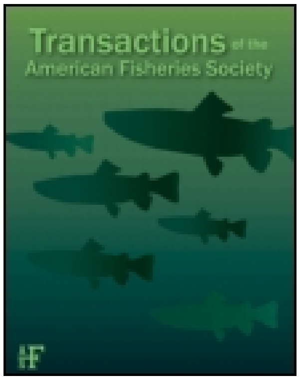

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Movement of Radio-Tagged Adult Pacific Lampreys during a Large-Scale Fishway Velocity Experiment

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NOTE

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Abstract

Optimization of fishways to pass multiple species is challenging because life history, swimming ability, and behavior often differ among species. For example, high fishway water velocities designed to attract adult Pacific salmon *Oncorhynchus* spp. at Columbia River dams inhibit fishway entrance and passage success of adult Pacific lampreys *Lampetra tridentata*, a species of conservation concern. We tested whether reduced water velocities (∼1.2 m/s, 0.15 m of head) at Bonneville Dam fishway openings improved entrance efficiency and other passage metrics for radio-tagged Pacific lampreys compared with control velocities (>1.98 m/s, 0.46 m of head) and near-zero ("standby") velocities. Lamprey entrance efficiencies were significantly higher in the reduced-velocity treatment (26–29%) than in the control (13–20%) or standby (5–9%) treatment. In some years, significantly more Pacific lampreys passed through fishway collection channels and transition pools and reached the fish ladder during reduced-velocity treatment conditions, indicating that benefits extended beyond fishway entrances. However, overall passage efficiency at the dam was relatively unchanged, suggesting that additional passage bottlenecks for Pacific lampreys exist upstream from fishway entrances. The experiment demonstrated how operational changes can improve passage performance and how exploiting behavioral differences among species can improve multispecies management.

An ideal fish passage structure would preserve the population, community, and ecosystem processes upstream and downstream from the passage obstacle. However, developing optimal fish passage structures is challenging because behavior, metabolic scope, and swimming performance differ significantly among species (Haro et al. 2004). Fishway design is influenced by historical, operational, and economic factors (Monk et al. 1989; Clay 1995; Mallen-Cooper and Brand 2007; Keefer et al. 2010) and consequently favors individual fish with specific traits within species (e.g., size; Mallen-Cooper and Brand 2007; Keefer et al. 2009) or selects for a subset of species present (Oldani and Baigún 2002; Stuart and Berghuis 2002; Agostinho et al. 2007). It is well recognized that successful passage is strongly influenced by hydraulic attributes, such as velocity and turbulence, but is rarely understood in detail (Haro et al. 1999; Bunt 2001).

Reducing fishway selection can be achieved by modifying fishway structures or operations. Structural changes to fishway features such as entrance areas, transition pools, and fishway weirs typically aim to reduce passage bottlenecks (Monk et al. 1989; Bunt et al. 2001; Naughton et al. 2007). Operational changes can include manipulation of discharge or tailwater elevation to improve fishway entrance discovery and use (Clay 1995; Laine et al. 2002; Pon et al. 2009) or temporal adjustments that take advantage of seasonal or diel passage differences among species (Hard and Kynard 1997; Bunt et al. 2001; Ellis and Vokoun 2009).

Fishways at many dams in the Pacific Northwest were designed and are operated to facilitate passage by strong-swimming adult salmonids. Passage efficiency (defined as [number of adults passing fishways]/[number that approach the dam base]) at individual dams on the lower Columbia River is high (i.e., often >90%; Caudill et al. 2007) for adult salmonids, particularly when compared with the passage efficiency of adult

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Pacific lampreys *Lampetra tridentata* (<50%; Moser et al. 2002b; this study). In recent studies, just 4–5% of adult Pacific lampreys tagged with passive integrated transponder tags at Bonneville Dam were able to pass all four lower Columbia River dams (∼235 river km [rkm]) and only approximately 1% reached the Snake River, a major tributary where Pacific lampreys were once abundant (Keefer et al. 2009). Low passage efficiency appears to be related to differences in swimming performance between Pacific lampreys and salmonids. Specifically, adult Pacific lampreys have difficulty stemming high water velocities at many fishway entrances, in constricted fishway segments, and at ladder orifices (Moser et al. 2002b; Keefer et al. 2011). Pacific lamprey passage can also be impeded by design features inside fishways (e.g., vertical steps and metal grates) that do not affect salmonid passage (Keefer et al. 2010).

