

EVALUATIONS OF PACIFIC LAMPREY SWIMMING BEHAVIOR AND PERFORMANCE IN RELATION TO VELOCITY, SLOT LENGTH, AND TURBULENCE IN VERTICAL SLOT FISHWAY WEIRS, 2014



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M.A. Kirk, C.C. Caudill, and N. Hubbard
Department of Fish and Wildlife Sciences
University of Idaho, Moscow, ID 83844-1136

and

J. C. Syms and D. Tonina
Center for Ecohydraulics Research
University of Idaho
Boise, ID 83702

for

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

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Executive summary

Understanding the processes that limit Pacific lamprey passage through fishways is critical for improving passage of this species at Columbia and Snake River dams. High rates of lamprey turn-around and passage failure have been identified within some upper fishway sites, and thus we targeted these sites for mechanistic studies of lamprey passage failure. In particular, the hydraulic and structural environment within the serpentine weir sections at Bonneville Dam are associated with both high turbulence and relatively long sections of high velocity at individual weirs that may act as a deterrent or barrier for lamprey passage. We assessed lamprey passage rates and behaviors at an experimental weir by varying treatment combinations of velocity, weir length, and turbulence similar to conditions found in the Bonneville Dam serpentine weir sections. We also compared results from the experimental flume to *in-situ* video observations of lamprey behavior within the serpentine weir sections of Bonneville Dam.

We evaluated lamprey success rates and behavior in an experimental flume, which had a vertical slot structure similar in design to a serpentine weir at Bonneville Dam. This slot weir allowed us to manipulate three variables of interest. First, we had three different velocity treatments (1.2 m/s, 1.8 m/s, 2.4 m/s), which captured the range of velocities present within the Bonneville fishways. Second, we had three different slot lengths (0.33 m, 0.66 m, 1.00 m), because slot lengths differ considerably among serpentine weirs at Bonneville Dam. Third, we tested the effect of turbulence using treatments with or without a large deflector wall upstream of the weir, which produced large eddies representative of those in the serpentine weir sections. The overall experimental design consisted of 18 total treatment combinations ($3 \times 3 \times 2$) and each combination consisted of three replicates with 5-6 lamprey per replicate.

There was no significant overall effect of velocity, turbulence, or slot length on lamprey success rates through the weir. There was however, a turbulence \times slot length interaction, in which the lowest success rates (<70%) were observed for the high turbulence \times long length treatments. There was no indication of direct body size effects on passage, but adults with larger inter-dorsal fin distance were more likely to pass. Subsequent monitoring of adults during upstream migration post-release provided no evidence of a correlation between passage success in the experimental flume and upstream migration distance, whereby lamprey that did not pass the experiments had similar upstream escapement estimates throughout the hydrosystem as lamprey that did pass the experiments.

Lamprey showed a strong demersal orientation during the experiments, with the majority of upstream movements occurring along the floor. The frequency of lamprey attachments and the duration of attachment events increased under higher velocity and high turbulence treatments, suggesting greater physiological demands under these passage conditions. Attachment times also increased non-linearly across treatments, with more than a two-fold increase in the high velocity, high turbulence treatments compared to all others. The swim tracks of lamprey during experiments showed consistent movement patterns along one side of the flume, indicating that lamprey were potentially responding to lateral hydraulic gradients across the weir. Video observations from the serpentine weir section of the Bonneville Dam Bradford Island fishway revealed slightly different lamprey behaviors compared to the flume, which included a higher proportion of movements in the upper water column and a lower incidence of attachment

behaviors. Despite these behavioral differences, preliminary hydraulic measurements within the Bradford Island serpentine weirs using an Acoustic Doppler Velocimeter (ADV) showed that the turbulence and medium/high velocity treatments during flume experiments were most similar to the fishway conditions.

The ability of most lamprey to successfully navigate through the single weir in the experimental flume, particularly under the high velocity and turbulence treatments, was surprising given that only ~70% of lamprey successfully pass the Bonneville serpentine weir sections based on radiotelemetry studies. The poor passage associated with these sections may be associated with cumulative effects of passing multiple weirs, as lamprey must traverse 15 weirs within the serpentine weir sections in the fishway. Assuming constant single-weir passage probabilities, only 10% of lamprey would successfully traverse all 15 weirs based on the estimates of success from our experiments. Video observations provided some support for this hypothesis. Pacific lamprey event rates were lower at weirs farther upstream and a high frequency of downstream movements was observed at one of the upstream weirs. These results suggest that some threshold (i.e., an exhaustion threshold) may be exceeded in the serpentine weirs that is responsible for poor passage at these locations. Though speculative, it is also plausible that the complex flows and/or large turning angles required for traversing the serpentine weirs disrupts the orientation capabilities of lamprey.

Overall, our results suggest that passage through the serpentine weirs is driven by a complex set of biological and hydraulic parameters and that cumulative effects may be important. Improving Pacific lamprey passage through these sections will require a greater understanding of how flow complexity affects behavior and the role of biological thresholds (motivation, endurance, etc.) in determining lamprey passage. Improving passage may be best accomplished by providing alternative passage routes (i.e., Lamprey Passage Systems, LPS') that bypass these fishway locations or by providing more linear routes with improved hydraulic conditions (e.g., a series of 'lamprey orifices' similar to those at McNary and some lower Snake River dams).

Introduction

Improving the passage of native, anadromous Pacific lamprey (*Entosphenus tridentatus*) at large hydropower dams in the Columbia River basin has become an important priority for fisheries managers in the last decade. This is in part due to the considerable population declines lamprey have experienced in their native range (Moser and Close 2003; Clemens et al. 2010). Large hydropower dams have been identified as one potential agent for these declines, including on the Columbia River where low upstream passage by this species (often <50%) has been observed within fishways designed for Pacific salmonids (Moser et al. 2002a, 2002b; Keefer et al. 2013b). Efforts to improve passage have included installing lamprey-specific passage systems at several hydropower dams on the Columbia River (Moser et al. 2011), which provide inclined ramps for Pacific lamprey to climb using their oral discs. These systems have been quite successful and are becoming an effective alternative for passing Pacific lamprey at barriers. Nonetheless, climbing structures are not possible in all locations and future development of additional passage improvements will benefit from a mechanistic understanding of the limits on passage in existing fishways.

Radiotelemetry studies have been valuable in identifying the general locations of poor lamprey passage within fishways. These areas include fishway entrances, collection channels, transition areas, and serpentine weirs (Moser et al. 2002a, 2002b; Johnson et al. 2012; Keefer et al. 2013c). However, the spatial scale of radiotelemetry (5-10 m) is often too coarse to identify the specific factors responsible for lamprey passage failure. Past efforts to identify the mechanisms of lamprey passage failure have included observing behavior with a high-frequency sonar camera (Johnson et al. 2013; Kirk et al. 2014) and testing swimming performance in an experimental flume under simulated fishway conditions (Keefer et al. 2010, 2011). These experimental tests helped identify structural features resulting in lamprey passage failures (i.e., vertical steps, diffuser grating), as well as evaluated lamprey swimming capacity under strenuous, high water velocities. However, a broader understanding of how hydraulic conditions influence behavior and passage is still needed, particularly because of the high frequency of passage bottlenecks observed at mainstem Columbia River dams (Keefer et al. 2012, 2013b).

One location where a greater understanding is needed is at the serpentine weir (i.e., vertical slot) fishway sections at Bonneville Dam. These serpentine weirs are located in the upper portions of the fishway near the fishway exits and are associated with high lamprey turnaround rates (Clabough et al. 2012; Keefer et al. 2013b). Hence, improving passage at these locations has been a management priority given the proximity of lamprey to exiting into the forebay and because adult lamprey moving downstream of the weirs after attempting to pass very rarely successfully pass Bonneville Dam. Serpentine weir sections are a structurally and hydraulically dynamic environment with high water velocities, turbulent conditions, and weirs of varying slot lengths (i.e., distance from upstream-downstream end of each slot). Given that lamprey are hypothesized to have relatively lower swimming capacity compared with salmonids (Mesa et al. 2003, Keefer et al. 2010, 2011), the strenuous conditions within this section may be difficult for lamprey to overcome.

The primary objective of our study was to identify the hydraulic and structural mechanisms affecting lamprey passage success and behavior within the serpentine weir sections at Bonneville

Dam. We used a series of flume experiments with conditions similar to those within the serpentine weirs, as well as fishway camera observations inside the Bonneville fishways, to better understand lamprey passage. We experimentally tested the effects of three different features common to this location (velocity, turbulence, and slot length) to identify what factor(s) best explained elements of lamprey success and behavior. We hypothesized that lamprey success rates would be lower for experimental treatments with high velocity, high turbulence, and longer slot lengths. Observations from camera deployments in the serpentine weir sections at Bonneville Dam were used to supplement conclusions about passage derived from experimental tests.

Methods

Flume experiments

Adult Pacific lamprey ($n = 300$) were collected overnight from 18 May to 12 July, 2014 from trap boxes adjacent to fishway weirs near the adult fish facility (AFF) at Bonneville Dam (45.6°N, 121.9°W) on the lower Columbia River. Fish were removed from traps the following morning and were held in large aluminum tanks (92 × 152 × 122 cm) that had constantly recirculating river water. Lamprey were anesthetized with AQUI-S 20E (Aqua Tactics Fish Health, Kirkland, WA) using a concentration of 45-50 mL /50 L river water. Fish were weighed, measured for total length and body girth, and had a fin clip removed for complementary genetic studies. A measurement was also made between the end of the first dorsal fin and the beginning of the second dorsal fin, which has been shown to be a potential marker for maturation status and energetic condition in Pacific lamprey (Clemens et al. 2009). A small incision was then made on the fish's ventral side and a half-duplex passive integrated transponder tag (HD-PIT tag; 4 × 32 mm, Texas Instruments, Dallas, Texas) was inserted into the body cavity. Tagged fish were allowed to recover for 8-12 h in the large holding tanks at densities less than 20 individuals per holding chamber prior to experiments. 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). One lamprey died shortly after tagging and was not included in any analyses. Two additional fish were censored from some analyses because of an outage on HD-PIT detectors.

Experiments were conducted in an experimental flume (11.6 m long × 1.2 m wide × 2.4 m high) inside the adult fish facility at Bonneville Dam. The flume consisted of a 9 m long experimental section with a 10% slope, a downstream chamber with a removable gate where fish could be acclimated prior to experiments, and an upstream chamber at the top of the flume with fyke nets that fish could enter, but not exit (Figure 1A). 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. (2010, 2011).

