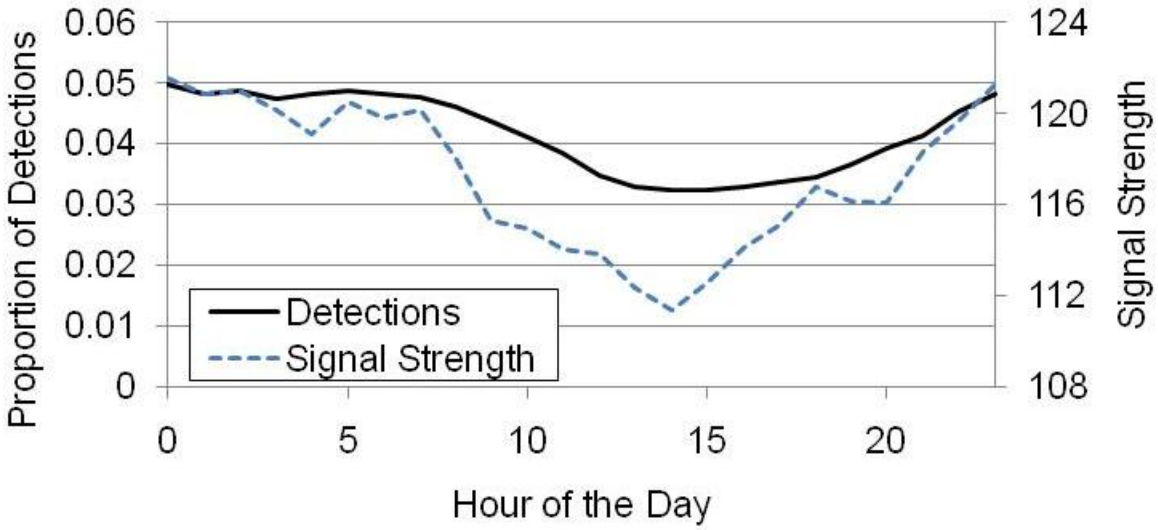

Figure 3.3. Proportion of lamprey detections and associated mean signal strength (indication of range) at Winchester Dam by the hour of the day between the months of June and August (n = 915947).

The spatial distribution of the daytime lamprey location at the dam was summarized for the summer/fall and winter/spring seasons using ArcGIS 10 (Figure 3.4). Types of habitat most frequently used by lamprey during the summer/fall season included the outside boundaries of the fish ladder, the southeast bank, interface zones between fast and slow water (eg. dam surface and bottom of the riffle), and highway bridge pilings. The locations were similar during the winter/spring season, but the boundaries of the fish ladder was used less compared to the summer/fall season. Spring spawning activity was observed near the side channel (E in Figure 3.5).

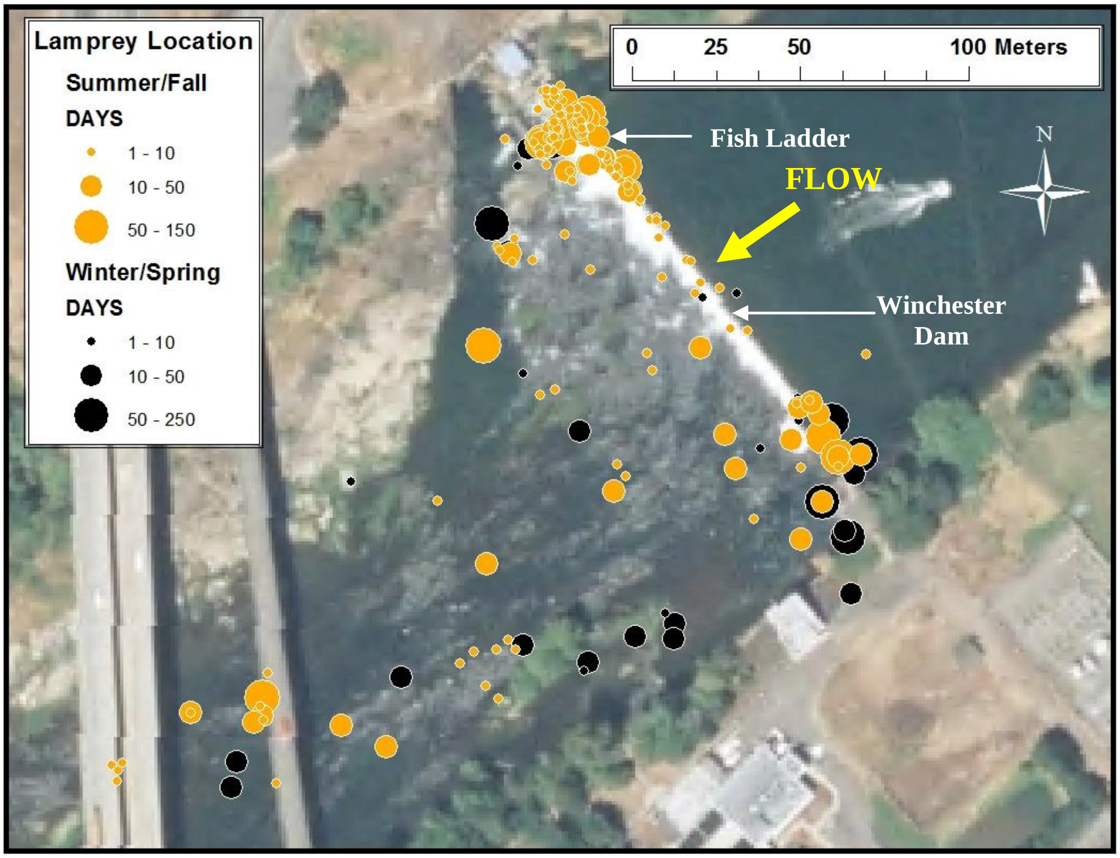

Figure 3.4. Locations of the tagged lamprey at Winchester Dam during the summer/fall season (2009 and 2010 data) and winter/spring season (2009 data). Each circle represents a specific detection location of a tagged lamprey and the number of days spent at each location is represented by the size of the circle.

The temporal shift in the spatial distribution was also analyzed using ArcGIS 10 (Figure 3.5). For the summer/fall season, we found that the fish ladder (A) and dam surface (B) had the highest use in the early season with a peak in August, but the magnitude of use decreased gradually thereafter. The use of southeast bank (C) increased only after September, suggesting that fish were migrating into this section during this period.

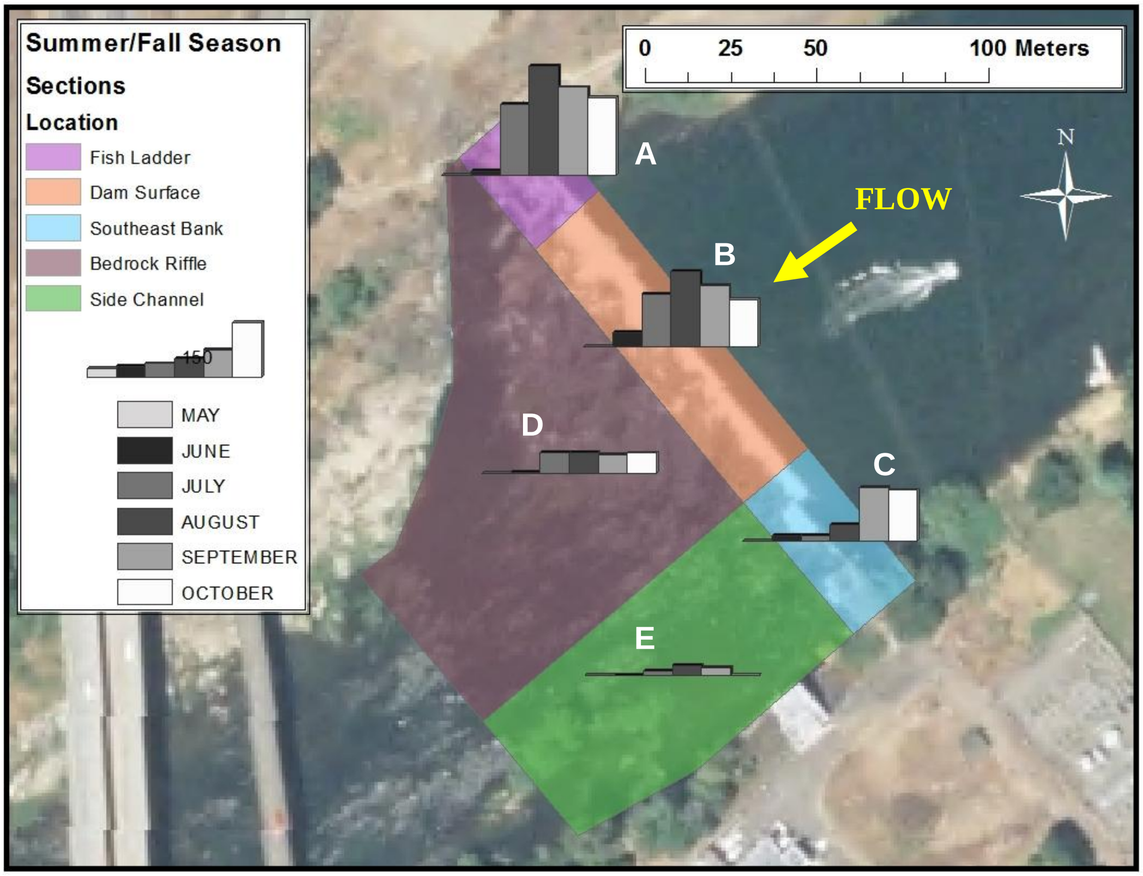

Figure 3.5. Spatiotemporal distribution of the tagged lamprey at Winchester Dam during the summer/fall season from 2009 and 2010 data. The total number of days spent by all tagged lamprey in each section are shown in the bar graph (A = fish ladder; B = dam surface; C = southeast bank; D = bedrock riffle; E = side channel). The reference bar graph inside the legend is included for size reference (the largest bar on the very right displays 150 days of lamprey residence).

During the winter/spring season, there were considerably fewer lamprey using the fish ladder side (A) and the dam surface (B) compared to the southeast bank (C) (Figure 3.6). There was a small peak in lamprey use at the fish ladder in March, and a separate peak for the bedrock riffle (D) in April. Although none of the tagged lamprey passed the dam during the second spring season, this small peak in the fish ladder may be an indication of their impetus to move past the dam. The use of the fish ladder and dam surface dramatically decreased by the end of April, whereas use of other sections persisted for one to two more months.

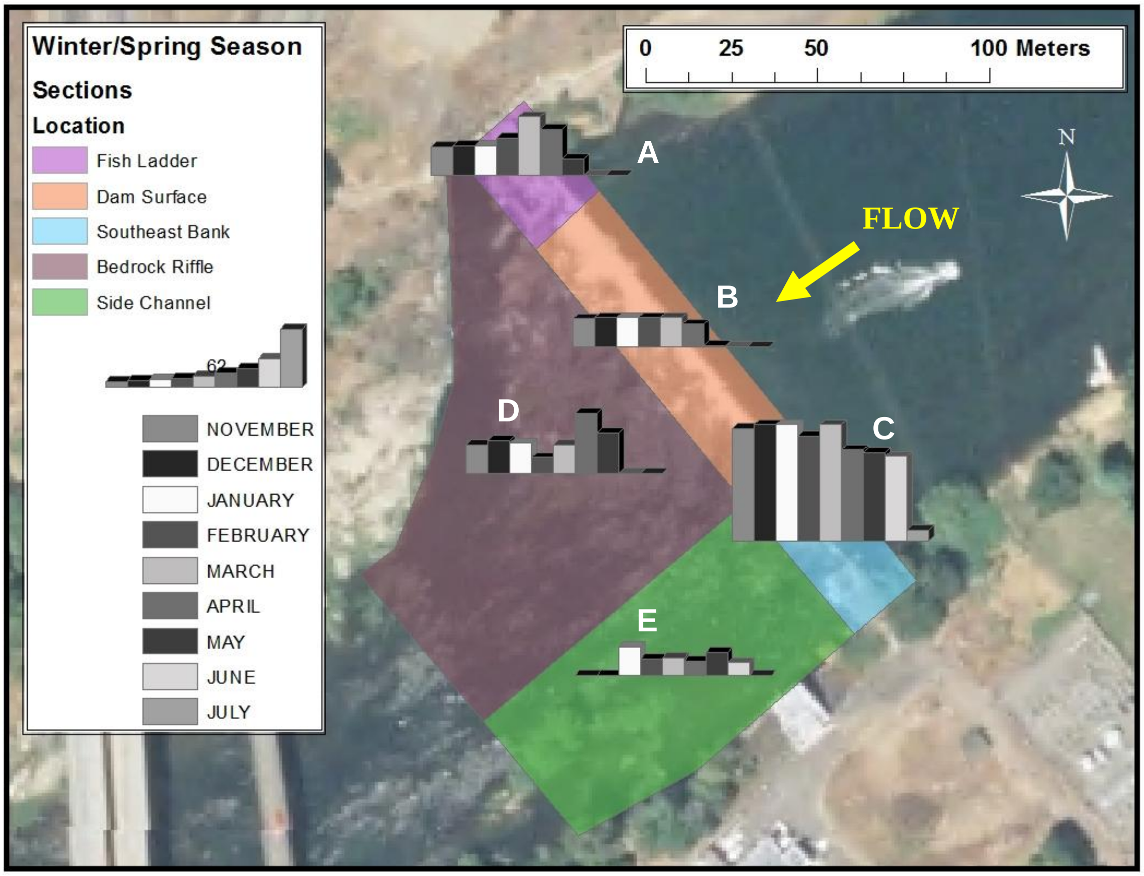

Figure 3.6. Spatiotemporal distribution of the tagged lamprey at Winchester Dam during the winter/spring season from 2009 data. The total number of days spent by all tagged lamprey in each section are shown in the bar graph (A = fish ladder; B = dam surface; C = southeast bank; D = bedrock riffle; E = side channel). The reference bar graph inside the legend is included for size reference (the largest bar on the very right displays 62 days of lamprey residence).

Using the detection and signal reading data from the two fixed receiver stations at the dam, we classified the approach locations of these fish into the following three sections: fish ladder, central area, and south bank (A, B, and C in Figure 3.5 and Figure 3.6, respectively). The central area was the most popular approach location for the first time returners in both 2009 (58%) and 2010 (85%); however, the majority of the tagged lamprey approached the dam from the fish ladder side for the approaches following the first approach in 2009 and 2010 (61% and 51%, respectively), and lamprey approaching the dam from the channel center decreased considerably thereafter (averaging 17% and 10%, respectively). During the winter/spring season, the approach locations shifted more towards the south bank side (76% and 63%, respectively) and only a small portion of the tagged lamprey approached the dam from the central area (1%).

There were also seasonal differences in the movement patterns. Tagged lamprey that only used one side of the dam during the summer/fall season were a minority in both 2009 and 2010 (25% and 15%, respectively). On the other hand, during the winter/spring season, a large portion of the tagged lamprey only used one side of the dam (57% and 44%, respectively). For each pair of entries and exits, we also determined how often the lamprey exited from a location that was different from its entry location. The rate of location change was relatively high during the summer/fall season (25% in 2009 and 26% in 2010), whereas during the winter and spring season, this rate was much lower (3% and 10%, respectively). These findings indicate that lamprey were not as active in exploring various areas within the dam during the winter/spring season (especially during winter) compared to the summer/fall season.

Many of the tagged lamprey released below the dam (33% in 2009 and 60% in 2010) spent over 50% of the initial migration phase at the dam. Out of the 11 tagged lamprey that approached the dam but failed to pass in 2009, 5 (45 %) ended up overwintering at the dam. We also discovered that most tagged lamprey repeatedly appeared and disappeared from the detection zone of many of the aerial and underwater antennas at the dam. During the summer/fall season, 67% and 70% of the lamprey returning to the dam made detectable movements across the sections (see Figure 3.5 for a delineation of the sections; typically >50 m distance) at least once every seven days in 2009 and 2010, respectively, based on fixed station data. During the winter season, none of them made detectable movements across the sections at that frequency (movement was detected only every 45-90 days).

On the fish ladder side, underwater antennas were set up in a variety of locations in 2009 and 2010 (Figure 3.1). Among the tagged lamprey that returned to the dam, 92% in 2009 and 96% in 2010 were detected by these antennas. Over 60% of the detections were from the timber crib section (3 in Figure 3.1) in both years, which lamprey most likely accessed from the lower fish ladder pool. In contrast to the other underwater antennas detections that peaked in July or August and decreased considerably thereafter, the detections from the timber crib section peaked in August, but had sustained detections through the end of October, indicating that lamprey used this area specifically for holding. In 2009, three additional underwater antennas were established in the lower and upper fish ladder (a, b, and c in Figure 3.1). Judging from the markedly higher number of detections at the south pool (a) (92% of all detections from a, b, and c), the majority of lamprey appeared to be accessing the fish ladder through this south entrance rather than the west entrance (c). Data from lamprey trapping also indicated that the majority of the lamprey (82%) were using the south entrance. Many of the early run lamprey (43%), however, were captured at the west entrance (b) when the flow level was comparatively high. Because the west entrance typically has a perched outflow, it is unknown how many of the lamprey that access the west entrance could actually pass there. Although there were some detections from inside the diffuser gratings (b) (5% of all detections from a, b, and c), use of this area appeared to be minimal. The majority of these readings appeared to be from lamprey in the south pool that were in close proximity to the underwater antenna inside the diffuser grating and detections were apparently made through the concrete wall.

Behavioral Thermoregulation

The daily mean body temperature profiles for all tagged lamprey were strongly correlated with the daily mean river water temperature ($r = 0.995$, $df = 110$, $t = 110.68$, $p\text{-value} < 0.0001$; Figure 3.7). Despite some seasonal fluctuations in the magnitude of the difference, the lamprey body temperature was consistently lower than the river temperature. The mean difference between the daily mean body temperature and river water temperature was 1.19 C° (ranging from 0.35 to 2.79 C°). The lamprey-to-lamprey variation was minimal with a mean daily standard error of 0.25 C° (ranging from 0.06 to 0.78 C°). The magnitude of difference between the mean river water temperature and the mean body temperature was consistently greater than the daily standard error associated with the mean body temperature for all measured dates from 9 July to 28 October, indicating that the temperature difference was significant.

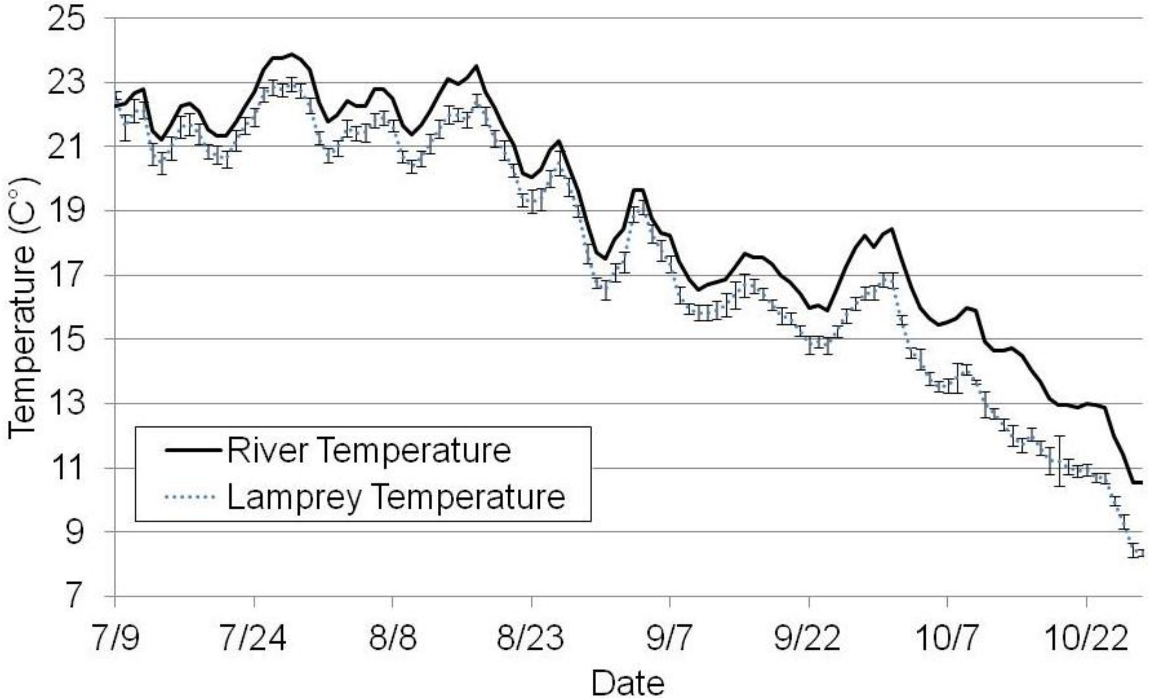

Figure 3.7. Mean daily temperature of river water and body temperature of the tagged lamprey (N = 17) at Winchester Dam between 9 July and 28 October in 2010. Body temperature reading was first detected on 24 June, 2010, but continuous data were not available until 9 July, 2010. Error bars represent standard error.

Because temperature can oscillate extensively within a day and lamprey were detected disproportionately more in the evening, it was critical to acquire time specific temperature data for comparison. When the hourly temperature difference between the lamprey body and river water was evaluated by month, we found that the temperature differential increased steadily and slowly between July and September, and a larger increase in this differential was detected in October (Figure 3.8). This suggests that the tagged lamprey were using coldwater thermal refuges at the dam throughout the migration season, but that the duration or frequency of use increased from summer to fall, especially after October. On average, the hourly lamprey body temperature was 0.78 (±0.16 standard error) C° lower in July, 0.92 (±0.04) C° lower in August, 1.00 (±0.04) C° lower in September, and 1.93 (±0.05) C° lower in October compared to the river water temperature. We also discovered that the lamprey body and river temperature gap was less during early evenings compared to mornings from July through September, but the pattern was less distinct in October (which could be due to the smaller sample size). From July through October, the mean temperature gap during the early evening hours (16:00~0:00) was 0.63 C°, 0.41 C°, 0.32 C°, and 0.29 C° less compared to that during the morning hours (4:00~12:00), respectively, displaying a gradual decrease in this gap.

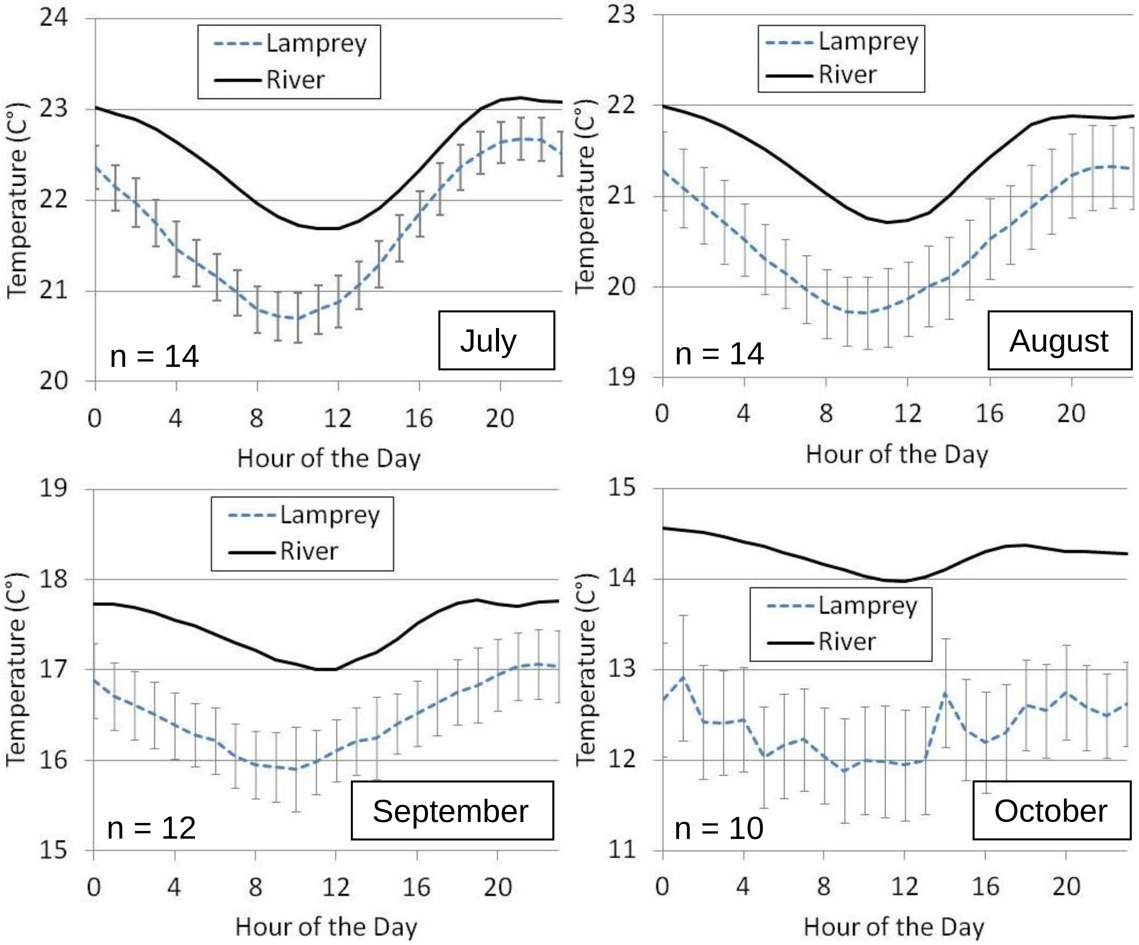

Figure 3.8. Mean hourly temperature of the river water and the lamprey body from July through October, 2010**.** The y-axis temperature ranges are all 5 C° (different maximum and minimum values). The body temperature profile for the month of October was more roughened compared to that of other months due to the reduced temperature readings associated with the scheduled tag programming. Error bars represent standard error.

Discussion

Spatiotemporal Movement

Compared to the passage efficiency at other mainstem dams in the northwestern USA [50~80% (Moser et al. 2002b; Cummings 2007)], the rates of passage at Winchester Dam appear considerably low (8.3% in 2009 and 18.5% in 2010). In Chapter 2, we found that relative tag size and migration timing of individual lamprey within the run also affected dam passage efficiency; those that migrated early within the run or with a smaller tag had a significantly higher rate of passage compared to others. Nevertheless, some lamprey may be deliberately using the dam as overwintering holding habitat and are less motivated to pass the dam.

The small openings on the dam are quite prevalent and observations of lamprey exiting out of small crevices at the top of the dam have been made by Oregon Department of Fish and Wildlife (ODFW) personnel (Fabian Carr, ODFW, pers. comm. 2009). Maintenance projects aimed at filling these holes have occurred on average every six years (range 1-14 years) since 1946. Recently in 2009, reservoir water above Winchester Dam was drained during the low flow period in early September to repair and fill the enlarged holes on the dam surface. During the very first day of dewatering, over 250 adult lamprey were observed retreating from inside one of these enlarged openings (Figure 3.9). From the second and third day of the operation, 160 more adult lamprey were captured from the lower fish ladder and bedrock spaces below the dam (Figure 3.10). These observations confirmed that many lamprey were holding at the base of the dam.

Figure 3.9. The enlarged opening on the surface of Winchester Dam during the first day of the reservoir dewatering event on 31 August, 2009. Within an hour after this photo was taken, many adult Pacific lamprey began to retreat from within the timber crib structure (arrow symbol), totaling over 250 adults this day.

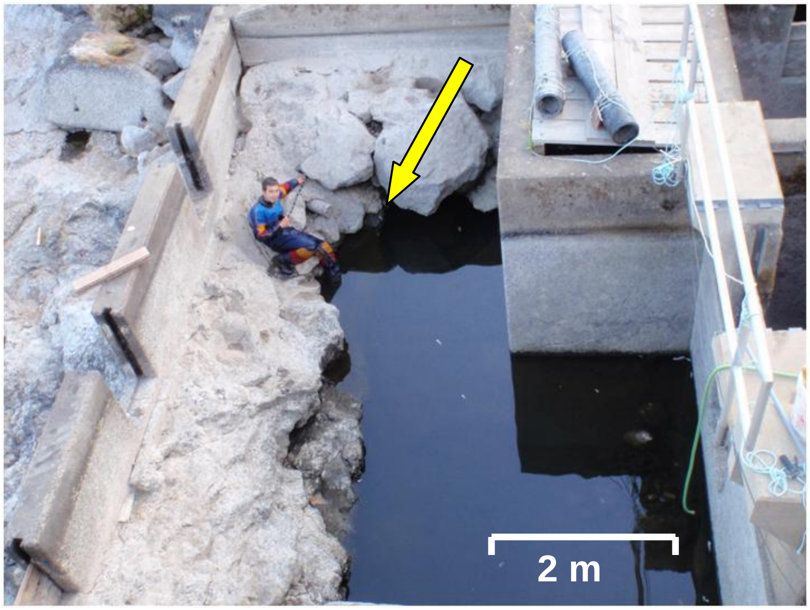

Figure 3.10. The lower fish ladder during a dewatering event in 2009. On the second and third day of dewatering, we found a total of 160 adults that emerged from the bottom of the boulder and bedrock structures from this area (arrow symbol) and the immediately surrounding area.

Our study indicated that the frequency of movements decreased sharply between August and September. We observed an overall shift in the holding locations at the dam around this same time period, during which many of the tagged lamprey moved to the southeast bank away from the fish ladder side. This coincided with the end of the lamprey run as indicated by the lamprey capture data; 90% of the run was captured by 9 August, 2010. These results suggest that lamprey were more active during the summer/fall season (especially up to August) compared to the winter/spring season.

According to Savina and Gamper (1998), the respiration rate of overwintering adult European river lamprey (*Lampetra fluviatilis l.*) were 2.5~3 times slower than that observed during the migratory season in autumn and the following spring. The availability of fatty acids for oxidation appear to control the hepatocyte energy metabolism and associated change in respiration (Gamper and Savina 2000). Therefore, if the biological process is similar for Pacific lamprey, lamprey may be forced to transition into a sedentary physiological state in late summer as a result of some shift in metabolic processes controlled by the deficiency or reduction in available fatty acids. At this point, their focus transitions from upstream migration to finding overwintering habitat to conserve their limited available energy reserves for the springtime spawning season. In our study lamprey displayed a high level of activity during the early and mid summer months, but they altered their behavior markedly and became sedentary sometime in August.