High water velocities at fishway entrances have been implicated as a passage bottleneck to Pacific lampreys because past radiotelemetry studies have revealed low fishway entrance efficiencies ([number of fishway entries]/[number of fishway approaches]) but relatively high passage efficiencies through middle and upper fishways (Moser et al. 2002b). Fishway entrances at Columbia River dams often have water velocities that exceed 2.0 m/s (Clay 1995; Naughton et al. 2007), which is considerably higher than the adult Pacific lampreys' critical swimming speed of 0.8 m/s (Mesa et al. 2003) and may exceed the burst-swimming capabilities (2.5–3.0 m/s range) of some lampreys (Keefer et al. 2010).

The primary objectives of this study were to experimentally reduce water velocity at a fishway entrance and evaluate the effects on the behavior and entrance success of radio-tagged adult Pacific lampreys. Dam passage by adult Pacific lampreys is predominantly nocturnal (Moser et al. 2002b), whereas Pacific salmon *Oncorhynchus* spp., steelhead *O. mykiss*, and American shad *Alosa sapidissima* primarily pass dams during the day (Quinn and Adams 1996; Hatch et al. 1998; Naughton et al. 2005; Caudill et al. 2007). Therefore, entrance velocities were manipulated only at night to maximize benefits for Pacific lampreys while minimizing potential negative effects on other species. We hypothesized that reducing fishway entrance velocity would (1) increase Pacific lamprey fishway approach rates and entrance efficiencies, (2) reduce Pacific lamprey fishway entrance times (time from fishway approach to fishway entry), and (3) improve passage through the lower fishway.

METHODS

Study site and velocity experiment.—The experiment was conducted at entrances to the Powerhouse 2 (PH2) fishway (Washington shore) at Bonneville Dam (Figure 1) on the lower Columbia River. The entire dam spans three channels separated by islands, and PH2 dams the northernmost channel. Paired openings at the south and north fishway entrances feed into collection channels that merge below a transition pool (Figure 1). From the transition pool, fish enter a series of pools and weirs that ascend to the forebay on the north shore of the dam.

Water velocities at entrances to the PH2 fishway are determined by differences in elevation (head) between the inside of the fishway entrance and the dam tailrace. The three target head levels for our experiment were 0.45 m (control), 0.15 m (reduced velocity), and 0 m (standby) and corresponded to mean entrance velocities of greater than 1.96, 1.20, and 0 m/s, respectively. Head at PH2 fishway entrances was controlled by operation of two turbines ("fish units") that provided water to the fishway collection channel. Control velocities corresponded to operational criteria thought to be optimal for upstream migrating salmonids and occurred during daytime hours throughout the duration of the experiment. Each night (typically between 2200 and 0400 hours), experiment velocity treatments were alternated in a randomized block design, with control or reduced treatment velocities applied each night within each 2-d block. Changes from control head levels to treatment levels generally took less than 15 min at the four main PH2 entrances as determined from water-level loggers located inside the fishway and in the tailrace near the fishway. Standby conditions occurred intermittently during the season by stopping fish units in order to float debris off the fish unit trash racks as required by operations guidelines. Operational constraints precluded application of the reduced-velocity treatment in 2008 and standby was more frequent in 2008, a year with more debris. Standby conditions occurred for minutes to hours each night and occurred haphazardly with respect to treatment.