We constructed an experimental section within the flume that simulated a vertical slot design and allowed for manipulation of the three treatment variables. We had three velocity levels (2.4 m/s, 1.8 m/s, 1.2 m/s), three different slot lengths (1 m, 0.66 m, 0.33 m), and two turbulence levels (treatment and control) for a total of 18 treatment combinations with a target of three replicates per treatment combination. We note that slot length treatments were unbalanced due

to several preliminary experiments that occurred during the final week of tests (Table 1). Velocity was manipulated by changing the flow rates of the supply pipes and by altering hydraulic head using wooden boards placed on the downstream overflow section. Treatment velocities were determined from measurements at the hydraulic jump of the weirs and along the flume floor using a Marsh-McBirney flow meter (Hach Company, Loveland, Colorado). Measurements indicated that velocities near the surface and velocities near the floor were relatively consistent (Appendix Figure A).

A 3-m long false floor was fixed to the bottom and placed in the middle of the flume, and three pairs of 2.44-m high weirs were placed within this experimental section. Each weir was 33-cm long and 38-cm wide, which created a 46-cm wide slot that fish had to traverse under manipulated slot lengths of 0.33 m (short), 0.66 m (medium), and 1 m (long). The first set of weirs was permanently fixed in the false floor and represented the short slot length treatment (Figure 1D), whereas the other two sets were removable in order to create the medium (Figure 1C) and long (Figure 1B) treatments. Two aluminum HD-PIT antennas were custom designed to slide into the frame of the first and last set of weirs to monitor individual fish movements. A 2.44-m high turbulence wall was placed ~1.5-m upstream from the weirs and projected halfway out into the flume (Figure 1). Turbulence was induced by the addition of this wall, which produced large, circular eddies upstream of the experiment weirs (the treatment condition). The control tests involved removal of the turbulence wall.

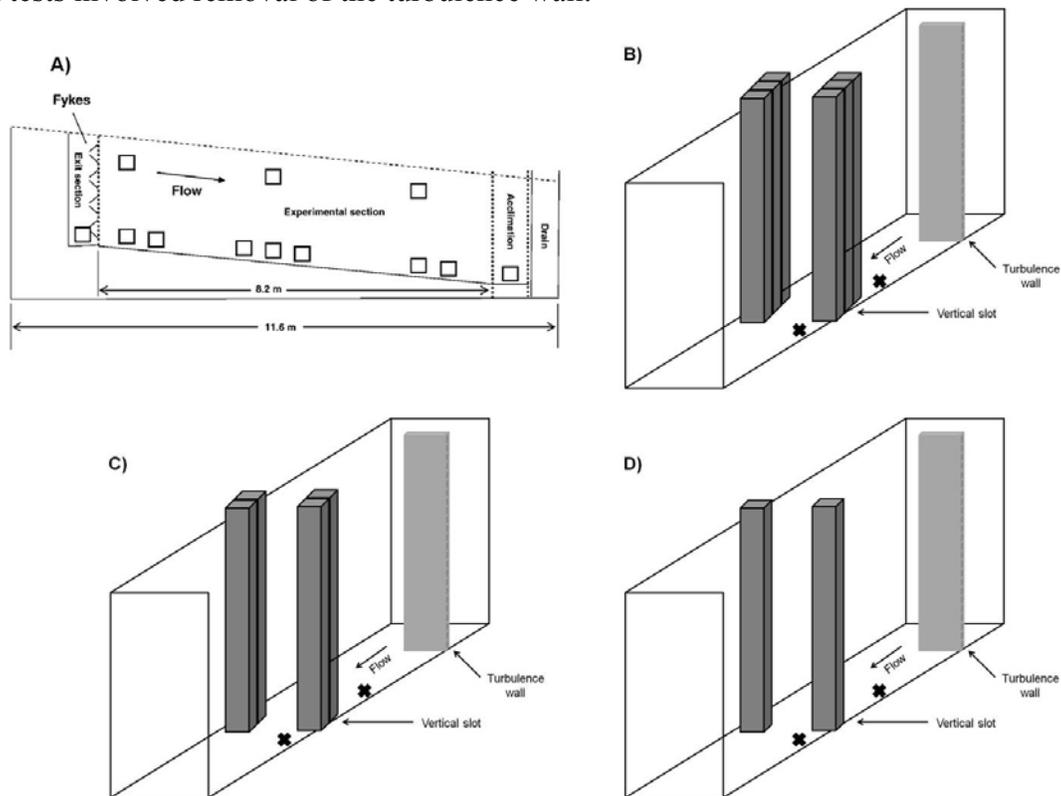


Figure 1. Upper left panel is a side view of the experimental flume (A) with the different flume sections. Three-dimensional cross sections of the flume show how the 6 experimental weirs manipulated a vertical slot design with varying slot lengths of (B) 1.00 m (long), (C) 0.66 m (medium), and (D) 0.33 m (short). The turbulence wall was removed from the experimental flume for control treatments. X's indicate camera locations. Note that the 3-D figures are not drawn to scale.

Table 1. Summary data for the number of replicates, number of Pacific lamprey, and the mean length and standard deviation of lamprey for each treatment in this study.

Factor	Level	Number of replicates	Number of lamprey	Mean length (cm)	Standard deviation
Velocity	2.4 m/s	18	102	68.2	4.81
	1.8 m/s	18	100	68.4	4.46
	1.2 m/s	18	98	67.6	4.16
Turbulence	Treatment	27	150	67.8	4.48
	Control	27	150	68.3	4.49
Slot length	1.00 m	21	115	68.2	4.48
	0.66 m	16	90	67.7	4.79
	0.33 m	17	95	68.2	4.22

All experiments were conducted at night (2100-0520), since Pacific lamprey are primarily nocturnal during their migration phase (Keefer et al. 2010, 2013a). Five to six lamprey were first placed in the acclimation section of the flume for 10 minutes at low velocity conditions (1.2 m/s). The velocity was then raised to test conditions and fish were allowed to acclimate for another 10 minutes. 90 minute tests were initiated by raising the gate of the acclimation section, which allowed fish to move upstream through the flume. Lamprey movements and behaviors were video-recorded using infrared lamps and four optical cameras placed on the upstream and downstream sections of the experimental weirs (X's in Figure 1). Camera placement allowed for near full coverage of lamprey activity in the experimental weirs and ~ 0.5 m upstream and downstream of the weirs. Behaviors were tied to individual fish from time-stamps of video files and HD-PIT antenna records. Upon completion of each trial, the flume was drained and the position of all fish was noted. Fish were removed by hand from the fykes or netted from the flume, scanned for HD-PIT tags, and allowed at least 30 minutes recovery before being released upstream at Stevenson, WA following all experiments.

Video and HD-PIT data from the flume experiments were used to quantify six elements of Pacific lamprey performance and behavior; three at the trial-level (success, fallbacks, and percent of attachment events) and three at the individual fish level (approach time, weir passage time, and total passage time). Success was defined as the number of unique fish that passed the experimental weirs divided by the number of unique fish that approached the weirs in each trial; individuals that never approached the experimental weirs were censored from further analyses. The number of fallbacks was defined as the number of times in each trial that a fallback occurred from upstream of the weirs to downstream of the weirs. The percent of attempts with attachment events was the percent of all observed upstream movements in a trial that involved an attachment by a fish, including all passage events for those individuals that fell back and reascended. Approach time was measured as the time from the initiation of a trial (S1) until an individual fish approached the first downstream camera or the first detection at the downstream antenna (A1). Weir passage time (WPT) was calculated as the time when individual fish were first observed on the downstream camera or the first detection on the downstream antenna (A1) until an individual fish passed the last upstream camera or the last detection at the upstream antenna (P1). Finally, total passage time (TPT) was calculated as the time from the initiation of a trial (S1) until an individual fish passed the last upstream camera or the last detection at the upstream antenna (P1).

The experimental design of the flume studies was a split-split-plot because all variables were not replicated together. Instead, it was a restricted randomized design where each factor was hierarchically randomized. Slot length was the whole plot factor that was randomized first, turbulence was the split-plot factor that was randomized next within slot length treatments, and velocity was the split-split-plot factor that was randomized last within turbulence treatments (Kuehl 1999). This design minimized the time and effort associated with the logistical constraints of manipulating the slot length and turbulence conditions for each experiment. Treatments were randomized within three blocks across time to account for potential seasonal differences in Pacific lamprey behavior. The blocking variable was defined as ‘run date’ and the blocking groups were early (trials from 18 May to 3 June), middle (4-25 June), and late (26 June to 12 July). All factors were treated as fixed effects. A linear mixed effects model (lmer, lme4 packages in R v. 3.0.3, R Development Core Team, 2014) was used to evaluate the effects of the different treatment conditions on the six behavioral metrics. The model equation was:

$$\text{Behavior/Success} = \text{run date} + \text{slot length} + \text{turbulence} + \text{velocity} + \text{slot length} \times \text{turbulence} + \text{slot length} \times \text{velocity} + \text{turbulence} \times \text{velocity} + \text{slot length} \times \text{turbulence} \times \text{velocity} + \text{Error1} (\text{run date} \times \text{slot length}) + \text{Error2} (\text{run date} \times \text{slot length} \times \text{turbulence}) + \text{Error3} (\text{residual sum of squares})$$

A mixed effects model ($\alpha < 0.05$) was necessary to account for the additional error effects from the different randomization levels at the whole plot and split-plot levels (Kuehl 1999). Data for the number of fallbacks and weir passage times were log-transformed to satisfy the assumption of homogeneity of variances. Further differences in treatment groups were analyzed using Tukey’s post hoc test based on least square means comparisons (lsmeans package in R v. 3.0.3).

Two additional hypotheses we sought to test regarding passage in the flume were that: 1) larger lamprey would have a higher probability of passing the experiment; and 2) lamprey that passed the experiment would have a higher probability of post-release escapement to upstream sites. To test the body size hypothesis, we used logistic regression (GLM function with binomial distribution, R v. 3.0.3) with ‘passed the weirs’ vs. ‘did not pass the weirs’ as the binary response variable. The logistic regression predictor variables included all three treatment variables, run date, fish weight, dorsal distance, and residual weight estimated from a linear regression between length and weight, hereafter referred to as ‘condition’ (Brodersen et al. 2008). To test the hypothesis about escapement, we used a two-sample Kolmogorov-Smirnov test to determine whether the upstream distribution of lamprey was similar between fish that passed the experimental weir and fish that did not pass the experimental weir. The upstream distribution of lamprey was determined from the river kilometer of final detection post-release.