Behavioral Thermoregulation

The thermoregulation analysis using temperature sensor tags demonstrated that lamprey body temperature was consistently lower than the water temperature during their summer/fall migration period at Winchester Dam, and the gap between the two temperatures increased as the season progressed. The gap between the river water and lamprey body temperature only increased from 0.78 C° to 1.00 C° between July and September, but between September and October the gap increased rapidly to 1.93 C°, suggesting a more abrupt shift in behavior. We used the temperature data provided by the Winchester Water Treatment Plant, which appeared to be a reasonable representative for the standard river water temperature immediately below the dam, but this could be examined further by documenting hourly temperatures at multiple locations below the dam using more temperature probes.

According to Fanelli and Lautz (2008), riffles immediately downstream of small dams were rich in oxygen content, and the thermal exchange rate between the streambed and the stream was markedly high, effectively buffering stream temperature. Thermal infrared remote sensing surveys covering 90 km on the North Umpqua River (July, 2002) has identified two locations on the mainstem river with a large drop in surface water temperature (Watershed Sciences 2003). One of these was found between river km 9 and 11.5, enclosing Winchester Dam at river km 11.2, and a 0.8 C° drop in surface water temperature was observed here. Considering that there is no major tributary that enters the river at this location, this drop in temperature may be caused by hyporheic flow and/or groundwater exchange at the dam. Another possibility is thermal stratification in the reservoir water (which could be verified by measuring temperatures at various depths in the reservoir water seasonally). Our study indicated that the tagged lamprey used the thermal coldwater refuges made available downstream of the dam as time progressed from summer to fall. If lamprey are indeed keying into microhabitat with hyporhiec flow and/or influxes from thermal stratification at the dam, their microhabitat water temperature during the winter is expected to be modulated and higher compared to the mean river water temperature.

The difference between lamprey body and river water temperature was the lowest in the early evenings (21:00~22:00), which corresponds to the time of day when high levels of lamprey activity generally began (Figure 3.3). On the other hand, the temperature gap was the highest in the mornings (4:00~8:00), which corresponds to the time of day when high levels of activity began to cease. Hence, lamprey activity levels could potentially be associated with these changes in lamprey/river temperature dynamics. The tendency for the lamprey body temperature to elevate more at night compared to the river water temperature may also be related to their diel behavior. During the day, lamprey are usually holding at the bottom of the river underneath boulders and bedrock cracks, which may have slightly colder water temperature compared to the mid-column and surface water they swim in at night for passage.

Although the dam appeared to provide unique overwintering habitat with thermal coldwater refuges during the summer and fall, there are other factors to consider. If coldwater thermal refuges were indeed important for adult lamprey during the summer and fall, lamprey could reach colder water if they travel farther upstream past the dam. In fact, the mean hourly water temperature 17.6 km and 22.0 km upstream of Winchester Dam was on average 2.0 and 2.1 C colder than the mean hourly water temperature available at the dam (from temperature probe data). Migrating farther upstream could also be beneficial for the larval lamprey because it provides access to more potential habitat for these larva to occupy as they drift downstream.

During the early and mid summer, many lamprey were actively using the fish ladder and other migration corridors below the dam. In 2009 and 2010, four tagged lamprey were confirmed dead in their first summer (well after the typical spawning season), and all of them were detected at Winchester Dam within two days prior to their deaths. Several other fish were also detected making long downstream migration immediately after residing at the dam, but we were unable to confirm their survival. There are many avian and mammalian predators (great blue heron, osprey, river otters, etc.) that frequent the base of the dam, and many of them were repeatedly sighted near known lamprey migration corridors and early summer holding habitat. Therefore, the physiological effects of passage delay as well as the impacts from the predators that take advantage of this delay need to be considered as part of the overall impact of Winchester Dam on Pacific lamprey reproduction.

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CHAPTER 4: SEASONAL MIGRATORY ACTIVITY OF PRE-SPAWNING ADULT PACIFIC LAMPREY WITHIN THE NORTH UMPQUA BASIN, OREGON, USA

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Abstract

The yearlong spawning migration of Pacific lamprey, *Entosphenus tridentatus,* within the North Umpqua Basin in southwest, Oregon, USA, were monitored in 2009 and 2010 using radio telemetry. Ninety-five percent of the overall upstream migration took place during the first spring/summer period, and only small-scale upstream movements were observed during the winter and second spring/summer (4% and 1%, respectively). The median rate of upstream migration was the fastest during the initial migration phase and was 1.9 km/day (ranging from 0.3 to 11.0 km/day) for tagged lamprey released above Winchester Dam. During the pre-spawning phase (a 5-month period in winter), 71% of the lamprey remained in the exact same location where they initiated holding behavior. Multiple regression analysis indicated that the total upstream migration distance traveled by individual lamprey was most strongly related to presence/absence of a local dam, relative tag size, and the water temperature and photoperiod conditions at release. The presence of Winchester Dam, large relative tag size, and high water temperature / short photoperiod conditions at release significantly reduced upstream migration distance. Therefore, incorporating the effects of environmental conditions and relative tag size into the analysis can be critical for Pacific lamprey passage studies using radio telemetry. We also detected a significant interaction between the interval length of the two dorsal fins (a rough reflection of sexual maturity) and the water temperature at release; lamprey with long dorsal fin intervals traveled further compared to those with short dorsal fin invervals when they were released during high water temperature conditions, but the relationship was reversed during low water temperature conditions.

Introduction

Pacific lamprey, *Entosphenus tridentatus*, is a native anadromous fish distributed in rivers and streams along the Pacific Rim from Baja California, Mexico, to eastern Honshu Island, Japan (Ruiz-Campos and Gonzalez-Guzman 1996, Yamazaki et al. 2005). Spawning migrations of Pacific lamprey typically last over a year (Clemens et al. 2010) and can span up to 800 km (Hamilton et al. 2005). Spawning takes place in tributary systems in the spring and summer approximately a year after they enter freshwater systems. During this period, lamprey halt feeding, survive on their stored fat accumulated during the marine phase, and navigate through a wide variety of predation risks and altered freshwater environments. An improved understanding of the migratory behavior and its underlying biological mechanism during this freshwater stagecould help managers make informed management decisions to facilitate lamprey recovery.

Literature suggests that there are three distinct phases in Pacific lamprey spawning migration (Beamish 1980; Robinson and Bayer 2005), which can be referred to as initial migration, pre-spawning holding, and final migration phases (Clemens et al. 2010). The timing of the spawning migration can vary considerably depending on the latitude (Clemens et al. 2010) as well as the distance from the ocean (Brumo et al. 2009; Gunckel et al. 2009). Research on passage at major hydroelectric facilities indicated that May through September is the primary migration season for Pacific lamprey in the lower Columbia River (Moser et al. 2002b) and movement is primarily nocturnal (Moser et al. 2002a). A telemetry study conducted in the John Day River (a Columbia River tributary in Oregon, USA) observed exclusive nighttime passage at fixed stations and migratory behavior ceased predominantly in September (Robinson and Bayer 2005). The final migration in this study began in mid-March and ended in mid-May the following year. A telemetry study on the Willamette River (Columbia River tributary) also displayed similar results in relation to the migration timing and behavior (Clemens et al. 2011). In the lower Klamath River, a correlation between lamprey migration and rising temperature was documented, which also coincided with decreasing river discharge (McCovey Jr. et al. 2007). The mean rate of travel for the tagged lamprey were 11.1 km/day (ranging from 1.0 to 20.9 km/day) in the John Day River study and 1.97 km/day (ranging from 0.46 to 5.75 km/day) in the Klamath River study.

Few studies have focused on the pre-spawning migration behavior of Pacific lamprey outside the Columbia River system. The two primary objectives of our study were to 1) describe in detail the spawning migration behavior of adult Pacific lamprey within the North Umpqua Basin in southwest Oregon, and 2) use multiple regression analysis to identify biotic and abiotic factors that are strongly associated with the total distance they migrate by the end of the initial migration phase. Radio telemetry was used to monitor the behavior of adult Pacific lamprey captured in the lower North Umpqua River in 2009 and 2010. The fish migration characteristics, including direction, distance, rate of travel, and timing, are provided for general overview. Based on a multiple regression analysis, we examined the role of various environmental, morphological, and physiological factors on the total upstream migration distance traveled by individual lamprey. We used an information-theoretic approach to evaluate the relative support for multiple hypothesized models based on Akaike's information criterion (AIC) as described by Burnham and Anderson (2002).

Methods

Study Area

The study area includes the North Umpqua River from its river mouth to Soda Springs Dam including all its tributaries in southwest Oregon, USA (Figure 4.1). Anadromous species, including Pacific lamprey and salmonid (*Oncorhynchus*) species, migrate 179 km in the Umpqua River from the Pacific Ocean to reach the mouth of the North Umpqua River. The North Umpqua Basin (3,520 km^2) holds roughly 110 km of anadromous fish habitat in the mainstem river and 450 km in all of its tributaries (Umpqua Basin Explorer, available at: http://oregonexplorer.info/umpqua/). The historical extent of salmonid species and Pacific lamprey distribution is considered to be very similar in many basins within the Northwestern USA (Hamilton et al. 2005; Moyle 2002; Scott and Crossman 1973). The river originates from Maidu Lake at an elevation of 1,824 m on the western slope of central Cascade Mountains and joins the South Umpqua River northwest of Roseburg, Oregon, at an elevation of 110 m. Over 20% of the basin lies above 1,700 m elevation, which supplies strong, cool flows from snowmelt runoff that last through the summer. Furthermore, the flow is augmented by large-volume groundwater systems stemming from the upper reaches (Wallick et al. 2010).

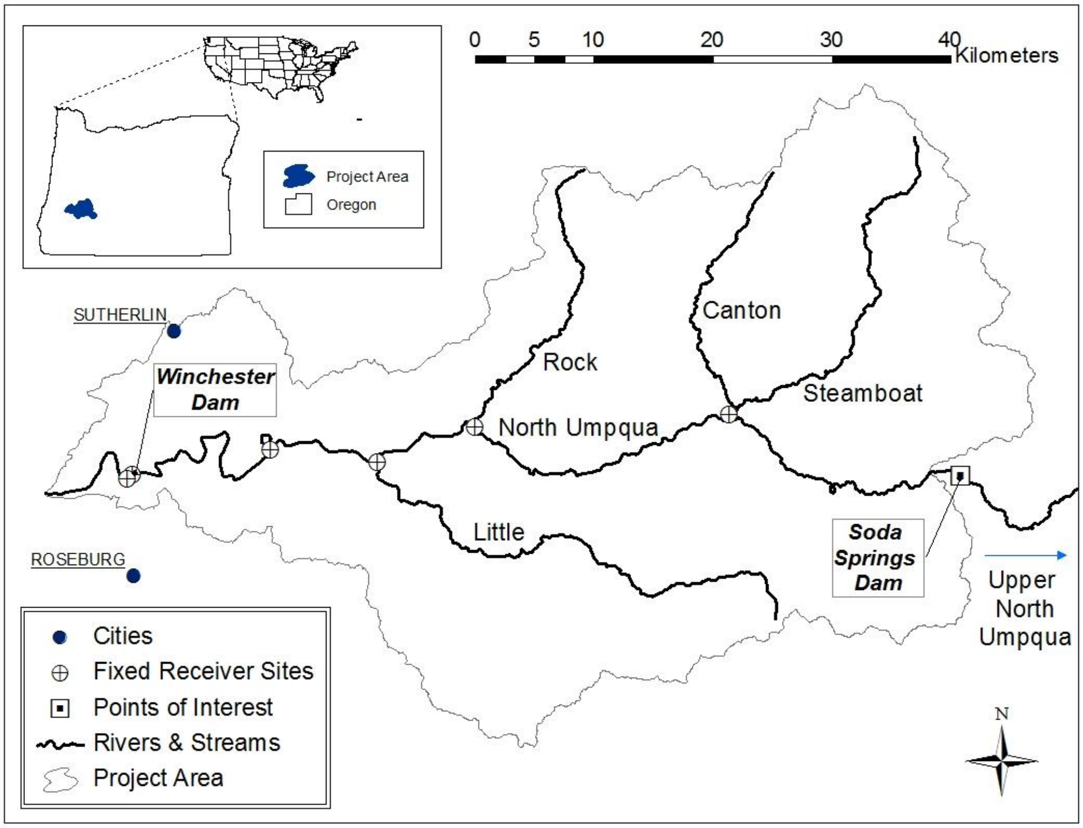

Figure 4.1. Map of North Umpqua River below Soda Springs Dam, including major tributaries. Locations of fixed receiver sites and Soda Springs Dam are identified. Soda Springs Dam has been the upper extent of the anadromous fish habitat, but new fish ladders will enable anadromous fish to use the upper North Umpqua watershed starting in 2012.

Sampling and Tagging

In 2009 and 2010, adult Pacific lamprey were collected and radio-tagged during the initial migration phase (May-September) at Winchester Dam (river km 11.2). Water discharge at Winchester Dam typically ranges from 30 m^3/s during the summer low flow period (July-September) to 180 m^3/s during the winter-spring high flow period (December-February), with a mean annual flow of 105 m^3/s. Adults were captured inside the lower fish ladder or within 50 m downstream of the dam using dip nets, an assortment of traps, or by hand. Traps were designed to capture adult Pacific lamprey of all sizes.

Traps were checked in the morning and then reset allowing them to fish 24 hours. Netting and hand-capture methods were used during the day, predominantly in the morning. For more details on lamprey capture methods, see Appendix A.

Captured lamprey were handled immediately or held in a permeated flow-through container (30 – 70 L) in the river for 2 – 48 hours before surgically implanting radio tags. Lamprey were individually anesthetized, measured, and surgically implanted with radio transmitter tags following the surgical techniques described by Moser et al. (2002a) and the training and practice provided by lamprey telemetry experts. Post surgery, lamprey recovered in an aerated recovery bucket for 1-3 hours to allow monitoring of their conditions before release. All tagged lamprey were released in calm water of a pool or a side pool to minimize post-release stress.

Winchester Water Treatment Plant (City of Roseburg) routinely collects data on water temperature 35 m downstream from Winchester Dam on the southest bank of the North Umpqua River. The daily mean temperature of water withdrawn from this deep, swift segment of the river at a depth of 3.7 m was used to represent the river water temperature at the dam. Photoperiod data were from the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneDay.php).

Radio Tags and Monitoring of Location

To ensure that the tags represented less than 8% of the fish's cross-sectional area, only captured lamprey that met the minimum mid-girth criterion of 102 mm were surgically implanted with the Lotek NTC-6-2 nano tags (4.3 g in air, 9x30 mm) in 2009. In 2010, two additional types of tags were deployed: Lotek NTC-3-2 nano tags (1.1 g, 6x16 mm) and MST-820T temperature sensor tags (2.2 g, 8x22 mm). The minimum girth threshold was reduced to 73 mm and 90 mm, respectively, for these smaller tags, using the same 8% area ratio criterion. All tagged lamprey had a tag/lamprey weight ratio smaller than 1.2%. Sex was identified during tagging for 52.9 % of the fish in 2009 and 77.8 % of the fish in 2010. Females made up 66.7 % and 61.8 % of the sample, respectively. Based on 10 years of lamprey run timing from Winchester Dam fish ladder counts, the peak of the run occurs primarily between late June and early July (Figure 4.2). One of the objectives for both years was to tag a sizeable number of lamprey from the early, middle, and late run of the population.

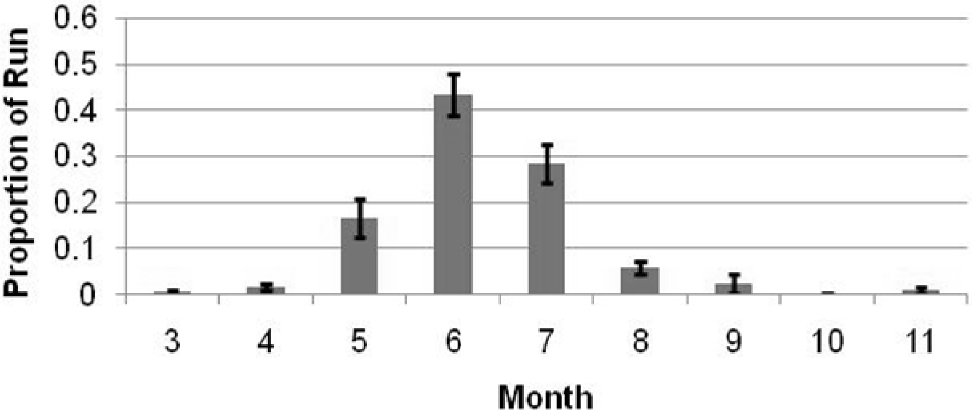

Figure 4.2. Mean proportion of lamprey counts at Winchester Dam by month using 10 years of data between 1999 to 2008. The error bars represent the standard error. Data was provided by Oregon Department of Fish and Wildlife.

Radio-tagged lamprey were tracked using manual tracking and fixed sites. Fixed sites were established at Winchester Dam and directly above major tributary junctions (Little River [river km 46.7], Rock Creek [river km 57.5], and Steamboat Creek [river km 84.9]) (Figure 4.1). Additional fixed sites were added downstream (river km 10.6) and upstream (river km 33.2) from the dam starting in September, 2010, to detect small scale movements, including fallbacks. All fixed sites had a minimum of two aerial antennas to detect both lamprey presence and direction of movement. The fixed stations operated 24 hours of the day for the majority of the project period.

Manual tracking involved mainly vehicle tracking using the extensive road network in the basin, but when the tagged lamprey were detected, more precise locations (< 15 m) were found by on-foot mobile tracking using triangulation when feasible. Tracking by rafts was also used in mid-summer in both years to cover a portion of the river that was otherwise hard to access. Each radio-tagged lamprey was manually tracked at least once a week (usually 2~4 times a week) between May and September. This frequency was reduced to once every two weeks between October and February in accordance with the extensive reduction in movement. During spring spawning migration (April - July) tracking was conducted on a weekly basis.

Overview of Migratory Behavior

In 2009, 15 radio-tagged lamprey were released 0.9 km downstream of Winchester Dam while 2 were released above the dam (2.5 km and 23.9 km upstream of dam). Seven additional lamprey captured during a two-week-long reservoir water dewatering event for dam maintenance on 1 September, 2009, were also radio-tagged; 4 were released immediately upstream of the dam in the dewatered reservoir water, and the remaining 3 were released immediately downstream of the dam. In 2010, 31 radio-tagged lamprey were released 0.9 km downstream of the dam while 14 were released 2.5 km upstream of the dam (end of reservoir water).

Because of the distinct changes in lamprey behavior observed in association with the migration phases, their movement was analyzed separately for each phase. The initial migration phase (May-September) is generally characterized by the active upstream migration during the first summer. The pre-spawning holding phase (October-February) is the period of prolonged holding and metabolic depression during the winter (Gamper and Savina 2000). The final migration phase (March-July) is characterized by the enhanced level of activity associated with the beginning of the spawning migration in the spring. Tags from 2009 and 2010 were included in the initial migration phase analysis. Only tags from 2009 were included in the analysis for the pre-spawning holding and final migration phases.

All lamprey holding locations were given a best approximate start and an end date as determined by manual tracking and fixed station data to monitor the duration of the holding behavior (in days). For each detected individual lamprey movement event, the rate of movement (km/day) for the individual fish was calculated using the following equation:

$$\frac{river\ km_{n,t} - river\ km_{n,t-1}}{start\ date_{n,t} - end\ date_{n,t-1}}$$

where $river\ km_{n,t}$ represents the river km (0.1 km resolution) of an individual lamprey location at time t; $river\ km_{n,t-1}$ represents the river km of the lamprey location immediately prior to $river\ km_{n,t}$; $start\ date_{n,t}$ represents the first date the fish (n) was identified at $river\ km_{n,t}$; and $end\ date_{n,t-1}$ describes the last date the fish was identified at $river\ km_{n,t-1}$. Because the relation between distance and time is most likely non-linear (i.e. variable movement rates within a set of time) and because fish detections were not always made right after lamprey stopped moving, these movement rates only provide a conservative measure of ground speed and actual rates could have been higher. For any of the rate of movement calculations, holding lamprey (those showing no movement temporarily) were excluded from the calculation.

Data and Modeling Analysis

Statistical analyses were performed using R statistical software (R Development Core Team 2011). Variables were analyzed for normality of distribution using normal probability plots and Shapiro-Wilk normality test. Variables with normal distributions were analyzed using means, and a two-sample t-test was conducted for any comparisons. Variables with skewed distributions were analyzed using medians, and a Wilcoxon two-sample test was conducted for comparison. A significance level of p-value = 0.05 was used for all statistical tests performed in this study.

For the regression analysis, we used an information-theoretic approach as described by Burnham and Anderson (2002). Any predictor variable that was strongly correlated with other predictor variables (a Pearson correlation coefficient > 0.7) was removed from the list of candidate variables for all analyses to avoid multicollinearity (Moore and McCabe 2003). Linear multiple regression models were fit using R statistical software (R Development Core Team 2011) and an AIC score corrected for small sample size (AICc) was calculated for each model (Hurvich and Tsai 1989):

$$\mathrm{AICc} = n\log(\frac{\mathrm{RSS}}{n}) + 2K + \frac{2K(K+1)}{n-K-1}$$

where n is the sample size, K is the number of estimable parameters, and RSS is the residual sum of squares. Akaike weight (w_i) for each model was calculated using differences in AICc scores ($\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{min}$):

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{r=1}^{R}\exp(-0.5\Delta_r)}$$

Multimodel inference and model averaging were used to incorporate model selection uncertainty of the predictor variables (Burnham and Anderson 2002). Evidence ratio ($\frac{w_{max}}{w_i}$) was also calculated for each model as a reference for the confidence in the model; a model with an evidence ratio of 10 or higher would indicate that it is 10 times less likely to be better than the best-approximating model (Burnham and Anderson 2002). The Akaike importance weight for each variable was calculated by summing the model weights from all models that contained the variable of interest. Model averaged parameter estimates and unconditional standard errors were computed for all parameters using the modavg function from "AICcmodavg" package in R. The precision of each parameter was estimated by computing 90% confidence intervals using the unconditional standard errors. Finally, model averaged parameter estimates were standardized using the standard deviation of each variable to evaluate the expected effects given the range of variable values.

Analysis of Total Upstream Migration Distance

Our objective in this analysis was to evaluate whether certain properties associated with the lamprey could be used effectively to predict their overall migration distance. To identify the factors that most strongly influenced the upstream migration distance of individual tagged lamprey, linear multiple regression analysis was conducted using the total upstream migration distance traveled by each tagged lamprey as the response variable. The response variable was obtained by subtracting the river km of the release location from the maximum river km for each fish at the end of the initial migration phase.

Nine predictor variables were examined in this multiple regression analysis (Table 4.1). Four of these variables were endogenous to the lamprey and were associated with lamprey morphology or physiology. The remaining five variables were exogenous to the lamprey and included environmental and anthropogenic factors. The release location (upstream or downstream of Winchester Dam) was included in all models as a base variable because of the known effect of the dam on upstream migration (see Chapter 2 for more information). The two main factors (run timing and relative tag size) described in Chapter 2 appeared to have a similar effect on the upstream migration of lamprey regardless of their release location. As a result, we determined that including both upstream and downstream release groups together in the model is a logical approach given that the release location is included in the model as a base variable. Due to the limited sample size (n = 62), only parsimonious linear regression models containing a maximum of three variables (including the release location) were constructed and compared using a combination of the nine predictor variables (totaling 37 models).

Table 4.1. List of predictor variables used in the multiple regression analysis for maximum upstream migration distance. x_{release} was included in all models as a base variable. The specific categories for the two categorical variables are listed in the description (baseline category is denoted by 1).

Variable	Theme	Type	Description
x_{release}	exogenous	categorical	release location (1. downstream of dam and 2. upstream of dam)
x_{weight}	endogenous	linear	weight of the lamprey (g)
$x_{\text{condition}}$	endogenous	linear	Fulton's condition factor of the lamprey $[(10^\wedge 5*\text{weight})*(\text{body length})^\wedge 3)^{-1}]$
x_{dorsal}	endogenous	linear	standardized dorsal gap [distance between 1st and 2nd dorsal fin (mm) divided by the body length]
x_{color}	endogenous	categorical	color of the ventral side of the lamprey (1. black, 2. gold/silver light spots, 3. gold/silver heavy spots, and 4. white)
x_{temp}	exogenous	linear	mean water temperature (C°) on the release date
x_{photo}	exogenous	linear	photoperiod (day length in hours per day) on the release date
x_{tag}	exogenous	linear	ratio of tag / lamprey mid-girth cross-sectional area (%)
x_{holding}	exogenous	linear	number of days between lamprey capture and release

The distance between the two dorsal fins gauges the level of sexual maturity (Clemens et al. 2009), and was incorporated into the analysis to assess its effect on total upstream migration distance. Because of the positive correlation between body length and dorsal fin interval length (r = 0.32), we standardized the dorsal fin interval length by dividing it by the body length of the fish. We hypothesized that those with a longer standardized dorsal fin interval would travel more than those with a shorter standardized dorsal fin interval (which suggests a higher degree of sexual maturity). Lamprey body length, weight, and mid-girth were highly correlated (> 0.7) with each other, so we only included weight in the analysis. Discharge and the Julian date of lamprey capture (indicating the migration timing of the individual lamprey within the overall run) were also eliminated due to the high correlation (> 0.7) with mean water temperature and/or photoperiod on the release date.

Some predictors may influence the upstream migration differently depending on the conditions of other predictor variables (such as the release location). To explore the potential presence of interaction between the variables, we constructed two-way interaction terms using a combination of the nine predictor variables. All 36 combinations of the interaction terms were added to the best simple additive model to explore potential interaction effects and the resulting models were ranked based on the AICc values. Whenever an interaction term was added to the best simple additive model, the main effects of the two variables that constructed the interaction term were also included in the model.

Results

Overview of Migratory Behavior

The run timing projected from the capture dates in 2009 and 2010 was similar to the run timing displayed in the previous 10 years, with the 50th percentile capture dates falling on July 6 and July 11, respectively (Figure 4.3). There was a strong correlation between the daily number of lamprey captured and the daily mean temperature in both years ($r = 0.334$, df = 123, p-value = 0.00016 in 2009; $r = 0.350$, df = 122, p-value = 0.00008 in 2010). Based on the multimodal distribution of the capture data and the associated breakpoints, tagged lamprey captured before July 1 were classified as the "early run," those captured between July 1 and July 15 were classified as the "middle run," and those captured after July 16 were classified as the "late run."

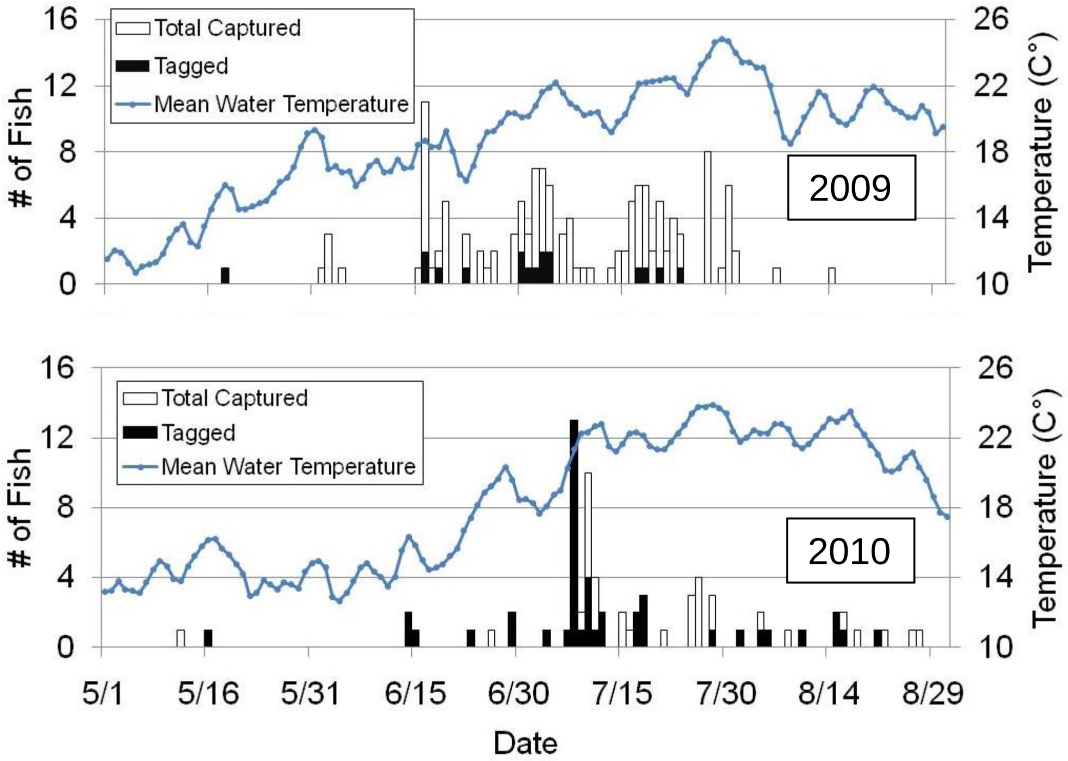

Figure 4.3. Number of adult Pacific lamprey captured in 2009 (n = 131) and 2010 (n = 77) shown in conjunction with the mean water temperature at Winchester Dam. The filled bars display the number of lamprey that were tagged for this study.

The majority of the upstream migration movements were observed between June and August during the initial migration phase (Figure 4.4 and Figure 4.5). Tagged lamprey released below Winchester Dam that never passed the dam were excluded from the data set due to the identified effects of the dam on upstream migration. Because all tagged lamprey released above the dam in 2009 were released late in the season (after 17 July), the data prior to this date are limited in scope (only represented by the tagged lamprey that passed the dam on its own). However, the general pattern of summer seasonal movement was similar between the two years in that the majority of the upstream migration was observed between mid June and mid August. Limited, concentrated movement upstream during the winter pre-spawning holding phase was followed by small but distinct upstream movements during the final migration phase starting in mid-March (Figure 4.4). Downstream movement was detected mostly during the final migration phase and appeared to follow the small, upstream movements during the spring spawning season.

