Technical Report 2019-3

EVALUATING THE INFLUENCE OF PAST EXPERIENCE ON SWIMMING BEHAVIOR AND PASSAGE SUCCESS IN ADULT PACIFIC LAMPREY USING EXPERIMENTAL FLUMES AND ACCELEROMETER TELEMETRY, 2018

A Report for Study Code: LMP-P-17-1

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S.A. Hanchett and C.C. Caudill
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University of Idaho, Moscow, ID 83844-1136

for

U.S Army Corps of Engineers
Portland District, Portland, OR

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Executive Summary

Radio-telemetry studies have revealed that bottlenecks and high-turn around rates in fishways contribute to low passage success of Pacific Lamprey at Columbia river dams. Structural and operational modifications to fishways and installation of lamprey-specific passage structures have improved fishway entrance and dam passage efficiencies, but conditions in the upper fishways continue to result in low overall passage success. In particular, lamprey turnaround rates are high in the Bonneville Dam serpentine weir sections, areas characterized by high water velocities and hydraulic complexity through a series of more than a dozen weirs. Approximately one quarter to one third of lampreys that reach the serpentine weirs fail to pass the dam. While previous research has demonstrated most lamprey readily pass a single challenge with high water velocity (2.4 m/sec), the low passage success suggests fatigue during passage of multiple weirs in series may be problematic. Our primary research objective in 2018 tested this hypothesis using exercise trials that manipulated exercise histories of lamprey prior to a single weir passage challenge at high velocity in an experimental flume (11.6-m long × 1.2-m wide × 2.4-m high). Treatments were applied using a 2 × 2 factorial design with two exercise velocity levels (1.0 m/s and 1.4 m/s) and two exercise duration levels (1 × 20 min and 2 × 20 min with a 10 min recovery interval in between repetitions; 6 replicates/treatment with 6 lamprey/replicate) as well as control. Passage success was then evaluated with a 1-m long vertical weir at 2.2 m/sec water velocity. In a second study, we evaluated the feasibility of a moderate (10°) slope prototype flume with and without weirs as a potential design element in future lamprey passage structures. Lastly, we conducted a pilot evaluation of accelerometer biotelemetry as a tool for estimating lamprey activity levels and energy expenditure in fishways.

In the exercise trials, we found that point estimates of mean passage success were lower in the high pre-challenge velocity treatments (52-56%) than in controls (86%) regardless of the pre-challenge exercise duration. Mean passage success in the 1 × 20 min low pre-challenge velocity treatment was similar to the control, and the 2 × 20 min mean passage success (72%) was intermediate between control and high velocity treatments. Passage success in the low-velocity, low-duration exercise treatment was significantly higher than in the low-velocity, high-duration treatment ($Z = 2.57$, $P = 0.01$) and the high-velocity, low-duration treatment ($Z = 3.64$, $P < 0.01$). Lamprey that were characterized as ‘late’ run were more likely to fail at passing compared to those earlier in the season. This effect was particularly magnified for the high-velocity treatments. Overall, the results indicate the past exercise history of lamprey affects passage success rate through the vertical slot weir section of the experimental flume, consistent with the hypothesis that lamprey reach an endurance threshold and/or incur loss of motivation when passing multiple high velocity obstacles in succession (i.e., the serpentine weirs).

Passage success in the prototype flume was slightly lower without weirs (64%) compared to when weirs were present (83%), but this difference was not statistically significant ($Z = 0.57$, $P =$

0.36. Length was not associated with passage success ($Z = 0.07$, $P = 0.13$). Passage time was considerably faster with weirs present (median = 2 min) versus without weirs (median = 13.5 min) ($W = 110.5$, $P < 0.05$). The high passage success and relatively rapid passage times in both treatments highlight the potential for the design as a flexible element in lamprey passage systems that may also be more cost effective than current lamprey passage structure (LPS) designs.

The pilot accelerometer trial compared tag acceleration records to simultaneous video observations and revealed some, but not all, important behaviors could be discerned from the tag output. Burst movement behavior was clearly distinguished from swimming and attachment in low water velocities. Telemetry data from a single *at-liberty* lamprey released to the fishway suggested strong differences in activity between day and night. The efficacy of accelerometer biotelemetry as a method for estimating the energy expenditure associated with passage of specific routes and obstacles in fishways at Bonneville Dam will be tested in 2019.

Introduction

Lampreys have experienced major declines, including populations of the anadromous Pacific lamprey (*Entosphenus tridentatus*) found in the Pacific Northwest (Close et al. 2002). Blocked or poor passage at dams and other barriers, habitat degradation, and deliberate eradication efforts have been implicated in the declines of Pacific lamprey (Close et al. 2004). Traditional fishways developed at hydroelectric dams in the Columbia River basin, known as the Federal Columbia River Power System (FCRPS), were primarily designed for passage of adult salmonids, and thus are less suitable for the anguilliform swimming behavior of lamprey (Clay 1995; Moser et al. 2011). Differences in swimming behavior, morphology, and migration strategy, as compared to salmonids, all contribute to low success rates for lamprey navigating fishways (e.g., Mesa et al. 2003; Kemp et al. 2009; Moser et al. 2009; 2011; Kirk et al. 2017a).

In past telemetry studies, approximately 50% of all upstream migrating adult Pacific lamprey failed to pass Bonneville Dam, the lowermost dam on the Columbia River and only ~1% successfully passed Ice Harbor dam, the first dam on the Snake River (Moser et al. 2002a, 2002b; Keefer et al. 2009, 2013, 2019). High water velocities (>2 m/s) present throughout fishways may be partially responsible for low lamprey passage success, as such velocities exceed the critical swimming speed of Pacific lamprey (~0.86 m/s) (Mesa et al. 2003). Furthermore, lampreys do not have the endurance and burst speed capabilities of salmonids, instead relying on their oral disk to attach and then burst forward ("saltatory" motion) in high velocity/turbulent conditions (Reinhardt et al. 2008). Grating and other surfaces present in fishways prevent oral disk attachment, thus further contributing to unfavorable passage conditions (Moser et al. 2002a).

Efforts have been made to improve passage conditions, including implementation of structures specifically suited for lamprey passage at Bonneville and John Day dams (Moser et al. 2002b, 2011). These structures, referred to as lamprey passage structures (LPS), take advantage of the natural climbing ability of lamprey and reroute them through difficult passage areas (Moser et al. 2002b; 2011). Lamprey passage structures have steep-angled climbing ramps (45° - 60°) that lead to low-slope ducts terminating in either a collection box or into the forebay above the dam (Reinhardt et al. 2008). Structures were placed in areas of high lamprey densities where milling and turn-around behaviors were observed (Moser et al. 2005, 2006, 2008, 2011). Once lamprey enter the structures, passage success rates are generally greater than 90% (Moser et al. 2006, 2008, 2011). However, despite the promising use of lamprey-specific passageways, the complex nature of the lower Columbia River dams continues to result in local areas of poor passage (i.e., bottlenecks, Keefer et al. 2013). In particular, the serpentine weir section near the exits of both fishways at Bonneville Dam are areas with ~25-30% turn-around rates for lamprey, despite having similar velocities and turbulence to obstacles encountered previously during passage (Keefer et al. 2013, 2014b) and experimental demonstration of generally high passage rate of high velocity obstacles in experimental settings (e.g., Kirk et al. 2016). These patterns highlight the need for mechanistic understanding of the factors affecting turnaround behaviors.

Additionally, although previous studies have shown that lamprey exhibit fairly high success rates once they engage in climbing, many lamprey initially bypass the structure when moving upstream (Moser 2005). Furthermore, recent research has shown that many lamprey only use some LPSs after turning around when failing to pass upstream through the traditional fishway (Clabough et al. 2019). Energetic costs associated with climbing are largely unknown, as well as any effects of size selection that may be occurring in lamprey that successfully use these structures. Qualitative observations of lamprey climbing up ramps has revealed that lamprey may take several attempts to pass after falling back, indicating that climbing may prove to be energetically costly and/or may affect exhaustive condition or motivational state.