Tagging and monitoring.—Pacific lampreys were captured, handled, tagged, and released according to protocols described previously (Moser et al. 2002a, 2007). Pacific lampreys were trapped at night in the PH2 fishway and fishway entrance. Lampreys with a girth circumference greater than 9 cm (at the insertion of the first dorsal fin) were anesthetized in a 60-ppm (3 mL/50 L) solution of eugenol. An approximately 12-mm ventral incision was made directly below the anterior edge of the first dorsal fin fold. A 14-cm-long sterile catheter (Abbocath-T, Hospira, Lake Forest, Illinois) was placed inside the body cavity and pushed through the body wall approximately 5 cm posterior to the incision. The antenna of the radio transmitter was guided through the catheter, and the transmitter was gently inserted. A minimum of two simple, interrupted sutures were applied to close the incision (Ethicon 46-cm [18-in], 3–0 coated vicryl braided sutures with an FS-2 cutting needle in 2007 and 2008; Ethicon 69-cm [27-in], 3–0 undyed monofilament sutures with an RB-1 cutting needle in 2009). In 2007, transmitters were 30.1 mm long × 9.1 mm in diameter, weighed 4.5 g in water, and had a burst rate of 5 s and an expected tag life of 235 d (Model NTC-6–2, Lotek Wireless, Newmarket, Ontario). In 2008 and 2009, transmitters were 18.3 mm long × 8.3 mm in diameter, weighed 2.1 g in water, and had a burst rate of 8 s and an expected tag life of 127 d (Model NTC-4–2L, Lotek Wireless). After at least 2 h, radio-tagged Pacific lampreys were released approximately 3 rkm downstream from the dam. Surgery and handling