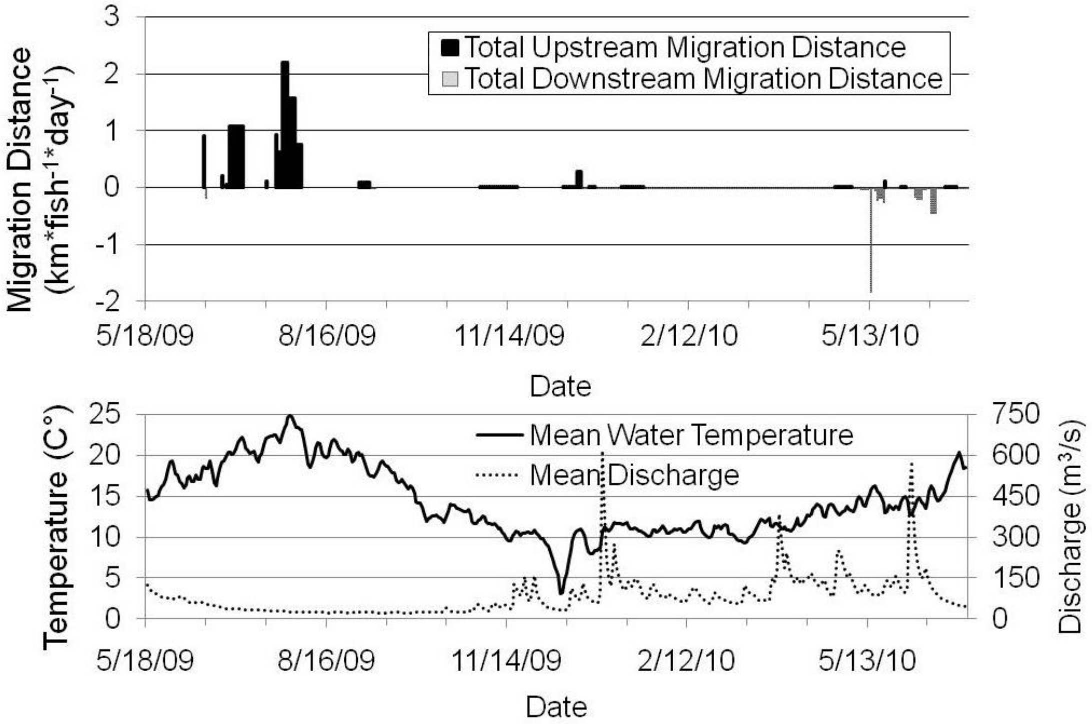

Figure 4.4. Daily mean upstream and downstream migration distance traveled by tagged fish in 2009 that either were released above Winchester Dam or passed the dam on their own during the initial migration, pre-spawning, and final migration phases. The corresponding daily mean water temperature and discharge during this period are shown in the bottom graph. The x-axis tick mark interval is 30 days.

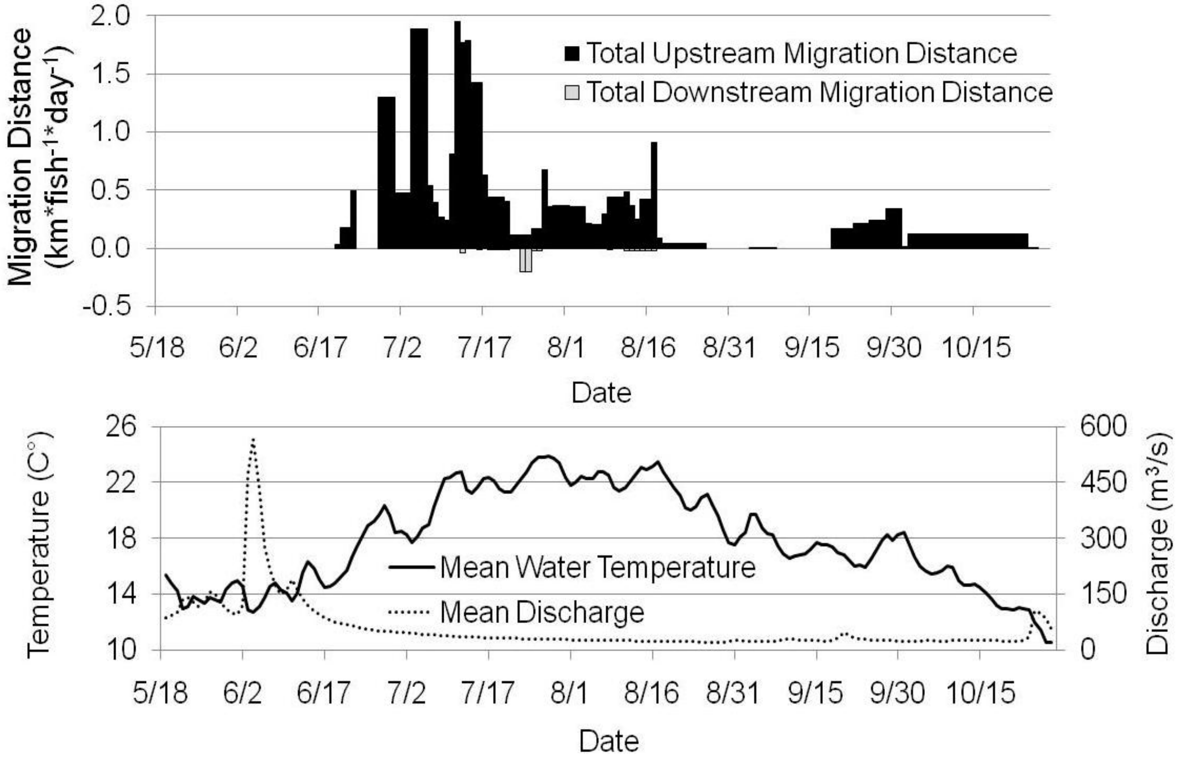

Figure 4.5. Daily mean upstream and downstream migration distance traveled by tagged fish in 2010 that either were released above Winchester Dam or passed the dam on their own during the initial migration phase in 2010. The corresponding daily mean water temperature and discharge during this period are shown in the bottom graph. The x-axis tick mark interval is 15 days.

The majority of the overall upstream migration (95.4%) took place during the initial migration phase, whereas only 3.9% and 0.7% of the movement was observed during the pre-spawning holding phase and final migration phase, respectively. On the other hand, downstream movement was most prevalent during the final migration phase (88.0% of the overall downstream migration) in comparison to the pre-spawning holding phase and initial migration phase (8.5% and 3.5%). Downstream migration was typically observed shortly after upstream migration peaks, and during the final migration phase this was mostly in May and June.

On average, lamprey from the early run travelled farther compared to those from the middle and late run. This was observed for tagged lamprey released upstream (Figure 4.6) and downstream (Figure 4.7) of Winchester Dam (W = 473, df = , p-value = 0.0146). Many tagged lamprey released below the dam halted their upstream migration when they returned back to the dam. For more details on the lamprey behavior at the dam, see Chapter 2.

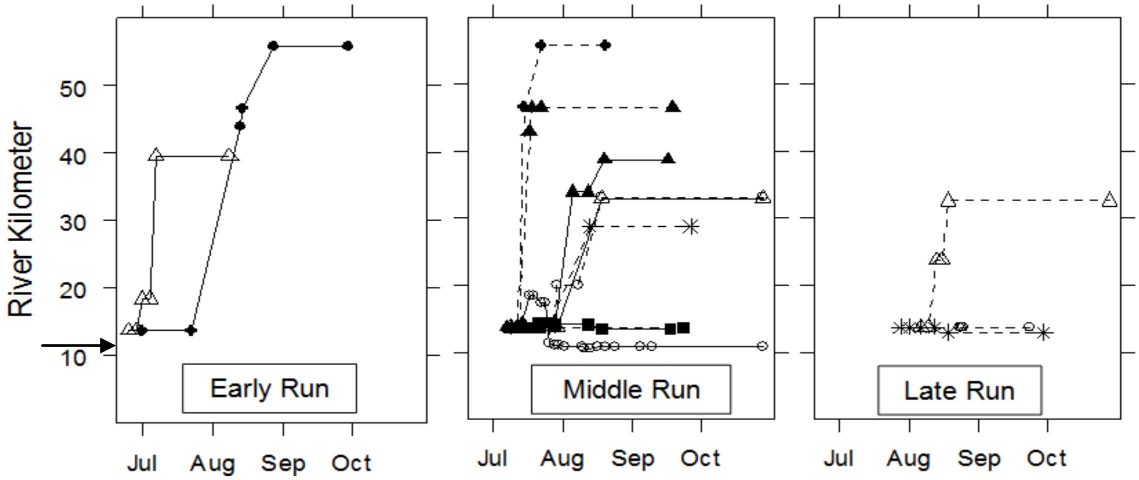

Figure 4.6. Upstream migration of Pacific lamprey that were released above Winchester Dam at river km 13.7 in 2010 displayed separately by run timing (early run [N = 2], middle run [N = 9], late run [N = 3]). The unique symbols denote the detection locations of individual lamprey following their release. The black arrow on the y-axis represents the location of Winchester Dam (river km 11.2).

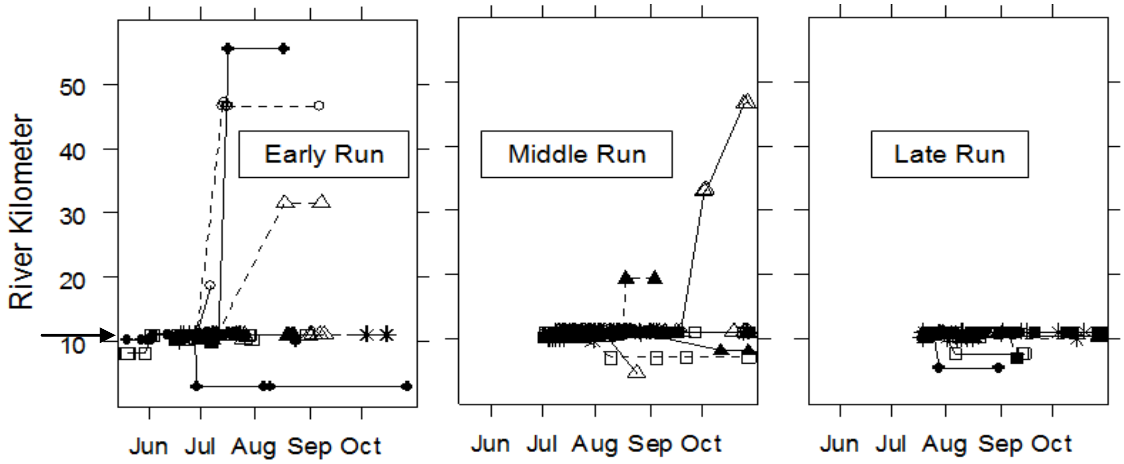

Figure 4.7. Upstream migration of Pacific lamprey released below Winchester Dam at river km 10.3 in 2009-2010 displayed separately by run timing (early run [N = 12], middle run [N = 21], late run [N = 13]). The unique symbols denote the detection locations of individual lamprey following release. The black arrow on the y-axis represents the location of Winchester Dam (river km 11.2).

The median date for the start of pre-spawning holding was August 6 in 2009 (ranging from July 6 to September 14) and August 18 in 2010 (ranging from July 15 to October 25), reflecting the slightly later run timing observed in 2010 compared to 2009. The median date for the start of pre-spawning holding was about one week earlier for female lamprey compared to male lamprey in both years (4 and 7 days earlier in 2009 and 2010, respectively).

The median rate of upstream migration during the initial migration phase was 1.9 km/day (ranging from 0.3 to 11.0 km/day) for tagged lamprey released above Winchester Dam. Due to the presence of the dam, the median rate of upstream migration for tagged lamprey released downstream of the dam was much lower than those released above the dam (W = 1357.5, $P < 0.00001$) and was 0.6 km/day (ranging from 0.1 to 8.3 km/day). Upstream migration rates also varied by tag size; median rate was 0.3 km/day for the large tags (4.3 g) and 0.9 km/day for the medium (2.2 g) and small tags (1.1 g) (W =

1557, P = 0.0066). No difference in migration rates were observed between male and female lamprey (W = 423, P = 0.9694). During the pre-spawning holding and final migration phases, the median rate of upstream migration was much reduced (0.1 and 0.2 km/day, respectively; W = 970.5, P = 0.0027).

Downstream movement behavior was displayed by a portion of the tagged lamprey. During the initial migration phase, the proportion of lamprey that showed any downstream movement was lower for the group of lamprey released above the dam (33% in 2009 and 28% in 2010) compared to the group of lamprey released below the dam (61% in 2009 and 52% in 2010) showing the possible impacts of the dam. Downstream movement was only a small portion (3%) of the overall movement for lamprey released above the dam, but it constituted 25% of the overall movement for lamprey released below the dam. During the final migration phase, on the other hand, downstream movement made up 91% of the overall movement for fish released below the dam, whereas it constituted 98% of the overall movement for fish released above the dam.

Downstream movements during the initial migration phase were significantly correlated with the lunar phase, and longer movements were displayed near the full moon (df = 164, r = -0.178 for 2009, df = 161, r = -0.143 for 2010, p-value < 0.04 for both years). During the final migration phase, however, downstream movements were strongly associated with the new moon phase (r = 0.251 [df = 121], p-value = 0.0027).

Analysis of Total Upstream Migration Distance

The regression analysis modeling the total upstream migration distance produced only one model with an evidence ratio smaller than 10 (Table 4.2). The second best model had an evidence ratio of 25.1, indicating that the best model is at least 25 times better than the second best model in approximating the total upstream migration distance. Normality plots for the top two models were symmetrical and the assumption of equal variance was met adequately. Mean temperature was included in both of the top models, and this is reflected in its high Akaike importance weights (0.95; Table 4.3). The variables with the second and third highest Akaike importance weights were tag/lamprey cross-sectional area ratio (0.86) and photoperiod during release (0.05), and the top three variables in addition to the base variable had a 90% CI estimate that excluded zero.

Table 4.2. Summary of the top-ranked models from the multiple regression analysis modeling total upstream migration distance traveled by lamprey at the end of the initial migration phase (null model included for comparison). The base variable, x_{release}, were included in all candidate models. [n = sample size; k = number of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; Δ_i = $\text{AICc}_i - \text{AICc}_{\text{min}}$; w_i = Akaike weight; w_{max} / w_i = evidence ratio]

Models (x_{release} included in all models)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{temp}} + x_{\text{tag}}$	62	5	0.440	466.5	0.0	0.81	1.0
$x_{\text{temp}} + x_{\text{condition}}$	62	5	0.378	472.9	6.4	0.03	25.1
null model	62	3		484.2	17.7	0.0001	8071.0

Table 4.3. Akaike importance weights, model averaged parameter estimates, standard errors (SE), lower and upper 90% confidence intervals (CI), parameter standard deviations (SD), and standardized parameter estimates (Estimate × SD) for the nine variables in the multiple regression analysis modeling the total upstream migration distance. Akaike importance weight values in bold text indicate parameter estimates with non-zero CIs.

Parameter	Weight	Estimate	SE	Lower CI	Upper CI	SD	Standardized Estimate	Standardized Lower CI	Standardized Upper CI
$x_{\text{release: up}}$	**NA**	15.97	2.96	11.10	20.85	NA	NA	NA	NA
x_{temp}	**0.95**	-2.02	0.59	-2.99	-1.04	2.27	-4.58	-6.79	-2.37
x_{tag}	**0.86**	-393.10	131.87	-610.00	-176.20	0.01	-3.87	-6.01	-1.74
x_{photo}	**0.05**	5.98	3.64	0.002	11.96	0.40	2.40	0.00	4.79
$x_{\text{condition}}$	0.04	-127.44	105.41	-300.82	45.95	0.02	-1.96	-4.62	0.71
x_{holding}	0.03	2.19	1.84	-0.83	5.21	0.80	1.75	-0.67	4.16
x_{weight}	0.02	-0.01	0.03	-0.07	0.05	57.34	-0.61	-3.84	2.61
$x_{\text{dorsal.gap}}$	0.01	-2.92	204.22	-338.84	333.00	0.01	-0.02	-2.47	2.43
$x_{\text{color: light}}$	0.00	7.04	3.37	1.49	12.58	NA	NA	NA	NA
$x_{\text{color: heavy}}$	0.00	3.65	3.88	-2.73	10.04	NA	NA	NA	NA
$x_{\text{color: white}}$	0.01	2.56	4.54	-4.91	10.04	NA	NA	NA	NA

There were three models with a two-way interaction term that had a lower AICc value compared to the best simple additive model approximating the total upstream migration distance traveled by lamprey at the end of the initial migration phase (Table 4.4). The second model had an evidence ratio of 21.1, indicating that the top model is at least 21 times better than the second best model in approximating the response variable. The best simple additive model had an evidence ratio of 73.6, showing a very strong support for the top two-way interaction model. The top interaction model included the interaction between mean water temperature at release and the standardized dorsal fin interval, suggesting that the effect of standardized dorsal fin interval varied depending on the water temperature during release. When the water temperature during release was high, lamprey with long standardized dorsal fin interval migrated further upstream.

When the water temperature during release was low, on the other hand, lamprey with long standardized dorsal fin interval tended to migrate less upstream, indicating a different effect of lamprey dorsal fin interval depending on the water temperature (Figure 4.8).

Table 4.4. Summary of the models with a two-way interaction term that had a lower AICc value compared to the best simple additive model approximating the total upstream migration distance traveled by lamprey at the end of the initial migration phase. The base variable, x_{release}, were included in all candidate models. [n = sample size; k = number of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; $\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$; w_i = Akaike weight; w_{max} / w_i = evidence ratio]

Models (x_{release} included in all models)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{temp}} + x_{\text{tag}} + x_{\text{temp}} * x_{\text{dorsal.gap}}$	62	7	0.534	457.9	0.0	0.86	1.0
$x_{\text{temp}} + x_{\text{tag}} + x_{\text{photoperiod}} * x_{\text{holding}}$	62	8	0.498	464.0	6.1	0.04	21.1
$x_{\text{temp}} + x_{\text{tag}} + x_{\text{release}} * x_{\text{temp}}$	62	6	0.464	465.1	7.3	0.02	37.7
$x_{\text{temp}} + x_{\text{tag}}$	62	5	0.378	466.5	8.6	0.01	73.6

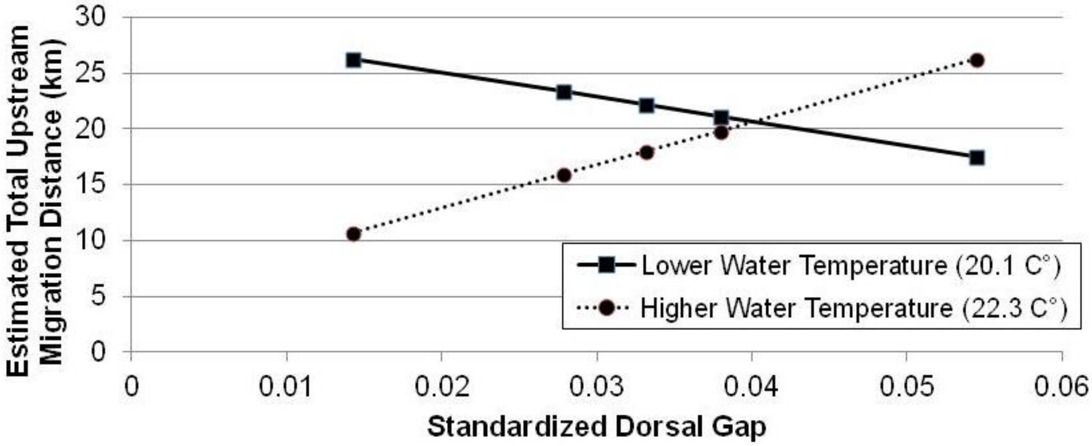

Figure 4.8. The interactive effect of standardized dorsal fin interval (dorsal fin interval divided by the body length) on the estimated total upstream migration distance depending on the mean water temperature conditions on the release date of the lamprey. The relationship was based on a lamprey that had a median value for the tag/lamprey cross-sectional area ratio (= 0.069) and was released above the dam. The lower water temperature (20.1 C°) represents the first quartile value whereas the higher water temperature (22.3 C°) represents the third quartile value for mean water temperature during release.

Discussion

Overview of Migratory Behavior

Past radio telemetry studies that monitored the entire freshwater phase of the adult Pacific lamprey movement have all reported that the greater part of their upstream migration takes place during the initial migration phase in early summer (Clemens et al. 2011; Robinson and Bayer 2005; Beamish 1980). Our study in the North Umpqua River reaffirmed this hypothesis and demonstrated distinct shifts in migration behavior in relation to seasonal changes. During the initial migration phase, upstream migration was mostly observed between June (when the water temperature started to rise sharply) and August (when the water temperature started to drop sharply). During the entire pre-spawning holding phase (a 5-month period), as many as 71% of the lamprey remained in the exact same location where they initiated holding behavior. This indicates that lamprey may be transitioning into a depressed metabolic state or hibernation mode as suggested by Gamper and Savina (2000) for European river lamprey (*Lampetra fluviatilis*).

Because most of the spring downstream movements were not observed until well after the spring freshets occurred, we suspect the majority of the tagged fish that survived the summer successfully overwintered and remained alive until the spring season. For two of the tagged lamprey, we observed spring downstream movement followed immediately by upstream movement, indicating that they were not only drifting downstream, but also actively moving upstream. Although higher flow conditions made it difficult to survey during this period, some redds were confirmed in the downstream locations where the tagged lamprey remained for several days at a time. Furthermore, two tagged lamprey upstream of the dam in two separate locations 4.3 km apart synchronized their downstream movement on May 14, 2010 during a low flow period, and spent 2.5 days at Winchester Dam in identical locations before they moved downstream in synchrony.

Some distinct individual differences in migratory activity were detected within the overall population. Regardless of the lamprey release location (upstream or downstream of Winchester Dam), on average lamprey from the early run traveled farther upstream when compared to the later run. This trend has not been confirmed in other Pacific lamprey case studies with the exception of a small group of lamprey in the Snake River basin (Keefer et al. 2009b). Our results indicated that on average female lamprey initiated pre-spawning holding about a week earlier than male lamprey in both 2009 and 2010, which is in agreement with the results observed in Robinson and Bayer (2005). The rate of upstream migration ranged widely from 0.1 to 11.0 km/day, and was highly dependent on the migration timing and season, release location (signifying potential impacts of Winchester Dam), and tag size (demonstrating the effect from the relative tag size).

None of the tagged lamprey were detected moving into tributary streams and all fish appeared to remain solely in the North Umpqua River. This may be due to the fact that the major tributaries to North Umpqua River typically have higher peak water temperatures compared to the mainstem river during the summer. According to a thermal infrared survey of the North Umpqua River and its major tributaries by Watershed Sciences, Inc. (2003), the water temperature was approximately 4.5 C° higher for Little River and Steamboat Creek and 1.5 C° higher for Rock Creek in comparison to the North Umpqua River.

Analysis of Total Upstream Migration Distance

Keefer et al. (2009a) showed that larger lamprey were more successful in passing through multiple hydroelectric facilities in the Columbia River. In our study, the best morphologic lamprey feature in predicting the ensuing upstream migration distance was Fulton's condition factor. Although the evidence was only suggestive, the results showed that the increase in condition factor was generally associated with reduced total upstream migration. Research suggests that Pacific lamprey shrink in length by approximately 18% (male 14% and female 22%) over the course of its one year residence in freshwater as adults, while the reduction in weight is much less due to the increase in its water content (Hardisty 2006). Therefore, increases in the condition factor could be linked to the degree of sexual maturity, and those that are further along this maturation process may not have the energy to travel very far.

Exogenous factors to lamprey, on the other hand, were shown to play more significant roles in the total upstream migration distance compared to the endogenous factors to lamprey. We found that the relative tag size in relation to the lamprey size influenced upstream migration distance; those with higher tag/lamprey cross-sectional area ratios (0.07~0.08) traveled significantly less distance compared to those with lower area ratios (0.04~0.06). Water temperature and photoperiod length on the release date was strongly related to upstream migration distance as well. Lamprey that were released early in the migration season when the water temperature was still low and the photoperiod was long made significantly longer migrations than those released later in the season. The significant differences in the travel distance associated with the lamprey migration timing (early run traveling further) appears to be due to the combination of temperature and photoperiod conditions; early run lamprey experience significantly lower temperature and longer photoperiod compared to the middle and late run lamprey. Some of the lamprey that were released in late summer also experienced lower water temperature conditions compared to the peak temperatures, but the length of day (i.e. photoperiod) was considerably short by then, and this most likely contributed to their generally reduced upstream migration. Therefore, incorporating the effects of environmental conditions and relative tag size into the analysis can be critical for Pacific lamprey passage studies using radio telemetry. Finally, the presence of the dam significantly affected migration, and on average those released above the dam traveled 15.97 (±2.96) km more than those released below the dam. Most lamprey released below the dam only traveled 0.9 km back to Winchester Dam.

Interaction of Factors

Significant improvements were made to the best simple additive model by adding some two-way interaction terms. The top model with the interaction term contained a two-way interaction between mean water temperature on the release date and the standardized dorsal fin interval and. This highlights the increase in travel distance by lamprey with long standardized dorsal fin interval during the mid-summer when temperature was high. As in condition factor, the standardized dorsal fin interval may be an indicator of maturation. Lamprey with a longer standardized dorsal fin interval may have entered freshwater relatively more recently with more energy to travel upstream compared to those with a shorter standardized dorsal fin interval. The positive association between the dorsal fin interval and the total upstream migration distance may only manifest when the temperature conditions are high and energetically demanding.

One of the interaction term models that performed better than the best simple additive model contained an interaction term between the release location and the mean temperature during release. This indicated that the negative effects of warm water temperature were more severe for the upstream release group compared to the downstream release group. Aside from this difference, the overall impacts of the various factors on total upstream migration appeared to be very similar and consistent regardless of whether the lamprey were released above or below the dam.

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CHAPTER 5: SUMMARY AND CONCLUSIONS

Lampreys (*Petromyzontidae*), a family of jawless fish that represents one of the most ancient vertebrates, have inhabited the streams, rivers and coastal waters of the earth relatively unchanged for 360 million years (Gess et al. 2006). Although long-term, continuous historical records are significantly lacking, anecdotal and short-term data (spanning ~30 years) overwhelmingly indicate that many lamprey species worldwide are in decline (Renaud 1997). Among the 34 lamprey species in the Northern Hemisphere, 20 species were recognized as either extinct (3%), endangered (29%), or vulnerable (26%), while the status of many others had not yet been evaluated. Renaud (1997) claimed that human disturbance, such as habitat degradation and stream regulation, was the major cause of their decline.

In light of the ubiquitous, declining trend in lamprey numbers observed in the northwestern USA in the late nineteenth century, 11 environmental groups petitioned for the Endangered Species Act (ESA) listing of four species of lamprey (Pacific lamprey, western brook lamprey, Kern brook lamprey, and river lamprey) in 2003 (Nawa 2003). The U.S. Fish and Wildlife Service in 2004 concluded that the listing was not warranted, mainly due to insufficient information on biological requirements and historical abundance (USDI-FWS 2004). The status of Pacific lamprey and western brook lamprey were recently reviewed by the Oregon Department of Fish and Wildlife, and despite the paucity of overall information, these populations were found to be “at risk” of extinction due to passage barriers, habitat loss, and pollution (ODFW 2005).

Fish counts from hydroelectric dam facilities in the northwestern USA suggest that the number of Pacific lamprey have declined sharply sometime between the 1970s and 1980s (Kostow 2002). Winchester Dam (Oregon, USA) on the North Umpqua River has continuous, long-term records of Pacific lamprey counts since 1965, and the records show that lamprey numbers decreased dramatically in the early 1970s (see Chapter 2). This study investigated three main topics related to adult Pacific lamprey in the freshwater environment: 1) passage efficiency at Winchester Dam and the preferred migration routes; 2) seasonal movement below the dam and use of coldwater refuges; and 3) seasonal migration behavior and the effects of various biotic and abiotic factors on upstream migration.

In Chapter 2, we demonstrated that the passage efficiency at Winchester Dam for adult Pacific lamprey was low in both 2009 and 2010 (8% and 19%, respectfully). The migration timing within the run had a significant impact on passage, and the early run group had the highest passage efficiency (33%), followed by the middle run and late run groups (12% and 0%, respectfully). Among those released above the dam, the early run group of lamprey traveled further compared to the middle and late run groups. Lamprey in the middle and late run groups were exposed to higher water temperatures (>20 C°) during their release, whereas those in the early run group experienced milder water temperatures (14-20 C°). We speculate that the physiological stress associated with high water temperatures may have contributed to the low passage rates in the later portions of the run.

Passage efficiency research at hydroelectric dams in the Columbia River system have mandatory fish collection stoppages when the water temperature exceeds 21 C° (due to U.S. Army of Corps Engineers regulations), resulting in under-representation of the later portions of the run (Keefer et al. 2009b). In our study, as many as 42% of the captured lamprey were trapped when the daily mean water temperature was over 22 C°, indicating that these later portions of the run exposed to high temperatures make up a large portion of the run. We speculate that these lamprey may be moving upstream in search of cooler water to evade the rising water temperature, and upstream passage during this time period may be especially crucial for their survival and successful reproduction. Given the results we observed, the under-representation of the later portions of the run, therefore, may result in significant overestimation of the overall passage rates in other river systems.

In addition to the physiological stress associated with high water temperatures in the river environment, the surgery operations conducted in high water temperature conditions may have further contributed to the low passage rates by the later portions of the run. Although the degree to which the tagging procedure contributed to the low passage rates is difficult to verify, the fact that those lamprey from the middle and late run group released above the dam actively migrated upstream (median travel distance of 19.3 km and 11.3 km, respectfully) show that they are indeed capable of swimming upstream.