Swim tracks were estimated for a random subset of individual fish from each trial (6-9 fish per treatment combination) to provide more ‘fine-scale’ evaluations of Pacific lamprey responses to the hydraulic environment, and are presented here for descriptive purposes. A simple grid system was established within the experimental weirs consisting of 6 cells, (left-right; upper, middle, lower; each cell was 6.23 cm. \times 31 cm.) to compare the movement of fish on each side of the flume (turbulence wall was adjacent to right side; Figure 1). Swim tracks were only selected for fish that had a known grid of entrance and exit and for fish that moved upstream.

Fish were denoted as right-side or left-side based on their head position relative to the flume centerline, and the lateral precision of these estimates was estimated to be +/- 2-3 cm.

Fishway Camera Observations

We deployed cameras inside the Bradford Island serpentine weir section at Bonneville Dam in July and August of 2014 to supplement our observations from the flume trials. From 16-25 July, two optical cameras and two infrared lamps were fixed to a steel trolley and captured imagery in the lower and middle water column. These cameras were deployed on I-beams at the downstream ends of three different serpentine weirs (Weir #5, #7, #9; Figure 2), in order to compare lamprey distribution and behavior along a longitudinal gradient (downstream to upstream; Figure 2). The three weirs monitored had FDX-PIT arrays and were ~1.5-m. in slot length. However, while characterizing longitudinal patterns, these deployments did not document the depth distribution of lamprey within the serpentine weirs. Hence, three optical cameras and three infrared lamps were deployed from August 12-20 on the upstream and downstream sides of Slot #5 that captured the lower, middle, and upper water column.

The review of video files was similar to the methods described in Kirk et al. (2014). Briefly, a random and equal subset of nighttime files (2300-0300) was processed for each of the three different weir locations (July deployments) and for each of the three camera depths (August deployments). July and August deployments were analyzed separately given the different objectives of each deployment. Reviewers watched 5 minute video files for the July deployments and watched either 5 or 10 minute video files for the August deployments, depending on the camera location (Table 2). We treated each video file as an independent replicate and the number of lamprey observed was standardized as ‘events per hour.’ Each event scored as a lamprey was assigned a confidence level by reviewers (high, medium, low), with the majority of events from all cameras yielding high confidence in lamprey identification (>69%). For each lamprey event, viewers documented lamprey orientation (fish facing upstream/downstream), movement direction (upstream/downstream), swimming behavior (free-swimming/attached), and attachment duration.

Table 2. Summary data for the video watched from the Bradford Island serpentine weir camera deployments. July deployments had two cameras and August deployments had three cameras. Cameras in the middle water column at Weir #9 could not be analyzed due to poor image quality.

Deployment Date	Water column location	Weir Number	Number of files watched	Hours watched	Number of events	Events per hour
July	Middle	5	80	6.67	247	37.05
	Lower	5	80	6.67	410	61.50
	Middle	7	80	6.67	234	35.10
	Lower	7	80	6.67	258	38.70
	Middle	9	-	-	-	-
	Lower	9	80	80	6.67	258
August	Upper*	5	33	2.5	206	39.68
	Middle*	5	31	4.67	159	34.29
	Lower	5	31	5.17	111	44.80

*Video files from these deployments were ten minutes; all others were five minute files.

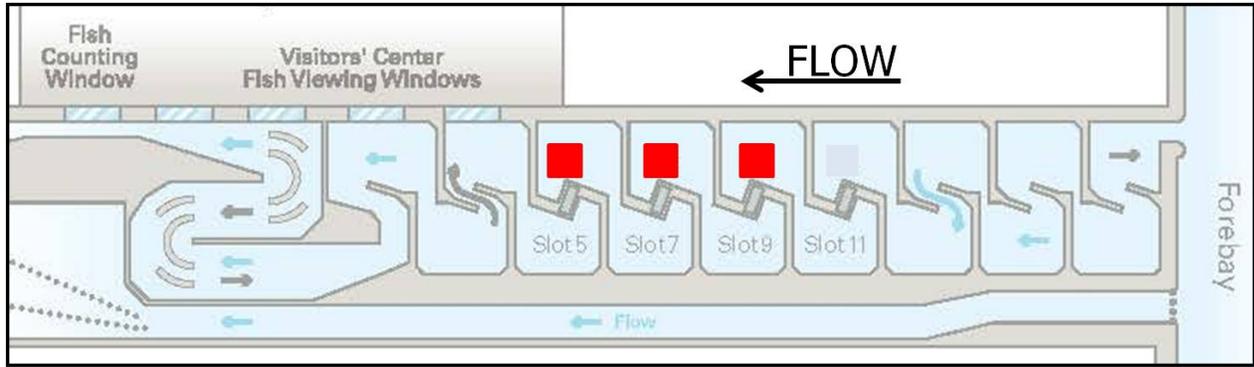


Figure 2. Overhead view of the Bradford Island fishway serpentine weir section at Bonneville Dam. Red boxes indicate the camera deployments at Weir 5 (most downstream), Weir 7 (middle), and Weir 9 (most upstream). There are approximately 15 weirs which fish must overcome to reach the fishway exit. Flow is from right to left.

Results

Experimental weir passage success

Across treatments, success rates were slightly lower (69.8%) in the block of early run dates compared with the middle (84.9%) and late (88.3%) groups ($F_{2, 34} = 3.12$, $P = 0.057$, Figure 3). Run date was also associated the behavior of lamprey, where the early run group had a higher percentage of fish that never approached the experimental weirs (47.9%) compared with the middle (23.2%) and late (16.2%) groups. Both observations are consistent with previously reported seasonal increases in lamprey passage rate (e.g., Keefer et al. 2009b).

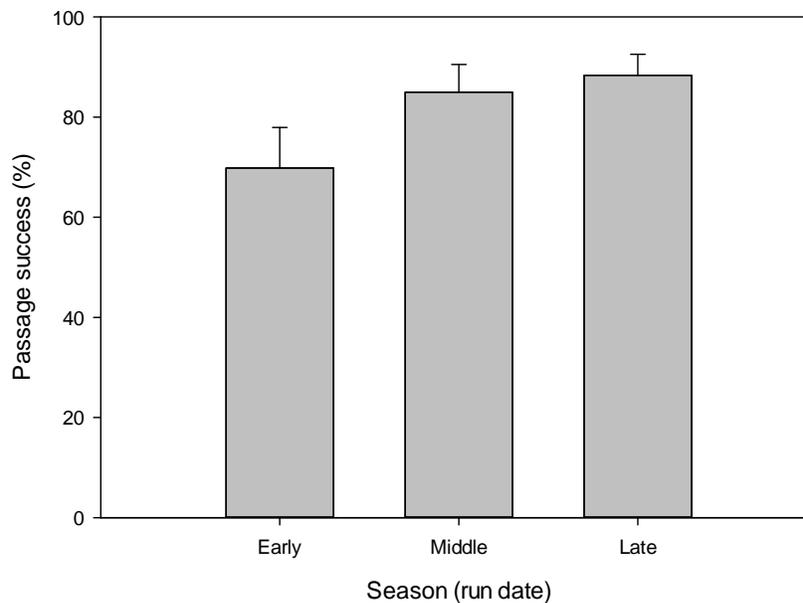


Figure 3. Mean success rates (+SE) for Pacific lamprey by the blocking variable run date.

Hydraulic parameters had complex effects on lamprey passage, with few significant effects on lamprey passage. There were no significant main effects of velocity ($F_{2,34} = 1.31, P = 0.280$), turbulence ($F_{2,34} = 0.53, P = 0.470$), or slot length ($F_{2,34} = 0.20, P = 0.920$) on lamprey passage success. The only significant hydraulic effect was a turbulence \times slot length interaction ($F_{2,34} = 4.35, P = 0.021$), where mean success rates within the high turbulence treatments were lowest for long slot lengths (69.4% across all velocity treatments) compared with the short (91.7% across all velocity treatments) and medium (90.8% across all velocity treatments; Figure 4A). In contrast, passage success was highest under the long slot length treatments (92.1% across all velocity treatments) in the turbulence control treatments (Figure 4B).

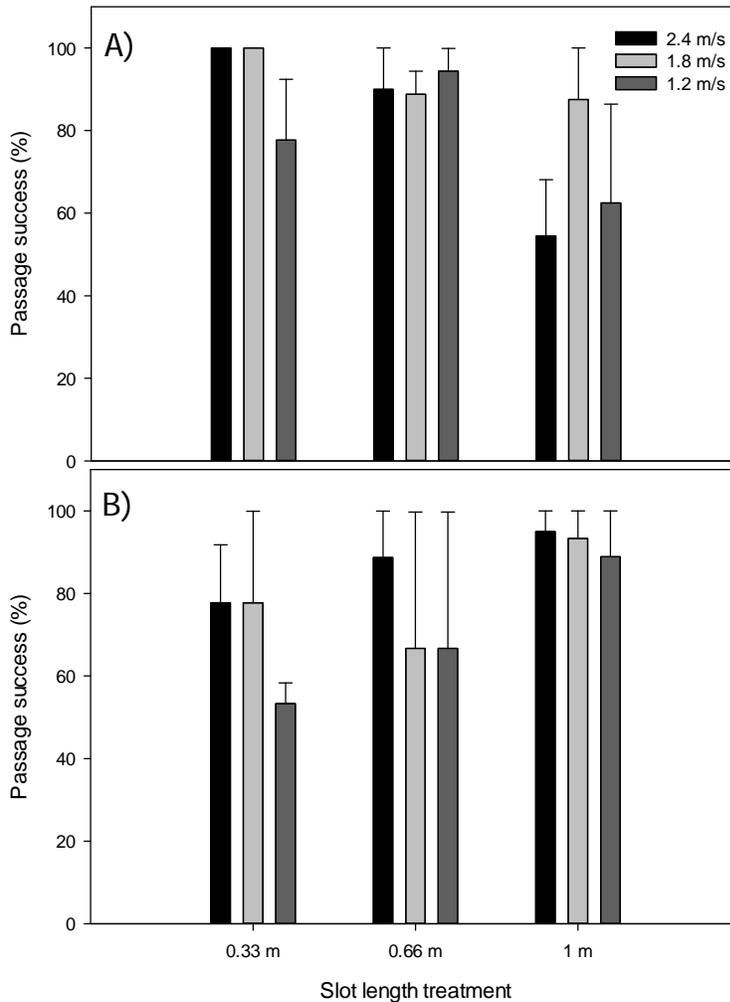


Figure 4. Mean success rates (+SE) of Pacific lamprey for all trials ($n = 54$) sorted by slot length and velocity treatments for (A) turbulence and (B) control treatments.