Understanding the metabolic costs of passing individual dams and the FCRPS hydrosystem may also be important to understanding lamprey declines as metabolic and energetic condition may influence behavioral decisions during migration, individual fitness, and population productivity. As velocity increases, both swimming speed and relative energy expenditure also increases (Brett 1964). When encountering high velocities and turbulent conditions, lampreys frequently employ an 'attach and burst' method that may induce a high physiological cost from anaerobic metabolism (Kemp et al. 2009). Quintella et al. (2009) found that the occurrence and rate of attachment increased over time in response to ongoing strenuous conditions for upstream migrating sea lamprey (*Petromyzon marinus*), indicating that lampreys required longer rest periods under prolonged strenuous conditions. The ability to quantify the cost of different behaviors would prove to be advantageous when designing fish passage routes. A common and well-studied method to estimate fish metabolic rate is through the use of respirometry, or measurement of oxygen consumption (Norin and Clark 2016). However, these estimates do not always translate well into the field, often underestimating a fish's true aerobic scope (Norin and Clark 2016). Recent advances in the use of biotelemetry accelerometers offer the opportunity to simultaneously monitor fine-scale behavior and estimate the energy budget for a fish in natural environments by linking specific activities to respirometer measurements (Thiem et al. 2015; Metcalf 2016; Bouyoucos et al. 2018; Fuchs and Caudill 2019). Using accelerometers to relate metabolic cost to swimming activity would provide the ability to estimate total energy expenditure under various scenarios.

This report summarizes results from the first year of a two-year study. The objectives are as follows:

1) Exhaustive Exercise Flume: The first and primary objective was to investigate the effects of exercise history (i.e., fatigue) on adult Pacific lamprey swimming performance and

passage using an experimental flume in the Bonneville Dam adult fish facility (AFF). Given that multiple obstacles and high velocities such as those encountered in the serpentine weirs will have a greater energetic demand and require increased endurance capacity, we hypothesized that 1) fish subjected to longer swim durations and strenuous velocities prior to a passage challenge will result in decreased passage success. Additionally, we hypothesized that 2) the traits of individual fish will affect endurance thresholds among fish subjected to the same treatment, resulting in varied passage success due to physiological, and/or morphological (body size) differences.

2) Prototype Flume: The second objective was to evaluate the swimming performance of lamprey in a prototype flume to test feasibility of the design for application as a passage structure. Passage success rates and overall passage time were evaluated in response to the presence or absence of weirs (i.e., rounded, semi-circular pvc pipes attached width-wise at ~1-m intervals) along the length of a 6-m wetted ramp with a 10% slope.

3) Accelerometer Biotelemetry: The third objective was to evaluate the application of accelerometer biotelemetry to quantify activity of lamprey as the first step to quantifying energy expenditure for fish navigating through the serpentine weir section at the WA-shore fishway. In this pilot study, accelerometer radio-tagged lamprey were placed in an experimental flume and swum at various water velocities, both free-swimming and attached, to assign different behaviors according to the tag output. Fish were subsequently released in the WA-shore fishway downstream of the upstream migration tunnel (UMT) junction and monitored with fixed telemetry sites, using a combination of aerial and underwater antennas, as they moved upstream.

Methods

Exhaustive Exercise Flume Experiments

Adult Pacific lamprey (*n* = 180) were collected at night from June 20 to August 5, 2018 from a newly installed lamprey flume structure (LFS) located near the adult fish facility (AFF) at Bonneville Dam (45.6°N, 121.9°W) on the lower Columbia River. Fish were removed from the collection box the following morning and were held in large aluminum tanks (92-cm wide × 152-cm long × 122-cm high) that had constantly recirculating aerated river water. Lamprey were anesthetized in a 60-ppm (3 mL/50 L) solution of eugenol (AQUI-S 20E). An approximate 12-mm ventral incision was made directly below the anterior insertion of the first dorsal fin and a half-duplex passive integrated transponder tag (HD-PIT tag; 4 × 32 mm) was inserted into the body cavity. Fish were weighed (g), measured for total length (cm), body girth (cm), and dorsal distance (cm), percent body fat (lipid), and had a fin clip removed for a future genetic study.

A subset of 50 fish had a blood sample taken during the 'late' run (7/2 – 8/5). After insertion of a PIT tag, the fish was turned with ventral side facing up in a moistened trough. A 5 ml, 1-inch, 23-gauge needle was inserted ~2 cm posterior to the vent at a slight angle (angled towards caudal fin, away from vent). Approximately 40 µl of blood was removed from caudal vasculature. The blood sample was processed using a VetScan i-STAT® 1 handheld analyzer (Abaxis products, Union City, CA) for hematocrit, hemoglobin, ionized calcium, glucose, sodium, potassium, pH, pCO_2, HCO_3, TCO_2, base excess, PO_2, and sO_2. A Lactate Plus meter (Sports Resource Group Inc., U.S.A) was used to measure plasma lactate. Tagged fish were allowed to recover for 8-12 hours prior to the experiment. All surgical and handling methods were approved by the University of Idaho Animal Care and Use Committee. Further details on collection and tagging procedures can be found in Moser et al. (2002a) and Johnson et al. (2012).

Experiments were conducted in an experimental flume (11.6-m long × 1.2-m wide × 2.4-m high) inside the AFF at Bonneville Dam. The flume consisted of a 9-m long experimental section with a 10% slope, and an upstream chamber at the top of the flume with fyke nets that fish could readily enter, but which limited exit. An aluminum frame structure (1.1-m long × 0.91-m wide × 0.61-m high) outlined with mesh to prevent oral-disk attachment at the downstream end served as an acclimation and exercise chamber (Figure 1). A vertical slot weir (1-m long) was situated upstream of the mesh chamber (Figure 2). The flume was supplied with river water via two supply pipes that were capable of generating flow rates of 835 L/s. Additional details of the flume can be found in Keefer et al. (2011) and Kirk et al. (2016, 2017b).

Figure 1. Mesh exercise chamber located in the downstream portion of the experimental flume

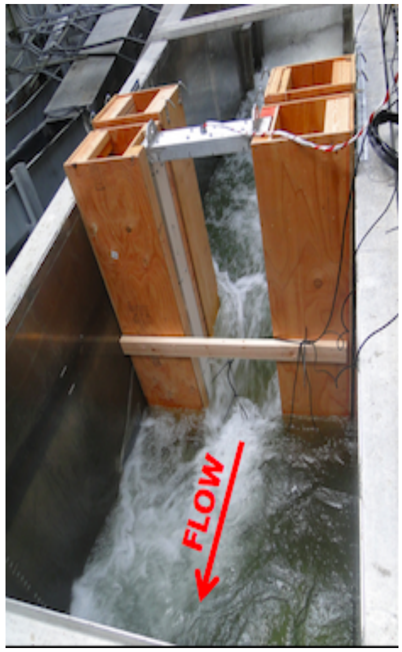

Figure 2. Experimental flume with vertical slot weir. The downstream PIT antenna is visible as the metal frame at the downstream end of the weir. Weir slot length was 1.0-m rather than 0.66-m as pictured.