Because Pacific lamprey spawning migration typically extends for over a year, lamprey researchers need tags with long battery life, which also tends to be bulky. As a result, smaller lamprey have often been underrepresented in most of the past lamprey radio telemetry studies due to the minimum threshold size for girth. In 2010, we acquired two types of smaller tags (Lotek NTC-3-2 nano tags [1.1 g, 6x16 mm] and MST-820T temperature sensor tags [2.2 g, 8x22 mm]) so that we could successfully tag lamprey of all sizes to better represent the overall run in the North Umpqua River. This was especially critical in the North Umpqua basin because the average lamprey size in this basin was much smaller than that from the lower Columbia River (43.5% difference in weight and

15.3% difference in girth; see Chapter 3 and Appendix C for more information). In our study, we did not find any association with sizes of the lamprey and passage rates, but for large-scale hydroelectric dams, the larger lamprey appear to have an advantage over the smaller lamprey in terms of passage efficiency (Keefer et al. 2009a).

Although lamprey size was not influential in upstream migration in our study, we found that the relative tag size played a major role in upstream migration. There was a strong negative correlation between the tag/lamprey cross-sectional area ratio and their total upstream migration distance. Lamprey tagged with the smallest tags (1.1 g, 6x16 mm) displayed the highest passage rate (33%), followed by those lamprey with the medium tags (2.2 g, 8x22 mm) and large tags (4.3 g, 9x30 mm) (18% and 7%, respectively).

Our research also showed that the count data at Winchester Dam were underestimating the Pacific lamprey numbers that actually migrate past the dam considerably. Our population estimates based on mark-recapture data (960 in 2009 and 556 in 2010) are low, however, when compared to the historical count data from the late 1960s and early 1970s (14,532~46,785). Furthermore, the extent to which lamprey were using alternate routes in the earlier period is completely unknown, which suggests that the lamprey numbers in this period could have been even higher than what the fish count records indicate. Despite the substantial adjustment factor associated with the fish count efficiency, the number of lamprey above the dam in recent years appears to be considerably depressed compared to historical counts.

In Chapter 3, we examined the seasonal movement patterns of adult Pacific lamprey at Winchester Dam. The majority of lamprey that did not pass Winchester Dam remained and held at the base of the dam at the end of their summer migration (63% in

2009 and 67% in 2010). Types of habitat most frequently used by lamprey downstream from the dam included dam surface, interface zones between fast and slow water, and highway bridge pilings. The movement behavior and holding locations changed considerably between August and September; the frequency of movements decreased sharply during this period as many lamprey started to use the dam surface away from the fish ladder. This also coincided with the end of the lamprey run as indicated by the lamprey capture data; 90% of the run was captured by 9 August in 2010. Lamprey used coldwater thermal refuges that were 0.4 C° to 2.8 C° colder than the mean river temperature immediately downstream of the dam and this differential continued to increase as the summer progressed. We suspect that hyporheic flow and/or influxes from thermal stratification in the reservoir water may be responsible for this differential, which could be verified by measuring the static liquid pressures below the dam and seasonal temperature profiles in the reservoir water. We concluded that lamprey displayed a high level of activity during the early and mid summer months, but they altered their behavior markedly, becoming sedentary to initiate their pre-spawning holding sometime between August and September.

The timber crib design of Winchester Dam offers unique interstitial spaces for adult Pacific lamprey, and we found many tagged lamprey holding in these spaces for extended periods. In fact, over 410 adult lamprey were captured at the base of the dam in late summer of 2009 during the first three days of a dewatering event for dam maintenance, indicating that many untagged lamprey were holding at the base of the dam. We also identified lamprey using the cold-water thermal refuges at the dam, and the interstitial spaces within the timber crib structure may provide access to hyporheic flow which modulates temperature extremes. Therefore, one could argue that the lamprey that remained below the dam may not have had the motivation to pass the dam and were instead using the holding habitat at Winchester Dam to simply overwinter.

Some considerations related to the reproduction of the adult lamprey may provide additional insights into this matter. Although we observed suitable spawning habitat and identified multiple lamprey redds below the dam in both the main channel (> 2 m deep) as well as a smaller side channel (~1 m deep) during the spring of 2009-2011, the spawning habitat immediately below the dam was unlikely to be sufficient for the estimated 3003~5109 adult lamprey (see Chapter 2) that halted their migration at the base of the dam. We speculate that not all lamprey could spawn successfully without a high degree of superimposition given the habitat conditions. Furthermore, spawning habitat of Pacific lamprey is typically observed in rivers and streams that are considerably smaller than the size of the mainstem North Umpqua River (Gunckel et al. 2009; Brumo et al. 2009) and there is only one tributary downstream of Winchester Dam (Sutherlin Creek located 3.6 km downstream of the dam) that could potentially provide suitable tributary spawning habitat. In the North Umpqua River, we observed lamprey spawning in deep water habitat (> 2 m deep), but uncertainty remains as to whether this is part of their natural spawning habitat. Lamprey may have been forced to spawn in this habitat because there were simply no other choices. Besides the issue of spawning habitat availability, the physiological effects of passage delay and the impacts from predators (such as great blue heron, osprey, river otters, etc.) need to be considered as indirect effects of the dam on Pacific lamprey reproduction.

Habitat conditions for larval lamprey may also be relevant to the question at hand. Because a considerable portion of the fine substrate and organic matter from the upstream environment is collected and artificially concentrated above the dam in the reservoir water, only limited amount of optimal larval habitat is currently available below the dam (Wallick et al. 2010). Furthermore, the optimal temperature for Pacific larval lamprey growth is near 18 C° (Meeuwig et al. 2005) and the cooler upper reaches above the dam would most likely provide more suitable habitat conditions for the larval lamprey than the warmer lower reaches by Winchester Dam. The concentration and high density of adult Pacific lamprey found below the dam where water temperature conditions frequently exceed 24 C° in midsummer appear to be counterproductive to the growth and survival of larval lamprey.

In our study, adult lamprey that were either released above the dam or passed the dam on their own distributed themselves widely in the upstream environment (Figure 5.1). This was also observed in four other radio telemetry studies that monitored the lamprey spawning location using a combination of fixed stations and manual tracking (Clemens et al. 2011; S. Starcevich pers. comm. 2011; McCovey et al. 2007; Robinson and Bayer 2005). Although Winchester Dam was not the only location where multiple lamprey held for an extensive period of time within the North Umpqua basin, there were always some distance among the holding lamprey (usually >100 m) or temporal lag in their usage of the habitat in other locations (A-D in Figure 5.1), and none of the tagged lamprey appeared to share the same location concurrently. Interestingly, we confirmed several incidences in which a tagged lamprey moved into the exact same habitat occupied by another tagged lamprey only after the habitat was vacated by the former holding lamprey. These results suggest that holding lamprey are inclined to maintain some distance among themselves, and the holding behavior shown at the dam where multiple tagged lamprey and hundreds of untagged lamprey were holding together in a relatively small area appears extremely atypical of holding behavior exhibited in other areas.

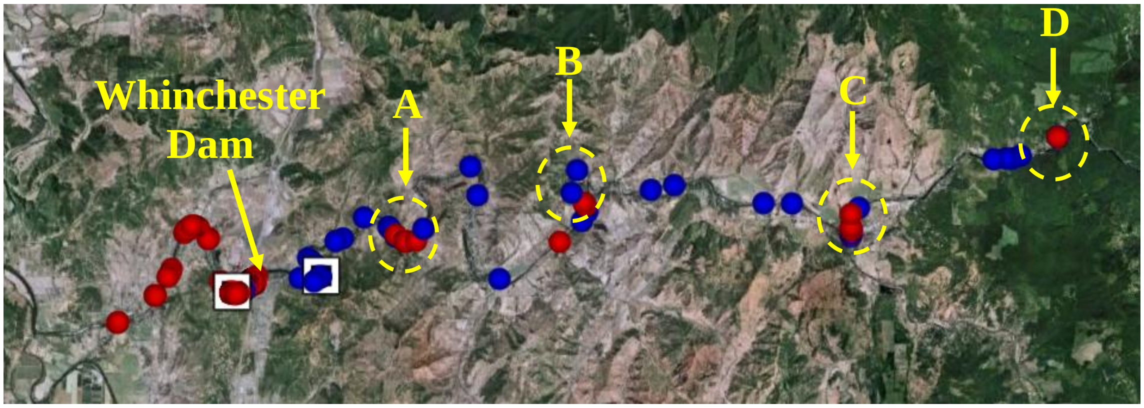

Figure 5.1. Holding habitat of adult Pacific lamprey from 2009 and 2010 in lower North Umpqua River. Blue circles show the lamprey released above Winchester Dam, whereas the red circles show the lamprey released below the dam. The white square to the left of Winchester Dam represents the release location downstream of the dam and the white square to the right of Winchester Dam represents the release location upstream of the dam. The yellow dotted circles represent the locations where multiple tagged lamprey held extensively (A, B, C, and D): A is river km 19 (upper end of Page Road), B is river km 33 (downstream of Whistler's Bend campground), C is river km 46 (confluence of Little River), and D is river km 56 (downstream of Rock Creek confluence).

Based on our results and circumstantial evidence, we speculate that lamprey that remained at Winchester Dam were initially attempting to pass the dam in search of better habitat conditions upstream, but due to innate, physiological changes associated with the end of the summer, they were compelled to use the abundant holding habitat at the base of the dam to overwinter. The presence of coldwater thermal refuges available at the base of the dam may have also contributed to the high density of adult lamprey using this area.

In Chapter 3, the seasonal migratory activity of adult Pacific lamprey was evaluated in the North Umpqua River. The majority of the overall upstream migration (95%) took place during the initial migration phase, and only small-scale upstream movements were observed during the pre-spawning holding and final migration phases (4% and 1%, respectively). The median rate of upstream migration was the fastest during the initial migration phase and was 1.9 km/day (ranging from 0.3 to 11.0 km/day) for tagged lamprey released above Winchester Dam. During the pre-spawning phase (a 5-month period in winter), 71% of the lamprey remained in the exact same location where they initiated holding behavior. Summer pre-spawning mortality (five confirmed) was mostly observed during the mid-summer at or immediately downstream from Winchester Dam when water temperature was generally high. Winter mortality, on the other hand, appeared to be absent or very low. For example, the majority of the tagged lamprey exhibited downstream migration during the spring spawning season when the discharge level was considerably low (hence, not influenced by the high water events).

The majority of the lamprey upstream migration was detected between June and August in both 2009 and 2010. Because many of the lamprey initiated holding behavior in August when the water temperature began to drop from the summer temperature peaks, we hypothesize that water temperature, and in particular the relative change in water temperature, may be influencing their upstream migration. Downstream movement during the final migration phase was strongly associated with the new moon phase (df = 121, r = 0.251, p-value = 0.0027). For more information on the environmental factors that influence lamprey seasonal upstream migration, see Appendix A.

Multiple regression analysis indicated that the total migration distance traveled by individual lamprey was most strongly associated with Winchester Dam presence/absence, relative tag size, and water temperature and photoperiod conditions at release. In Chapter 2, we showed that the migration timing of lamprey, in addition to dam presence/absence and relative tag size played a key role in influencing the total upstream migration of lamprey. This indicates that water temperature and photoperiod may be the two environmental variables that drive migration timing. The early run lamprey that arrived when water temperature was low and the photoperiod was long traveled much longer distances compared to the later portions of the run that arrived when water temperature was higher and the photoperiod shorter. The effect of water temperature was considerably higher than that of photoperiod based on the Akaike importance weights (95% and 5%, respectfully).

Although the main effect of fish morphology and physiology on total upstream migration distance was largely absent, we detected a significant interaction effect between the dorsal fin interval length and the water temperature conditions at release. Lamprey with longer interval length migrated further compared to those with shorter interval length when the water temperature conditions at release were high, and the reverse relation was observed during low water temperature conditions.

We also investigated the habitat use of pre-spawning adult Pacific lamprey in three spatial scales (for more information, see Appendix B). At the macro scale, as represented by 1.5 km reaches, the radio-tagged lamprey were concentrated in reaches with a high number of individual habitat units (regardless of the habitat type). At the meso scale, as represented by individual habitat units (~100 m), run habitat and boulder substrate were used significantly more in comparison to available habitat. At the micro scale, as represented by the precise locations within the habitat units (<3 m), the interface of habitats (head and tail locations) were used significantly more for riffle and run habitats, while no distinct pattern was observed for pool and glide habitats. We hypothesized that lamprey may be actively seeking intermediate flow and/or depth in the fast, shallow habitat units (riffles and runs).

The original goal of this project was to assess the passage efficiency and passage routes selected by pre-spawning adult Pacific lamprey at Winchester Dam. This information was critical for estimation of the number of lamprey that migrate to and pass Winchester Dam. However, the discovery of adult lamprey holding within the wooden structure of the dam and in other areas surrounding the dam raised an important question: are lamprey moving to Winchester Dam to use the holding habitat (and hence not motivated to pass)? To answer this question, it was critical that we had a good understanding of their migration and movement behavior in general to compare with the specific behavior observed at Winchester Dam. In the three main chapters, we answered the following questions systematically: 1) "what is the passage efficiency and how does the migration pattern differ between lamprey that were released downstream vs. upstream of the dam?"; 2) "For the lamprey that approached the dam, what was the spatiotemporal patterns in movement behavior and how did water temperature affect their movement and/or lack of movement (Chapter 3)?"; and 3) "How can we characterize the upstream migration behavior of lamprey that were released above the dam or passed the dam on their own (Chapter 4)?"

For Pacific lamprey conservation and recovery, some important questions still remain: 1) "If improvements were made for lamprey passage, would a large number of lamprey still hold at the base of the dam?"; 2) "What is the reproductive success of the lamprey that remain below Winchester Dam (in comparison with those upstream of the dam)?"; and 3) "What are the most critical factors that continue to limit their overall population recovery within the North Umpqua basin (predation by exotic species, freshwater habitat, dam passage, high temperature, pollution, dewatering activities during low flow conditions, etc.)?" Passage improvements for adult Pacific lamprey (including lamprey passage structures similar to the ones at the Bonneville Dam on lower Columbia River) are scheduled to be implemented at Winchester Dam in the spring of 2012, which would help determine the answer to question (1). The answer to question (2) would help determine the role of Winchester Dam in relation to the reproductive success of Pacific lamprey and is also critical in resolving the answer to question (3), which is a much broader, comprehensive question. These questions will need to be answered promptly; otherwise conservation and restoration efforts may not be able to restore the steadily declining lamprey populations within the North Umpqua River basin.

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APPENDICES

Appendix A: THE INFLUENCE OF THERMAL, HYDROLOGIC, AND METEOROLOGIC FACTORS ON THE SEASONAL MIGRATORY ACTIVITY OF PRE-SPAWNING ADULT PACIFIC LAMPREY WITHIN THE NORTH UMPQUA BASIN, OREGON, USA

Abstract

The seasonal spawning migration of Pacific lamprey, *Entosphenus tridentatus*, within the North Umpqua Basin in southwest, Oregon, USA, was monitored in 2009 and 2010 using radio telemetry. Our main objective was to conduct a series of multiple regression analyses to identify the factors most strongly associated with seasonal migratory activity of pre-spawning adult Pacific lamprey. The first set of regression analyses revealed effects of thermal, hydrologic, and metereologic variables on seasonal upstream migration activity. Increase in short-term day-to-day change in mean water temperature was associated with upstream movement during the initial migration phase (first spring/summer). Low lunar illumination, short photoperiod, and high short-term daily amplitude in water temperature were related to upstream movement during the pre-spawning holding phase (winter). High short-term temperature amplitude and low short-term day-to-day change in mean water temperature, and high lunar illumination were associated with upstream movement during the final migration phase (second spring/summer). In the second set of regression analyses, lamprey migration activity was assessed using lamprey capture rates as the response variable. High mean water temperature and long photoperiod were strongly associated with increases in the daily lamprey capture rates, indicating a potentially different mechanism at work compared to the daily migration analysis. Interaction terms using meteorologic variables were also evaluated in all of the multiple regression analyses; interaction terms that included

photoperiod, lunar cycle, and short-term mean wind speed improved the fit of the models significantly for the two sets of regression analyses.

Introduction

Evidence suggests that populations of Pacific lamprey, *Entosphenus tridentatus*, have declined sharply since the 1970s and 1980s across their native range (Kostow 2002; Moser and Close 2003). Spawning migrations of anadromous Pacific lamprey in freshwater habitat typically last over a year (Clemens et al. 2010) and can span up to 800 km (Hamilton et al. 2005). During this period, lamprey stop feeding, survive on their stored fat accumulated during the marine phase, and navigate through a wide variety of predation risks and altered freshwater environments. An improved understanding of the migratory behavior and its biological mechanism during this freshwater stage, therefore, could help managers make informed management decisions to facilitate their natural upstream migration and successful reproduction.

The primary objective of our study was to identify biotic and abiotic factors that are strongly associated with the seasonal migration of adult Pacific lamprey. Radio telemetry was used to monitor the behavior of adult Pacific lamprey captured in the lower North Umpqua River in 2009 and 2010. Few studies have focused on the pre-spawning migration behavior of Pacific lamprey outside the Columbia River system, and the autoecological mechanism of the migration behavior is still largely unknown for the species. Long-term data on adult lamprey migration timing from the lower Columbia River indicated that temperature and discharge were effective in predicting Pacific lamprey run timing and may play a role in controling upstream movement (Keefer et al. 2009). May through September was the primary migration season (Moser et al. 2002a), and movement was primarily nocturnal (Moser et al. 2002b). The migration rates of PIT-tagged lamprey in the same basin were also positively correlated with temperature and negatively correlated with discharge (Keefer et al. 2009). A telemetry study conducted in the John Day River (a Columbia River tributary) observed exclusive nighttime passage at fixed stations and migratory behavior ceased predominantly in September (Robinson and Bayer 2005). The final migration in this study began in mid-March and ended in mid-May the following year. In the lower Klamath River, a correlation between lamprey migration and rising temperature was documented, which coincided with decreasing river discharge (McCovey Jr. et al. 2007).

Spawning migration of other lamprey species in relation to environmental variables has been more thoroughly described. Applegate (1950) and Skidmore (1959) both showed the importance of temperature in the migration activity of Great Lakes sea lamprey (*Petromyzon marinus*), although the former depicted a curvilinear relationship with the absolute temperature whereas the latter denoted the significance of the relative changes in temperature. Binder et al. (2010) suggested that absolute and relative temperatures were the best predictor variables, whereas flow was only important for smaller streams in predicting migration activity based on 10 years of trap capture data. This particular study found no association between lunar cycle and migration, but other studies documented the significance of lunar illumination and/or circumlunar rhythm (Tesch 1967; Hardisty and Potter 1971; Sjöberg 1980). The importance of large discharge, especially for lamprey species that migrate predominatly during the fall/winter season [such as European brook lamprey (*Lampetra planeri*), European river lamprey (*Lampetra fluviatilis*), and sea lamprey] has been reported (Malmqvist 1980; Masters et al. 2006; Andrade et al. 2007). A key difference between Pacific lamprey and sea lamprey is that the freshwater residence of the adult Pacific lamprey is longer (~1 year) compared to that of the adult sea lamprey (~ 3 months), which could have large implications for their migratory behavior.

Two sets of multiple regression analyses were conducted to identify the factors most strongly related to lamprey migratory activity. We used an information-theoretic approach to evaluate the relative support for multiple hypothesized models based on Akaike's information criterion (AIC) as described by Burnham and Anderson (2002). The first set of analyses modeled the combined daily upstream migration rates, expressed as 'upstream migration distance per lamprey per day' for each of the three pre-spawning migration phases using hydrologic, thermal, and meteorologic factors. To account for the seasonally-distinct mechanism in upstream migratory behavior, data for the daily upstream migration rate were categorized into three migration phases [i.e. initial migration, pre-spawning holding, and final migration phases (Clemens et al. 2010)] and were analyzed separately. The second set of analyses identified the factors most strongly related to the daily lamprey capture rate using the same predictor variables from the first analysis. Trap catches of lamprey have been demonstrated to be an effective proxy for the general migratory activity of sea lamprey in Lake Ontario tributaries (Binder et al. 2010). We compared the best predictor variables from the two sets of analyses and evaluated the effectiveness of using trap catch data as a surrogate for the daily migratory activity of lamprey.

Methods

Study Area

The study area included the North Umpqua River from its mouth to Soda Springs Dam including all its tributaries in southwest Oregon, USA (Figure A.1). Anadromous species, including Pacific lamprey and salmonids (*Oncorhynchus* spp.), migrate 179 km in the Umpqua River from the Pacific Ocean to reach the mouth of the North Umpqua River. The North Umpqua Basin (3,520 km^2) holds roughly 110 km of anadromous fish habitat in the mainstem river and 450 km in all of its tributaries (Umpqua Basin Explorer, available at: http://oregonexplorer.info/ umpqua/). The historical extent of Pacific salmonids and Pacific lamprey distribution is very similar in many basins within the northwestern USA (Hamilton et al. 2005; Moyle 2002; Scott and Crossman 1973). The river originates from Maidu Lake at an elevation of 1,824 m on the western slope of central Cascade Mountains and joins the South Umpqua River northwest of Roseburg, Oregon, at an elevation of 110 m. Over 20% of the basin lies above 1,700 m elevation. Thus, strong, cool flows from snowmelt runoff last through the summer. Furthermore, the flow is augmented by large-volume groundwater systems stemming from the upper reaches (Wallick et al. 2010).

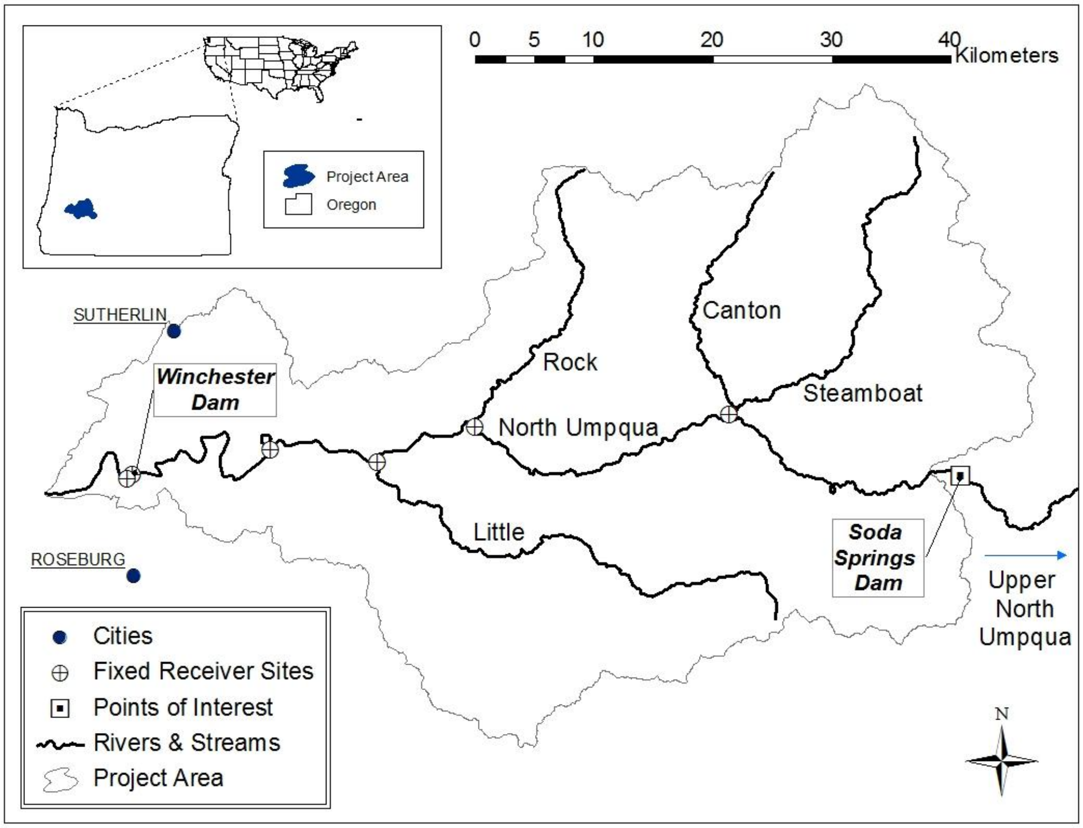

Figure A.1. Map of North Umpqua River below Soda Springs Dam, including major tributaries. Locations of fixed receiver sites and Soda Springs Dam are identified. Soda Springs Dam has been the upper extent of the anadromous fish habitat, but new fish ladders will enable anadromous fish to use the upper North Umpqua watershed starting in 2012.

Sampling and Tagging

In 2009 and 2010, adult Pacific lamprey were collected and radio-tagged during the initial migration phase (May-September) at Winchester Dam (river km 11.2). Water discharge at Winchester Dam typically ranges from 30 m^3/s during the summer low flow period (July-September) to 180 m^3/s during the winter-spring high flow period (December-February), with a mean annual flow of 105 m^3/s.

Adults were captured inside the lower fish ladder or within 50 m downstream of the dam using dip nets, an assortment of traps (Figure A.2), or by hand. Traps were designed to capture adult Pacific lamprey of all sizes. These traps were placed in a wide variety of locations on both banks and within 2 km downstream of Winchester Dam to diversify the sample. However, lamprey were only captured within 50 m downstream of the dam, and many were captured in the south entrance of the fish ladder (37%). To increase the sample size, a portion of the sample (37%) was captured in the middle section of the fish ladder just below the high velocity current. Traps were checked in the morning and then reset allowing them to fish 24 hours, while netting and hand-capture methods were used during the day, predominantly in the morning. The two most effective traps were 1) the Karuk Tribe traps, which worked best in swift water, and 2) tube traps, which performed best in slow, deep water.

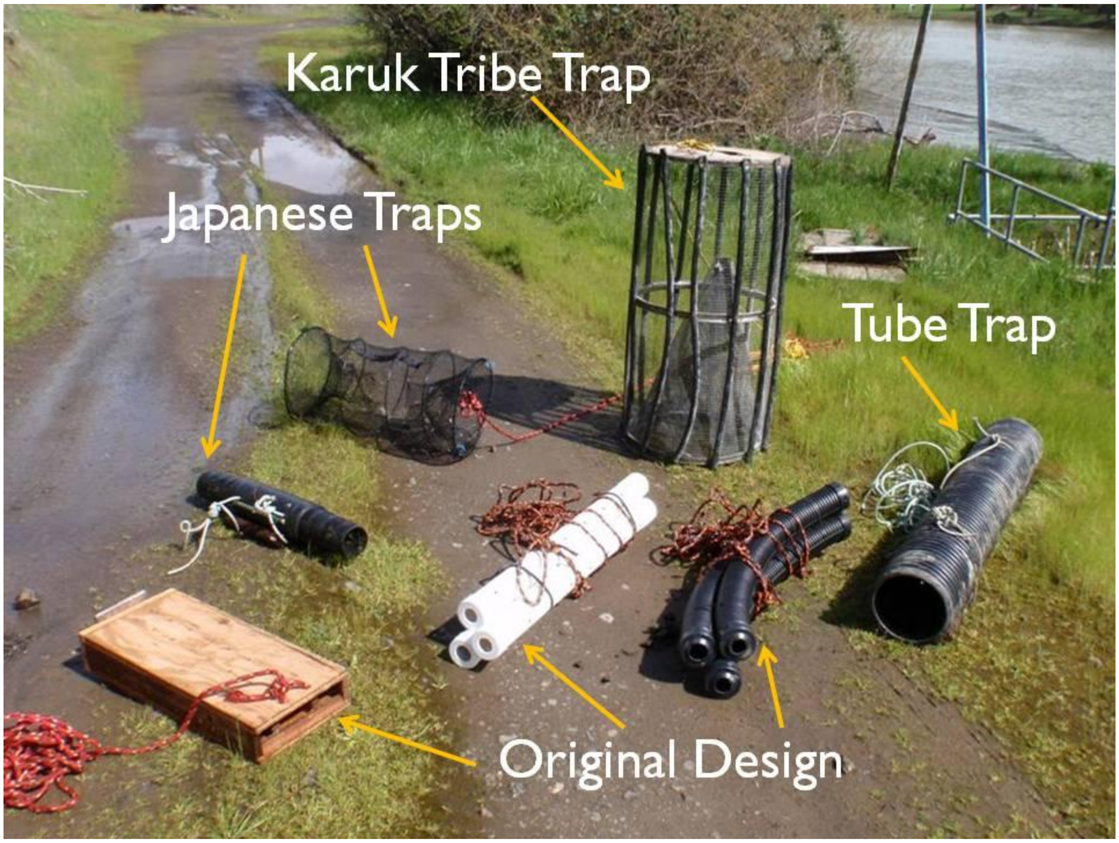

Figure A.2. Examples of traps used in capturing lamprey (clockwise: Karuk Tribe trap, tube trap, original design [bundles of small tubes & wood boxes], and Japanese eel traps). The Karuk Tribe trap is 1.2 meter in length, for size reference.

Captured lamprey were handled immediately or held in a flow-through container (30 – 70 L) in the river for 2 – 48 hours before surgically implanting radio tags. Lamprey were individually anesthetized, measured, and surgically implanted with radio transmitter tags following the surgical techniques described by Moser et al. (2002a) and the training and practice provided by lamprey telemetry experts. Post surgery, lamprey recovered in an aerated recovery bucket for 1-3 hours to allow monitoring of their conditions before release. All tagged lamprey were released in calm water of a pool or a side pool to minimize post-release stress.

Winchester Water Treatment Plant (City of Roseburg) routinely collects data on water temperature 35 m downstream from Winchester Dam on the southest bank of the North Umpqua River. The daily mean temperature of water withdrawn from this deep, swift segment of the river at a depth of 3.7 m was used to represent the river water temperature at the dam. Flow measurements were taken by Douglas County (Station #14319500) at the same location and were available from the U.S. Geological Survey website (http://waterdata.usgs.gov/nwis/uv?14319500). Data for the photoperiod and lunar phases were collected online from the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). All other meteorologic data were collected at the weather station in Roseburg, Oregon (Coop ID #357331) and were downloaded from the National Climatic Data Center website (http://www.ncdc.noaa.gov/oa/climate/stationlocator.html).

Radio Tags and Monitoring of Location

To ensure that the tags represented less than 8% of the fish's cross-sectional area, only captured lamprey that met the minimum mid-girth criterion of 102 mm were surgically implanted with the Lotek NTC-6-2 nano tags (4.3 g in air, 9x30 mm) in 2009. In 2010, two additional types of tags were deployed: Lotek NTC-3-2 nano tags (1.1 g, 6x16 mm) and MST-820T temperature sensor tags (2.2 g, 8x22 mm). The minimum girth threshold was reduced to 73 mm and 90 mm, respectively, for these smaller tags, using the same 8% area ratio criterion. All tagged lamprey had a tag/lamprey weight ratio smaller than 1.2%. One of the objectives for both years was to tag a sizeable number of lamprey from the early, middle, and late run of the population.