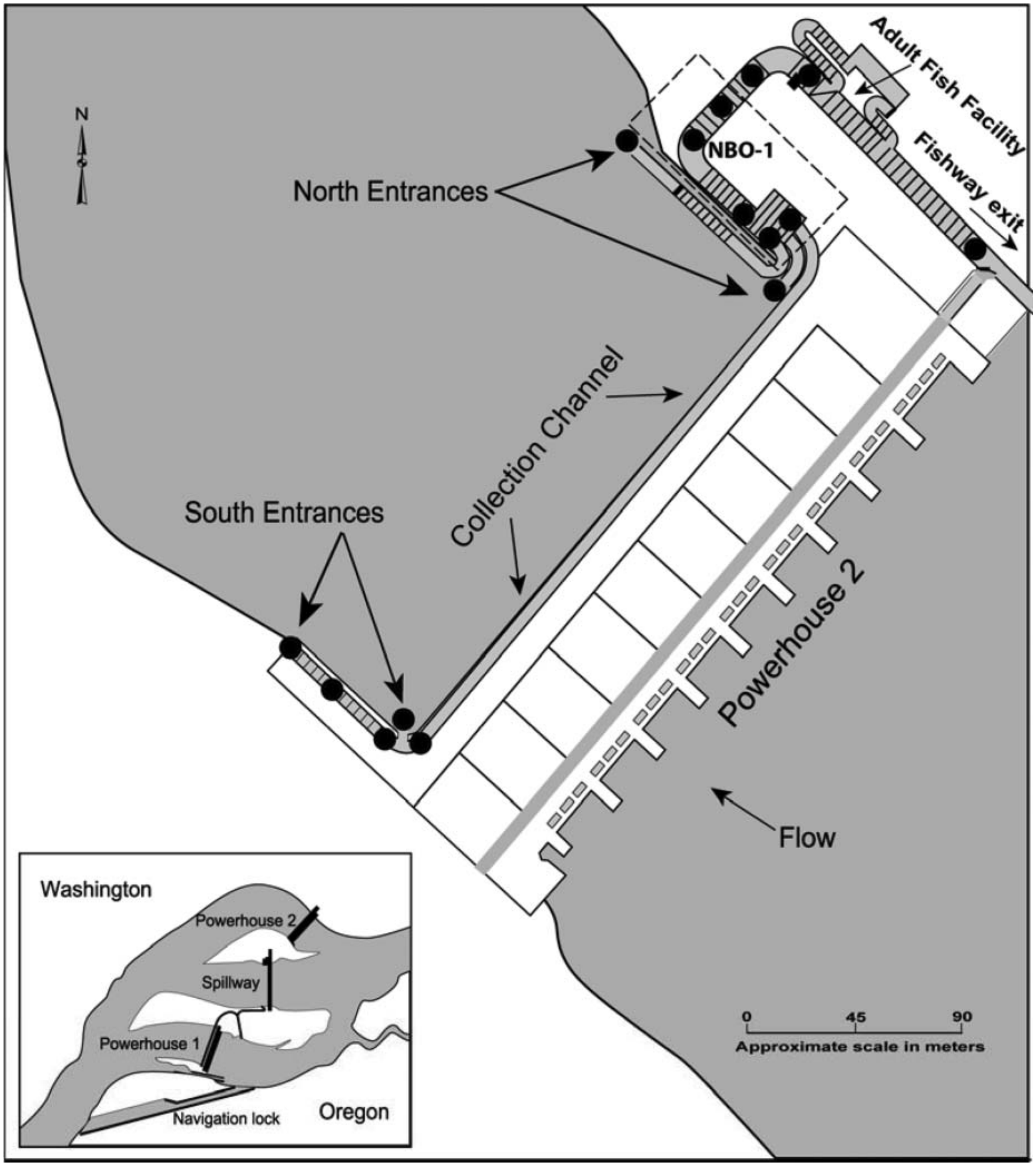

FIGURE 1. Map of Powerhouse 2 (PH2) at Bonneville Dam (Columbia River), showing the north and south fishway entrance locations (where nighttime water velocity was manipulated) and the location of the transition pool (dashed rectangle). Solid circles indicate locations of underwater antennas. The NBO-1 antenna was located at the downstream end of the transition pool. Inset shows the location of PH2 at Bonneville Dam.

protocols were reviewed and approved by the University of Idaho Animal Care and Use Committee (Protocol 2009–41).

Radio-tagged Pacific lamprey movements were monitored with an array of fixed-site receivers at Bonneville Dam and in the tailrace. Radio receivers were equipped with digital spectrum processors to receive transmissions on multiple frequencies simultaneously. Radio receivers coupled with a scanning receiver and one or more underwater coaxial cable antennas were positioned at fishway entrances and inside fishways to detect fish as they approached and entered fishways, moved within collection channels, transition pools, and fish ladders, or exited a fishway. Radiotelemetry data were downloaded from receivers weekly.

Entrance rates, ratios, and passage times.—We tested for treatment effects at several scales by using metrics that evaluated different aspects of Pacific lamprey passage behavior. Fishway approach metrics examined the potential influence of treatment effects on attraction to the entrances. Fishway entry metrics included both the entry rate (number of entries per hour) and entrance efficiency ([entries]/[approaches at the same site]) to test for local treatment effects at the manipulated entrances. For these metrics, fishway entries that occurred during a different treatment than the approach treatment were discarded; consequently, the estimated effect sizes were probably conservative. Fishway exit metrics included exit rate (exits per hour) and net entry ratio ([total fishway entries]/[total exits to the tailrace]).

We examined individual Pacific lamprey routes to evaluate whether a treatment affected successful passage through the PH2 entrances and the lower fishway (collection channel and transition pool). We calculated the percentages of radio-tagged Pacific lampreys that ascended to the base of the Washington shore ladder (defined as detection at antenna site NBO-1; Figure 1) of those that approached and entered the fishway during each experimental treatment (hereafter referred to as approach-to-lower-ladder and entry-to-lower-ladder ratios). Each unique approach or entry event was included (i.e., a fish could approach or enter a fishway more than one time).

We also tested for local treatment effects on passage time. Passage times were calculated for two segments at Bonneville Dam: (1) the time from first fishway approach to first fishway entry, defined as the elapsed time between the first detection at an antenna outside a fishway entrance to the first detection inside a fishway, for those fish that approached and entered the same entrance during the same treatment; and (2) the time from first fishway entry to transition pool entry, defined at the first detection at an antenna inside a fishway to the first detection at NBO-1 (Figure 1). Treatment comparisons were categorized by treatment condition encountered at the time of fishway entry. Entrance efficiencies, approach-to-lower-ladder ratios, and entry-to-lower-ladder ratios among velocity treatments were compared by using Pearson's χ^2 tests. We used a Yates continuity correction to adjust computed χ^2 values to compensate for 1 df (Zar 1999).