All experiments were conducted at night (1900-0700) because Pacific lamprey are primarily nocturnal during their migration phase. The experiment consisted of a 2 × 2 factorial design with a control that manipulated two treatment variables (Table 1). The design had two pre-challenge exercise velocity levels (1.0 m/s and 1.4 m/s) and two pre-challenge exercise duration levels (20 min and 2 × 20 min with a 10 min recovery interval in between repetitions). The control consisted of no exercise. Hereafter, the treatments will be referred to as C (control), L1 (1.0 m/s, 20 min), L2 (1.0 m/s, 2 x 20 min), H1 (1.4 m/s, 20 min) and H2 (1.4 m/s, 2x20 min). All lamprey were acclimated in the mesh chamber for 20 min prior to exercise, including the control treatment. Depending on the exercise treatment, the lamprey spent 20 min – 70 min in the chamber. After the pre-challenge exercise treatment, lamprey were immediately given access to the flume for the passage trial. Velocity at the weir was 2.2 m/s for all treatments and lamprey were given two hours to pass. A complete randomized block design consisting of 6 blocks accounted for seasonal variation in river temperature and lamprey traits (see Results). To account for seasonal variation, blocks were divided into “early”, “mid”, and “late” categorizations (block 1-2 “early”, block 3-4 “mid”, block 5-6 “late”). Treatment velocities were measured at three equidistant points directly in front of the mesh covered cage at 60% of the depth and averaged to determine exercise velocity. Three additional measurements were made at the vertical slot weir at 20% and 80% depth and averaged to determine velocity for conditions experienced post-exercise release into the flume. All measurements were made using a Marsh-McBirney flow meter. After the conclusion of each experiment, lamprey were removed from the flume, scanned for HD-PIT tags, and allowed at least 25 minutes recovery before being released upstream of Bonneville Dam at the Stevenson, WA boat launch. After release, lamprey were monitored during upstream migration using methods detailed in Clabough et al. (2019).

Table 1. Summary of exercise velocities, duration of exercise treatments, and number of replicates in the 2018 experiment. Each replicate included 6 adult lamprey with a total of 180 lamprey across all replicates.

Exercise Velocity (m/s)	Exercise Duration (min)		
	0	20	2x20
0	6		
1		6	6
1.4		6	6

Lamprey movements and behaviors were video-recorded using two underwater cameras placed on the upstream end and two cameras on the downstream end sections of the vertical slot weir. Two cameras were placed in the mesh chamber for behavioral observations. HD-PIT antennas were placed at the downstream and upstream ends of the vertical slot weir, as well as at the entrance to the fyke section to record approach and finishing times. PIT tag records for individual lamprey were used to score each individual as having passed the weir or not, and to calculate passage times.

To test the hypotheses regarding predictor variables effects on passage and to test for treatment effects, we used multiple logistic regression (GLM function with binomial distribution, nnet package, R v. 3.3.3) with ‘passed’ vs. ‘did not pass’ as the binary response variable. The logistic regression predictor variables included all treatment variables, run date (block), fish length, dorsal distance, and body fat. We also tested for factors associated with upstream escapement past dams with a multinomial logistic regression model (nnet package, R v. 3.3.3) that evaluated subsequent passage at four upstream dams: The Dalles, John Dam, McNary, and Priest Rapids dams. Individual lamprey were scored into one of the following classes: (1) final record between release and below The Dalles Dam; (2) passing The Dalles Dam; (3) passing John Day Dam; (4) passing McNary Dam, or (5) passing Priest Rapids dam. Predictor variables included run date, dorsal distance, and length.

Prototype Flume Experiment

Adult Pacific lamprey (n = 100) were collected overnight from July 6 to 18, 2018 from the lamprey flume structure (LFS) located adjacent to the AFF. All lamprey were tagged and assessed as described above for the exhaustive exercise flume experiments.

Experiments were conducted in a prototype flume (6.1 m long x 0.41 m wide x 0.30 m high with 0.61 m × 0.91 m boxes on either end) with a 10% slope (Figure 3). Passage success rates were evaluated in the presence or absence of weirs (i.e., 25 cm diameter pvc half-pipes attached transversely across the channel at 1 m intervals) (Figure 4). HD-PIT tag antennas were placed at the upstream and downstream end of the flume in order to record lamprey approach and finishing events and times. The flume was supplied with river water by a pipe regulated with valves. Discharge was 0.03 m^3/s (1.06 cfs) and velocity was 0.30 m/s. Velocity was measured using a Marsh-McBirney flow meter.

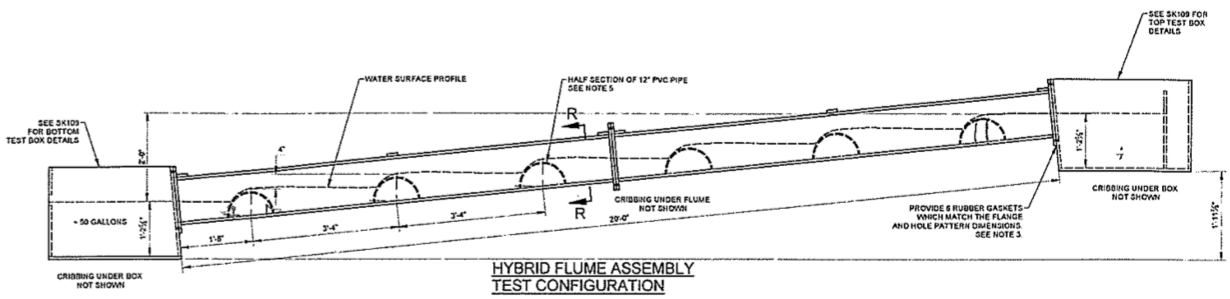

Figure 3. Schematic of prototype flume. Image provided by USACE.

Figure 4. Prototype flume with weirs in place.

The experiment was a completely randomized design consisting of two treatments: either presence or absence of weirs. Each treatment had 5 replicates for 10 total trials with a sample size of 10 lamprey per trial (*n* = 50 per treatment). Lamprey were allowed to acclimate for a minimum of 15 minutes in the downstream chamber before being released into the flume and were given one hour to pass. All trials were conducted in the early evening. Passage success was defined as the number of lamprey that successfully passed divided by the number that approached the first antenna. All lamprey that did not approach the first antenna were excluded from analysis. Additionally, passage time of the first successful passage attempt was recorded for each individual. Subsequent events were excluded from analysis. Video observations were made for one replicate within each treatment to qualitatively assess lamprey behavior.

Multiple logistic regression (GLM function with binomial distribution, nnet package, R v. 3.3.3) with 'passed' vs. 'did not pass' as the binary response variable. Length was included as the predictor variable. Passage time was square root transformed in order to meet the assumption of normality. A Welch's t-test was used to test for differences between passage time among the two groups. All analyses were conducted in R v. 3.3.3.

Accelerometer Biotelemetry Pilot Study

Adult Pacific lamprey (*n* = 13) were collected overnight from August 13 to September 5, 2018. All lamprey were tagged and assessed as described above, with the additional implantation of an accelerometer tag (9 × 42 mm, 6.8 g, Lotek Wireless, Newmarket, ON). After the incision was made, a 14-cm long sterile catheter was placed inside the body cavity and pushed through the body wall approximately 3-5 cm posterior to the incision. The accelerometer tag antenna was threaded through the catheter and the tag was inserted into the body cavity. Three sutures were placed to close the incision.

The accelerometer tag measured acceleration at 12.5 Hz and reported the maximum acceleration in any vector every 5 seconds (referred to as the burst interval, BI), with a maximum value of 1.5 g (gravity, m/s^2). Prior to release at the WA-shore fishway, a subset of lamprey (*n* = 9) were placed in the AFF experimental flume to observe behaviors under velocities ranging from 0.8 m/s to 2.2 m/s in order to correlate behaviors with the tag output. Lamprey were initially placed in a mesh chamber that prevented attachment of the oral disk in order to observe free-swimming behavior. They were allowed to acclimate at a velocity of 0.8 m/s for 10 min, velocity was increased to 1.2 m/s for 5 min, and then increased to 1.4 m/s for 5 min. Lamprey were released from the chamber into the flume at a velocity of 2.2 m/s for 1 hour. Video was used to record lamprey behavior. Start and end times for behaviors (attachment, free swimming) were recorded and aligned to telemetry records. Lamprey tagged with accelerometer radio-tags were released into the WA-shore fishway on the following dates: August 13 (*n* = 3), August 15 (*n* = 3), September 5 (*n* = 6), and September 6 (*n* = 1). We used Lotek SRX 800 receivers and a combination of aerial and underwater antennas to monitor behaviors; locations are shown in Figure 5.