Radio-tagged lamprey were tracked using manual tracking and fixed sites. Fixed sites were established at Winchester Dam and directly above major tributary junctions (Little River [river km 46.7], Rock Creek [river km 57.5], and Steamboat Creek [river km 84.9]) (Figure A.1). Additional fixed sites were added downstream (river km 10.6) and upstream (river km 33.2) from the dam starting in September, 2010, to detect small scale movements, including fallbacks. All fixed sites had a minimum of two aerial antennas to detect both lamprey presence and direction of movement. The fixed stations operated 24 hours of the day for the majority of the project period.

Manual tracking involved mainly vehicle tracking using the extensive road network in the basin, but when the tagged lamprey were detected, more precise locations (< 15 m) were found by on-foot mobile tracking using triangulation when feasible. Tracking by rafts was also used in mid-summer in both years to cover a portion of the river that was otherwise hard to access. Each radio-tagged lamprey was manually tracked at least once a week (usually 2~4 times a week) between May and September. This frequency was reduced to once every two weeks during the winter between October and February in accordance with the extensive reduction in movement. The spring spawning migration between April and July was tracked on a weekly basis.

In 2009, 15 radio-tagged lamprey were released 0.9 km downstream of Winchester Dam while 2 were released above the dam (2.5 km and 23.9 km upstream of dam). Seven additional lamprey captured during a two-week-long reservoir water dewatering event for dam maintenance on 1 September, 2009, were also radio-tagged; 4 were released immediately upstream of the dam in the dewatered reservoir water, and the remaining 3 were released immediately downstream of the dam. In 2010, 31 radio-tagged lamprey were released 0.9 km downstream of the dam while 14 were released 2.5 km upstream of the dam (end of reservoir water).

Because of the distinct changes in lamprey behavior observed in association with the migration phases, their movement was analyzed separately for each phase. The initial migration phase (May-September) is generally characterized by the active upstream migration during the first spring/summer. The pre-spawning holding phase (October-February) is a period of prolonged holding and metabolic depression during the fall/winter (Gamper and Savina 2000). The final migration phase (March-July) is characterized by the enhanced level of activity associated with the beginning of the spawning migration in the second spring/summer. Tags from 2009 and 2010 were included in the initial migration phase analysis. Only tags from 2009 were included in the analysis for the pre-spawning holding and final migration phases

All lamprey holding locations were given a best approximate start and an end date as determined by manual tracking and fixed station data to monitor the duration of the holding behavior (in days). For each detected individual lamprey movement event, the rate of movement (km/day) for the individual fish was calculated using the following equation:

$$\frac{river\ km_{n,t} - river\ km_{n,t-1}}{start\ date_{n,t} - end\ date_{n,t-1}}$$

where $river\ km_{n,t}$ represents the river km (0.1 km resolution) of an individual lamprey location at time t; $river\ km_{n,t-1}$ represents the river km of the lamprey location immediately prior to $river\ km_{n,t}$; $start\ date_{n,t}$ represents the first date the fish (n) was identified at $river\ km_{n,t}$; and $end\ date_{n,t-1}$ represents the last date the fish was identified at $river\ km_{n,t-1}$. Because the relation between distance and time is most likely non-linear (i.e. variable movement rates within a set of time) and because fish detections were not always made right after lamprey stopped moving, these movement rates only provide a conservative measure of ground speed and actual rates could have been much higher.

Data and Modeling Analyses

Statistical analyses were performed using R statistical software (R Development Core Team 2011). For the regression analyses, we used an information-theoretic approach as described by Burnham and Anderson (2002). Any predictor variable that was strongly correlated with other predictor variables (a Pearson correlation coefficient > 0.7) was removed from the list of candidate variables for all analyses to avoid multicollinearity (Moore and McCabe 2003). Linear multiple regression models were fit using R statistical software (R Development Core Team 2011) and an AIC score corrected for small sample size (AICc) was calculated for each model (Hurvich and Tsai 1989):

$$\mathrm{AICc} = n\log(\frac{\mathrm{RSS}}{n}) + 2K + \frac{2K(K+1)}{n-K-1}$$

where n is the sample size, K is the number of estimable parameters, and RSS is the residual sum of squares. Akaike weight (w_i) for each model was calculated using differences in AICc scores ($\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{min}$):

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{r=1}^{R}\exp(-0.5\Delta_r)}$$

Multimodel inference and model averaging were used to incorporate model selection uncertainty of the predictor variables (Burnham and Anderson 2002). Evidence ratio ($\frac{\mathrm{w_{max}}}{\mathrm{w_i}}$) was also calculated for each model as a reference for the confidence in the model; a model with an evidence ratio of 10 or higher would indicate that it is 10 times less likely to be better than the best-approximating model (Burnham and Anderson 2002). The Akaike importance weight for each variable was calculated by summing the model weights from all models that contained the variable of interest. Model averaged parameter estimates and unconditional standard errors were computed for all parameters using the modavg function from “AICcmodavg” package in R. The precision of each parameter was estimated by computing 90% confidence intervals using the unconditional standard errors. Finally, model averaged parameter estimates were standardized using the standard deviation of each variable to evaluate the expected effects given the range of variable values.

Analysis of Daily Upstream Migration

We modeled the combined daily upstream migration rate of radio-tagged lamprey as a response variable to help describe the biological mechanism behind their migration behavior. For each given day, the sum of distance traveled by all lamprey in the sample was divided by the total number of lamprey to estimate the mean distance traveled per lamprey per day. The upstream and downstream movement was evaluated separately to account for potentially unique processes involved in migration directionality. Because the migration activity of the tagged lamprey released below Winchester Dam was considerably inhibited by the presence of the dam, only lamprey that were released above the dam or those that passed the dam on their own were included in this analysis (n = 7 in 2009 and n = 19 in 2010). The main objective was to identify the hydrologic, thermal, and meteorologic variables most strongly related to the migration activity of pre-spawning Pacific lamprey in each of the three migration phases.

For the initial migration phase and pre-spawning holding phase analyses, we used two meteorologic variables (photoperiod and lunar cycle) and four hydrologic/thermal variables (discharge, mean water temperature, change in water temperature, and water temperature amplitude) (Table A.1). To avoid potential overfitting of models given the sample size for each analysis (n = 214 for the initial migration phase, n = 151 for the pre-spawning holding phase, n = 122 for the final migration phase), only parsimonious multiple linear regression models containing a maximum of four variables were constructed and compared using the combination of six predictor variables (excluding the base variables).

Table A.1. List of predictor variables used in the multiple regression analyses for phase-specific daily upstream migration activity and daily lamprey capture. [analysis code: a = initial migration phase migration, b = pre-spawning holding phase migration, c = final migration phase migration, d = daily lamprey capture]. For all four analyses, x_{lag} was in all candidate models to correct for first-order positive serial correlation. For the initial migration phase analysis, x_{year} was in all candidate models to account for the year-to-year variability in migration rates. *$x_{visibility.10}$ and $x_{wind.10}$ were only included in the interaction term analyses.

Variable	Type	Analysis	Description
x_{lag}	log(x) for a,b,c asin(sqrt(x)) for d	a,b,c,d	response variable value from the previous day (C°)
x_{year}	categorical	a	year in which lamprey were captured and released (1. 2009, 2. 2010)
x_{temp}	linear	a,b,d	daily mean water temperature (C°)
$x_{change.10}$	linear	a,b,c,d	10-day moving average of [day-to-day change in x_{temp} (C°)]
$x_{amplitude.10}$	linear	a,b,c,d	10-day moving average of [daily water temperature amplitude (C°)]
$x_{discharge}$	log(x)	a,b,c	daily mean discharge (m^3/s)
x_{photo}	linear	a,b,d	photoperiod (length of daylight hours per day)
x_{moon}	linear	a,b,c,d	fraction of the moon illuminated
$x_{visibility.10}$	linear	a,b,c,d*	10-day moving average of [daily atmospheric visibility (km)]
$x_{wind.10}$	linear	a,b,c,d*	10-day moving average of [daily mean wind speed (knot)]

To account for the absolute and relative properties of water temperature and their effects on lamprey migration, we included variables depicting the day-to-day change and daily amplitude in temperature as well as mean temperature. Based on past research and observations that suggested enhanced migration and spawning activity by lamprey during or near the full moon phase (Hardisty and Potter 1971; Sjöberg 1980), we also included lunar cycle in the global model.

Short-term predictor variables that expressed the 10-day moving averages of daily predictor variables were included in the regression analysis for two reasons. We hypothesized that lamprey movement may be linked to short-term (~10 day) conditions more than the instantaneous condition from one day alone. For instance, lamprey may be stimulated to move upstream only when temperature has been rising continuously for the past several days. Although fixed station monitoring provided 24-hour, continuous data, manual tracking monitored each individual fish at a somewhat reduced frequency (daily to weekly, depending on the season). Hence, it was also important to incorporate short-term variables to partially account for the lack of precision in the daily movement data. As a result, predictor variables that fluctuated widely on a daily basis, such as daily temperature amplitude and day-to-day change in temperature, were converted to short-term variables for the two sets of regression analyses. For the final migration phase, mean temperature and photoperiod were removed from the global model due to their high correlation with the short-term daily amplitude in temperature ($r > 0.7$).

The response variable for the daily migration activity analysis (all three migration phases) were transformed using natural log transformation to normalize the residuals as closely as possible, and a small constant (exponential of the integer value of the natural log of the minimum non-zero response value) was added to enable the transformation for zero values with minimum data distortion (McCune and Grace 2002). After transformation, normality plots improved considerably (became symmetrical) and the assumption of equal variance was met adequately. The discharge variable was also transformed using natural log transformation. Preliminary data analysis suggested positive first-order serial correlation among residuals from the global models (serial correlation coefficients ranging from 0.25-0.70), indicating that the error term from a given day was significantly correlated to the error term from the previous day. To meet the assumption of independence, we included a lagged dependent variable in the base model, and this effectively reduced the serial correlation to below 0.1. We also included a categorical variable “year” in the base model for the initial migration phase to account for the variation in migration rate between 2009 and 2010.

Modeling studies on the spawning migration of European river lamprey (*Lampetra fluviatilis*) from Finland showed that four variables were strongly related to the winter upstream migration: lunar cycle, wind speed, atmospheric visibility, and discharge level (Aronsuu et al. 2002). Although we did not include wind speed and atmospheric visibility in any of the simple additive models, we hypothesized that these two variables could potentially interact with other meteorologic variables from each of the global model. To determine the presence of interaction between the meteorologic variables, we constructed interactive terms using a combination of four meteorologic predictor variables: photoperiod, lunar cycle, short-term wind speed, and short-term atmospheric visibility (Table A.2). All six combinations of the meteorologic interaction terms were added to the top-ranked simple additive model from each phase-specific analysis and the resulting models were ranked based on the AICc values. Because photoperiod was removed from the global model in the final migration phase analysis due to multicollinearity ($r > 0.7$), only the three combination of interactive terms using the remaining three meteorologic variables were evaluated for this analysis. Whenever an interaction term was added to the top-ranked simple additive model, the main effects of the two variables that constructed the interactive term were also included in the model.

Table A.2. List of six interaction terms used in the multiple regression analyses for phase-specific daily migration activity and daily lamprey capture. [analysis code: a = initial migration phase, b = pre-spawning holding phase, c = final migration phase, d = daily lamprey capture]. These six interaction terms were each added to the top-ranked simple additive model for each phase-specific analyses and were compared based on AICc values.

Interaction Term	Analysis
$x_{\text{photoperiod}} * x_{\text{moon}}$	a,b,d
$x_{\text{photoperiod}} * x_{\text{visibility.10}}$	a,b,d
$x_{\text{photoperiod}} * x_{\text{wind.10}}$	a,b,d
$x_{\text{moon}} * x_{\text{visibility.10}}$	a,b,c,d
$x_{\text{moon}} * x_{\text{wind.10}}$	a,b,c,d
$x_{\text{visibility.10}} * x_{\text{wind.10}}$	a,b,c,d

Analysis of Daily Lamprey Capture

Multiple linear regression models were also constructed using data from the daily capture of adult Pacific lamprey at Winchester Dam in the spring/summer of 2009 and 2010. Binder et al. (2011) have demonstrated that trap catch data of sea lamprey served as a reliable measure for their migratory activity. Our objective was to identify the most strongly associated factors for the daily capture rate of lamprey and evaluate how these were similar or different from those selected for the daily migration activity analysis during the initial migration phase. Any lamprey with signs of sexual maturity (e.g. closed dorsal interval, stunted body length, pseudo-anal fin, distended abdomen) were eliminated from the dataset to restrict the sample to newly arriving migrants in their first year. To standardize for the annual variation in run size, we used the proportion of the total run (proportion of run = daily catch / total annual catch) as the response variable. To normalize the model residuals as closely as possible, these proportions were transformed using arcsine-square-root transformation. All variables from the initial migration analysis except discharge were part of the global model for this analysis; discharge variable was removed due to its high correlation with mean temperature ($R > 0.7$). The same six interaction terms evaluated in the daily migration analysis were also evaluated in the daily capture analysis using the top-ranked simple additive model for the daily lamprey capture as the base model.

Results

Analysis of Daily Upstream Migration

The regression analysis for the daily upstream movement rate during the initial migration phase produced 24 models with an evidence ratio larger than 10, indicating that the top-ranked model is at least 10 times better than those 24 models. The null model with just the two base variables had an evidence ratio of 1190, indicating that the top-ranked model is 1190 times better than the null model (Table A.3). Short-term day-to-day change in water temperature was included in all top 23 models and was the only predictor with a model-averaged parameter 90% CI estimate that excluded zero, which is reflected in its high Akaike importance weight of 0.98 (Table A.4). The standardized model-averaged parameter estimates of this predictor after back transformation indicated that an increase in the variable values by 1 standard deviation (0.21 C°) resulted in a change in the median of the daily upstream migration rate by 1.60 (90% CI: 1.28, 1.99). Although the model-averaged parameter 90% CI estimate for mean water temperature and short-term daily amplitude in water temperature both included zero, these two predictor variables also had moderately high Akaike importance weights (0.55 and 0.38, respectively).

Table A.3. Summary of the five top-ranked models from the multiple regression analysis modeling daily upstream migration rate during the initial migration phase. The null model is also listed for comparison (lowermost on the list). The base variables, x_{lag} and x_{year}, were included in all candidate models. [n = sample size; k = number of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; Δ_i = AICc$_i$ – AICc$_{\text{min}}$; w_i = Akaike weight, w_{max} / w_i = evidence ratio]

Models ($x_{\text{lag}} + x_{\text{year}}$ included in all models)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{change.10}} + x_{\text{temp}}$	214	6	0.752	796.16	0.00	0.12	1.0
$x_{\text{change.10}}$	214	5	0.751	796.25	0.09	0.11	1.0
$x_{\text{change.10}} + x_{\text{temp}} + x_{\text{amplitude.10}}$	214	7	0.753	796.33	0.17	0.11	1.1
$x_{\text{change.10}} + x_{\text{discharge}}$	214	6	0.750	797.86	1.70	0.05	2.3
$x_{\text{change.10}} + x_{\text{amplitude.10}}$	214	6	0.750	797.94	1.78	0.05	2.4
(null model)	214	4	0.732	810.93	14.77	<0.001	1190.0

Table A.4. Akaike importance weights, model averaged parameter estimates, standard error (SE), lower and upper 90% confidence intervals (CI), parameter standard deviation (SD), and standardized parameter estimate (Estimate × SD) for the six candidate variables in the multiple regression analysis modeling the daily upstream migration rate during the initial migration phase. Akaike importance weight values in bold text indicate parameter estimates with non-zero CIs.

Parameter	Weight	Estimate	SE	Lower CI	Upper CI	SD	Standardized Estimate	Standardized Lower CI	Standardized Upper CI
$x_{\text{change.10}}$	**0.98**	2.26	0.64	1.21	3.32	0.21	0.47	0.25	0.69
x_{temp}	0.55	0.11	0.07	-0.02	0.23	2.88	0.30	-0.05	0.66
$x_{\text{amplitude.10}}$	0.38	-0.59	0.53	-1.46	0.28	0.27	-0.16	-0.40	0.08
$x_{\text{discharge}}$	0.28	0.02	0.86	-1.39	1.44	0.64	0.01	-0.88	0.91
$x_{\text{photoperiod}}$	0.26	-0.16	4.83	-8.11	7.78	0.05	-0.01	-0.38	0.37
x_{moon}	0.24	0.12	0.32	-0.40	0.65	0.35	0.04	-0.14	0.23

There were three models with a two-way interaction term that had a lower AICc value compared to the top-ranked simple additive model approximating the daily migration activity during the initial migration phase (Table A.5). A combination of pairs between three variables, $x_{\text{visibility.10}}$, $x_{\text{photoperiod}}$, and $x_{\text{wind.10}}$, comprised all of the interaction terms in these top-ranked models. The top-ranked simple additive model had an evidence ratio of 3.4, showing a moderate support for the top two-way interaction model. The top interaction model included the interaction between photoperiod and lunar cycle, signifying that the effect of lunar cycle varied depending on the daylight length. When the photoperiod was long, lamprey moved upstream at a higher rate during the new moon compared to full moon. When the photoperiod was short, on the other hand, lamprey moved upstream at a higher rate during full moon compared to new moon.

Table A.5. Summary of the models with a two-way interaction term that had a lower AICc value compared to the top-ranked simple additive model (lowermost on the list) approximating the daily upstream migration rate during the pre-spawning holding phase. The base variables, x_{lag} and x_{year}, were included in all candidate models. [n = sample size; k = # of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; Δ_i = $\text{AICc}_i - \text{AICc}_{\text{min}}$; w_i = Akaike weight]

Models (top-ranked simple additive model + interaction term)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{change.10}} + x_{\text{temp}} + x_{\text{photoperiod}} * x_{\text{moon}}$	214	9	0.759	793.7	0.00	0.33	1.0
$x_{\text{change.10}} + x_{\text{temp}} + x_{\text{moon}} * x_{\text{wind.10}}$	214	9	0.758	794.3	0.56	0.25	1.3
$x_{\text{change.10}} + x_{\text{temp}} + x_{\text{photoperiod}} * x_{\text{wind.10}}$	214	9	0.758	794.3	0.60	0.25	1.4
$x_{\text{change.10}} + x_{\text{temp}}$	214	6	0.752	796.2	2.43	0.10	3.4

The regression analysis for the daily upstream migration rate during the pre-spawning holding phase produced 39 models with an evidence ratio larger than 10, indicating that the top-ranked model is at least 10 times better than those 39 models. The null model with just the base variable, x_{lag}, had an evidence ratio of 12.4 , indicating that the top-ranked model is 12.4 times better than the null model (Table A.4). Lunar cycle, photoperiod, and short-term daily amplitude in water temperature all had a model-averaged parameter 90% CI estimate that excluded zero, which is reflected in their high Akaike importance weight of 0.75, 0.68, and 0.55, respectively. After back transformation, the standardized model-averaged parameter estimates of these predictors indicated that an increase in the variable values by 1 standard deviation (SD) resulted in a change in the median of the daily upstream migration rate by the following factors: 0.85

(90% CI: 0.75, 0.97) for x_{moon} (1 SD = 0.36 increase in illumination fraction); 0.84 (90% CI: 0.72, 0.97) for x_{photo} (1 SD = 0.79 hours); and 1.13 (90% CI: 1.00, 1.28) for $x_{\text{amplitude.10}}$ (1 SD = 0.18 C°).

Table A.6. Summary of the five top-ranked models from the regression analysis modeling daily upstream migration rate during the pre-spawning holding phase. The null model is also listed for comparison (lowermost on the list). The base variable, x_{lag}, was included in all candidate models. [n = sample size; k = number of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; $\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$; w_i = Akaike weight, w_{max} / w_i = evidence ratio]

Models (x_{lag} included in all models)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{moon}} + x_{\text{photoperiod}} + x_{\text{amplitude.10}}$	151	6	0.660	385.37	0.00	0.13	1.0
$x_{\text{moon}} + x_{\text{photoperiod}} + x_{\text{amplitude.10}} + x_{\text{change.10}}$	151	7	0.661	386.10	0.73	0.09	1.0
$x_{\text{photoperiod}} + x_{\text{moon}} + x_{\text{amplitude.10}} + x_{\text{discharge}}$	151	7	0.660	386.57	1.20	0.07	1.1
$x_{\text{moon}} + x_{\text{photoperiod}}$	151	5	0.655	386.62	1.25	0.07	2.3
$x_{\text{moon}} + x_{\text{photoperiod}} + x_{\text{amplitude.10}} + x_{\text{temp}}$	151	7	0.658	387.54	2.17	0.04	2.4
(null model)	151	3	0.641	390.40	5.03	0.01	12.4

Table A.7. Akaike importance weights, model averaged parameter estimates, standard error (SE), lower and upper 90% confidence intervals (CI), parameter standard deviation (SD), and standardized parameter estimate (Estimate × SD) for the six candidate variables in the multiple regression analysis modeling the daily upstream migration rate during the pre-spawning holding phase. Akaike importance weight values in bold text indicate parameter estimates with non-zero CIs.

Parameter	Weight	Estimate	SE	Lower CI	Upper CI	SD	Standardized Estimate	Standardized Lower CI	Standardized Upper CI
x_{moon}	**0.75**	-0.45	0.22	-0.80	-0.10	0.36	-0.16	-0.29	-0.03
$x_{\text{photoperiod}}$	**0.68**	-5.39	2.81	-10.01	-0.77	0.03	-0.18	-0.33	-0.03
$x_{\text{amplitude.10}}$	**0.55**	0.67	0.41	-0.01	1.35	0.18	0.12	0.00	0.24
x_{temp}	0.33	-0.05	0.05	-0.14	0.04	1.89	-0.09	-0.26	0.07
$x_{\text{change.10}}$	0.27	-0.21	0.41	-0.89	0.47	0.22	-0.05	-0.20	0.11
$x_{\text{discharge}}$	0.25	-0.05	0.15	-0.30	0.21	0.64	-0.03	-0.19	0.13

There were four models with a two-way interaction term that had a lower AICc value compared to the top-ranked simple additive model approximating the daily migration activity during the pre-spawning migration phase (Table A.8). The top three models (with an evidence ratio less than 10) all had lunar cycle in their interaction term, indicating that the effect of lunar cycle varied depending on the other atmospheric predictor variables (wind speed, photoperiod, and visibility). The top-ranked simple additive model had an evidence ratio of 196.5, showing strong support for the top two-way interaction model. The top interaction model indicated that when the short-term mean wind speed was low, lamprey moved upstream at a higher rate during the new moon compared to full moon. When the short-term mean wind speed was high, on the other hand, lamprey moved upstream at a higher rate during full moon compared to new moon, signifying a contrasting effect of the lunar cycle depending on the wind speed.

Table A.8. Summary of the models with a two-way interaction term that had a lower AICc value compared to the top-ranked simple additive model (lowermost on the list) approximating the daily upstream migration rate during the pre-spawning holding phase. The base variable, x_{lag}, were included in all candidate models. [n = sample size; k = # of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; $\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{\mathrm{min}}$; w_i = Akaike weight]

Models (top-ranked simple additive model + interaction term)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\mathrm{moon}} + x_{\mathrm{photoperiod}} + x_{\mathrm{amplitude.10}} + x_{\mathrm{moon}} * x_{\mathrm{wind.10}}$	214	8	0.688	374.8	0.00	0.67	1.0
$x_{\mathrm{moon}} + x_{\mathrm{photoperiod}} + x_{\mathrm{amplitude.10}} + x_{\mathrm{moon}} * x_{\mathrm{photoperiod}}$	214	7	0.680	377.3	2.52	0.19	3.5
$x_{\mathrm{moon}} + x_{\mathrm{photoperiod}} + x_{\mathrm{amplitude.10}} + x_{\mathrm{moon}} * x_{\mathrm{visibility.10}}$	214	8	0.681	378.3	3.54	0.11	5.9
$x_{\mathrm{moon}} + x_{\mathrm{photoperiod}} + x_{\mathrm{amplitude.10}} + x_{\mathrm{photoperiod}} * x_{\mathrm{wind.10}}$	214	8	0.673	381.8	7.01	0.02	33.4
$x_{\mathrm{moon}} + x_{\mathrm{photoperiod}} + x_{\mathrm{amplitude.10}}$	214	6	0.660	385.4	10.56	0.00	196.5

The regression analysis for the daily upstream migration rate during the final migration phase produced 11 models with an evidence ratio larger than 10, indicating that the top-ranked model is at least 10 times better than those 11 models. The null model with just the base variable, x_{lag}, had an evidence ratio of 88.5, indicating that the top-ranked model is 88.5 times better than the null model (Table A.9). Short-term daily amplitude in water temperature, short-term day-to-day change in water temperature, and lunar cycle all had a model-averaged parameter 90% CI estimate that excluded zero, which is reflected in their high Akaike importance weight of 0.96, 0.80, and 0.74, respectively. After back transformation, the standardized model-averaged parameter estimates of these predictors indicated that an increase in the variable values by 1 standard deviation (SD) resulted in a change in the median of the daily upstream migration rate by the following factors: 1.16 (90% CI: 1.07, 1.27) for $x_{\text{amplitude.10}}$ (1 SD = 0.28 C°); 0.90 (90% CI: 0.82, 0.97) for $x_{\text{dca.10}}$ (1 SD = 0.17 C°); and 1.09 (90% CI: 1.02, 1.18) for x_{moon} (1 SD = 0.36 increase in illumination fraction).

Table A.9. Summary of the five top-ranked models from the regression analysis modeling daily upstream migration rate during the final migration phase. The null model is also listed for comparison (lowermost on the list). The base variable, x_{lag}, was included in all candidate models. [n = sample size; k = number of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; Δ_i = AICc$_i$ – AICc$_{\text{min}}$; w_i = Akaike weight, w_{max} / w_i = evidence ratio]

Models (x_{lag} included in all models)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{amplitude.10}} + x_{\text{change.10}} + x_{\text{moon}}$	122	6	0.266	159.28	0.00	0.37	1.0
$x_{\text{amplitude.10}} + x_{\text{change.10}} + x_{\text{moon}} + x_{\text{discharge}}$	122	7	0.266	160.57	1.29	0.20	1.9
$x_{\text{amplitude.10}} + x_{\text{change.10}}$	122	5	0.247	161.21	1.92	0.14	2.6
$x_{\text{amplitude.10}} + x_{\text{moon}}$	122	5	0.244	161.78	2.50	0.11	3.5
$x_{\text{amplitude.10}} + x_{\text{change.10}} + x_{\text{discharge}}$	122	6	0.247	162.46	3.18	0.08	4.9
(null model)	122	3	0.187	168.26	8.98	<0.01	88.5

Table A.10. Akaike importance weights, model averaged parameter estimates, standard error (SE), lower and upper 90% confidence intervals (CI), parameter standard deviation (SD), and standardized parameter estimate (Estimate × SD) for the six candidate variables in the multiple regression analysis modeling the daily upstream migration rate during the final migration phase. Akaike importance weight values in bold text indicate parameter estimates with non-zero CIs.

Parameter	Weight	Estimate	SE	Lower CI	Upper CI	SD	Standardized Estimate	Standardized Lower CI	Standardized Upper CI
$x_{\text{amplitude.10}}$	**0.96**	0.55	0.19	0.23	0.86	0.28	0.15	0.07	0.24
$x_{\text{change.10}}$	**0.80**	-0.66	0.31	-1.16	-0.16	0.17	-0.11	-0.19	-0.03
x_{moon}	**0.74**	0.25	0.12	0.05	0.46	0.36	0.09	0.02	0.16
$x_{\text{discharge}}$	0.33	-0.08	0.10	-0.24	0.08	0.50	-0.04	-0.12	0.04

None of the interaction terms improved the top-ranked simple additive model in approximating the daily upstream migration rate during the final migration phase. The top-ranked model with an interaction term had an evidence ratio of 4.0, indicating that the top-ranked simple additive model (with an evidence ratio of 1.0) was 4.0 times better than this model with the interaction term.

Table A.11. Summary of the top-ranked models with a two-way interaction term compared to the top-ranked simple additive model (lowermost on the list) approximating the daily upstream migration rate during the final migration phase. The base variable, x_{lag}, were included in all candidate models. [n = sample size; k = # of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; Δ_i = $\text{AICc}_i - \text{AICc}_{\text{min}}$; w_i = Akaike weight]

Models (top-ranked simple additive model + interaction term)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{photoperiod}} * x_{\text{wind.10}}$	259	7	0.339	-690.0	0.00	0.98	1.0
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{photoperiod}} * x_{\text{visibility.10}}$	259	7	0.313	-680.4	9.64	0.01	123.7
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{wind.10}} * x_{\text{visibility.10}}$	259	8	0.315	-679.7	10.33	0.01	174.5
$x_{\text{temp}} + x_{\text{photoperiod}}$	259	5	0.305	-679.4	10.59	0.00	199.4

Analysis of Daily Lamprey Capture

We captured and measured 131 adult Pacific lamprey in 2009 and 77 in 2010 through trapping efforts. None of the captured lamprey, except one female in 2010, displayed any signs of sexual maturity (e.g. small dorsal interval, stunted body length, pseudo-anal fin, distended abdomen) and appeared to be in their initial migration phase. The run timing projected from the capture dates in 2009 and 2010 was similar to the run timing displayed in the previous 10 years, with the 50th percentile capture dates falling on July 6 and July 11, respectively.

The regression analysis for the daily lamprey capture rate during the initial migration phase produced 24 models with an evidence ratio larger than 10, indicating that the top-ranked model is at least 10 times better than those 24 models. The null model with just the two base variables had an evidence ratio of 10^8, indicating that the top-ranked model is 10^8 times better than the null model (Table A.12). Daily mean water temperature and photoperiod were included in all the top-ranked models with an evidence ratio smaller than 89 and both had a high Akaike importance weight (1.00 and 0.99, respectively) and a model-averaged parameter 90% CI estimate that excluded zero (Table A.13). Although the model-averaged parameter 90% CI estimate for the three remaining predictor variables (short-term day-to-day change and amplitude in water temperature and lunar cycle) all included zero, these predictor variables had moderately high Akaike importance weights (0.45, 0.38, and 0.34, respectively), suggesting that increases in the short-term day-to-day change in temperature and decreases in the short-term daily temperature amplitude and moon illumination may contribute partially to increases in the daily lamprey capture rate.