Regarding our two additional hypotheses about lamprey success, multiple logistic regression analyses showed that the morphological metric of dorsal distance was the only significant predictor of passage probability. Odds ratio indicated that passage probability for lamprey

increased 2.5 times for every 1 cm increase in dorsal distance ($\chi^2 = 7.40, P = 0.007$). In contrast, the metrics of body weight and condition displayed no relationship with probability of success (Table 3). There appeared to be slightly higher probability of escapement to the upper Columbia and Snake River dams for lamprey that did pass the experiments (Figure 5). Over twice as many lamprey that passed the experiment (35) were detected above McNary compared with the number of lamprey that did not pass the experiment (13). However, Kolmogorov-Smirnov tests indicated that the distribution of final detections was similar between lamprey that did and did not pass the flume experiments when assessed across all sites ($D = 0.07, P = 0.863$).

Table 3. Multiple logistic regression results testing for the effects of Pacific lamprey body size on probability of passage. Bolded values are significant ($P < 0.05$).

Factor	χ^2	P	Odds ratio	95% CI
Weight	0.15	0.694	1.00	0.99-1.01
Dorsal	7.29	0.007	2.60	1.31-5.30
Condition	0.14	0.706	6.30	0.01-8.04
1 m – 0.66 m	0.01	0.914	1.06	0.35-3.29
1 m – 0.33 m	0.47	0.491	0.71	0.26-1.87
1.2 m/s – 2.4 m/s	1.13	0.287	0.61	0.24-1.51
1.8 m/s – 2.4 m/s	0.75	0.386	1.67	0.55-5.80
Treatment - Control	0.01	0.913	0.96	0.42-2.20
Late-Early run date	2.07	0.150	2.10	0.76-5.87
Mid-Early run date	1.30	0.253	1.81	0.65-5.10

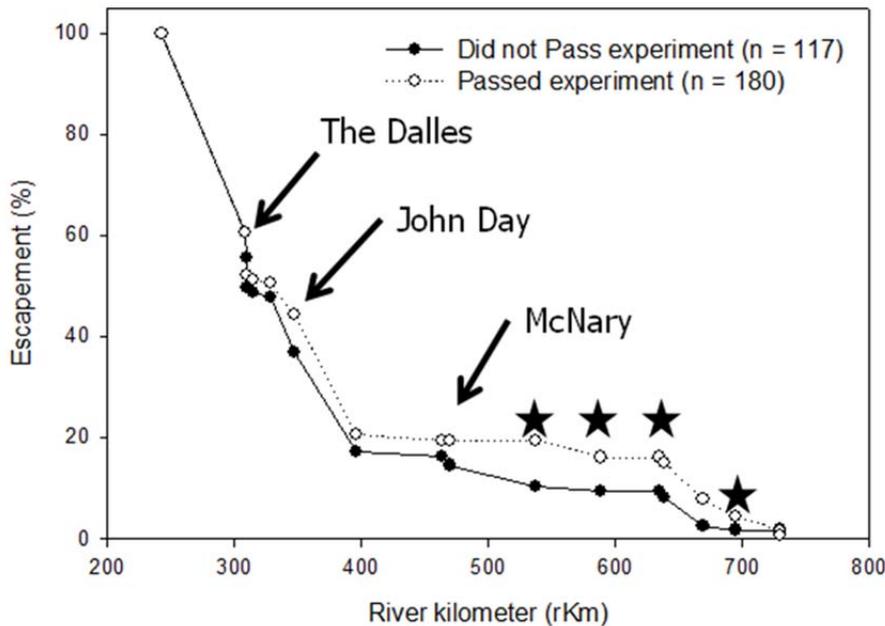


Figure 5. Escapement estimates for the HD-PIT tagged sample of experimental flume fish ($n = 297$) based on lamprey that passed the experimental weir and lamprey that did not pass the experimental weir. Stars indicate the locations of Snake River dams. Numbers in parentheses indicate sample sizes.

Experimental weir passage behaviors

The effects of hydraulic parameters on Pacific lamprey behavior were complex and differed among the five passage behaviors. Velocity had a significant effect on both the percent of attachment events for each trial ($F_{2,34} = 14.54$, $P < 0.001$; Figure 6) and weir passage times for individual fish ($F_{2,96} = 23.11$, $P < 0.001$; Figure 7). Both metrics increased with higher velocities. The higher weir passage times were associated with fish being attached for longer durations rather than multiple passage attempts. There was also a significant turbulence \times velocity interaction on weir passage times ($F_{2,96} = 5.85$, $P = 0.004$), whereby lamprey were observed attaching for ~ 2.5 times longer during high-velocity treatments in the turbulence treatment (12.5 min) compared with the turbulence control (4.7 min).

There were no clear effects of treatment on approach time (start of trial to first weir approach) or total passage time (start of trial to passage of weir), suggesting treatments did not differ in attraction or guidance cues to the weir. Relationships were similar between approach times and total passage times for the different treatment conditions, which was a result of the correlation between these two metrics ($r = 0.74$, $P < 0.001$). The only significant effects were a three way interaction ($F_{2,174} = 4.75$, $P = 0.001$) and a slot length \times velocity interaction ($F_{2,171} = 2.66$, $P = 0.034$) on lamprey approach times. Specifically, approach times were twice as fast for short slot length, high velocity conditions under the turbulence control ($mean = 22.7$ min) compared with turbulence treatments ($mean = 46.4$ min). However, this interaction was hard to interpret given the large variability observed in the individual approach time among fish (0.5-89 min; Figure 8).

The average number of swim tracks constructed for each treatment combination was 7.5; with most treatment combinations having 7-9 lamprey that fit the necessary criteria. Pacific lamprey appeared to prefer to move upstream along the right side of the experimental weirs, regardless of treatment. In both turbulence treatments for the long and medium slot lengths nearly every fish exhibited one of two behaviors. Lamprey either: 1) entered and exited along the right-side of the weirs; or 2) entered along the left-side of the weirs before switching sides to exit on the right-side (Figures 9-10). Hence, some preferential passage conditions may have existed on the right-side of the experimental weirs. There were two notable differences between the turbulence treatment and control pairs as well: at high velocity and short slot lengths, lamprey were uniformly distributed under low turbulence and passed on the right side in the high turbulence treatment. The converse was true at medium velocity (Figures 9-10). Although there was potential for cameras to be biased towards right side detections (Figure 1), the detection efficiency for cameras averaged 85% for all upstream movements based on comparisons with HD-PIT detections and thus detection bias is unlikely to explain the observed patterns.

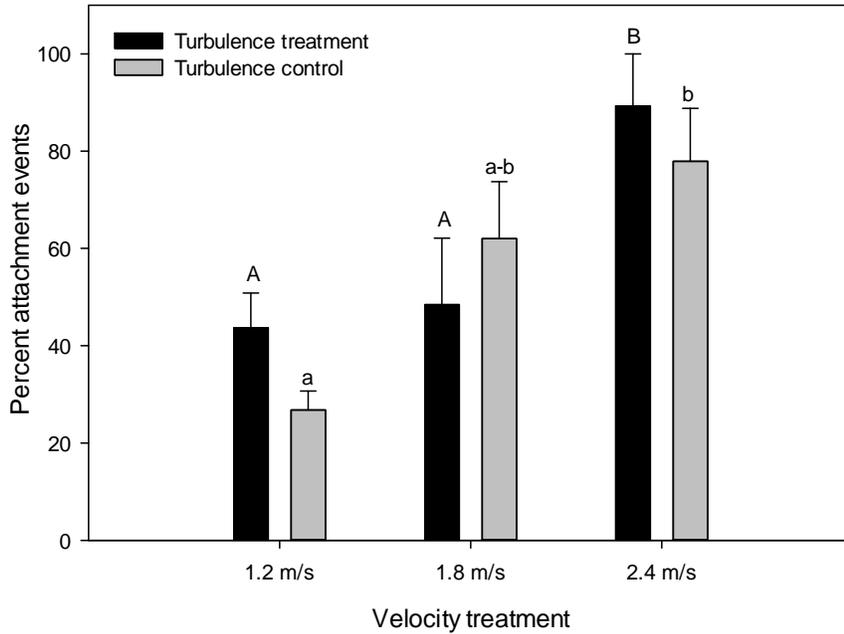


Figure 6. Percentage of upstream events (+SE) that involved an attachment for all velocity treatments sorted by turbulent (black) and non-turbulent (gray) conditions. Treatments with different capital letters were significantly different from each other within turbulent conditions and treatments with lower-case letters were significantly different from each other within non-turbulent conditions ($P < 0.05$).

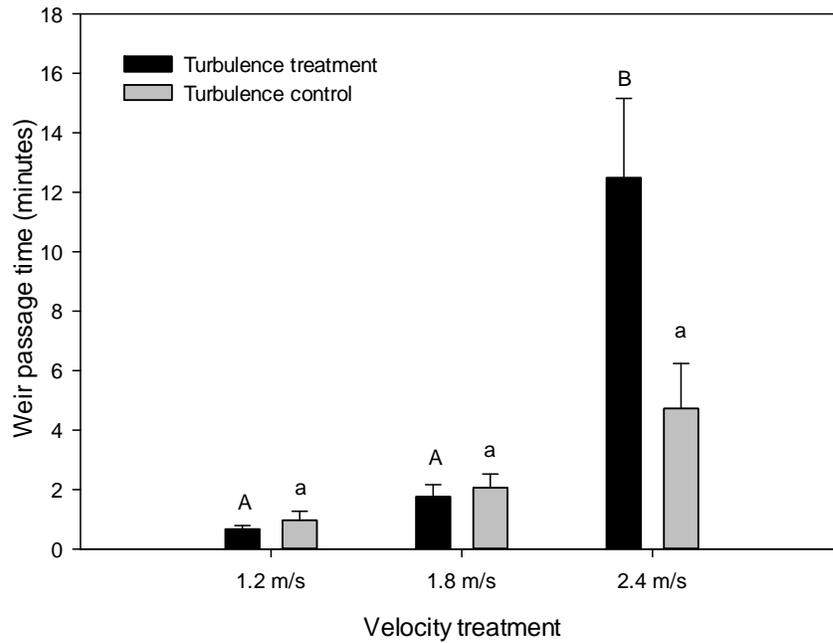


Figure 7. Weir passage times (+SE) for all velocity treatments sorted by turbulent (black) and non-turbulent (gray) conditions. Treatments with different capital letters were significantly different from each other within turbulent conditions and treatments with lower-case letters were significantly different from each other within non-turbulent conditions ($P < 0.05$).