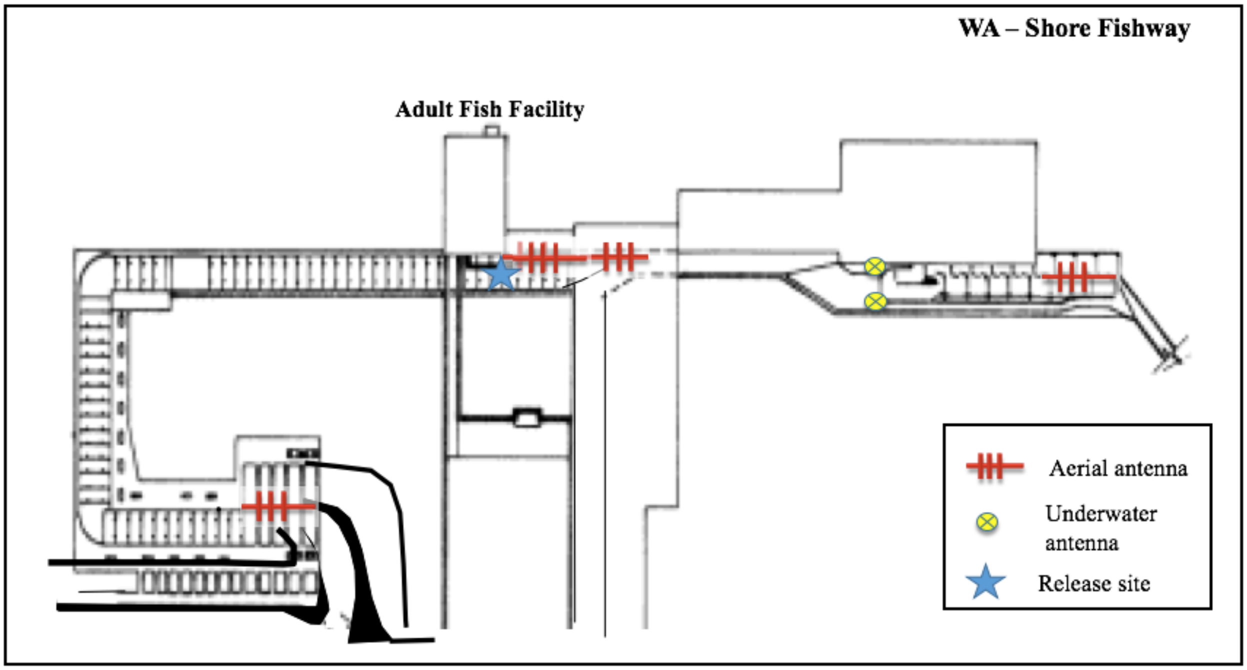

Figure 5. WA-shore fishway at Bonneville Dam, with locations of monitoring locations and the release site for lamprey tagged with accelerometer radio-tags (n = 13).

Results

Exhaustive Exercise Flume Experiments

Mean lamprey size and dorsal distance did not differ systematically among blocks during the experimental period (T-tests, all $P > 0.05$) (Table 2).

Table 2. Summary of number of blocks and corresponding dates of mean (±SD) dorsal distance, mean (±SD) length, and mean (±SD) weight of lamprey

Block	Dates	N	Mean dorsal distance (cm)	Mean weight (g)	Mean length (cm)
1	6/20 - 6/25	36	3.66 (±0.70)	497.33 (±108.46)	67.44 (±5.25)
2	6/29 - 7/03	36	3.84 (±0.55)	534.07 (±113.66)	68.96 (±4.82)
3	7/07 - 7/10	36	3.92 (±0.52)	529.43 (±88.80)	69.71 (±3.91)
4	7/19 - 7/22	36	4.40 (±1.00)	494.57 (±105.55)	67.88 (±5.39)
5	7/25 - 7/27	36	3.72 (±0.59)	493.80 (±106.04)	67.13 (±5.04)
6	8/02 - 8/05	36	3.65 (±0.51)	419.67 (±88.93)	64.22 (±3.21)

In the exercise trials, we found that point estimates of mean passage success were lower in the high pre-challenge velocity treatments (52-56%) than the control treatment (86%) regardless of the pre-challenge exercise duration (Figure 6). Mean passage success in the 1 × 20 min low pre-challenge velocity treatment was were similar to the control and the 2 × 20 min low velocity mean passage success (72%) was intermediate between control and high velocity treatments (Figure 6). Passage success in the low velocity, low duration exercise treatment was significantly different from the low velocity, high duration treatment ($Z = 2.57$, $P = 0.01$) and the high velocity, low duration treatment ($Z = 3.64$, $P < 0.01$) (Table 3).

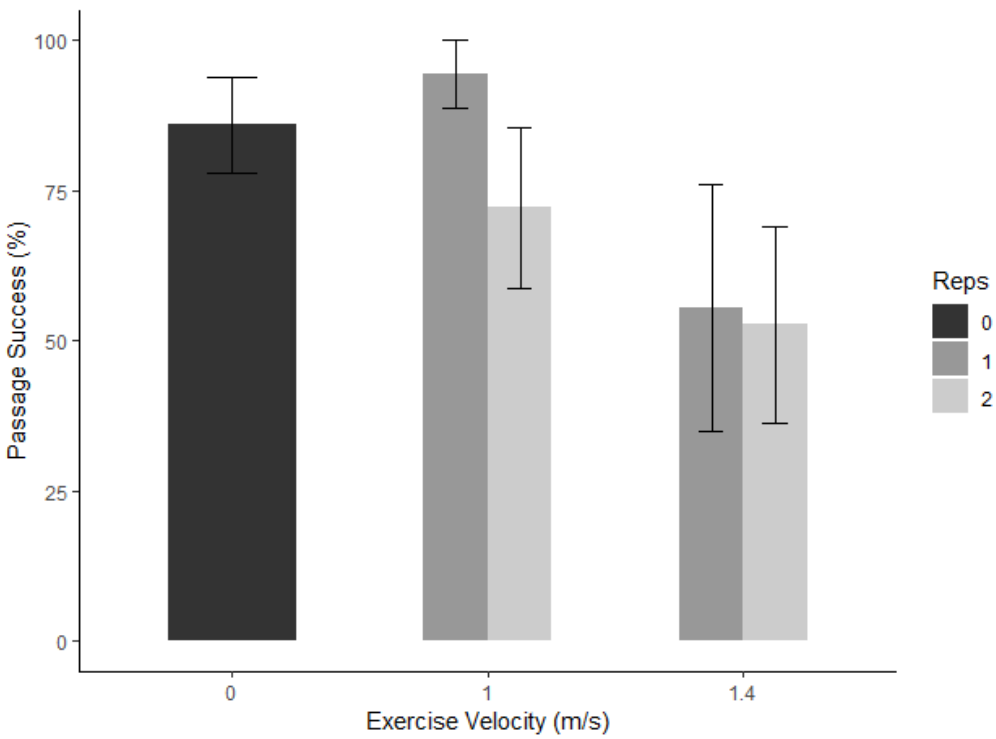

Figure 6. Percentage of lamprey that successfully passed the experimental flume by treatment. Reps refers to the duration of exercise (Control [0 min], 1 × 20 min or 2 × 20 min).

Dorsal distance was the only morphological covariate associated with passage success (Table 4). For every 1 cm increase in dorsal distance, the probability of success decreased by 63% (Table 3). Lamprey categorized as "mid" or "late" run were less likely to pass as compared to those classified as "early" run (Table 3). This effect was particularly magnified for the high velocity treatments.

No blood physiological parameter was associated with passage success (all $P > 0.05$) and were subsequently excluded from the model. Values for blood lactate, glucose, hematocrit, and pH were fairly similar across individuals (Figure 7, 8, 9, 10).