Table A.12. Summary of the five top-ranked models from the regression analysis modeling daily lamprey capture rate during the initial migration phase. The null model is also listed for comparison (lowermost on the list). The base variable, x_{lag}, was included in all candidate models. [n = sample size; k = number of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; Δ_i = AICc_i – AICc_{min}; w_i = Akaike weight, w_{max} / w_i = evidence ratio]

Models (x_{lag} included in all models)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{temp}} + x_{\text{photoperiod}}$	259	5	0.305	-679.4	0.00	0.19	1.0
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{change.10}} + x_{\text{amplitude.10}}$	259	7	0.311	-679.3	0.10	0.18	1.0
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{change.10}}$	259	6	0.308	-679.2	0.21	0.17	1.1
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{moon}}$	259	6	0.307	-679.0	0.38	0.16	1.2
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{amplitude.10}}$	259	6	0.306	-678.5	0.95	0.12	1.6
(null model)	259	3	0.205	-646.5	32.86	<0.001	$>10^8$

Table A.13. Akaike importance weights, model averaged parameter estimates, standard error (SE), lower and upper 90% confidence intervals (CI), parameter standard deviation (SD), and standardized parameter estimate (Estimate × SD) for the five candidate variables in the multiple regression analysis modeling the daily lamprey capture rate during the initial migration phase. Akaike importance weight values in bold text indicate parameter estimates with non-zero CIs.

Parameter	Weight	Estimate	SE	Lower CI	Upper CI	SD	Standardized Estimate	Standardized Lower CI	Standardized Upper CI
x_{temp}	**1.00**	0.007	0.001	0.005	0.010	3.49	0.026	0.018	0.033
$x_{\text{photoperiod}}$	**0.99**	0.600	0.162	0.334	0.867	0.03	0.018	0.010	0.026
$x_{\text{change.10}}$	0.45	0.034	0.024	-0.006	0.073	0.21	0.007	-0.001	0.015
$x_{\text{amplitude.10}}$	0.38	-0.024	0.020	-0.056	0.009	0.22	-0.005	-0.012	0.002
x_{moon}	0.34	-0.014	0.012	-0.033	0.006	0.35	-0.005	-0.012	0.002

There were three models with a two-way interaction term that had a lower AICc value compared to the top-ranked simple additive model approximating the daily lamprey capture rate during the initial migration phase (Table A.14). A combination of pairs between three predictor variables, $x_{\text{photoperiod}}$, $x_{\text{wind.10}}$, and $x_{\text{visibility.10}}$, comprised all of the interaction terms in these top-ranked models. The top-ranked simple additive model had an evidence ratio of 199.4, showing a strong support for the top two-way interaction model. The top interaction model contained the interaction between photoperiod and short-term wind speed, signifying that the effect of photoperiod varied depending on the wind speed. The model indicated that daily lamprey capture rates always increased in association with longer daylight length, but the rate of increase was significantly higher when short-term wind conditions were high instead of low.

Table A.14. Summary of the models with a two-way interaction term that had a lower AICc value compared to the top-ranked simple additive model (lowermost on the list) approximating the daily lamprey capture rate during the initial migration phase. The base variable, x_{lag}, were included in all candidate models. [n = sample size; k = # of parameters; adj. R^2 = adjusted R^2; AICc = Akaike's information criterion corrected for small sample size; $\Delta_i = \text{AICc}_i - \text{AICc}_{\text{min}}$; w_i = Akaike weight]

Models (top-ranked simple additive model + interaction term)	n	k	adj. R^2	AICc	Δ_i	w_i	w_{max}/w_i
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{photoperiod}} * x_{\text{wind.10}}$	259	7	0.339	-690.0	0.00	0.98	1.0
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{photoperiod}} * x_{\text{visibility.10}}$	259	7	0.313	-680.4	9.64	0.01	123.7
$x_{\text{temp}} + x_{\text{photoperiod}} + x_{\text{wind.10}} * x_{\text{visibility.10}}$	259	8	0.315	-679.7	10.33	0.01	174.5
$x_{\text{temp}} + x_{\text{photoperiod}}$	259	5	0.305	-679.4	10.59	0.00	199.4

Discussion

Analysis of Daily Upstream Migration

Past radio telemetry studies on the spawning migration of adult Pacific lamprey generally have only monitored part of the migration (either the initial migration or the final migration, but rarely the entire migration). Our study delved into the underlying biological mechanisms of the spawning migration during a whole year. Daily migratory activity was analyzed separately for the initial migration, pre-spawning holding, and final migration phases in light of the discrete shifts in lamprey migratory behavior. We hypothesized that the environmental factors most strongly associated with their upstream migration rate may change considerably with season. Although the regression analysis for the initial migration phase and daily lamprey capture included two years of data (2009 and 2010), the pre-spawning holding and final migration phases were only analyzed using only one year of data (2009). Daily upstream migration activity during the initial migration phase was most strongly related to the short-term day-to-day change in water temperature (Akaike importance weight = 0.98). As a single parameter, water temperature was strongly correlated to the lamprey migration rate (df = 212, t = 6.331, r = 0.399, p-value < 0.0001), but the bulk of the migration took place before the water temperature ever reached its peak in late July and early August. Photoperiod was also strongly correlated to the lamprey migration rate (df = 212, t = 6.015, r = 0.382, p-value < 0.0001), but the peak migration rate in both years took place 10 to 15 days after the peak length in photoperiod (20 June) was reached in both years. The short-term day-to-day change in water temperature was a better predictor variable for upstream migration compared to mean water temperature and photoperiod because movement appeared to be influenced more by the cumulative conditions of the relative changes in temperature rather than the absolute value itself.

The short-term daily amplitude in water temperature had the third highest Akaike importance weight (0.38), and the regression analysis indicated that the smaller the short-term daily amplitude in water temperature, the higher the lamprey migration rate. A small amplitude is an indication that maximum and minimum water temperatures were small, and lamprey may be more apt to swim upstream when the gap stayed small over the short-term period (10 days). We speculate that large amplitudes in daily temperature could make the physiological detection of the subtle day-to-day changes in mean temperature more difficult for lamprey due to the increased level of noise lamprey experience daily from this temperature amplitude. In our study, lamprey were most active between the hours of 22:00 and 8:00, which means that lamprey initiate their migration soon after the daily water temperature peak (~21:00) and halt their migration just before the daily water temperature hits the lowest point (~10:00). If water temperature decreases too quickly towards the early morning consistently over the short-term period (~10 days), this may deter lamprey from initiating their upstream migration.

The best approximating factors in predicting the daily upstream migration activity during the pre-spawning holding phase were lunar phase, photoperiod, and short-term daily amplitude in water temperature. The model-averaged parameter estimates indicated that more upstream migration was observed on days that had lower fraction of lunar illumination (i.e. new moon), shorter photoperiod, and higher short-term daily water temperature amplitude. Interestingly, the sign of the parameter estimate for most of the predictor variables during the initial migration phase was reversed during pre-spawning holding phase; predictor variables with positive estimates became negative and those with negative estimates became positive. For instance, lamprey may be keying into both summer and winter solstices as a biological signal for upstream migration. During the winter season when water temperature stays consistently low, the large water temperature amplitude over a 10-day period may be a clue for the lamprey that the spring season is around the corner and it is time to initiate their upstream migration. Indeed, the 10-day moving average of the daily water temperature amplitude increases rapidly in the beginning of spring after late March.

Lunar phase was one of the most important variables during both the pre-spawning holding and final migration phases. Interestingly, lamprey preferred lack of illumination for upstream migration during the pre-spawning holding phase, yet reversed their preference and opted for full moon during the final migration phase. The lack of illumination from the moon during the new moon phase may help lamprey avoid predators during their upstream migration. On the other hand, during the final migration phase in spring, finding their spawning partners may be a more important factor than avoiding predators; the illumination from the full moon may indeed help lamprey discover the location of their potential partners. There were also significantly more upstream movements when the lunar cycle was increasing (waxing) rather than decreasing (waning) during the spring.

The impact of the lunar phase is considerably harder to detect because the relationship is often non-linear (fish may prefer both new and full moon) and the break points in categorical variables often end up being arbitrary (for instance, how many days before and after the full moon do you include in the "full moon" category?). In our regression analysis, lamprey appeared to key in on entirely different lunar phases depending on the specific migration phase, and this can further muddle the relationship in modeling.

Besides the illumination factor, lamprey may be able to perceive the changes in gravity or have a circumlunar rhythm that is linked closely to their physiology. The anomalistic month, which influences tides, refers to the lunar cycle between perigree (when moon orbits closest to the earth) and apogee (when moon orbits farthest from the earth). This anomalistic month cycle is very similar in length to the synodic or lunar phase month cycle (~29.53 days), but slightly shorter (~27.21 days). In 2009 and 2010, the new moon phase during the winter seasons and the full moon phase during the summer seasons roughly matched the apogee period. Therefore, it is possible that lamprey are keying into the apogee period instead of the two diametrically opposite lunar illumination phases.

Analysis of Daily Lamprey Capture

Binder et al. (2010) demonstrated that lamprey capture rates were a reliable index of migration activity as they relate closely to the number of individuals that were moving upstream on a given night. By conducting two separate regression analyses on the daily upstream migration rate and the daily lamprey capture rate, we assessed whether the daily lamprey capture rate would prove to be a good indicator for the daily migratory activity. The main effects of the temperature parameters were similar across the two regression analyses; higher rates of migration and capture were generally observed when mean temperature was high, short-term day-to-day change in mean temperature was high, and short-term daily temperature amplitude was low. One main difference between the two analyses was the importance of the photoperiod and mean temperature. While the Akaike importance weight of the photoperiod was 0.99 for the daily capture analysis, it was only 0.26 for the daily migration analysis. Similarly, the Akaike importance weight of mean temperature was 1.00 for the daily capture analysis, but only 0.55 for the daily migration analysis. Under extremely high temperature conditions (>22 C°), lamprey may not be capable of swimming long distances due to physiological stress, whereas lamprey that are already at Winchester Dam may be more inclined to use the traps to rest during these physiologically demanding conditions (hence the difference in the Akaike importance weight).

Interaction of Factors

Substantial improvements were made to each of the top-ranked simple additive models by adding interaction terms composed of atmospheric variables, except for the model from the final migration phase. The effects of these interaction terms revealed yet another interesting dimension of the lamprey migratory behavior. For the initial migration phase, all combinations of interactions between photoperiod, lunar cycle, and short-term wind speed were important. Similarly, the best approximating interaction term for the daily lamprey capture modeling was that between photoperiod and short-term wind speed and it highlighted the importance of photoperiod during the summer. In all of these cases, the increase in wind speed during days of long photoperiod significantly increased their daily upstream migration rates. The combination of high wind speed and high visibility also enhanced the daily migration activity. Fishes' perception of longer day length may be confounded if the sky remains overcast and stagnant with no wind to clear the skies. Therefore, the combination of these two variables may indeed help lamprey perceive longer day light hours and stimulate upstream migration.

On the other hand, during the pre-spawning holding phase, it was mainly the combination of interaction terms that included lunar phase that produced the best approximating models for daily upstream migration activity. During the winter season, lamprey were more likely to move upstream during the new moon, when the visibility was low (i.e. cloudy) and wind speed slow, illustrating the opposite effects observed during the summer season.

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Appendix B: HABITAT USE OF PRE-SPAWNING ADULT PACIFIC LAMPREY AT THREE SPATIAL SCALES IN THE NORTH UMPQUA SUBBASIN, WESTERN OREGON, USA

Summary

Evidence suggests that Pacific lamprey, *Lampetra tridentata*, populations have declined precipitously in the Northwestern USA (Kostow 2002, Moser and Close 2003). State, federal, and tribal agencies have expressed concern at the apparent widespread decline of this culturally and ecologically important lamprey species (Close et al. 2003), which has prompted more monitoring and research on the species in recent years. There have been several research projects that examined the spawning migration of Pacific lamprey in recent years, but most have focused primarily on the migratory behavior (Clemens et al. 2011; Cummings 2007; Moser et al. 2002) and spawning activity (Gunckel et al. 2008; Luzier et al. 2005; Stone 2004) of Pacific lamprey. Although Pacific lamprey are known to hold for an extensive period during the winter, little information is currently available to describe the type of habitat that adult Pacific lamprey use for overwintering.

Our primary goals were 1) to assess the holding and overwintering habitat selected by adult Pacific lamprey in freshwater at three spatial scales (macro, meso, and micro scales; Figure B.1), and 2) to evaluate the temperature conditions of the habitat selected by adult lamprey using FLIR data from 2006 (Watershed Sciences 2007). Radio telemetry was used to monitor the behavior of adult Pacific lamprey captured in the lower North Umpqua River in 2009 and 2010. Because Pacific lamprey are known to spend over an entire year in freshwater prior to spawning (Clemens et al. 2010), finding suitable habitat during this period is crucial to reach sexual maturity and successfully complete

reproduction. To conserve and restore this long-neglected native species, it is important that we recognize its complex relationship with the riverscape and target our management focus on the key habitat features at a wide range of spatial scales.

We describe the holding and overwintering habitat use of adult Pacific lamprey at the macro, meso, and micro spatial scales (Figure B.1) in the North Umpqua River (~3500 km^2). The macro scale is represented by 1.5 km reaches, and we assessed the role of gradient, sinuosity, valley width, mean habitat length, mean habitat width, habitat unit (pool, glide, run, and riffle) counts, and side channel counts on the duration of lamprey holding. The meso scale is represented by individual habitat units, and we examined the role of habitat unit type, length, width, and area on the duration of lamprey holding. The micro scale is represented by the precise positions (<3 m) within the habitat units, and we assessed the role of relative location (head vs. tail), depth, width, and substrate on the duration of lamprey holding.

During 2009-2010, 70 fish were radio-tagged between May and September and were released in the lower North Umpqua River. The general locations of these fish were detected using fixed stations and mobile tracking, and the more precise locations of these fish (< 3 m) were tracked by snorkeling surveys using underwater antennas. For the macro and meso scale analysis, the project area only included river km 0-46.5 on the North Umpqua River (between mouth and confluence with Little River). Habitat units were classified using the density of visible white water from aerial photography. Areas with 50% or more white water were classified as riffle habitat, those with 25-50% white water were classified as run and glide habitat, and those with 25% or less white water were classified as pool habitat. Ground-truthing was conducted in selected areas where the interpretation of aerial photography interpretation was particularly difficult. For all three spatial scale analyes, lamprey that held near Winchester Dam or either of the release locations (downstream and upstream of Winchester Dam) were eliminated from the sample due to the artificial, high concentration of lamprey found in these locations.

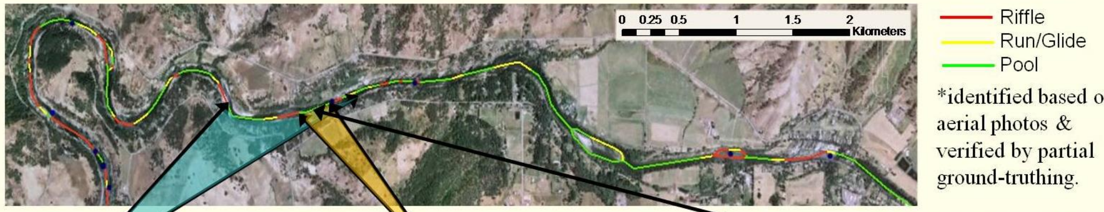
At the macro scale, we found that the radio-tagged lamprey were concentrated in reaches with many short segments of habitat. At the meso scale, run habitat was used significantly more and pool habitat was used significantly less in comparison to available habitat. At the micro scale, the interface of habitats (head and tail regions) were used significantly more for riffle and run habitats, whereas no distinct pattern was observed for pool and glide habitats. Boulder substrate was used by lamprey at a significantly higher frequency compared to the substrate availability in other areas (thalweg and channel margin) within the habitat unit. We hypothesize that lamprey may be actively seeking intermediate flow and depth in the fast and shallow habitat units represented by riffles and runs.

Temperature data suggests that at the macro scale, there was a tendency for lamprey to be found in relatively warm locations in the upper reaches (river km 12-60) where water temperature was comparatively cold, whereas in the lower reaches (river km 0-12) where water temperature was comparatively high, lamprey were found in relatively cold locations. At the micro scale, there was circumstantial evidence that cold water pockets are actively sought by lamprey, and this pattern was especially evident in the lower reaches, where water temperature was high.

Additionally, we compared the habitat use of the radio-tagged lamprey at the macro spatial scale with results from the intrinsic potential model (IPM) developed for rearing habitats of juvenile coho salmon (Burnett et al. 2007). Our analysis suggested that adult Pacific lamprey held positions in two distinct types of habitat: habitat with very high values for the juvenile coho IPM as well as habitat with very low values. This indicates that restoration efforts focusing solely on high intrinsic potential habitat for coho salmon would benefit pre-spawning adult Pacific lamprey to some extent, but less desirable coho potential habitat will also need to be targeted to support the full range of holding habitat used by Pacific lamprey. Finally, using the results from the combination of radio tracking, digital elevation models, and thermal infrared surveys, we hypothesize that hyporheic exchange flow may be a potential driver in lamprey selection of holding and overwintering habitat at all three spatial scales.

Results

Scale Reference



*identified based on aerial photos & verified by partial ground-truthing.

Macro Habitat

- Fish used reaches with higher number of habitat units ($R^2 = 0.1842$, p-value = 0.00003)

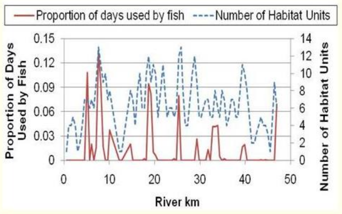


Figure 2. Fish use vs. number of habitat units within reach from river km 0-47

- Lamprey used reaches with very high & low Intrinsic Potential (IP) value for Coho juvenile rearing

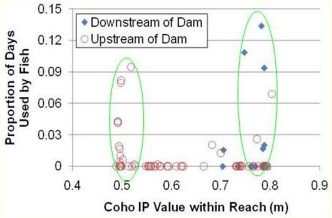


Figure 3. Fish use vs. Coho IP within reach

Meso Habitat

- Fish preferred run habitat

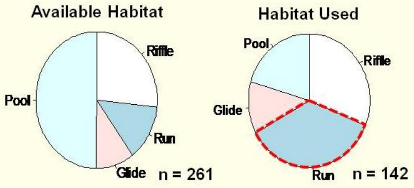


Figure 4. Available habitat vs. habitat used by fish

- Fish preferred boulder habitat

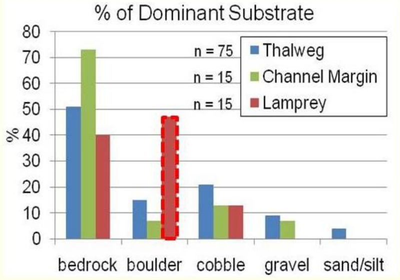


Figure 5. Substrate makeup for thalweg (fastest flow), channel margin, and fish location

Micro Habitat

- Fish found in habitat interface (heads & tails) for riffle & run habitats
- No observable pattern with pool and glide habitats

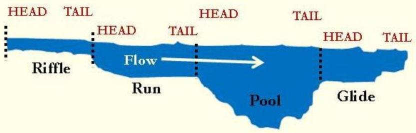


Figure 6. Illustration of 4 habitat types

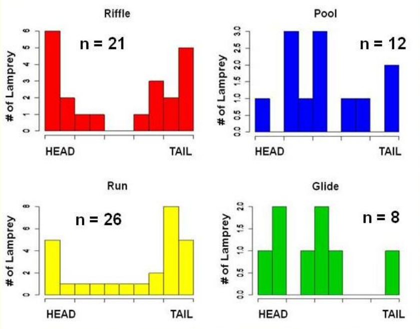


Figure 7. Fish location within habitat type

Discussion

- Management focusing protection only in reaches with high IP values for Coho species is insufficient for Pacific lamprey protection
- Abundance of all habitat units were important at macro scale
- Run habitat with boulder was important at meso scale
- Habitat interface were preferred in fast-flowing habitats
- Adult lamprey may be keying into hyporheic exchange (HE)
- HE is higher in habitat interface & upwelling is strongest at tail end of riffles (Brunke and Gonser 1997)
- HE is a refuge from shear stress of strong currents and more variable thermal conditions in the surface water

Figure 10. Conceptual model of why lamprey use habitat interface

Thermal Habitat Conditions

- Fish in warm lower reaches (river km 0-12) were found in cooler local zones (macro scale)
- Fish in cold upper reaches (river km 12-60) were found in warmer local zones (macro scale)
- Most fish (72%, n = 43) used thermal refugia habitat (colder surface water [>0.5 C°]) based on FLIR imageries (meso scale).

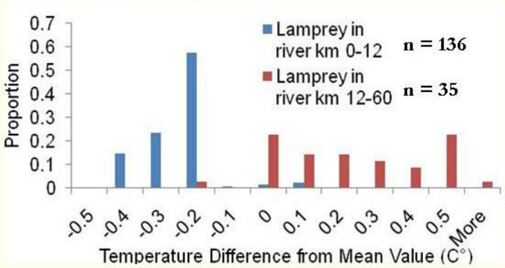


Figure 8. Diff. b/w temp. at lamprey location and mean temp. from the neighboring 10 km range

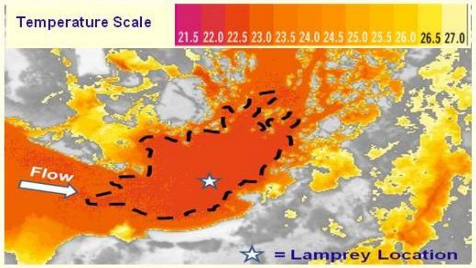


Figure 9. Site specific thermal conditions surrounding a lamprey location. Dotted black line shows area with colder surface water

Appendix C: TRACKING DATA SUMMARY BY INDIVIDUAL LAMPREY

Column Heading	Description
ID	ID name of lamprey [type of tag (L= NTC-6-2 tag, M = MST-820-T temperature sensor tag, S = NTC-3-2 tag) followed by the radio code ID number]
Start Date	Date when the lamprey was first detected at the location
Status	Movement Categories ["release" = release location, "up" = moved upstream, "down" = moved downstream, "new" = small movement (<0.1 km)]
River km	River km of the location (0.1 km increments)
Above/Below Dam?	Whether the location is "Above" or "Below" Winchester Dam
Previous Date	Date when the lamprey was last detected at the previous location
Travel Days	Days spent on the last migration
River km Δ	Change in River km from previous location to current one (0.1 km increments)
travel speed	Speed of migration (km/day)
End Date	Date when the lamprey was last detected at the location
Holding Days	Days spent holding at the location
HU	Habitat Unit categories ("1P" = pool, "2G" = glide, "2R" = run, "3R" = riffle)
Pre-HU	HU categories for the habitat directly upstream of the current one
Post-HU	HU categories for the habitat directly downstream of the current one

*This only shows new locations (multiple repeat detections were typically made while lamprey remained in the same location).

Year: 2009, Release Location: Downstream of Winchester Dam
L20, L21, L22, L23, L24, L25, L26, L27, L28, L29, L30, L31, L32, L35, L36, L41, L42, L44

Year: 2009, Release Location: Upstream of Winchester Dam
L34, L37, L38, L39, L40, L43

Year: 2010, Release Location: Downstream of Winchester Dam (until 10/28/2010)
L45, L47, L48, L49, L50, M1, M3, M4, M5, M6, M7, M11, M12, M14, M17, M18, M19, M20, M21, M22, M24, M26, M27, M28, S1, S2, S91, S92, S198, S199, S172

Year: 2010, Release Location: Upstream of Winchester Dam (until 10/28/2010)
L46, M2, M8, M9, M10, M13, M15, M16, M23, M25, M29, S19, S93, S94

*Photos were added to the lamprey tagged in 2009 to display the variety of habitat used across the three spawning migration phases (initial migration, pre-spawning holding, and final migration phases).

ID: L20

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L20	5/19/2009	release	8.2	Below	na	na	na	na	5/19/2009	2			
L20	5/20/2009	new	8.2	Below	5/19/2009	1	0.0	0.00	5/30/2009	12	1P	3R	2G
L20	6/2/2009	up	11.2	Below	5/30/2009	3	3.0	1.00	6/2/2009	1			
L20	6/3/2009	down	11.0	Below	6/2/2009	1	-0.2	-0.20	7/4/2009	32			
L20	7/5/2009	up	11.2	Below	7/4/2009	1	0.2	0.20	7/5/2009	1			
L20	7/6/2009	down	11.0	Below	7/5/2009	1	-0.2	-0.20	7/28/2009	23			
L20	7/29/2009	up	11.1	Below	7/28/2009	1	0.1	0.10	7/29/2009	1			
L20	7/30/2009	down	10.3	Below	7/29/2009	1	-0.8	-0.80	7/30/2009	1	2R	3R	3R

Photo 1: 7/30/2009
(Possibly already mortality status by then)

ID: L21

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L21	6/16/2009	release	10.3	Below	na	na	na	na	6/16/2009	2			
L21	6/17/2009	up	10.4	Below	6/16/2009	1	0.1	0.10	6/18/2009	3	3R	2G	2R
L21	6/19/2009	up	11.2	Below	6/18/2009	1	0.8	1.60	6/19/2009	1			
L21	6/20/2009	new	11.2	Below	6/19/2009	1	0.0	0.00	6/23/2009	4			
L21	6/24/2009	new	11.2	Below	6/23/2009	1	0.0	0.00	6/27/2009	4	3R	1P	2R
L21	6/28/2009	new	11.2	Below	6/27/2009	1	0.0	0.00	6/28/2009	1			
L21	6/28/2009	new	11.2	Below	6/28/2009	1	0.0	0.00	7/5/2009	8	3R	1P	2R
L21	7/7/2009	down	9.7	Below	7/5/2009	2	-1.5	-0.75	7/7/2009	1	3R	2G	2R

Photo 1: 6/17/2009
(at the head of riffle habitat)

Photo 2: 7/7/2009
(general location where carcass was found)

Photo 3: 7/7/2009
(decomposing body in the stream)

Photo 4: 7/7/2009
(possible spawning grounds nearby)

ID: L22

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L22	6/16/2009	release	10.3	Below	na	na	na	na	6/16/2009	1			
L22	6/16/2009	up	11.2	Below	6/16/2009	1	0.9	1.80	6/17/2009	2			
L22	6/17/2009	down	11.0	Below	6/17/2009	1	-0.2	-0.40	6/25/2009	10	1P	2R	3R
L22	6/26/2009	up	11.1	Below	6/25/2009	1	0.1	0.20	6/27/2009	2			
L22	6/29/2009	up	11.2	Below	6/27/2009	2	0.1	0.05	6/29/2009	1			
L22	7/6/2009	up	18.7	Above	6/29/2009	7	7.5	1.07	12/11/2009	159	1P	2G	3R
L22	12/21/2009	up	19.1	Above	12/11/2009	10	0.4	0.04	3/19/2010	89	1P	2G	3R
L22	4/2/2010	new	19.1	Above	3/19/2010	14	0.0	0.00	5/1/2010	30	1P	2G	3R
L22	5/4/2010	new	19.1	Above	5/1/2010	3	0.0	0.00	6/18/2010	47	1P	2G	3R
L22	6/23/2010	new	19.1	Above	6/18/2010	5	0.0	0.00	7/1/2010	9	1P	2G	3R

Photo 1: 6/19/2009
(in a pool by the highway piling)

Photo 2: 8/21/2009
(at the head of a pool with residual current from the glide above)

Photo 3: 9/10/2009
(underwater view of the holding habitat)

Photo 4: 3/5/2010 (by boulder complexes)

ID: L23

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L23	6/18/2009	release	10.3	Below	na	na	na	na	6/18/2009	2			
L23	6/19/2009	up	11.2	Below	6/18/2009	1	0.9	1.80	6/20/2009	3	3R	1P	2R
L23	6/24/2009	new	11.2	Below	6/20/2009	4	0.0	0.00	6/27/2009	4	3R	1P	2R
L23	6/28/2009	new	11.2	Below	6/27/2009	1	0.0	0.00	7/21/2009	24	3R	1P	2R
L23	7/21/2009	new	11.2	Below	7/21/2009	1	0.0	0.00	7/22/2009	2			
L23	7/22/2009	new	11.2	Below	7/22/2009	1	0.0	0.00	7/23/2009	2	3R	1P	2R
L23	7/24/2009	new	11.2	Below	7/23/2009	1	0.0	0.00	10/4/2009	73	3R	1P	2R
L23	10/5/2009	new	11.2	Below	10/4/2009	1	0.0	0.00	10/15/2009	11			
L23	10/16/2009	new	11.2	Below	10/15/2009	1	0.0	0.00	4/24/2010	191			
L23	4/25/2010	new	11.2	Below	4/24/2010	1	0.0	0.00	4/25/2010	1			

Photo 1: 9/2/2009 (never left the inside of the dam even after the dam dewatering event)

Photo 2: 9/2/2009 (Close-up of the precise location at the dam)

ID: L24

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L24	6/22/2009	release	10.3	Below	na	na	na	na	6/22/2009	2			
L24	6/23/2009	up	11.2	Below	6/22/2009	1	0.9	1.80	6/24/2009	2	3R	1P	2R
L24	6/25/2009	new	11.2	Below	6/24/2009	1	0.0	0.00	7/3/2009	9	3R	1P	2R
L24	7/7/2009	new	11.2	Below	7/6/2009	1	0.0	0.00	7/8/2009	2	3R	1P	2R
L24	7/9/2009	down	11.0	Below	7/8/2009	1	-0.2	-0.20	7/12/2009	4	3R	2G	2R
L24	7/13/2009	new	11.2	Below	7/12/2009	1	0.0	0.00	7/22/2009	10	3R	1P	2R
L24	7/23/2009	new	11.2	Below	7/22/2009	1	0.0	0.00	7/26/2009	4	3R	1P	2R
L24	7/27/2009	new	11.2	Below	7/26/2009	1	0.0	0.00	8/22/2009	27	2R	3R	1P
L24	8/24/2009	down	9.9	Below	8/22/2009	2	-1.3	-0.65	8/24/2009	1	2R	3R	1P