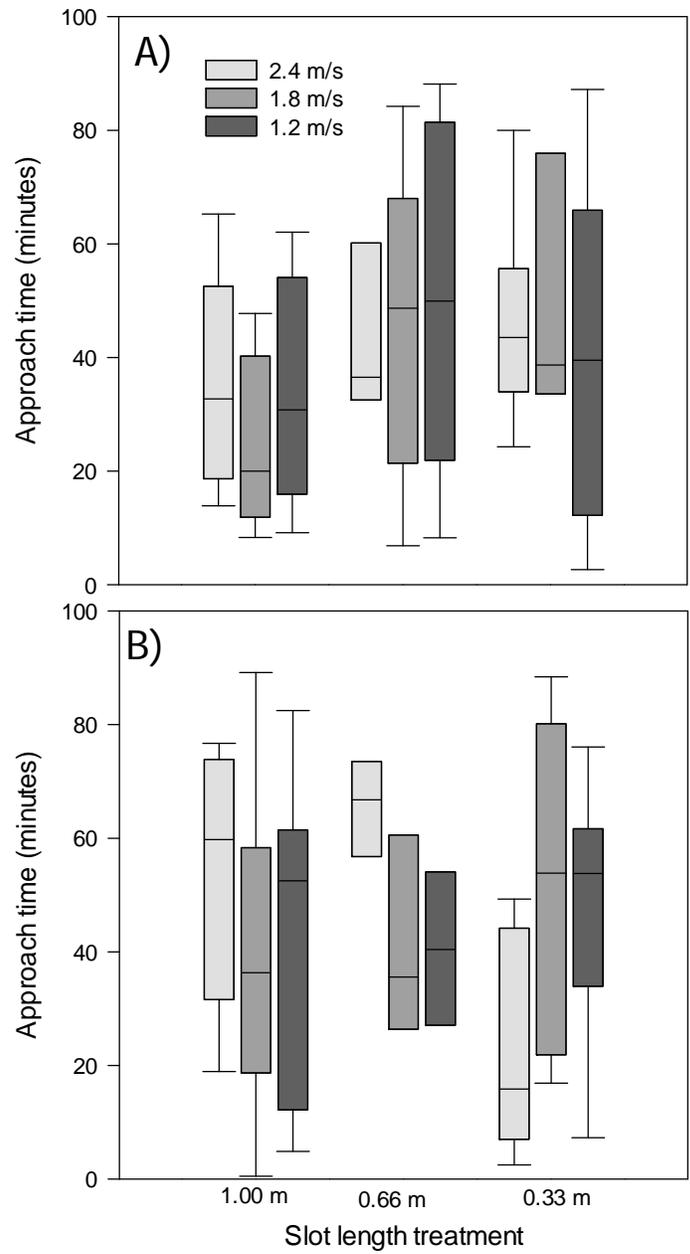


Figure 8. Approach times of Pacific lamprey sorted by slot length and velocity conditions for (A) turbulence and (B) control treatments. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

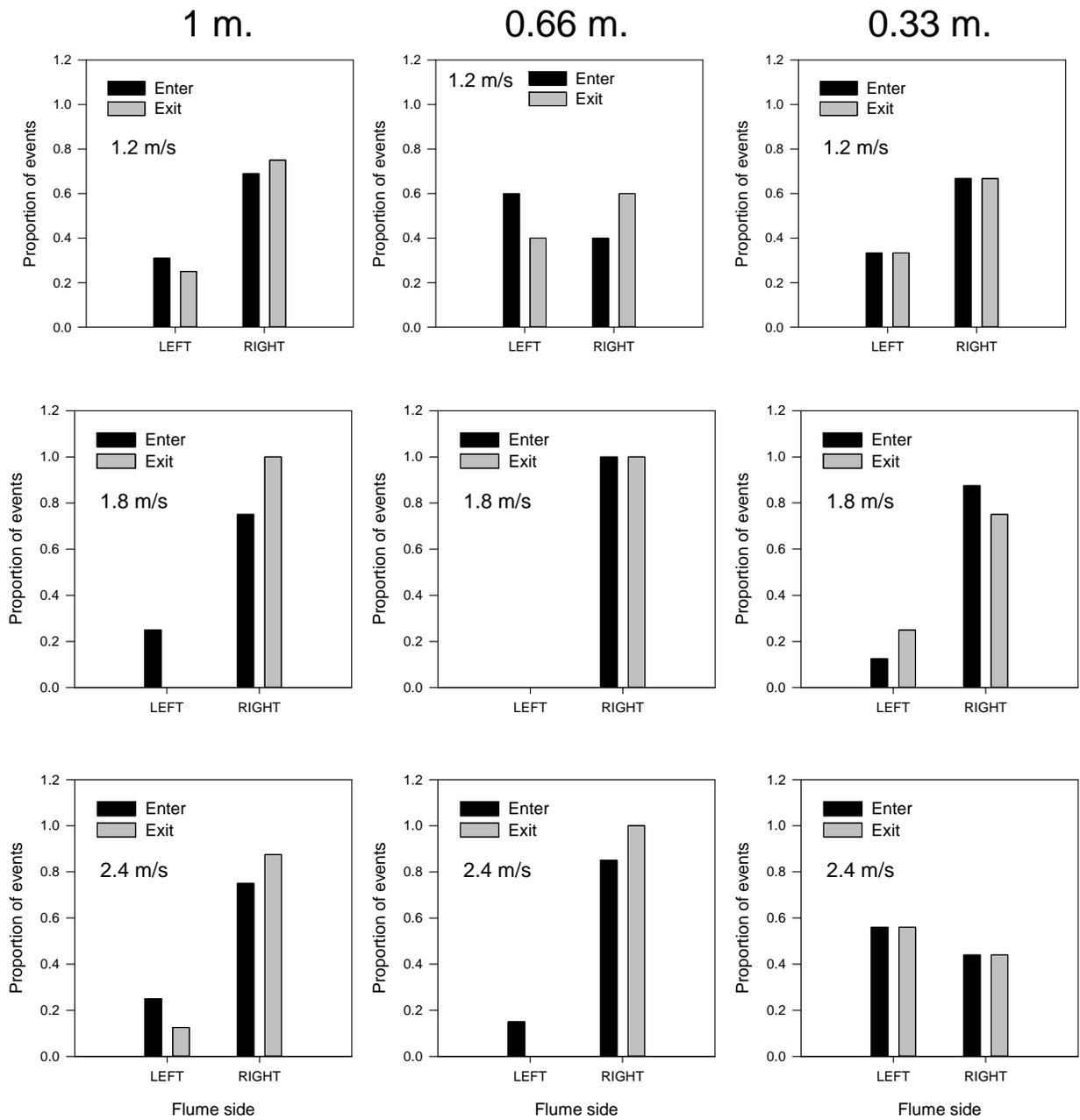


Figure 9. Proportion of upstream movements in low turbulence treatments for Pacific lamprey entering (black bars) and exiting (gray bars) the experimental weirs on the left and right side of the flume. The direction of flow was from top to bottom. Columns are sorted by slot length (1 m = left, 0.66 m = middle, 0.33 m = right) and rows are sorted by velocity (top = 1.2 m/s, middle = 1.8 m/s, bottom = 2.4 m/s).

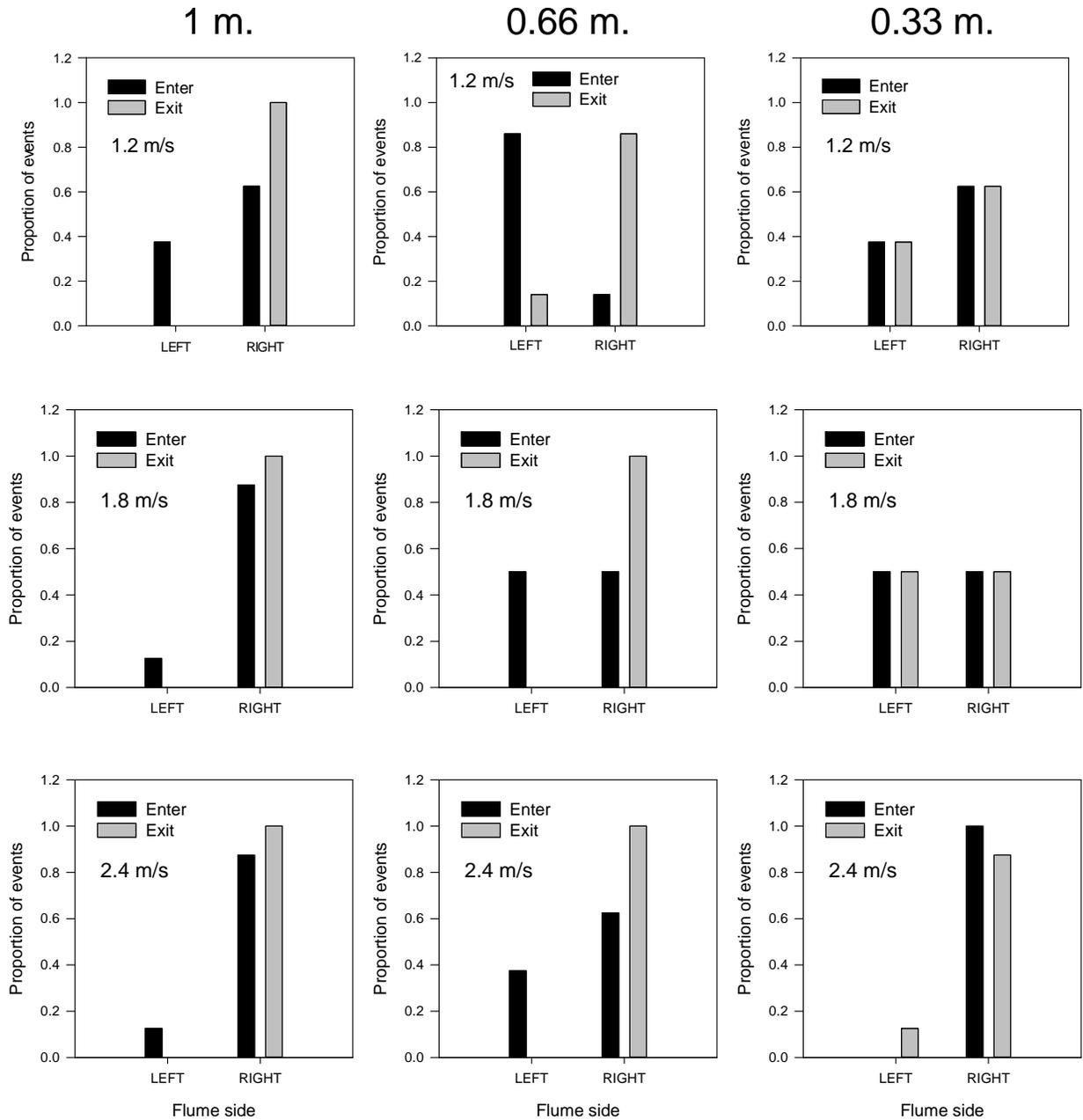


Figure 10. Proportion of upstream movements in high turbulence treatments for Pacific lamprey entering (black bars) and exiting (gray bars) the experimental weirs on the left and right side of the flume. The direction of flow was from top to bottom. Columns are sorted by slot length (1 m = left, 0.66 m = middle, 0.33 m = right) and rows are sorted by velocity (top = 1.2 m/s, middle = 1.8 m/s, bottom = 2.4 m/s).