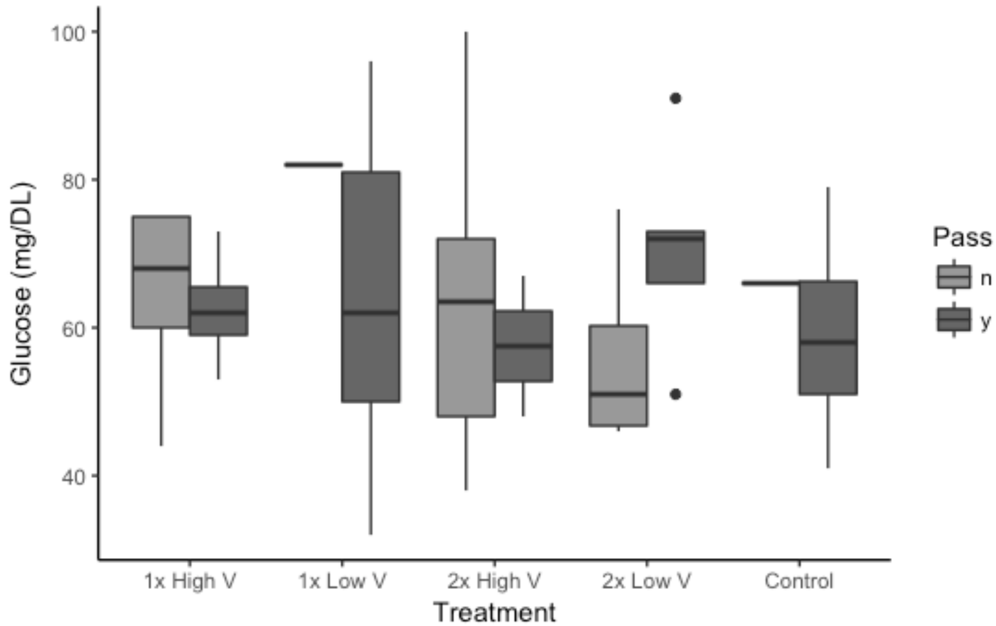

Figure 7. Whole blood glucose levels (mg/DL) according to treatment among lamprey (n=50) who passed and those who failed to pass the experimental flume. Blood was collected prior to the flume trial.

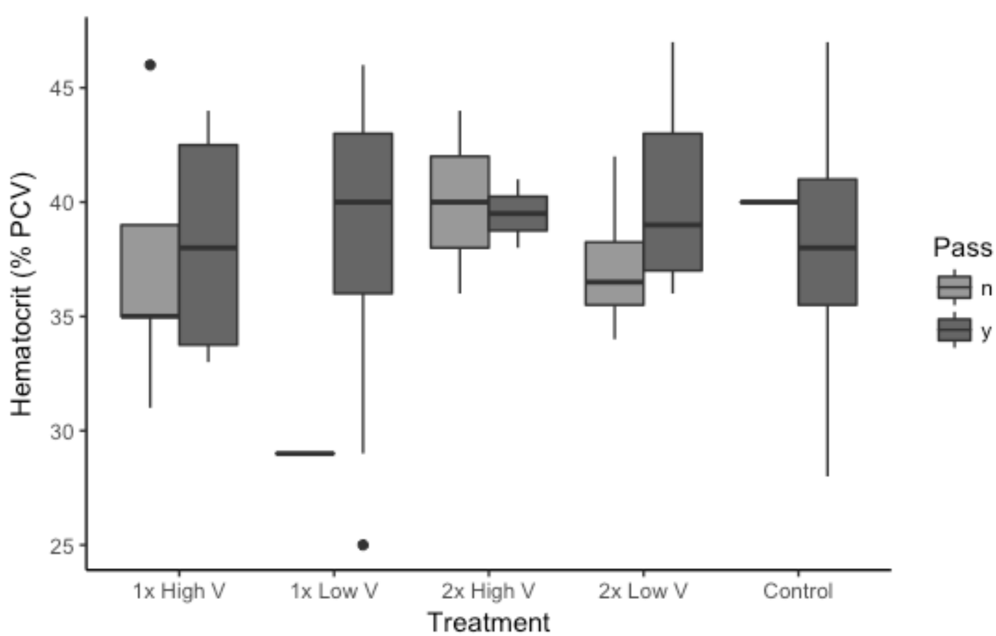

Figure 8. Hematocrit levels (%PCV) according to treatment among lamprey (n=50) who passed and those who failed to pass the experimental flume.

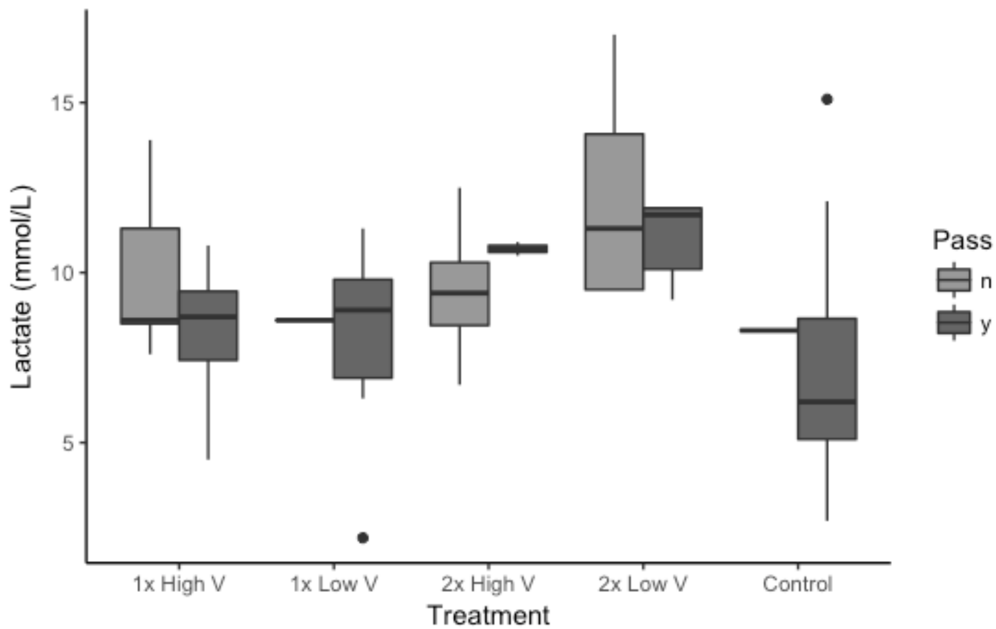

Figure 9. Whole blood lactate levels (mmol/L) according to treatment among lamprey (n=50) who passed and those who failed to pass the experimental flume.

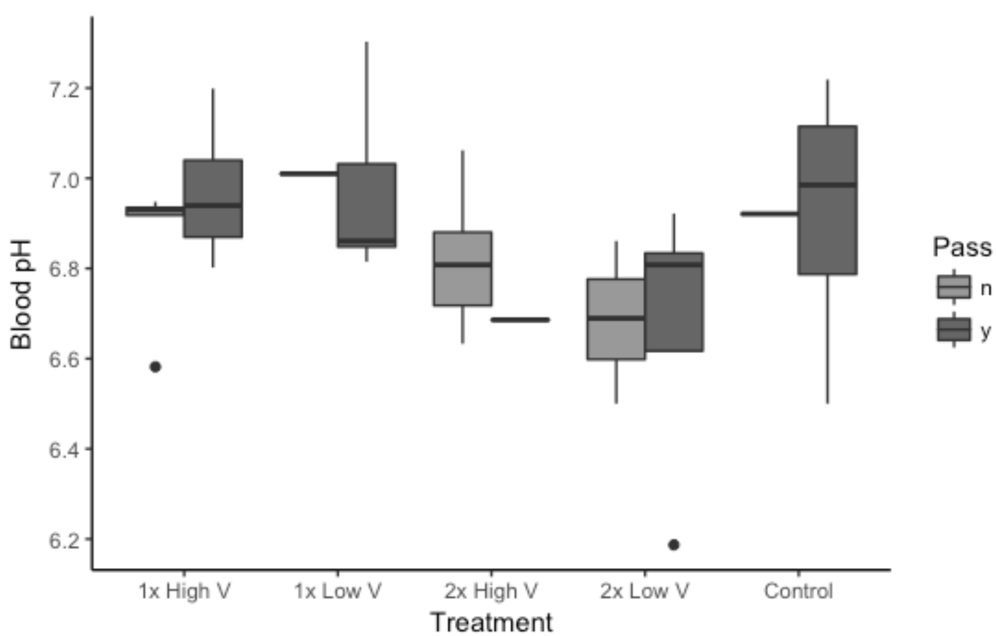

Figure 10. Blood pH levels (mmol/L) according to treatment among lamprey (n=50) who passed and those who failed to pass the experimental flume.