Photo 1: 7/31/2009
(by the highway piling)

Photo 2: 8/14/2009
(underwater view of the holding habitat)

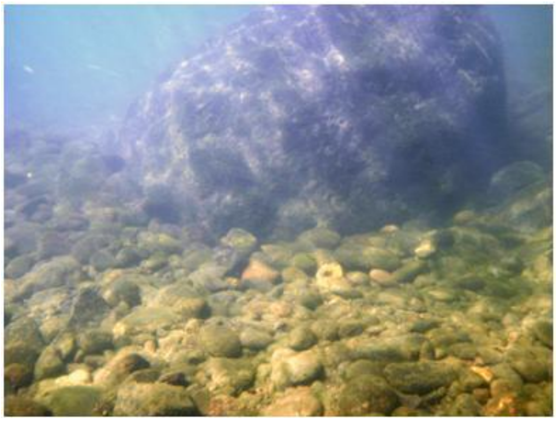


Photo 3: 8/20/2009
(hole under boulder where lamprey was seen)

Photo 4: 8/24/2009
(dead lamprey found in a side pool)

ID: L25

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L25	6/30/2009	release	10.3	Below	na	na	na	na	6/30/2009	2			
L25	7/1/2009	new	10.3	Below	6/30/2009	1	0.0	0.00	7/5/2009	5	3R	2G	2R
L25	7/6/2009	new	10.3	Below	7/5/2009	1	0.0	0.00	7/6/2009	2	2R	3R	3R
L25	7/7/2009	new	10.3	Below	7/6/2009	1	0.0	0.00	7/25/2009	19	3R	2G	2R
L25	7/26/2009	up	11.1	Below	7/25/2009	1	0.8	0.80	9/1/2009	38	2R	3R	1P
L25	9/3/2009	new	11.2	Below	9/1/2009	2	0.1	0.05	9/7/2009	6	3R	1P	2R
L25	9/10/2009	new	11.2	Below	9/7/2009	3	0.0	0.00	1/2/2010	115	3R	1P	2R
L25	1/3/2010	new	11.2	Below	1/2/2010	1	0.0	0.00	5/10/2010	128	3R	1P	2R
L25	5/11/2010	new	11.2	Below	5/10/2010	1	0.0	0.00	5/19/2010	9	3R	1P	2R
L25	5/20/2010	new	11.2	Below	5/19/2010	1	0.0	0.00	7/1/2010	43	3R	1P	2R

Photo 1: 9/4/2009 (holding just above the dam soon after the dam dewatering event; it appeared to move past the dam through the by-pass channel flow with fast current)

Photo 2: 5/26/2010 (holding? just downstream of the dam on the southeast side – may have been preyed on by a river otter during the dewatering event)

ID: L26

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L26	6/30/2009	release	10.3	Below	na	na	na	na	6/30/2009	1			
L26	6/30/2009	new	11.2	Below	6/30/2009	1	0.9	1.80	7/3/2009	4	3R	1P	2R
L26	7/4/2009	new	11.2	Below	7/3/2009	1	0.0	0.00	7/4/2009	1			
L26	7/5/2009	new	11.2	Below	7/4/2009	1	0.0	0.00	7/8/2009	4	3R	1P	2R
L26	7/9/2009	new	11.2	Below	7/8/2009	1	0.0	0.00	7/16/2009	8			
L26	7/17/2009	new	11.2	Below	7/16/2009	1	0.0	0.00	7/19/2009	3			
L26	7/20/2009	new	11.2	Below	7/19/2009	1	0.0	0.00	7/22/2009	3	3R	1P	2R
L26	7/22/2009	new	11.1	Below	7/22/2009	1	0.1	0.20	7/22/2009	2	3R	1P	2R
L26	7/23/2009	new	11.1	Below	7/22/2009	1	0.0	0.00	8/19/2009	28	3R	1P	2R
L26	8/20/2009	new	11.2	Below	8/19/2009	1	0.0	0.00	8/22/2009	3			
L26	8/23/2009	new	11.1	Below	8/22/2009	1	-0.1	-0.10	1/1/2010	132	2R	3R	1P
L26	1/2/2010	down	10.8	Below	1/1/2010	1	-0.3	-0.30	3/17/2010	75	2R	3R	1P
L26	3/18/2010	up	11.1	Below	3/17/2010	1	0.3	0.30	4/8/2010	23			
L26	4/9/2010	down	10.8	Below	4/8/2010	1	-0.3	-0.60	4/20/2010	13	2R	3R	1P

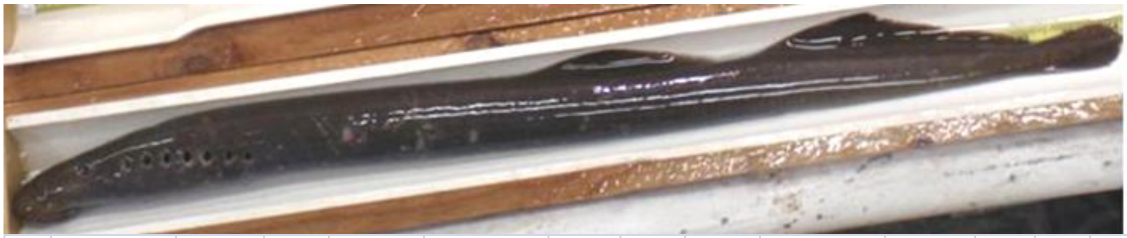
Photo 1: 9/2/2009 (below the dam in pool habitat – did not move after dewatering

Photo 2: 9/1/2009 (overview of the detection area)

Photo 3: 9/17/2009 (best detection inside an old irrigation pipe)

Photo 4: 4/4/2010 (detected by a trestle piling downstream)

ID: L27



ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L27	7/2/2009	release	10.3	Below	na	na	na	na	7/2/2009	1			
L27	7/2/2009	new	10.3	Below	7/2/2009	1	0.0	0.00	7/2/2009	1	3R	2G	2R
L27	7/3/2009	up	10.6	Below	7/2/2009	1	0.3	0.30	7/3/2009	1	2R	3R	1P
L27	7/3/2009	up	11.2	Below	7/3/2009	1	0.6	1.20	7/3/2009	1			
L27	7/4/2009	new	11.2	Below	7/3/2009	1	0.0	0.00	7/6/2009	3	3R	1P	2R
L27	7/7/2009	new	11.2	Below	7/6/2009	1	0.0	0.00	7/12/2009	6	3R	1P	2R
L27	7/13/2009	new	11.2	Below	7/12/2009	1	0.0	0.00	7/15/2009	3	3R	1P	2R
L27	7/16/2009	new	11.2	Below	7/15/2009	1	0.0	0.00	7/16/2009	1			
L27	7/17/2009	new	11.2	Below	7/16/2009	1	0.0	0.00	7/17/2009	1	3R	1P	2R
L27	7/18/2009	new	11.2	Below	7/17/2009	1	0.0	0.00	7/18/2009	1	3R	1P	2R
L27	7/19/2009	new	11.2	Below	7/18/2009	1	0.0	0.00	7/21/2009	3	3R	1P	2R
L27	7/22/2009	new	11.2	Below	7/21/2009	1	0.0	0.00	7/23/2009	2	3R	1P	2R
L27	7/24/2009	new	11.2	Below	7/23/2009	1	0.0	0.00	8/1/2009	9	3R	1P	2R
L27	8/2/2009	new	11.2	Below	8/1/2009	1	0.0	0.00	9/14/2009	44	3R	1P	2R
L27	9/27/2009	new	11.2	Below	9/14/2009	13	0.0	0.00	2/17/2010	144	3R	1P	2R
L27	2/18/2010	new	11.2	Below	2/17/2010	1	0.0	0.00	2/18/2010	1			
L27	2/19/2010	new	11.2	Below	2/18/2010	1	0.0	0.00	5/17/2010	89	3R	1P	2R

Photo 1: 7/3/2009 (holding in run habitat)

Photo 2: 7/3/2009 (underwater view)

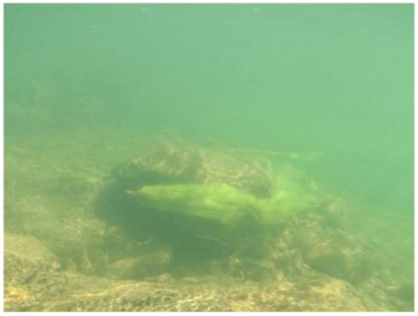


Photo 3: 8/10/2009 (above the dam in reservoir water)

Photo 4: 9/2/2009 (still inside the dam during the dewatering event)

ID: L28

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L28	7/2/2009	release	10.3	Below	na	na	na	na	7/2/2009	1			
L28	7/2/2009	new	10.3	Below	7/2/2009	1	0.0	0.00	7/8/2009	7	3R	2G	2R
L28	7/9/2009	new	10.3	Below	7/8/2009	1	0.0	0.00	7/9/2009	1	3R	2G	2R
L28	7/10/2009	up	11.2	Below	7/9/2009	1	0.9	0.90	7/11/2009	2			
L28	7/13/2009	down	11.0	Below	7/11/2009	2	-0.2	-0.10	7/13/2009	2	1P	2R	3R
L28	7/14/2009	new	11.0	Below	7/13/2009	1	0.0	0.00	7/14/2009	1	2R	3R	1P
L28	7/14/2009	up	11.2	Below	7/14/2009	1	0.2	0.40	7/15/2009	2			
L28	7/15/2009	new	11.2	Below	7/14/2009	1	0.0	0.00	7/16/2009	2	3R	1P	2R
L28	7/17/2009	new	11.2	Below	7/16/2009	1	0.0	0.00	7/19/2009	3			
L28	7/20/2009	new	11.2	Below	7/19/2009	1	0.0	0.00	7/20/2009	1			
L28	7/23/2009	new	11.2	Below	7/20/2009	3	0.0	0.00	8/31/2009	40	3R	1P	2R
L28	9/1/2009	release	11.4	Above	na	na	na	na	9/1/2009	1			
L28	9/3/2009	down	11.2	Below	9/1/2009	2	0.0	0.00	3/25/2010	204	3R	1P	2R
L28	3/26/2010	new	11.2	Below	3/25/2010	1	0.0	0.00	4/6/2010	12	3R	1P	2R
L28	4/6/2010	new	11.1	Below	4/6/2010	1	-0.1	-0.20	4/7/2010	2			
L28	4/13/2010	down	5.4	Below	4/7/2010	6	-5.7	-0.95	7/1/2010	80	3R	1P	1P

Photo 1: 9/4/2009 (found in the bypass channel during the dewatering event; attempted to pass the dam?)

Photo 2: 5/19/2010 (possible spawning habitat downstream of the dam)

ID: L29

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L29	7/4/2009	release	10.3	Below	na	na	na	na	7/6/2009	4			
L29	7/9/2009	new	10.3	Below	7/6/2009	3	0.0	0.00	5/2/2010	298	3R	2G	2R
L29	5/6/2010	down	5.7	Below	5/2/2010	4	-4.6	-1.15	5/8/2010	4			

Photo 1: 8/24/2009 (holding in a side pool near riffle flow)

Photo 2: 9/16/2009 (underwater view of the holding habitat)

Photo 3: 11/19/2009 (during higher flows)

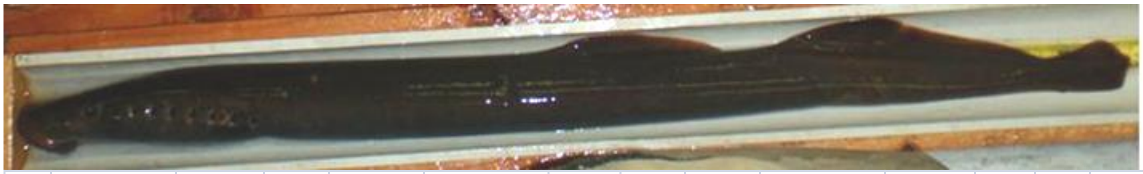
Photo 4: 4/4/2010 (during a flood in April)

ID: L30

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L30	7/4/2009	release	10.3	Below	na	na	na	na	7/5/2009	2			
L30	7/6/2009	new	10.3	Below	7/5/2009	1	0.0	0.00	7/13/2009	8	2R	3R	3R
L30	7/13/2009	up	11.2	Below	7/13/2009	1	0.9	1.80	7/14/2009	2			
L30	7/15/2009	down	10.8	Below	7/14/2009	1	-0.4	-0.40	7/27/2009	13			
L30	7/28/2009	up	11.1	Below	7/27/2009	1	0.3	0.30	7/28/2009	1			
L30	7/30/2009	down	9.8	Below	7/28/2009	2	-1.3	-0.65	7/30/2009	1			

Photo 1: 8/11/2009 (lamprey was found dead here in early September – may have been dead here since 7/30/2009)

ID: L31



ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L31	7/4/2009	release	10.3	Below	na	na	na	na	7/5/2009	2			
L31	7/6/2009	new	10.3	Below	7/5/2009	1	0.0	0.00	7/20/2009	16	3R	2G	2R
L31	7/21/2009	new	10.3	Below	7/20/2009	1	0.0	0.00	3/26/2010	249	2R	3R	3R
L31	3/27/2010	up	11.1	Below	3/26/2010	1	0.8	0.80	3/28/2010	2			
L31	3/30/2010	new	11.2	Below	3/28/2010	2	0.1	0.05	3/31/2010	2			
L31	3/31/2010	new	11.1	Below	3/31/2010	1	-0.8	-1.60	5/17/2010	48			
L31	5/18/2010	new	11.1	Below	5/17/2010	1	0.0	0.00	6/1/2010	15	2R	3R	1P
L31	6/2/2010	new	11.1	Below	6/1/2010	1	0.0	0.00	6/13/2010	12	2R	3R	1P

Photo 1: 9/16/2009 (in deep pool by the bedrock outcrop)

Photo 2: 11/19/2009 (same habitat during higher flow)

Photo 3: 4/4/2010 (moved upstream to the base of Winchester Dam)

Photo 4: 5/19/2010 (moved to the side channel below the dam for spawning)

ID: L32

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L32	7/4/2009	release	10.3	Below	na	na	na	na	7/5/2009	2			
L32	7/6/2009	new	10.3	Below	7/5/2009	1	0.0	0.00	7/19/2009	15	3R	2G	2R
L32	7/20/2009	new	10.3	Below	7/19/2009	1	0.0	0.00	8/7/2009	19	3R	2G	2R
L32	8/24/2009	down	4.7	Below	8/7/2009	17	-5.6	-0.33	5/10/2010	260	2G	1P	3R
L32	5/11/2010	new	4.7	Below	5/10/2010	1	0.0	0.00	5/25/2010	15	2G	1P	3R
L32	5/26/2010	new	4.7	Below	5/25/2010	1	0.0	0.00	7/1/2010	37	2G	1P	3R

Photo 1: 8/24/2009 (in deep pool habitat)

Photo 2: 4/4/2010 (still in same area)

Photo 3: 5/19/2010 (same area, but moved closer to the bank side?)

ID: L35

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L35	7/19/2009	release	10.5	Below	na	na	na	na	7/19/2009	1			
L35	7/20/2009	down	10.3	Below	7/19/2009	1	-0.2	-0.20	7/26/2009	7	3R	2G	2R
L35	7/28/2009	up	11.2	Below	7/26/2009	2	0.9	0.45	7/30/2009	3			
L35	7/31/2009	down	10.9	Below	7/30/2009	1	-0.3	-0.30	8/4/2009	6			
L35	8/6/2009	down	10.8	Below	8/4/2009	2	-0.1	-0.07	12/18/2009	135	2R	3R	1P
L35	12/21/2009	up	11.0	Below	12/18/2009	3	0.2	0.07	1/1/2010	12			
L35	1/2/2010	up	11.1	Below	1/1/2010	1	0.1	0.10	2/17/2010	47			
L35	2/18/2010	up	11.2	Below	2/17/2010	1	0.1	0.10	2/20/2010	3			
L35	3/3/2010	new	11.2	Below	2/20/2010	11	0.0	0.00	3/25/2010	23	3R	1P	2R
L35	3/26/2010	new	11.2	Below	3/25/2010	1	0.0	0.00	4/3/2010	9	3R	1P	2R
L35	4/4/2010	new	11.2	Below	4/3/2010	1	0.0	0.00	4/25/2010	23	3R	1P	2R
L35	4/28/2010	new	11.1	Below	4/25/2010	3	-0.1	-0.04	5/26/2010	29	2R	3R	1P
L35	5/26/2010	new	11.2	Below	5/26/2010	1	0.1	0.20	7/1/2010	37			

Photo 1: 8/6/2009 (holding just upstream of a tressle piling in deep water)

Photo 2: 9/17/2009 (underwater view of the habitat)

Photo 3: 3/24/2010 (downstream of dam)

Photo 4: 6/29/2010 (inside underground pipe at the water treatment plant)

ID: L36

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L36	7/21/2009	release	10.8	Below	na	na	na	na	7/21/2009	1			
L36	7/21/2009	new	10.8	Below	7/21/2009	1	0.0	0.00	7/22/2009	2	2R	3R	1P
L36	7/23/2009	new	10.8	Below	7/22/2009	1	0.0	0.00	7/23/2009	1	2R	3R	1P
L36	7/23/2009	up	11.2	Below	7/23/2009	1	0.4	0.80	7/23/2009	1			
L36	7/24/2009	down	11.0	Below	7/23/2009	1	-0.2	-0.20	7/28/2009	5			
L36	7/29/2009	new	11.2	Below	7/28/2009	1	0.2	0.20	7/30/2009	2			
L36	8/6/2009	down	7.7	Below	7/30/2009	7	-3.5	-0.50	9/14/2009	40	2G	1P	3R
L36	9/15/2009	new	7.7	Below	9/14/2009	1	0.0	0.00	1/16/2010	125	2G	1P	3R
L36	2/5/2010	down	7.6	Below	1/16/2010	20	-0.1	-0.01	4/3/2010	58	2R	3R	1P
L36	4/4/2010	new	7.5	Below	4/3/2010	1	-0.1	-0.10	4/27/2010	24	2R	3R	1P
L36	4/28/2010	new	7.5	Below	4/27/2010	1	0.0	0.00	6/4/2010	38	2R	3R	1P
L36	6/8/2010	new	7.4	Below	6/4/2010	4	-0.1	-0.02	6/27/2010	20	1P	2R	2G
L36	6/28/2010	new	7.5	Below	6/27/2010	1	0.1	0.10	7/6/2010	9	1P	2R	2G
L36	7/14/2010	new	7.4	Below	7/6/2010	8	-0.1	-0.01	7/14/2010	1			

Photo 1: 7/21/2009 (side channel by bank)

Photo 2: 8/24/2009 (by grass islands)

Photo 3: 9/15/2009 (detected inside an irrigation pipe)

Photo 4: 5/19/2010 (moved downstream by willow islands)

ID: L41

*Captured during dam dewatering event – no photo of lamprey

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L41	9/1/2009	release	11.1	Below	na	na	na	na	9/6/2009	6			
L41	9/11/2009	down	7.1	Below	9/6/2009	5	-4.0	-0.8	3/30/2010	201	1P	2R	2G

Photo 1: 3/15/2010 (pool with fast thalweg where it held extensively)

Photo 2: 9/11/2009 (underwater view of bedrock with crevices)

Photo 3: 12/14/2009 (during winter flows)

ID: L42

*Captured during dam dewatering event – no photo of lamprey

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L42	9/1/2009	release	11.1	Below	na	na	na	na	9/1/2009	1			
L42	9/2/2009	new	11.2	Below	9/1/2009	1	0.1	0.1	9/12/2009	11	3R	1P	2R
L42	9/13/2009	new	11.2	Below	9/12/2009	1	0.0	0.0	7/1/2010	292	3R	1P	2R

Photo 1: 5/26/2010 (detected from inside this water outlet at the base of the dam and stayed there for the entire time – either got stuck or may have been preyed and deposited by river otters)

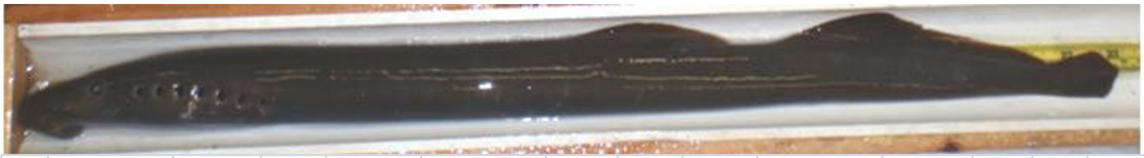
ID: L44

*Captured during dam dewatering event – no photo of lamprey

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L44	9/1/2009	release	11.1	Below	na	na	na	na	9/2/2009	2			
L44	9/3/2009	up	11.2	Below	9/2/2009	1	0.1	0.1	10/5/2009	33	3R	1P	2R
L44	10/5/2009	new	11.2	Below	10/5/2009	1	0.0	0.0	5/15/2010	223	3R	1P	2R

Photo 1: 9/4/2009 (found at the upstream end of the by-pass channel during dam dewatering – considering the extremely fast current, lamprey most likely was eaten by river otters and deposited inside their hang out inside the concrete wall [similar to L42?])

ID: L34



ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L34	7/17/2009	release	13.7	Above	na	na	na	na	7/17/2009	1			
L34	7/17/2009	new	13.9	Above	7/17/2009	1	0.2	0.40	7/22/2009	7			
L34	7/28/2009	up	25.0	Above	7/22/2009	6	11.1	2.02	12/14/2009	141	2R	3R	3R
L34	5/31/2010	down	18.7	Above	12/14/2009	168	-6.3	-0.04	6/4/2010	5	2G	1P	1P
L34	6/8/2010	down	16.0	Above	6/4/2010	4	-2.7	-0.68	6/19/2010	13	1P	2R	3R
L34	6/25/2010	up	16.2	Above	6/19/2010	6	0.2	0.04	7/1/2010	7	2G	1P	3R

Photo 1: 8/21/2009 (near bedrock outcrop)

Photo 2: 5/31/2010 (near bedrock outcrop)

Photo 3: 6/8/2010 (side channel habitat used for spawning?)

Photo 4: 6/25/2010 (last spawning habitat where tag was found – side channel with lots of gravel and cobble)

ID: L37

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L37	7/23/2009	release	13.7	Above	na	na	na	na	7/25/2009	4			
L37	8/1/2009	up	46.7	Above	7/25/2009	7	33.0	5.08	8/1/2009	1			
L37	8/4/2009	up	53.5	Above	8/1/2009	3	6.8	2.27	1/9/2010	159	2G	1P	1P
L37	1/21/2010	up	54.1	Above	1/9/2010	12	0.6	0.05	5/15/2010	115	2G	1P	3R
L37	5/17/2010	down	53.7	Above	5/15/2010	2	-0.4	-0.20	6/5/2010	21	2R	3R	1P
L37	6/10/2010	down	53.1	Above	6/5/2010	5	-0.6	-0.13	6/12/2010	4			
L37	6/15/2010	down	47.6	Above	6/12/2010	3	-5.5	-2.20	6/24/2010	10			

Photo 1: 8/4/2009 (deep glide habitat with lots of bedrock outcrops)

Photo 2: 9/8/2009 (underwater view of the habitat - lots of coarse substrate with spaces)

Photo 3: 3/4/2010 (new habitat with boulder/bedrock outcrop)

Photo 4: 6/24/2010 (last habitat – good spawning gravels and larva habitat [tag and unidentified flesh was found here])

ID: L38

*Captured during dam dewatering event – no photo of lamprey

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L38	9/1/2009	release	11.2	Above	na	na	na	na	9/1/2009	1			
L38	9/7/2009	up	13.0	Above	9/1/2009	6	1.8	0.3	12/18/2009	103	1P	2R	3R
L38	12/21/2009	up	18.9	Above	12/18/2009	3	5.9	2.0	3/19/2010	89	2R	3R	1P
L38	4/2/2010	down	18.7	Above	3/19/2010	14	-0.2	0.0	5/8/2010	37	2G	1P	1P
L38	5/12/2010	down	18.0	Above	5/8/2010	4	-0.7	-0.2	5/13/2010	2	2G	1P	1P
L38	5/14/2010	down	11.3	Above	5/13/2010	1	-6.7	-6.7	5/14/2010	1			
L38	5/15/2010	new	11.2	Below	5/14/2010	1	-0.1	-0.1	5/15/2010	1			
L38	8/10/2010	down	3.3	Below	5/15/2010	87	-7.9	-0.1	8/10/2010	1	1P	3R	3R

Photo 1: 9/7/2009 (riffle habitat during dam dewatering event before it returned to reservoir habitat – see right)

Photo 2: 10/13/2009 (lamprey did not move even after the riffle turned into a reservoir - in hibernation already?)

Photo 2: 10/13/2009 (new habitat upstream in willow islands)

Photo 4: 4/16/2010 (moved to a nearby habitat with bedrock outcrop under water)

ID: L39

*Captured during dam dewatering event – no photo of lamprey

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L39	9/1/2009	release	11.2	Above	na	na	na	na	9/1/2009	1			
L39	9/3/2009	down	11.2	Below	9/1/2009	2	0.0	0.0	9/8/2009	6	3R	1P	2R
L39	9/14/2009	down	10.8	Below	9/8/2009	6	-0.3	0.0	10/31/2009	49	3R	1P	2R
L39	11/19/2009	new	10.9	Below	10/31/2009	19	0.1	0.0	12/24/2009	37	2R	3R	1P
L39	12/28/2009	new	11.0	Below	12/24/2009	4	0.1	0.0	1/16/2010	21			
L39	2/5/2010	down?	9.8	Below	1/16/2010	20	-1.2	-0.1	2/5/2010	1			

Photo 1: 9/4/2009 (released upstream, but was detected at the by-pass channel outlet during the dewatering event)

Photo 2: 9/17/2009 (in an undercut bank below the highway bridge)

Photo 3: 9/17/2009 (underwater view of the undercut bank with lots of FW mussels)

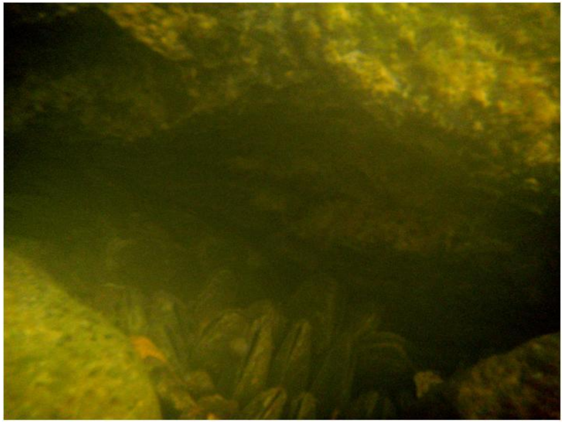


Photo 4: 12/15/2009 (moved upstream to a deeper pool during the winter)

ID: L40

*Captured during dam dewatering event

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L40	9/1/2009	release	11.2	Above	na	na	na	na	9/1/2009	1			
L40	9/7/2009	up	13.5	Above	9/1/2009	6	2.3	0.4	4/25/2010	231	3R	2G	2R
L40	5/4/2010	new	13.7	Above	4/25/2010	9	0.2	0.0	5/13/2010	10	3R	2G	2R
L40	5/14/2010	down	11.2	Below	5/13/2010	1	-2.5	-2.5	5/14/2010	1			
L40	5/15/2010	new	11.2	Below	5/14/2010	1	0.0	0.0	5/15/2010	1			
L40	5/16/2010	new	11.2	Below	5/15/2010	1	0.0	0.0	5/16/2010	1			
L40	5/19/2010	down	8.6	Below	5/16/2010	3	-2.6	-0.9	5/19/2010	2	3R	1P	1P
L40	5/20/2010	down	8.0	Below	5/19/2010	1	-0.6	-1.2	5/20/2010	2	1P	2G	2G
L40	5/21/2010	up	8.5	Below	5/20/2010	1	0.5	1.0	5/28/2010	9	1P	3R	3R
L40	5/31/2010	up	8.6	Below	5/28/2010	3	0.1	0.0	6/4/2010	5	3R	1P	1P
L40	6/8/2010	down	8.0	Below	6/4/2010	4	-0.6	-0.2	7/1/2010	24	1P	2G	2G

Photo 1: 9/7/2009 (in fast riffle habitat)

Photo 2: 9/10/2009 (underwater view)

Photo 3: 4/2/2010 (during a flood event)

Photo 4: 8/20/2010 (last location/spawning?)

ID: L43

*Captured during dam dewatering event – no photo of lamprey

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L43	9/1/2009	release	11.2	Above	na	na	na	na	9/1/2009	1			
L43	9/3/2009	down	11.1	Below	9/1/2009	2	-0.1	0.0	9/4/2009	3			
L43	9/5/2009	new	11.1	Below	9/4/2009	1	0.0	0.0	9/7/2009	4			
L43	9/10/2009	down	10.9	Below	9/7/2009	3	-0.2	-0.1	11/17/2009	69	3R	1P	2R
L43	11/19/2009	new	10.8	Below	11/17/2009	2	-0.1	0.0	12/18/2009	30	2R	3R	1P
L43	12/21/2009	new	10.8	Below	12/18/2009	3	0.0	0.0	12/24/2009	5	2R	3R	1P
L43	12/28/2009	up	11.2	Below	12/24/2009	4	0.4	0.1	2/17/2010	52	3R	1P	2R
L43	2/18/2010	new	11.2	Below	2/17/2010	1	0.0	0.0	3/25/2010	36	3R	1P	2R
L43	3/26/2010	new	11.2	Below	3/25/2010	1	0.0	0.0	4/19/2010	25	3R	1P	2R
L43	4/20/2010	new	11.1	Below	4/19/2010	1	-0.1	-0.1	4/25/2010	6			
L43	4/26/2010	new	11.1	Below	4/25/2010	1	0.0	0.0	5/9/2010	14			
L43	5/9/2010	new	11.1	Below	5/9/2010	1	0.0	0.0	5/11/2010	3			

Photo 1: 9/16/2009 (deeper section of a fast riffle with a large boulder)

Photo 2: 9/16/2009 (underwater view showing the large boulder and turbulence)

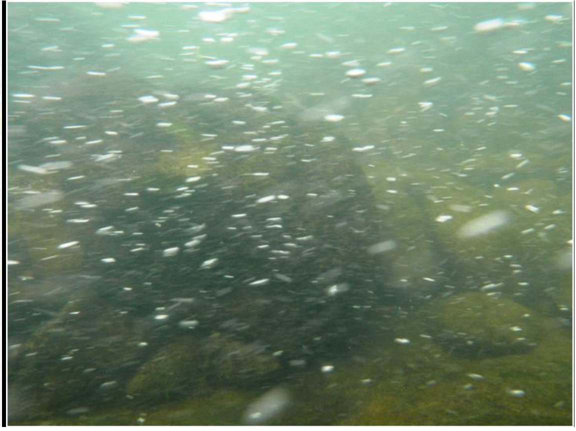


Photo 3: 4/1/2010 (moved up to the dam, hiding under artificial boulders)

Photo 4: 5/11/2010 (a heavily chewed up tag was found – eaten before spawning?)