Bradford Island fishway passage behaviors

The vertical distribution of lamprey observed during the August deployments indicated that lamprey were uniformly distributed with no strong demersal orientation (Figure 11; $F_{2,95} = 2.08$, $P = 0.131$). The frequency of attachment events was lower within the fishway (19.6%) than was observed in the flume (range: 26.8-89.3%). Movements in the upstream direction constituted 70-75% of all events at the three camera depths, indicating net upstream movement.

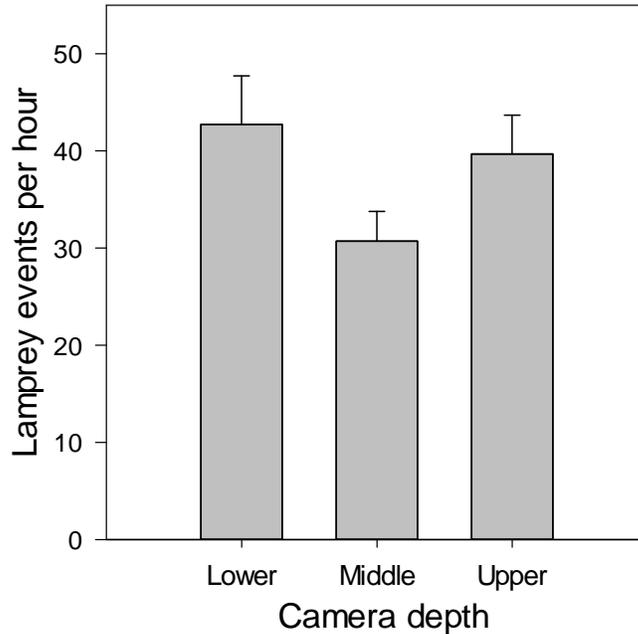


Figure 11. Vertical distribution of Pacific lamprey event rates (+SE) at three different camera deployments at Weir #5 in the Bradford Island serpentine weir section.

The longitudinal distribution of lamprey observed in the lower water column during the July deployments indicated a pattern of decreasing events from the downstream-most weir (Weir 5) to the upstream-most weir (Weir 9; Figure 12). Event rates at the lower camera were significantly higher at Weir 5 compared with Weirs 7 and 9 ($F_{2,236} = 14.85$, $P < 0.001$), where event rates were nearly the same. Interestingly, the proportion of lamprey attachment events was higher in July than August and decreased slightly from downstream to upstream, with a higher proportion at Weir 5 (32.7%) than Weirs 7 (26.4%) and 9 (24.0%). Event rates at the middle camera were not different between Weirs 5 and 7 ($F_{1,158} = 0.49$, $P = 0.486$), and were similar to the middle water column estimates from the August deployments.

When looking at movement patterns across the three weirs, Weir 7 had a higher proportion of fish moving downstream compared with Weirs 5 and 9 (Figure 13). 58% of movements at Weir 7 were downstream, suggesting a high degree of milling behaviors at this location. By comparison, only 37% of movements were downstream at Weirs 5 and 9. This same pattern was observed on the mid-water cameras as well, with a higher proportion of downstream movements at Weir 7 (73.8%) than at Weir 5 (39.6%).

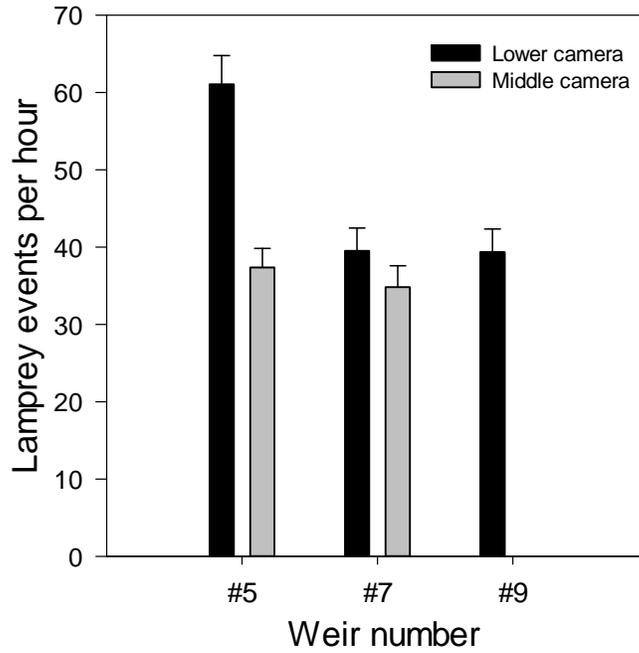


Figure 12. Longitudinal distribution of Pacific lamprey event rates (+SE) across three weirs within the Bradford Island serpentine weir section for cameras in the lower and middle water column. Data from the middle camera at Weir 9 could not be analyzed due to poor video quality.

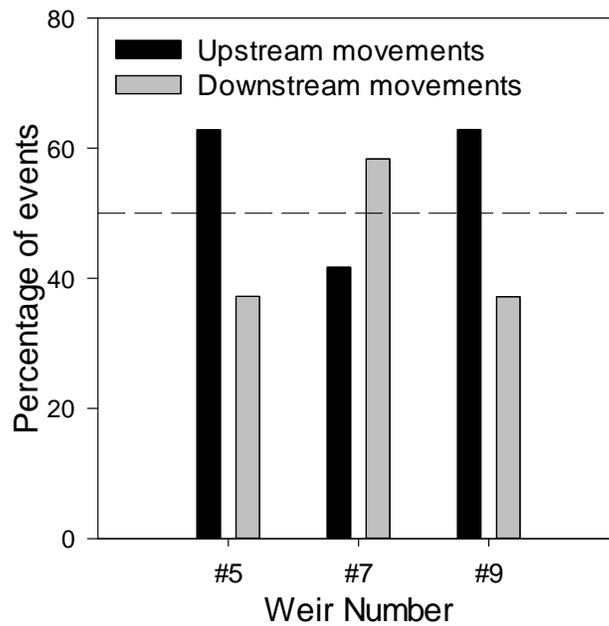


Figure 13. Proportion of upstream-downstream movements at the lower camera at three weir deployments within the Bradford Island serpentine weir section. Dashed line indicates a net upstream movement of zero (equal number of upstream and downstream movements).

Discussion

Passage implications

The primary mechanism suggested for the poor passage of Pacific lamprey at Columbia River dams arises from the lower swimming capacity of lamprey compared with salmonid species, for which many of these passage structures were specifically designed (Clay 1995; Rodriguez et al. 2006). For example, previous evidence has shown that Pacific lamprey may struggle in overcoming high velocity zones at some locations, such as fishway entrances (Moser et al. 2002a; Keefer et al. 2010; Kirk et al. 2014). In our study, the 1.2 m/s velocity treatment was representative of the reduced velocity conditions that occur during nighttime operations at Bonneville Dam, which have been shown to improve lamprey entrance efficiency (Johnson et al. 2012). In contrast, the 2.4m/s treatment was more reflective of the daytime velocity targets at entrances for salmonids. However, velocity did not have a major effect on Pacific lamprey success in any of our experiments. In fact, the overall success rates observed during experiments suggested that most lamprey were successfully passing the challenges, which was particularly surprising for the treatment conditions of higher velocity and turbulence. The ability of Pacific lamprey to overcome these treatment conditions is a testament to the species' swimming capabilities and ability to pass challenging obstacles. The successful passage of lamprey in our experiments presents an apparent contrast with the poor performance observed for lamprey in overcoming the Bonneville serpentine weir sections (~70% success observed in radiotelemetry studies by Keefer et al. 2013b). Below we discuss the implications of our results for explaining lamprey passage through the Bonneville serpentine weirs.

This apparent contradiction may have resulted from differences in fishway and experimental conditions and/or scale. The experimental weir in our study had a similar design to vertical slot weirs (Figure 1), which have been previously shown to be one of the more efficient passage designs among those tested for lamprey species (Laine et al. 1998; Foulds and Lucas 2013). For example, the vertical slots present at the top of The Dalles Dam are longitudinally aligned and are more similar to the turbulence controls in our flume experiments (Figure 15). These vertical slot sections at The Dalles are associated with low lamprey turn-around rates (Keefer et al. 2012). However, the serpentine weirs at Bonneville Dam do not provide a linear passage route for fish to ascend, but rather consist of a 'snake-pattern' design that generates large eddies with highly chaotic flow patterns instead of laminar flows. Preliminary results from hydraulic measurements using an Acoustic Doppler Velocimeter (ADV) showed that the turbulence and medium/high velocity treatments in our experiments were most similar to conditions within the Bonneville serpentine weirs (Syms et al., University of Idaho, *unpublished data*). Overall, we believe that the experimental weirs under the turbulence and high water velocity treatment conditions were most representative of the actual serpentine weirs within the fishways.