When evaluating upstream post-experiment escapement past upstream dams, multinomial logistic regression analysis indicated that lamprey length was the only significant predictor of migration distance for fish passing Priest Rapids dam ($Z = 2.51$, $P = 0.01$; all other $P > 0.05$ (Table 4). The probability of passing Priest Rapids dam increased by 33% for every 1 cm increase in length. Additionally, lamprey that were tagged and released later in the season were more likely to pass The Dalles Dam and there was some support for a run date effect at John Day Dam. The majority of fish had final telemetry records in the lower Columbia River (Figure 11).

Table 3**.** Multiple logistic regression results testing for the effect of treatment and morphometric measurements on passage success. Treatment factors refer to the following: C= control; L1 = low velocity, low duration; L2 = low velocity, high duration; H1 = high velocity, low duration; H2 = high velocity, high duration. Factors that are significant are indicated in bold.

Factor	*Z*	*P*	Odds Ratio	95% CI
C- L1	-1.47	0.142	0.26	0.04-1.56
C-H1	**2.81**	**0.005**	**6.24**	**1.74-22.39**
C- L2	1.32	0.188	2.37	0.66-8.56
C-H2	**3.00**	**0.003**	**7.02**	**1.96-25.05**
L1-L2	**2.57**	**0.010**	**9.05**	**1.69-48.46**
L1-H1	**3.64**	**0.0003**	**23.83**	**4.33-131.22**
L2-H2	1.87	0.06	2.96	0.94-9.25
Dorsal distance	**-2.27**	**0.023**	**0.371**	**0.15-0.84**
Mid-early run	**-4.05**	**<0.001**	**0.057**	**0.01-0.19**
Late-early run	**-4.24**	**<0.001**	**0.050**	**0.01-0.18**
Length	1.69	0.089	1.11	0.99-1.26

Table 4. Multinomial logistic regression results testing for the effect of experimental flume passage success, morphometric measurements, and run date on upstream escapement past dams. Factors that are significant are indicated in bold.

Logit	Variable	*Z*	*P*	Odds Ratio	95% CI
The Dalles	Passed weir	0.65	0.51	1.47	0.46-4.72
	Dorsal distance	-0.54	0.59	0.74	0.25-2.18
	Length	0.64	0.52	1.04	0.91-1.19
	Run date	**2.36**	**0.02**	**2.28**	**1.15-4.53**
John Day	Passed weir	-0.09	0.93	0.96	0.39-2.38

	Dorsal distance	-0.05	0.96	0.98	0.47-2.05
	Length	1.61	0.11	1.09	0.98-1.22
	Run date	1.78	0.07	1.63	0.95-2.81
Priest Rapids	Passed weir	0.67	0.50	2.18	0.22-21.30
	Dorsal distance	-0.85	0.39	0.52	0.11-2.35
	Length	**2.51**	**0.01**	**1.33**	**1.06-1.65**
	Run date	2.36	0.45	1.46	0.54-3.90

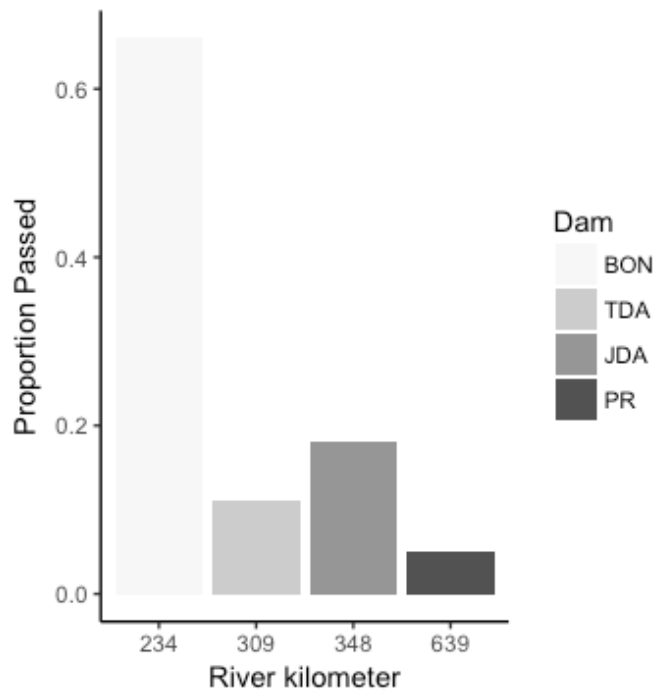

Figure 11. Proportion of lamprey released upstream of Bonneville Dam (*n* = 180) with final records at release (i.e., in Bonneville Tailrace; rkm 234), exiting The Dalles Dam (rkm 309), John Day Dam (rkm 348) or Priest Rapids Dam (rkm 639).

Prototype Flume Experiments

Mean lamprey passage success was slightly lower without weirs (64%) compared to when weirs were present (83%), but the difference was not significant ($Z = 0.57$, $P = 0.36$) (Table 5). Mean lamprey size did not differ between treatments (Table 6). Additionally, length was not associated with passage success ($Z = 0.07$, $P = 0.13$). Both treatments had a similar proportion of lamprey that approached the first antenna ($n = 37$ with weirs; $n = 39$ without) (Figure 12).

Passage time was considerably faster with weirs present (median = 2 min) versus without weirs (median = 13.5 min) (t = 3.152, *P* = 0.003, Figure 13).

Table 5. Multiple logistic regression results testing for the effect of treatment and body size (length) on passage success.

Factor	*Z*	*P*	Odds Ratio	95% CI
Weirs-Weirs absent	0.57	0.36	1.69	0.55-5.37
Length	0.07	0.13	1.10	0.97-1.27

Table 6. Summary of mean (±SD) length of lamprey according to treatment

Treatment	Mean length (cm)	N
Weirs	68.6 (±3.93)	37
Weirs Absent	68.1 (±4.19)	39

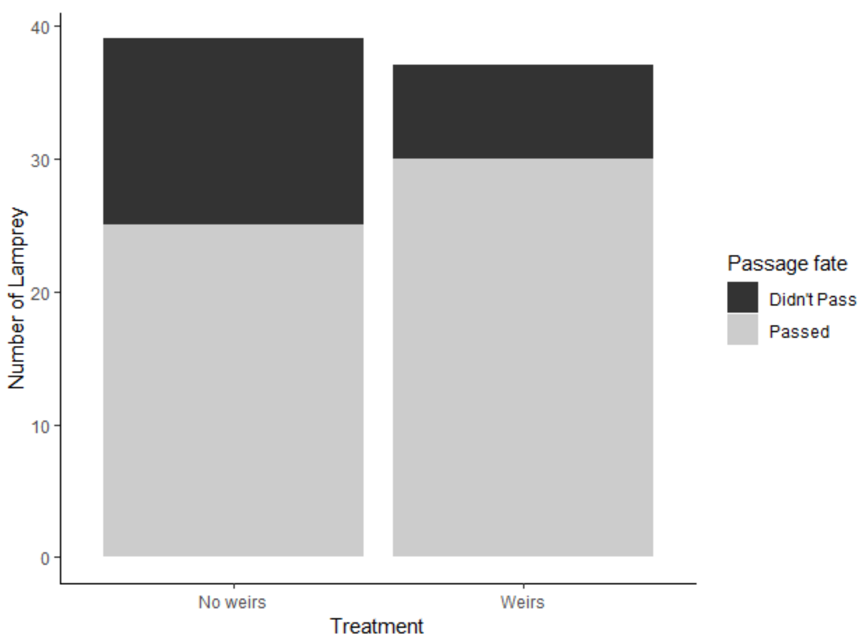

Figure 12. Total number of lamprey that either successfully passed or failed to pass prototype flume by treatment (i.e., the presence of absence of weirs).