ID: L45

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L45	5/19/2010	release	10.3	Below	na	na	na	na	5/19/2010	1			
L45	5/20/2010	new	10.3	Below	5/19/2010	1	0	0	5/28/2010	9	2R	3R	2R
L45	5/31/2010	new	10.3	Below	5/28/2010	3	0	0	6/2/2010	3	3R	2G	2R
L45	6/3/2010	up	11.2	Below	6/2/2010	1	0.9	0.9	6/11/2010	9			
L45	6/12/2010	new	11.2	Below	6/11/2010	1	0	0	6/25/2010	14			
L45	6/26/2010	new	11.2	Below	6/25/2010	1	0	0	6/27/2010	2			
L45	6/29/2010	down	3	Below	6/27/2010	2	-8.2	-4.1	8/6/2010	39	1P	3R	3R
L45	8/10/2010	new	2.9	Below	8/6/2010	7	-0.1	0	10/28/2010	79	1P	3R	3R

ID: L47

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L47	7/7/2010	release	10.3	Below	na	na	na	na	7/10/2010	3			
L47	7/13/2010	new	10.3	Below	7/10/2010	3	0	0	7/21/2010	9	3R	1P	2R
L47	7/24/2010	up	11.2	Below	7/21/2010	3	0.9	0.3	7/25/2010	2			
L47	7/26/2010	new	11.2	Below	7/25/2010	1	0	0	8/3/2010	9	3R	1P	2R
L47	8/4/2010	new	11.2	Below	8/3/2010	1	0	0	8/5/2010	2			
L47	8/6/2010	new	11.2	Below	8/5/2010	1	0	0	8/16/2010	11	3R	1P	2R
L47	8/18/2010	new	11.2	Below	8/16/2010	2	0	0	9/2/2010	16			
L47	9/3/2010	new	11.2	Below	9/2/2010	1	0	0	9/5/2010	3	3R	1P	2R
L47	9/6/2010	new	11.2	Below	9/5/2010	1	0	0	10/19/2010	44	3R	1P	2R
L47	10/25/2010	new	11.2	Below	10/19/2010	6	0	0	10/25/2010	1			
L47	10/26/2010	new	11.2	Below	10/25/2010	1	0	0	10/28/2010	2	3R	1P	2R

ID: L48

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L48	7/9/2010	release	10.3	Below	na	na	na	na	7/12/2010	5			
L48	7/16/2010	up	11.2	Below	7/12/2010	4	0.9	0.2	7/17/2010	2			
L48	7/28/2010	down	10.5	Below	7/17/2010	11	0.2	0	8/13/2010	17	2R	3R	1P
L48	8/16/2010	up	10.9	Below	8/13/2010	3	0.4	0.1	8/21/2010	5	1P	2R	3R
L48	8/22/2010	up	11.2	Below	8/21/2010	1	0.3	0.3	8/23/2010	2			
L48	10/12/2010	down	8.2	Below	8/23/2010	50	-2.7	-0.1	10/28/2010	16			

ID: L49

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L49	7/9/2010	release	10.3	Below	na	na	na	na	7/25/2010	16			
L49	8/10/2010	down	7.1	Below	7/25/2010	16	-3.2	-0.2	9/5/2010	27	2G	1P	1P
L49	9/22/2010	new	7.2	Below	9/5/2010	17	0.1	0	10/28/2010	36	1P	2R	2G

ID: L50

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L50	7/13/2010	release	10.3	Below	na	na	na	na	7/13/2010	1			
L50	7/13/2010	up	11.2	Below	7/13/2010	1	0.9	0.9	7/14/2010	3	3R	1P	2R
L50	7/15/2010	new	11.1	Below	7/14/2010	1	-0.1	-0.1	7/16/2010	3	3R	1P	2R
L50	7/17/2010	down	11	Below	7/16/2010	1	-0.1	-0.1	7/21/2010	5	2R	3R	1P
L50	7/22/2010	up	11.2	Below	7/21/2010	1	0.2	0.2	7/27/2010	7			
L50	7/28/2010	down	11	Below	7/27/2010	1	-0.2	-0.2	8/10/2010	15	2R	3R	1P
L50	8/11/2010	up	11.2	Below	8/10/2010	1	0.2	0.2	9/6/2010	27			
L50	9/7/2010	down	10.9	Below	9/6/2010	1	-0.3	-0.3	9/9/2010	2	1P	2R	3R
L50	9/9/2010	up	11.1	Below	9/9/2010	1	0.2	0.2	9/10/2010	2			
L50	9/17/2010	new	11.1	Below	9/10/2010	7	0	0	10/28/2010	42			

ID: M1

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M1	6/16/2010	release	10.3	Below	na	na	na	na	6/16/2010	2			
M1	6/17/2010	new	10.3	Below	6/16/2010	1	0	0	6/20/2010	4	2R	3R	3R
M1	6/23/2010	up	10.5	Below	6/20/2010	3	0.2	0.1	6/23/2010	2	1P	2R	2G
M1	6/24/2010	up	11.2	Below	6/23/2010	1	0.7	0.7	6/24/2010	1			
M1	6/25/2010	new	11.2	Below	6/24/2010	1	0	0	6/25/2010	1			
M1	6/27/2010	new	11.2	Below	6/24/2010	3	0	0	6/28/2010	2			
M1	7/13/2010	up	46.7	Above	6/28/2010	15	35.5	2.4	7/13/2010	1			
M1	7/15/2010	up	47.2	Above	7/13/2010	2	0.5	0.3	7/15/2010	1			
M1	7/16/2010	down	46.7	Above	7/13/2010	3	0	0	7/16/2010	1			
M1	7/17/2010	down	46.5	Above	7/16/2010	1	-0.2	-0.2	9/7/2010	54	2G	1P	1P

ID: M3

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M3	7/9/2010	release	10.3	Below	na	na	na	na	7/9/2010	1			
M3	7/9/2010	up	11.2	Below	7/9/2010	1	0.9	0.9	7/20/2010	12			
M3	7/21/2010	new	11.2	Below	7/20/2010	1	0	0	10/28/2010	100	3R	1P	2R

ID: M4

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M4	7/9/2010	release	10.3	Below	na	na	na	na	7/9/2010	1			
M4	7/9/2010	up	11.2	Below	7/9/2010	1	0.9	0.9	7/13/2010	5			
M4	7/14/2010	new	11.1	Below	7/13/2010	1	-0.1	-0.1	7/18/2010	5	2R	3R	1P
M4	7/19/2010	new	11.2	Below	7/13/2010	6	0	0	7/27/2010	9	3R	1P	2R
M4	7/28/2010	new	11.2	Below	7/27/2010	1	0	0	8/1/2010	5	3R	1P	2R
M4	8/2/2010	new	11.2	Below	8/1/2010	1	0	0	8/8/2010	7	3R	1P	2R
M4	8/9/2010	new	11.2	Below	8/8/2010	1	0	0	8/16/2010	8	3R	1P	2R
M4	8/17/2010	new	11.2	Below	8/16/2010	1	0	0	8/26/2010	10	3R	1P	2R
M4	8/27/2010	down	11	Below	8/26/2010	1	-0.2	-0.2	10/25/2010	60	2R	3R	1P

ID: M5

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M5	7/9/2010	release	10.3	Below	na	na	na	na	7/10/2010	3			
M5	7/11/2010	up	11.2	Below	7/10/2010	1	0.9	0.9	7/13/2010	3	3R	1P	2R
M5	7/14/2010	new	11.2	Below	7/13/2010	1	0	0	7/14/2010	2	3R	1P	2R
M5	7/15/2010	new	11.2	Below	7/14/2010	1	0	0	7/18/2010	4	3R	1P	2R
M5	7/19/2010	new	11.2	Below	7/18/2010	1	0	0	8/1/2010	13	3R	1P	2R
M5	8/2/2010	new	11.2	Below	8/1/2010	1	0	0	10/28/2010	87	3R	1P	2R

ID: M6

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M6	7/9/2010	release	10.3	Below	na	na	na	na	7/9/2010	1			
M6	7/10/2010	up	11.2	Below	7/9/2010	1	0.9	0.9	7/13/2010	4	3R	1P	2R
M6	7/13/2010	down	10.6	Below	7/13/2010	1	-0.6	-0.6	7/14/2010	2			
M6	7/14/2010	up	11.2	Below	7/14/2010	1	0.6	0.6	7/15/2010	2	3R	1P	2R
M6	7/17/2010	new	11.2	Below	7/15/2010	2	0	0	7/18/2010	2	3R	1P	2R
M6	7/19/2010	new	11.2	Below	7/18/2010	1	0	0	8/8/2010	21	3R	1P	2R
M6	8/13/2010	new	11.2	Below	8/8/2010	5	0	0	9/6/2010	25	3R	1P	2R
M6	9/16/2010	new	11.2	Below	9/6/2010	10	0	0	9/19/2010	4	3R	1P	2R
M6	10/2/2010	up	33.2	Above	9/19/2010	13	22	1.7	10/2/2010	1			
M6	10/3/2010	up	33.3	Above	10/2/2010	1	0.1	0.1	10/3/2010	1			
M6	10/25/2010	up	46.7	Above	10/3/2010	22	13.4	0.6	10/25/2010	1			
M6	10/27/2010	up	46.8	Above	10/25/2010	2	0.1	0	10/27/2010	1			

ID: M7

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M7	7/9/2010	release	10.3	Below	na	na	na	na	7/9/2010	1			
M7	7/9/2010	up	11.2	Below	7/9/2010	1	0.9	0.9	7/21/2010	13			
M7	7/22/2010	down	11	Below	7/21/2010	1	-0.2	-0.2	7/30/2010	9			
M7	7/31/2010	up	11.1	Below	7/30/2010	1	0.1	0.1	7/31/2010	1			
M7	8/2/2010	new	11.2	Below	7/31/2010	2	0.1	0	8/2/2010	1			
M7	8/2/2010	down	10.3	Below	8/2/2010	1	-0.9	-0.9	8/2/2010	1			

ID: M11

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M11	7/11/2010	release	10.3	Below	na	na	na	na	7/11/2010	1			
M11	7/11/2010	up	11.2	Below	7/11/2010	1	0.9	0.9	7/13/2010	3			
M11	7/13/2010	new	11.2	Below	7/13/2010	1	0	0	7/18/2010	6	3R	1P	2R
M11	7/19/2010	new	11.2	Below	7/18/2010	1	0	0	8/18/2010	31	3R	1P	2R
M11	8/19/2010	new	11.2	Below	8/18/2010	1	0	0	8/31/2010	13	3R	1P	2R
M11	9/1/2010	new	11.2	Below	8/31/2010	1	0	0	10/28/2010	58	3R	1P	2R

ID: M12

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M12	7/11/2010	release	10.3	Below	na	na	na	na	7/12/2010				
M12	7/13/2010	new	10.3	Below	7/12/2010	1	0	0	7/18/2010	6	3R	2G	2R
M12	7/20/2010	up	11.2	Below	7/18/2010	2	0.9	0.4	7/21/2010	2			
M12	7/21/2010	new	11.1	Below	7/21/2010	1	-0.1	-0.1	7/24/2010	5	3R	1P	2R
M12	7/28/2010	down	10.9	Below	7/24/2010	4	-0.2	0	8/19/2010	24			
M12	8/30/2010	new	11	Below	8/19/2010	11	0.1	0	9/4/2010	6	2R	3R	1P
M12	9/9/2010	new	11	Below	9/4/2010	5	0	0	9/19/2010	11	2R	3R	1P

ID: M14

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M14	7/11/2010	release	10.3	Below	na	na	na	na	7/11/2010	2			
M14	7/12/2010	up	11.2	Below	7/11/2010	1	0.9	0.9	7/19/2010	8	3R	1P	2R
M14	7/20/2010	new	11.2	Below	7/19/2010	1	0	0	7/29/2010	10	3R	1P	2R
M14	7/30/2010	new	11.2	Below	7/29/2010	1	0	0	8/10/2010	12	3R	1P	2R
M14	8/11/2010	new	11.2	Below	8/10/2010	1	0	0	8/13/2010	3	3R	1P	2R
M14	8/14/2010	new	11.2	Below	8/13/2010	1	0	0	8/17/2010	4	3R	1P	2R
M14	8/18/2010	new	11.2	Below	8/17/2010	1	0	0	8/20/2010	3	3R	1P	2R
M14	8/21/2010	new	11.2	Below	8/20/2010	1	0	0	9/1/2010	12	3R	1P	2R
M14	9/2/2010	new	11.2	Below	9/1/2010	1	0	0	9/9/2010	8	3R	1P	2R
M14	9/10/2010	new	11.2	Below	9/9/2010	1	0	0	10/28/2010	49	3R	1P	2R

ID: M17

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M17	7/13/2010	release	10.3	Below	na	na	na	na	7/13/2010	1			
M17	7/13/2010	down	10.2	Below	7/13/2010	1	-0.1	-0.1	7/18/2010	7			
M17	7/21/2010	up	11.2	Below	7/18/2010	3	1	0.3	8/2/2010	14			
M17	8/3/2010	new	11.2	Below	8/2/2010	1	0	0	8/13/2010	11	3R	1P	2R
M17	8/14/2010	new	11.2	Below	8/13/2010	1	0	0	8/17/2010	4	3R	1P	2R
M17	8/18/2010	up	19.5	Above	8/17/2010	1	8.3	8.3	9/4/2010	18			

ID: M18

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M18	7/13/2010	release	10.3	Below	na	na	na	na	7/13/2010	2			
M18	7/14/2010	up	10.6	Below	7/13/2010	1	0.3	0.3	7/15/2010	2			
M18	7/16/2010	down	10.4	Below	7/15/2010	1	-0.2	-0.2	7/21/2010	6	3R	2G	2R
M18	7/23/2010	up	10.5	Below	7/21/2010	2	0.1	0	7/24/2010	2			
M18	7/25/2010	up	11.2	Below	7/24/2010	1	0.7	0.7	8/1/2010	8	3R	1P	2R
M18	8/2/2010	new	11.2	Below	8/1/2010	1	0	0	8/14/2010	13	3R	1P	2R
M18	8/15/2010	new	11.2	Below	8/14/2010	1	0	0	8/21/2010	7			
M18	8/22/2010	new	11.2	Below	8/21/2010	1	0	0	9/8/2010	18			
M18	9/9/2010	new	11.2	Below	9/8/2010	1	0	0	10/25/2010	47	3R	1P	2R

ID: M19

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M19	7/19/2010	release	10.3	Below	na	na	na	na	7/21/2010	3			
M19	7/23/2010	up	10.6	Below	7/21/2010	2	0.3	0.1	7/23/2010	2			
M19	7/24/2010	up	11.2	Below	7/23/2010	1	0.6	0.6	7/27/2010	4	3R	1P	2R
M19	7/28/2010	new	11.2	Below	7/27/2010	1	0	0	9/8/2010	43	3R	1P	2R
M19	9/9/2010	new	11.2	Below	9/8/2010	1	0	0	9/21/2010	13	3R	1P	2R

ID: M20

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M20	7/19/2010	release	10.3	Below	na	na	na	na	7/21/2010				
M20	7/23/2010	new	10.3	Below	7/21/2010	2	0	0	7/23/2010	1			
M20	7/23/2010	up	11.2	Below	7/23/2010	1	0.9	0.9	8/1/2010	10	3R	1P	2R
M20	8/2/2010	new	11.2	Below	8/1/2010	1	0	0	8/23/2010	22	3R	1P	2R
M20	8/24/2010	new	11.2	Below	8/23/2010	1	0	0	8/29/2010	6	3R	1P	2R
M20	8/30/2010	new	11.2	Below	8/29/2010	1	0	0	9/9/2010	11	3R	1P	2R
M20	9/9/2010	new	11.2	Below	9/9/2010	1	0	0	10/28/2010	50	3R	1P	2R

ID: M21

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M21	7/19/2010	release	10.3	Below	na	na	na	na	7/19/2010	1			
M21	7/19/2010	up	11.2	Below	7/19/2010	1	0.9	0.9	8/10/2010	23	3R	1P	2R
M21	8/11/2010	new	11.2	Below	8/10/2010	1	0	0	9/13/2010	34	3R	1P	2R
M21	9/16/2010	new	11.2	Below	9/13/2010	3	0	0	10/20/2010	35	3R	1P	2R

ID: M22

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M22	7/19/2010	release	10.3	Below	na	na	na	na	7/19/2010	1			
M22	7/19/2010	up	11.2	Below	7/19/2010	1	0.9	0.9	7/25/2010	7	3R	1P	2R
M22	7/28/2010	down	5.6	Below	7/25/2010	3	5.6	1.9	8/31/2010	36	1P	2R	3R

ID: M24

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M24	8/4/2010	release	10.3	Below	na	na	na	na	8/4/2010	1			
M24	8/4/2010	new	10.3	Below	8/4/2010	1	0	0	8/7/2010	4	3R	2G	2R
M24	8/10/2010	down	10.1	Below	8/7/2010	3	-0.2	-0.1	8/13/2010	5	2R	3R	3R
M24	8/16/2010	up	10.5	Below	8/13/2010	3	0.4	0.1	10/28/2010	74	2R	3R	1P

ID: M26

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M26	8/11/2010	release	10.3	Below	na	na	na	na	8/13/2010	4			
M26	8/16/2010	up	10.5	Below	8/13/2010	3	0.2	0.1	10/28/2010	74	2R	3R	1P

ID: M27

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M27	8/16/2010	release	10.3	Below	na	na	na	na	8/20/2010	6			
M27	8/22/2010	up	11.2	Below	8/20/2010	2	0.9	0.4	8/22/2010	1			
M27	8/25/2010	new	11.2	Below	8/22/2010	3	0.9	0.3	10/28/2010	65	3R	1P	2R

ID: M28

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M28	8/16/2010	release	10.3	Below	na	na	na	na	8/16/2010	2			
M28	8/17/2010	up	11.2	Below	8/16/2010	1	0.9	0.9	8/19/2010	3	3R	1P	2R
M28	8/20/2010	new	11.2	Below	8/19/2010	1	0	0	9/8/2010	20	3R	1P	2R
M28	9/9/2010	new	11.2	Below	9/8/2010	1	0	0	10/28/2010	50	3R	1P	2R

ID: S1

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S1	6/16/2010	release	10.3	Below	na	na	na	na	6/16/2010	2			
S1	6/17/2010	up	10.4	Below	6/16/2010	1	0.1	0.1	6/20/2010	4	2G	1P	3R
S1	6/23/2010	new	10.4	Below	6/20/2010	3	0	0	6/24/2010	2	2G	1P	3R
S1	6/25/2010	up	11.2	Below	6/24/2010	1	0.8	0.8	6/25/2010	1			
S1	6/28/2010	down	10.6	Below	6/25/2010	3	0.2	0.1	7/3/2010	6	2R	3R	1P
S1	7/7/2010	new	10.5	Below	7/3/2010	4	-0.1	0	7/7/2010	1	2R	3R	1P
S1	7/7/2010	up	11.2	Below	7/7/2010	1	0.7	0.7	7/12/2010	6			
S1	7/13/2010	new	11.2	Below	7/12/2010	1	0	0	7/15/2010	3	3R	1P	2R
S1	7/16/2010	new	11.2	Below	7/15/2010	1	0	0	7/21/2010	6	3R	1P	2R
S1	7/21/2010	new	11.2	Below	7/21/2010	1	0	0	8/31/2010	42	3R	1P	2R

ID: S2

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S2	6/17/2010	release	10.3	Below	na	na	na	na	6/17/2010	1			
S2	6/17/2010	new	10.3	Below	6/17/2010	1	0	0	6/17/2010	5	3R	2G	2R
S2	6/24/2010	up	11.2	Below	6/21/2010	3	0.9	0.3	6/24/2010	1			
S2	6/25/2010	new	11.2	Below	6/24/2010	1	0	0	6/25/2010	1			
S2	6/27/2010	new	11.2	Below	6/25/2010	2	0	0	6/27/2010	1			
S2	6/28/2010	new	11.2	Below	6/27/2010	1	0	0	6/28/2010	1			
S2	6/30/2010	new	11.2	Below	6/28/2010	2	0	0	6/30/2010	1			
S2	7/2/2010	new	11.2	Below	6/30/2010	2	0	0	7/5/2010	4			
S2	7/11/2010	new	11.2	Below	7/5/2010	6	0	0	7/11/2010	1			
S2	7/17/2010	up	55.6	Above	7/11/2010	6	44.4	7.4	8/18/2010	33	3R	2R	2R

ID: S91

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S91	7/1/2010	release	10.3	Below	na	na	na	na	7/4/2010	4			
S91	7/7/2010	new	10.3	Below	7/4/2010	3	0	0	7/7/2010	2	2R	3R	3R
S91	7/8/2010	up	11.2	Below	7/7/2010	1	0.9	0.9	7/10/2010	3			
S91	8/18/2010	up	31.6	Above	7/10/2010	39	31.6	0.8	9/8/2010	22	2R	3R	3R

ID: S92

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S92	7/9/2010	release	10.3	Below	na	na	na	na	7/9/2010	1			
S92	7/9/2010	up	11.2	Below	7/9/2010	1	0.9	0.9	7/12/2010	4			
S92	7/13/2010	down	10.3	Below	7/12/2010	1	-0.9	-0.9	7/15/2010	3	3R	2G	2R
S92	7/16/2010	new	10.3	Below	7/15/2010	1	0	0	7/16/2010	1	3R	2G	2R

ID: S172

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S172	8/16/2010	release	10.3	Below	na	na	na	na	8/16/2010	1			
S172	8/16/2010	new	10.3	Below	8/16/2010	1	0	0	8/16/2010	1	2R	3R	3R
S172	8/16/2010	up	11.2	Below	8/16/2010	1	0.9	0.9	8/17/2010	2	3R	1P	2R
S172	8/21/2010	new	11.2	Below	8/17/2010	4	0	0	10/9/2010	50	3R	1P	2R
S172	10/12/2010	new	11.2	Below	10/9/2010	3	0	0	10/28/2010	17	3R	1P	2R

ID: S198

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S198	7/19/2010	release	10.3	Below	na	na	na	na	7/19/2010	1			
S198	7/19/2010	new	10.3	Below	7/19/2010	1	0	0	7/22/2010	4	3R	1P	2R
S198	7/25/2010	up	11.2	Below	7/22/2010	3	0.9	0.3	8/1/2010	8	3R	1P	2R
S198	8/2/2010	new	11.2	Below	8/1/2010	1	0	0	8/4/2010	3	3R	1P	2R
S198	8/5/2010	new	11.2	Below	8/4/2010	1	0	0	8/8/2010	4	3R	1P	2R
S198	8/9/2010	new	11.2	Below	8/8/2010	1	0	0	8/23/2010	15	3R	1P	2R
S198	8/24/2010	new	11.2	Below	8/23/2010	1	0	0	9/8/2010	16	3R	1P	2R
S198	9/9/2010	new	11.2	Below	9/8/2010	1	0	0	10/28/2010	50	3R	1P	2R

ID: L46

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
L46	7/1/2010	release	13.7	Above	na	na	na	na	7/22/2010	22			
L46	8/13/2010	up	44	Above	7/22/2010	22	30.3	1.4	8/13/2010	1	2G	1P	2R
L46	8/14/2010	up	46.7	Above	8/13/2010	1	2.7	2.7	8/14/2010	1			
L46	8/27/2010	up	55.7	Above	8/14/2010	13	9	0.7	9/29/2010	33	3R	2R	2R

ID: M2

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M2	7/7/2010	release	13.7	Above	na	na	na	na	7/12/2010	6			
M2	7/17/2010	up	43	Above	7/12/2010	5	29.3	5.9	7/17/2010	2			
M2	7/18/2010	up	46.6	Above	7/17/2010	1	3.6	3.6	7/18/2010	1			
M2	7/22/2010	down	46.5	Above	7/18/2010	4	-0.1	0	9/18/2010	59	1P	2G	2G

ID: M8

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M8	7/9/2010	release	13.7	Above	na	na	na	na	7/15/2010	7			
M8	7/16/2010	new	13.7	Above	7/15/2010	1	0	0	7/18/2010	4			
M8	7/21/2010	new	13.7	Above	7/18/2010	3	0	0	9/23/2010	66	2G	1P	3R

ID: M9

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M9	7/9/2010	release	13.7	Above	na	na	na	na	7/13/2010	5			
M9	7/17/2010	up	18.4	Above	7/13/2010	4	4.7	1.2	7/19/2010	4			
M9	7/22/2010	down	17.4	Above	7/19/2010	3	-1	-0.3	7/24/2010	3			
M9	7/26/2010	down	11.2	Below	7/24/2010	2	-6.2	-3.1	7/26/2010	1			
M9	7/28/2010	down	10.9	Below	7/26/2010	2	-0.3	-0.1	7/30/2010	4			
M9	8/2/2010	down	10.7	Below	7/30/2010	3	-0.2	-0.1	8/9/2010	9	1P	2R	3R
M9	8/10/2010	new	10.6	Below	8/9/2010	1	-0.1	-0.1	8/13/2010	5			
M9	8/16/2010	new	10.7	Below	8/13/2010	3	0.1	0	8/20/2010	5	1P	2R	3R
M9	8/24/2010	new	10.7	Below	8/20/2010	4	0	0	9/4/2010	12	2R	3R	1P
M9	9/9/2010	new	10.8	Below	9/4/2010	5	0.1	0	10/28/2010	50	2R	3R	1P

ID: M10

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M10	7/9/2010	release	13.7	Above	na	na	na	na	7/26/2010	19			
M10	8/13/2010	up	28.8	Above	7/26/2010	18	15.1	0.8	9/26/2010	45	1P	2G	2G

ID: M13

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M13	7/11/2010	release	13.7	Above	na	na	na	na	7/12/2010	3			
M13	7/14/2010	up	14.3	Above	7/12/2010	2	0.6	0.3	7/28/2010	16			
M13	8/5/2010	up	33.9	Above	7/28/2010	8	19.6	2.5	8/12/2010	8	3R	1P	1P
M13	8/19/2010	up	38.7	Above	8/12/2010	7	4.8	0.7	9/16/2010	30	2R	3R	1P

ID: M15

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M15	7/11/2010	release	13.7	Above	na	na	na	na	7/18/2010	9			
M15	7/21/2010	up	14.5	Above	7/18/2010	3	0.8	0.3	7/24/2010	5			
M15	7/28/2010	down	14.1	Above	7/24/2010	4	-0.4	-0.1	8/12/2010	16			
M15	8/18/2010	down	13.4	Above	8/12/2010	6	-0.7	-0.1	9/17/2010	31	2R	3R	1P

ID: M16

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M16	7/11/2010	release	13.7	Above	na	na	na	na	7/12/2010	3			
M16	7/14/2010	new	13.7	Above	7/12/2010	2	0	0	7/28/2010	16	3R	2G	2R
M16	7/29/2010	up	20	Above	7/28/2010	1	6.3	6.3	8/8/2010	11	2R	3R	3R
M16	8/18/2010	up	33.2	Above	8/8/2010	10	13.2	1.3	10/28/2010	72	3R	1P	2R

ID: M23

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M23	7/28/2010	release	13.7	Above	na	na	na	na	8/1/2010	6			
M23	8/6/2010	new	13.7	Above	8/1/2010	5	0	0	8/6/2010	1	3R	2G	2R
M23	8/6/2010	new	13.7	Above	8/6/2010	1	0	0	8/12/2010	7	2G	1P	3R
M23	8/18/2010	down	12.9	Above	8/12/2010	6	-0.8	-0.1	9/29/2010	43	1P	2R	3R

ID: M25

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M25	8/6/2010	release	13.7	Above	na	na	na	na	8/9/2010	5			
M25	8/13/2010	up	23.7	Above	8/9/2010	4	10	2.5	8/15/2010	4	2R	3R	3R
M25	8/18/2010	up	32.6	Above	8/15/2010	3	8.9	3	10/28/2010	72	2R	3R	3R

ID: M29

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
M29	8/23/2010	release	13.7	Above	na	na	na	na	8/23/2010	1			
M29	8/23/2010	new	13.7	Above	8/23/2010	1	0	0	8/24/2010	2	2G	1P	3R
M29	8/25/2010	new	13.7	Above	8/24/2010	1	0	0	9/23/2010	31	3R	2G	2R

ID: S19

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S19	6/25/2010	release	13.7	Above	na	na	na	na	6/28/2010	4			
S19	7/1/2010	up	18.3	Above	6/28/2010	3	4.6	1.5	7/4/2010	4			
S19	7/7/2010	up	39.5	Above	7/4/2010	3	21.2	7.1	8/8/2010	34			

ID: S93

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S93	7/9/2010	release	13.7	Above	na	na	na	na	7/12/2010	4			
S93	7/15/2010	up	46.7	Above	7/12/2010	3	33	11	7/15/2010	1			
S93	7/22/2010	up	55.7	Above	7/15/2010	7	42	6	8/20/2010	30	3R	2R	2R

ID: S94

ID	Start Date	Status	River km	Above/ Below Dam?	Previous Date	Travel Days	River km Δ	travel speed	End Date	Holding Days	HU	Pre-HU	Post-HU
S94	7/9/2010	release	13.7	Above	na	na	na	na	7/29/2010	21			
S94	8/18/2010	up	33	Above	7/29/2010	20	19.3	1	10/28/2010	72	3R	2R	2R

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