Because our experiments likely captured the range of conditions present at individual slots, we propose three mechanisms that may contribute to the poor passage observed for Pacific lamprey through the serpentine fishway sections. First, limited passage may be associated with one of our originally hypothesized factors, slot length. Success rates through the short (0.33 m) and medium (0.66 m) length treatments were ~25% higher than the long (1 m) treatments under high turbulence conditions (Figure 4A). While it may be possible that the length of the high

velocity barrier is the mechanism of poor performance (Castro-Santos 2004, 2006; Haro et al. 2004), the similarly low success rates between the low and high velocities (Figure 4A) suggest the treatment effects were not homogenous within the weir. The surprising absence of a main velocity effect also suggests that the relationships between passage success and treatment conditions were likely not a result of additive effects. The reduced success may have instead resulted from fine-scale hydraulic interactions between the flow and structural environment (e.g., weir wall), such as greater shear stress associated with the longer boundary layer for the long slot lengths (Vogel 1996; Weissburg 2000). Slot length may still play an important role in describing lamprey passage via non-linear, complex interactions with the flow environment. On-going analysis of hydraulic data in relation to fine scale movements of lamprey may reveal that other hydraulic measures, such as total kinetic energy, are more predictive of passage success than the treatment classes used in the present analysis.

The second hypothesis is that the poor passage observed through the fishway sections results from a cumulative effect of passing multiple weirs. Although Pacific lamprey only had to overcome one obstacle in the flume experiments, they must overcome ~15 of these weirs in the Washington-shore and Bradford Island fishways (Figure 2). Exploratory attempts to quantify Pacific lamprey response to exhaustive exercise revealed that experiments had produced physiologically demanding conditions for fish to overcome (Figure 14). Hence, we hypothesize that the physiological demands or motivation required for overcoming multiple weirs exceeds the endurance capacity of lamprey. Pacific lamprey require 1-4 hours to recover from exhaustive exercise (Mesa et al. 2003), so the constant re-exposure to the hydraulic conditions at these weirs during periods of recovery and attachment may inflict additional endurance based costs (Enders et al. 2003, 2005). Further research is needed regarding the physiological costs/benefits of attachment behaviors and how they may aid in recovery while simultaneously under exhaustive conditions.

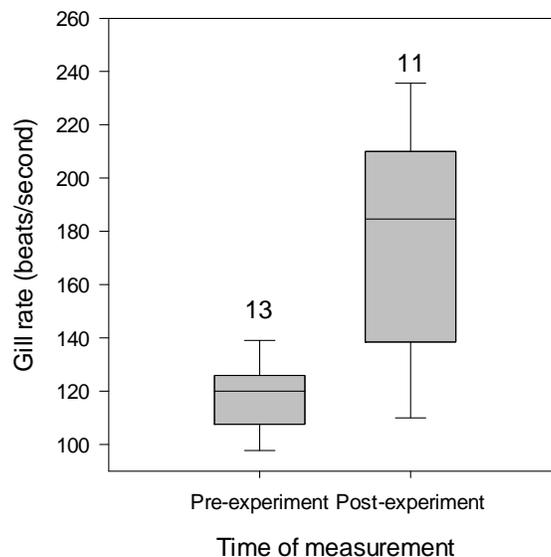


Figure 14. Estimates of Pacific lamprey gill beat rates before and after four experimental trials. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Numbers above bars are samples size of fish.

We modeled the cumulative passage success of Pacific lamprey through the actual serpentine weir sections using the average passage success observed from our experimental flume results for the slot length of each weir in the Bradford Island serpentine section (91% for short and medium slot lengths, 69% for long lengths). Using this approach, only 8% of lamprey would successfully pass all 15 weirs in the serpentine sections at Bonneville. In contrast, passage of individual weirs at a constant rate of 98% would result in a 73% success rate for the serpentine section, similar to the values obtained from radiotelemetry studies. Results from the fishway cameras provided some support for this hypothesis with lower lamprey event rates (Figure 12) at upstream weirs, but clearly also indicate substantial milling in this section (i.e., upstream movements were much less than 98%). Additionally, the high rate of milling behaviors observed at Weir 7 suggest that poor passage may not be resulting from a simple, linear decline; especially since higher upstream passage was observed at Weir 9 for the individuals that reached that point (Figure 13). Instead, it is plausible that the passage problem may be non-linear in nature, such that individuals may be exceeding some endurance or motivation threshold in the vicinity of Weir 7 that results in a higher number of “give-ups.” A non-linear effect was also observed for the weir passage times during the flume experiments, where the combined effect of both turbulence and high velocity generated a greater than two-fold increase in lamprey attachment times compared to any other treatment combination (Figure 7). Although the biological mechanism affecting any such threshold remains unknown, our evidence suggests the potential for a ‘giving up’ or exhaustion threshold as a proximate mechanism leading to passage failure in some lamprey.

A third and more speculative hypothesis is that the high rate of turning (i.e., changing swim directions) associated with the ‘snake-like’ design of serpentine weir sections may disrupt the orientation of Pacific lamprey. Fish must overcome 15 weirs involving sharp turns at either 90° or 180° (Figure 2). Such conditions are not present in natural riverine systems. As noted above, the orientation of vertical slots at The Dalles Dam (and dams upstream) do not require high turning angles to navigate (Figure 15) and are associated with higher passage rates for lamprey. Given that vision plays a minimal role in the migrations of lamprey species (Binder and McDonald 2007) and the ability of fishes to detect, orient, and navigate using magnetic fields (Quinn 2005; Putnam et al. 2013), Pacific lamprey may be dependent upon both rheotactic cues and magnetic cues during upstream migrations. Thus, the high degree of turning within the serpentine weirs sections may disrupt the upstream orientation capabilities of lamprey. Simple maze experiments could be conducted to test how the effects of turning would influence elements of behavior, aversion, and success, though we note that such experiments would need to control for the effects of turning angle on turbulence and velocity.



Figure 15: Vertical slot weirs at The Dalles Dam North fishway. Note linear alignment of slots compared to Bonneville Dam serpentine weirs.

Body size and escapement

There was limited evidence to support the hypothesis that body size was a significant predictor of experimental flume passage, with passage probability only being higher for Pacific lamprey with longer length-specific dorsal distances. Dorsal distance has been shown to be correlated with energetic status and maturation state in Pacific lamprey, in which shorter dorsal distances are associated with lower body weight and higher spawning readiness (Clemens et al. 2009). Hence, fish that have suffered a reduction in body weight or are physiologically close to spawning stage may lack the energetic capabilities for overcoming passage barriers. While other measurements of lamprey body size (i.e., weight, length) did not show significant relationships during experiments, size-selective processes may still manifest within the fishway when fish must pass multiple challenges. However, it is worth noting that there was a sampling bias towards shorter dorsal distances in long slot length and high turbulence treatments (Appendix Figure B). This was purely coincidental in our randomized experiment in that the high turbulence, long slot length treatments overlapped with the earliest group of migrants and occurred during the peak migration days (early July, ~200 fish trapped). Future studies should seek to confirm the relationships between dorsal distance, energetic status, and passage.

The mechanisms proposed to explain the patterns of size-selective passage in the Columbia River basin have included larger Pacific lamprey having higher energetic condition, as well as the homing of larger lamprey to upstream locations (Keefer et al. 2009a, 2013c; Hess et al. 2014). While we provided indirect evidence here for the role of energetic condition in describing passage, larger lamprey may have a higher amount of energetic reserves or possess greater burst swimming capabilities that allow them to overcome migration barriers. Although numerous studies have documented a correlation between swimming capacity and body size (Beamish 1974; Haro et al. 2004), our results did not appear to support the hypothesis that larger lamprey

have greater burst swimming capabilities in overcoming velocity barriers (Table 3). Overall, our results suggest that these ‘size-selective’ processes operating at Columbia River dams do not appear to be a result of overcoming single velocity barriers (Keefer et al. 2013b; Kirk et al. 2014). Instead, body size effects may manifest through motivation and/or giving-up thresholds associated with lamprey endurance for traversing multiple challenges. It is also possible that size effects were not detected due to the small scale of our experiments and these effects may only become observable at larger scales as lamprey encounter multiple obstacles.

Although the probability of post-experiment escapement within the hydrosystem was not significantly related to experimental passage success, lamprey that did pass the experiment had a slightly higher probability of escapement to the Upper Columbia and Snake River dams (Figure 5). It remains unknown whether this was a result of the lamprey that migrated further having greater swimming capacity or higher motivation. Overall, the pattern of attrition observed for both groups was similar to the rates documented previously (Moser et al. 2002a; Keefer et al. 2009). Hence, whether Pacific lamprey were successful in overcoming experimental challenges did not markedly affect the level of attrition the population experiences through the hydrosystem.

Tagging and handling effects have the potential to underestimate performance and need to be fully identified in order to develop accurate inferences from experiments (Wilkie et al. 1997; Keefer et al. 2010). While we did not have the ability to evaluate unhandled or untagged controls, a comparison of post release distribution indicated that the final upstream distribution of adults was largely similar to other tagged groups. However, there did appear to be some indirect evidence of a handling effect. A Kolmogorov-Smirnov test comparing the escapement between the lamprey used in flume experiments and a random subsample of 275 HD-PIT tagged lamprey (GM sample) that passed Bonneville revealed that the distribution of migration distances in the flume sample had a significantly shorter migration distance compared with the GM sample group ($D = 0.25$, $P = <0.001$).

However, we note that the GM sample and flume samples were not drawn from identical populations. The GM sample included adults successfully passing Bonneville whereas the flume sample included adults that would not have passed Bonneville Dam. Thus, these results potentially biased our escapement estimates because these adults would have been presumably less likely to pass other upstream dams. The distribution of migration distances in the flume group was similar to the escapement estimates of previous year’s lamprey samples double-tagged with JSATS and HD-PIT tags which were collected, tagged and released to the Bonneville Reservoir using similar protocols to the experimental flume lamprey (Figure 16). However, these effects could not be directly assessed given the available comparison groups. A substantial proportion of lamprey failed to approach during our experiments, which may have also been related to handling or tagging effects during the relatively short experimental period. Overall though, the broad concordance between our flume experiment and field experiments suggest tagging and handling effects were minor.