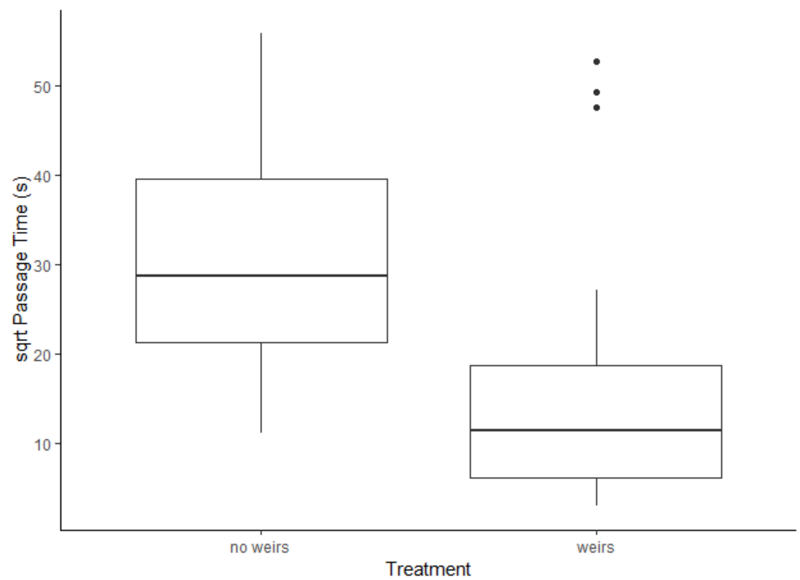

Figure 13. Passage time (square root transformed) for lamprey that successfully passed the prototype flume, by treatment.

Accelerometer Biotelemetry Pilot Study

Video observation of accelerometer-tagged lamprey in the experimental flume indicated two primary behaviors could be discerned from the tag output: burst swimming and oral disc attachment in low velocity conditions (Figure 14). Lamprey that were swimming in low velocity water or were attached at low velocities regularly exhibited between 0.0 and 0.25 g acceleration. Alternately, lamprey that engaged in 'burst' swimming had values between 1.1 and 1.5 g. Burst swimming was observed when lamprey initiated a swimming event from attachment just below the vertical slot weir and burst forward for several seconds. Lamprey classified as swimming at moderate velocities (1.2 – 2.0 m/s) and lamprey attached at high velocities (2.2 – 2.4 m/s) using video footage could not be differentiated using acceleration records.

Of the 13 lamprey released in the WA-shore fishway, only one fish successfully passed the dam. Several fish moved immediately downstream after release and were detected near the WA-shore junction pool. The individual that did pass the dam took 12 days to do so, was primarily nocturnal and had tag output values that suggested repeated brief periods of burst movements (with maximum recordable g values) followed by prolonged periods of low activity (Figures 15 & 16).

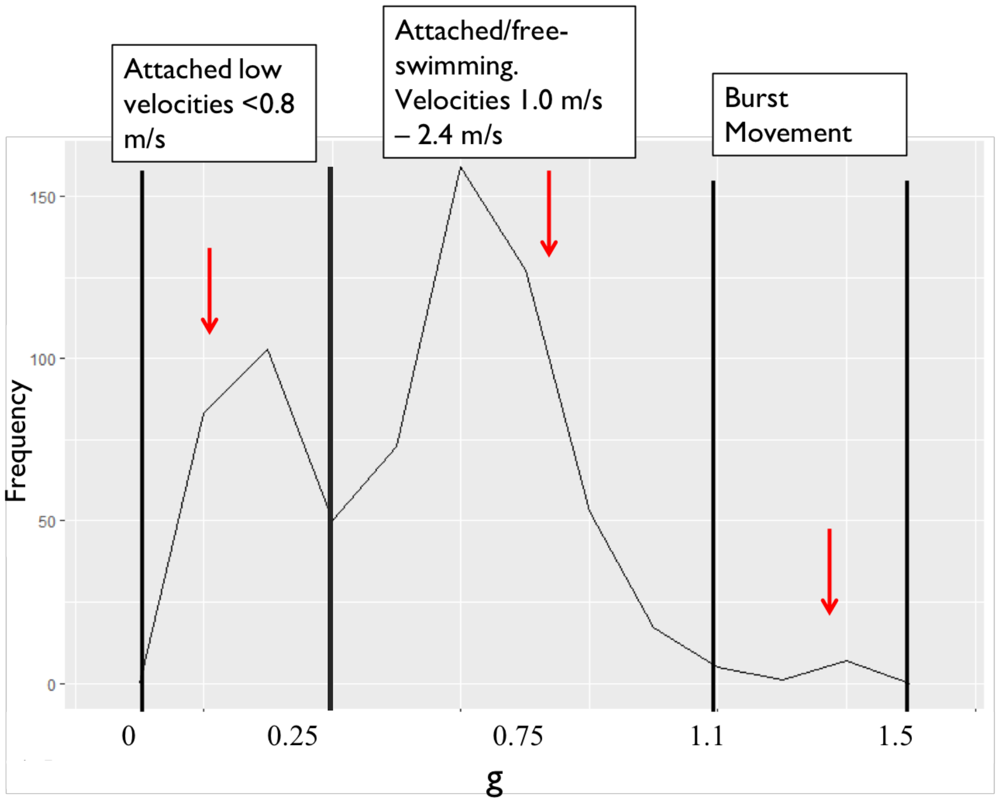

Figure 14. Frequency of tag output values (g) of one lamprey that was released into the experimental flume for 1 hour. Velocities ranged from 0.8 m/s – 2.4 m/s and represent both attached and free swimming behavior. Total number of records = 720. Lines and arrows indicate putative attachment, free-swimming, and burst movements.

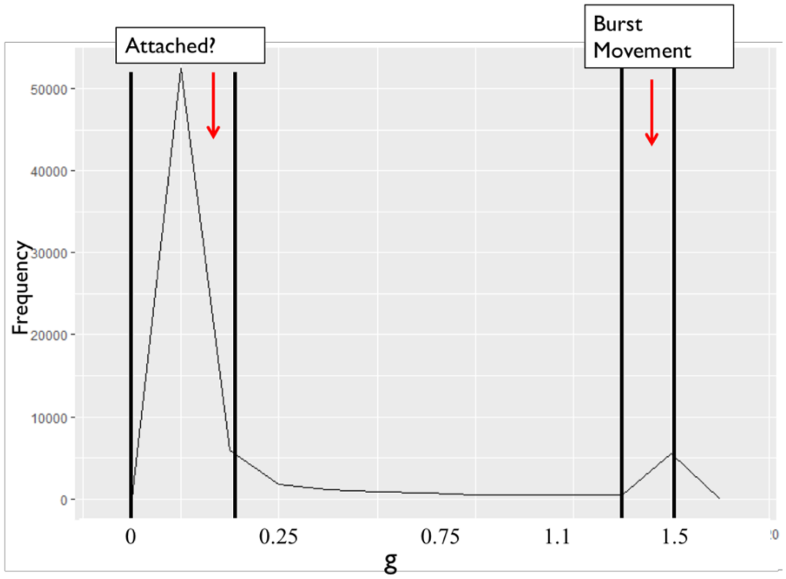

Figure 15. Frequency of tag output values (g) of one lamprey that was released into the WA-shore fishway on September 5, 2018. Successful passage through the WA-shore fishway occurred on September 17, 2018. Values include all records from the fishway during the 12 day period. Total number of records ~ 3400. Lines and arrows indicate putative attachment and burst movements

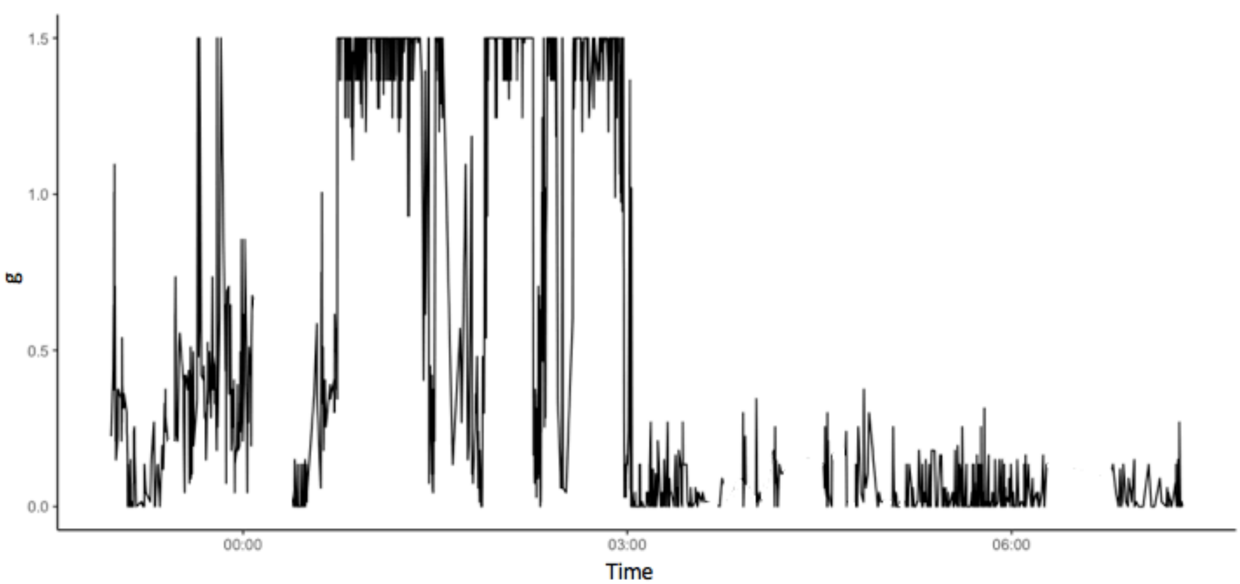

Figure 16. Time series of tag output values (g) for a single lamprey released into the WA-shore fishway recorded passing the dam. Time series from 2300 on September 15 to 0719 on September 16, 2018.

Discussion

Exhaustive Exercise Flume Experiment

We found the duration of prior exercise significantly lowered passage success rates through the vertical slot weir section of the experimental flume. As previously reported, high water velocity also had the same effect, with significantly lower passage success rates as velocity increased (Figure 6). The result indicates lamprey may be able to pass through high velocities at a single challenge, but may reach an endurance threshold when faced with overcoming multiple obstacles and/or incur loss of motivation. Lamprey are not philopatric (e.g., Hess et al. 2013), unlike salmonids (Keefer and Caudill 2014), and thus factors leading to the decision to turn-around in a fishway or cease upstream migration likely differ between the taxa but remain largely unclear. Approaching an energetic or physiological threshold may be a factor in this decision. Behavioral observations of lamprey attempting to pass through the weir revealed that lamprey rarely made multiple attempts. If they failed to pass the first time, they would attach below the weirs and remain there for the duration of the experiment. Lamprey also appeared to attach in close proximity to one another and would appear to "cue" off of each other – as one lamprey initiated movement others would follow shortly thereafter. During year two of this study (2019), we will replicate the experimental flume trials, perform exercise trials including respiration measurements, and conduct a preliminary test of the effects of social cues on lamprey migration behavior to further test for the effects of exercise history and social interactions on behavioral decisions during passage.

Our findings have shown that exhaustion may be limiting the ability for lamprey to successfully pass through fishways. Pacific lamprey passage through the serpentine weir sections at Bonneville Dam has been consistently poor (Keefer 2013, 2015, 2019). Previous studies have shown that velocities do not exceed lamprey swimming abilities (Kirk et al. 2015), suggesting that other mechanisms beyond water velocity alone contribute to passage failure through the section as a whole. Kirk et al. (2016) found that lamprey attachment time significantly increased at velocities of 2.4 m/s in the presence of a turbulence-inducing wall as compared to lower velocity and less turbulent conditions. Our results are consistent with this observed behavior. Specifically, high velocity alone does not pose a barrier, but the cumulative effect from multiple challenges might. Attachment and repeated burst swimming movements over a prolonged period of time have been related to behavioral patterns indicative of exhaustion (Quintella et al. 2004). Given lamprey pass through ~15 vertical slot weirs prior to exiting the fishway and the high turbulence in the serpentine weir section, anaerobic metabolism and exhaustion may be a contributing factor to passage failure.

One of the most consistent observations has been the increasing average size of lamprey reaching upstream sites during migration through the lower Columbia River (Keefer et al. 2009, 2019; Hess et al. 2014), while Kirk et al. (2016) found no evidence of size selection at the small scale of single velocity challenges. Though we did not have any evidence for a size effect in these trials, year two will provide an additional test of the relationship between lamprey size and passage success at small-scale challenges. In particular, we will test for an interaction between exercise and size whereby size selection may only be observed among lamprey that have previously experienced high exercise. Such an interaction would help explain the discordance between past flume studies (no size selection observed) and migration-scale studies (size selection consistently observed). While we did not observe size selection after release at The Dalles and John Day Dams, our sample size was smaller than previous studies and point estimates were consistent with size selection (Table 4). Thus we speculate a larger sample would have produced statistically significant effects. Fish that had a larger body size were more likely to pass Priest Rapids Dam on the upper Columbia. Furthermore, fish that were tagged later in the season were more likely to be unsuccessful in passing the experimental flume. Previous research has shown that migration timing is related to migration distance with earlier migrating fish going longer distances (Hess et al. 2014), consistent with the results presented here, indicating seasonal environmental or physiological effects on passage behavior and success. In fact, fish that were categorized in the high velocity, high duration treatment were more than 90% less likely to pass compared to those in the low velocity, low duration treatment within the same block late in the season. High water temperatures (>20°) during the majority of July and August may have contributed to low passage rates. Overall, we found evidence that the exercise trials induced physiological stress and physical "exhaustion" that contributed to passage failure.

Prototype Flume Experiment

Many of the current lamprey passage structures (LPS) at Bonneville Dam are steep-angled ramps of 45° or greater (Moser 2011). Due to the unknown energetic costs that are associated with climbing these structures, alternative passage systems that have a lower gradient may be useful in some passage areas, especially those that have high fallback rates.

Therefore, we tested the potential utility of a low-angled ramp. Although we did not observe a difference in the proportion of lamprey that successfully passed with weirs and without weirs, passage time was significantly faster when weirs were present (Figure 13). Additionally, although only the first successful passage attempt was scored for time, lamprey were allowed to move within the flume for the duration of the experiment. Anecdotal observations revealed that lamprey in the weir-present treatment passed back and forth at a much higher rate than lamprey in the weir-absent treatment, possibly indicating they were able to move more easily or were more motivated to move when weirs were present. This further supports the need for quantification of energetic costs associated with different passage systems. Currently, rest boxes in LPSs can be sources of bottlenecks and mortality and are relatively high maintenance. The weired prototype design could allow longer intervals between rest boxes or eliminate the need for rest boxes, and could add a cost-effective design element to lamprey passage systems. Overall, passage success rates were fairly high in both treatments (Figure 12), and the feasibility of the design as a passage structure should be further evaluated. Particular care should be taken to establishing sufficient flow at the terminal end to cue lamprey towards the structure.

Accelerometer Biotelemetry Pilot Study

The efficacy of accelerometer biotelemetry as a method for estimating the energy expenditure associated with passage of specific routes and obstacles in fishways at Bonneville Dam was assessed in this pilot study. Clear partitioning of burst movement behavior from swimming or attachment at low velocities is possible when analyzing output from the tag. Despite the inability to distinguish slow swimming from attachment at high velocity with a single axis accelerometer, the approach will likely provide important insights to lamprey passage behavior and energetics when coupled with physiological measurements, particularly if the costs of slow swimming are similar to attachment in high velocity and/or if these behaviors could be reliable distinguished in field settings using ancillary information on location (i.e., slow swimming is not possible in some fishway sections).

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