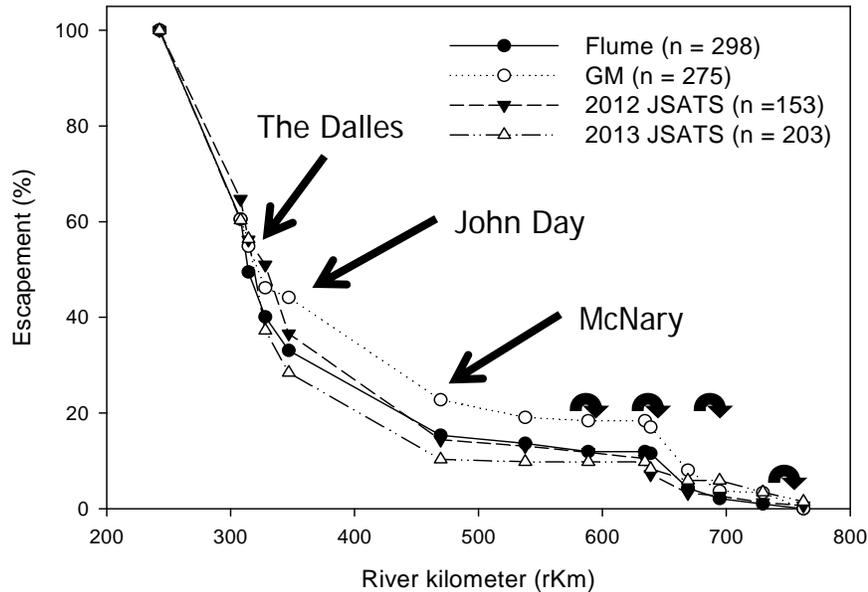


Figure 16. Escapement estimates for the HD-PIT tagged sample of experimental flume fish, HD-PIT tagged general migration sample, and 2012/2013 Juvenile Salmon Acoustic Tagged (JSATS) lamprey samples. Stars indicate the locations of Snake River projects. Numbers in parentheses indicate sample sizes.

Notes on lamprey behavior

The majority of Pacific lamprey showed a preference for moving upstream along the floor during the flume experiments regardless of hydraulic condition, which reflects the demersal nature and use of tactile cues that has been previously documented for lamprey species (Keefer et al. 2010, 2011; Kemp et al. 2010). However, lamprey did not display a strong demersal orientation within the serpentine weir sections in the Bradford Island video observations. Hence, ‘edge effects’ within the flume may explain the demersal behaviors observed during experiments given the shallower water depths in the flume. During the experiments, lamprey did alter their behavior from demersal and free-swimming versus demersal and saltatory (i.e., attach and burst) depending upon the hydraulic conditions encountered. Pacific lamprey had a greater incidence of saltatory movements as velocity and turbulence increased (Figure 6, 7).

These behavioral patterns have been previously observed under physiologically demanding passage conditions with high turbulence and high velocity for several different lamprey species (Quintella et al. 2004; Kemp et al. 2010; Kirk et al. 2014). The most strenuous conditions observed in our study were under these treatments, and some lamprey would hold location for long periods before incrementally bursting upstream to a new attachment point. This behavior likely minimizes the risk of lamprey being pushed downstream and provides some resting opportunity after periods of fatigue and exhaustion (Kemp et al. 2009, 2010). Lamprey may also employ attachment behaviors as a stabilizing mechanism given their lack of paired pectoral fins (Liao 2007), particularly under turbulent conditions with strong upwelling currents. These

observations, along with behaviors from *in situ* fishway observations (Kirk et al. 2014), have helped us develop a framework for understanding Pacific lamprey behavior at the fishway scale.

Swim track data provided indirect evidence for the ability of Pacific lamprey to detect ‘fine-scale’ changes within their hydraulic environment. Lamprey showed an affinity for both entering and exiting on the right side of the flume, and individuals that did enter the left side were most frequently observed exiting on the right side (Figure 9, 10). One hypothesis for this behavior is that lamprey were responding to changes in hydraulic cues, which could include either avoidance or attraction to turbulent forces (Silva et al. 2012; Goettel et al. 2014). Preliminary hydraulic data collected from a complementary study using an Acoustic Doppler Velocimeter (ADV) within the flume suggests that lamprey were avoiding locations of high turbulence (Syms et al., University of Idaho, *unpublished data*). A second hypothesis is that Pacific lamprey followed a similar swim path of previous conspecifics (Goettel et al. 2014). Lamprey were frequently observed attached in groups within only a few centimeters of each other, especially in the high velocity and high turbulence treatments. It is possible that these two mechanisms are complementary, whereby lamprey use social cues to reduce the costs of finding passable routes identified by earlier lamprey. Finally, unmeasured environmental cues such as magnetic fields or acoustic cues may have affected passage routes. Regardless of the mechanism(s), these data provide preliminary evidence that Pacific lamprey movements are driven by hydraulic, biological, or environmental cues at a scale smaller than previously quantified within fishway environments.

The lower success rates in the early season group were likely a result of behavioral or physiological changes associated with water temperature differences. Warmer water temperatures during late season trials may have raised the metabolic activity of lamprey and promoted faster upstream movement (Booth et al. 1997; Lee et al. 2003; Reinhardt et al. 2009; Keefer et al. 2009b). Warmer temperatures may have also promoted quicker recovery from potential tagging effects during late season trials (Wilkie et al. 1997). While success rates may have been higher if experiments lasted longer than 90 minutes, the vast majority of lamprey approached and attempted to pass during middle and late season groups. Early season Pacific lamprey exhibiting slower migration times has been observed previously in field populations and the specific mechanism, whether behavioral or physiological, remains unknown (Keefer et al. 2009a, 2009b).

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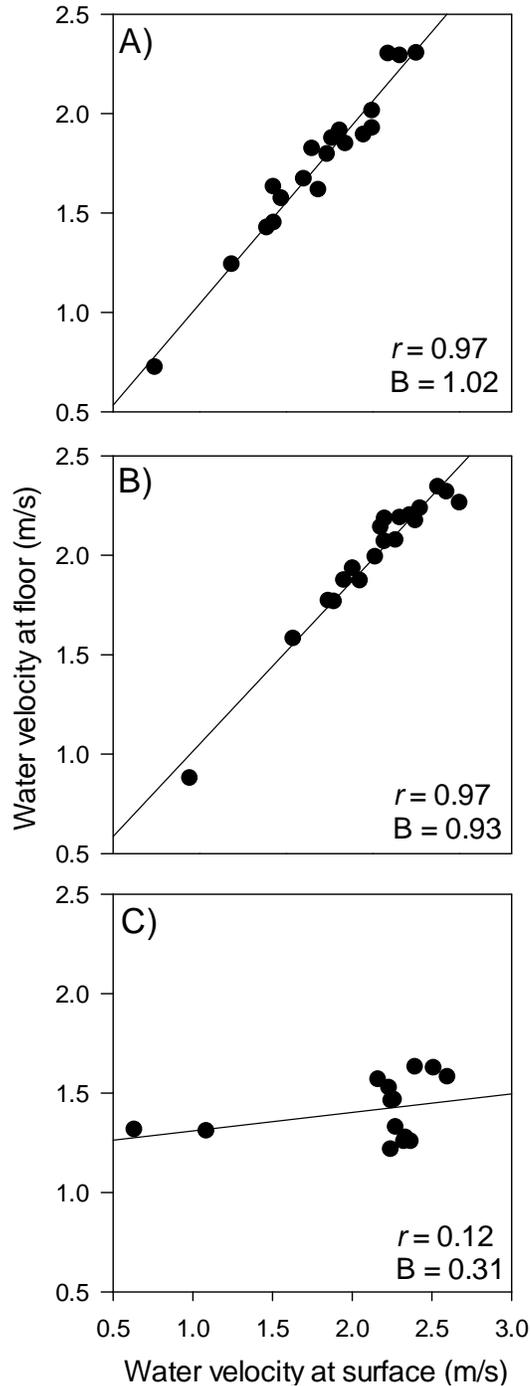
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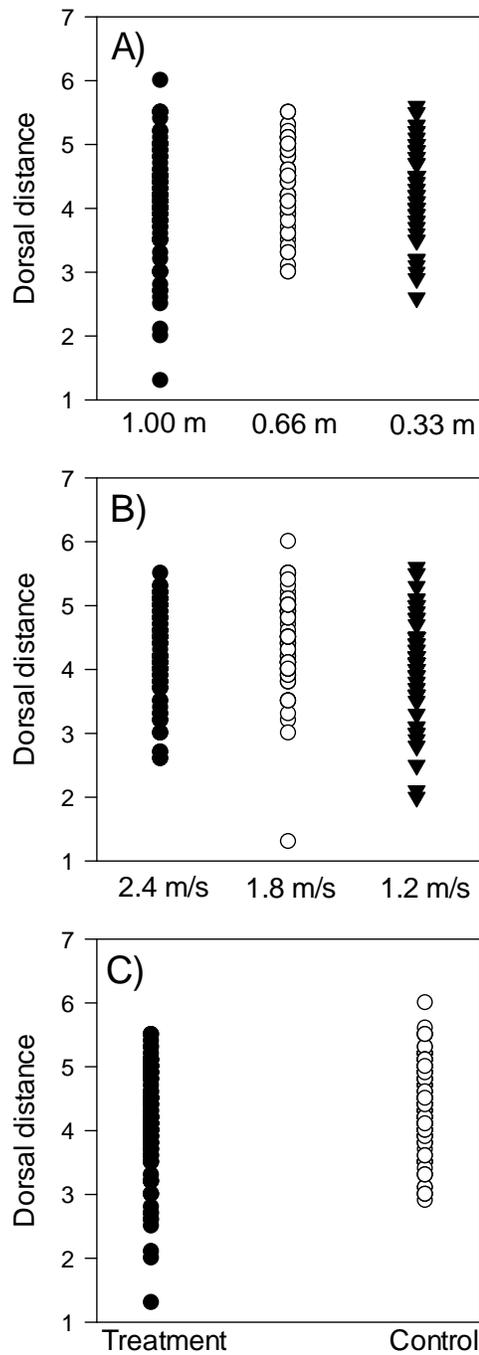
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Appendix



Appendix Figure A. Water velocity measurements taken within the experimental flume during the (A) short, (B) medium, and (C) long slot length treatments. Note that the slope for the short and medium length treatments was ~ 1 , indicating similar velocities between the flume floor and the water surface. In contrast, long length treatments did not show any strong correlation, which was potentially a result of sampling error since these measurements were collected first.



Appendix Figure B. Scatterplots of Pacific lamprey dorsal distance measurements for (A) slot lengths, (B) velocity, and (C) turbulence treatments. Notice the greater variation in dorsal measurements for the long slot lengths compared with short and medium lengths, as well as the variation in turbulence treatments compared with turbulence controls.