RESULTS

Trapping, Tagging, and General Passage Behavior of Pacific Lampreys

A total of 1,589 adult Pacific lampreys were radio-tagged during the 3-year study. Lamprey size was similar among years (mean mass ± SD: 2007, 466 ± 95 g; 2008, 464 ± 79 g; 2009, 473 ± 89 g), but the tag-to-lamprey girth ratio was lower in 2008 and 2009 than in 2007 as a result of using smaller diameter transmitters in the latter 2 years (tag ratio: 2007, 25.8 ± 2.1%; 2008, 23.1 ± 1.9%; 2009, 22.9 ± 1.8%).

Annual percentages of released Pacific lampreys detected at Bonneville Dam antennas ranged from 68% in 2007 to 79% in 2009 (Table 1). Annual percentages of Pacific lampreys known to have passed the dam ranged from 21% in 2007 to 31% in 2009. The majority of released Pacific lampreys detected at Bonneville Dam approached PH2 first before approaching other entrances (57% in 2009 to 63% in 2007). First approaches at Powerhouse 1 (Figure 1) ranged from 18% to 27%, and the fewest Pacific lampreys first approached entrances adjacent to the spillway (15–20%; Table 1).

Fishway Entrance Velocity Test: Passage Behavior

Reduced-velocity treatments at PH2 fishway entrances occurred on 48% (2007) and 47% (2009) of the nights from 1 June through 30 September. Control velocities occurred on 46% (2007), 65% (2008), and 42% (2009) of the nights. Standby operations occurred on 6% (2007), 35% (2008), and 11% (2009)

TABLE 1. Number of adult Pacific lampreys released downstream from Bonneville Dam and the number and percentage of released individuals that (1) were recorded in the tailrace and at dam fishways, (2) passed the dam, and (3) were recorded as approaching and entering a fishway opening.

	2007		2008		2009	
Passage metric	*n*	%	*n*	%	*n*	%
Released	398		595		596	
Recorded at tailrace	368	92.5	569	95.6	549	92.1
Recorded at dam	271	68.1	4,444	74.6	470	78.9
Known to pass dam	83	20.8	146	24.5	177	31.0
Recorded first fishway approach	266		396		444	
Powerhouse 2	167	62.8	228	57.6	254	57.2
Powerhouse 1	47	17.7	108	27.3	104	23.4
Spillway	52	19.5	60	15.2	86	19.4
Recorded first fishway entry	176		200		254	
Powerhouse 2	102	58.0	88	44.0	124	48.8
Powerhouse 1	32	18.2	60	30.0	53	20.9
Spillway	42	23.8	52	26.0	77	30.3

of the nights. Some Pacific lampreys approached and entered the PH2 fishway during different treatments ("treatment switching") in each year. In 2007, treatment switching rates were 24% after approaching the PH2 south entrances (n = 12 of 49) and 18% after approaching the PH2 north entrances (n = 12 of 66). The majority (83%) of those that switched approached during control conditions and entered during reduced velocity. In 2008, treatment switching rates were 8% ($n = 5$ of 59, PH2 south) and 17% ($n = 15$ of 87, PH2 north). Almost all (94%) that switched had approached during standby conditions and entered during control conditions. In 2009, treatment switching rates were 12% ($n = 9$ of 76, PH2 south) and 18% ($n = 24$ of 136, PH2 north). No single type of treatment switch predominated, but 50% entered during reduced velocity after approaching during either control or standby conditions.

Entrance efficiencies during reduced-velocity periods were 8–12% higher than during control periods in 2007 and 2009 (2007: Pearson's $\chi^2 = 13.1$, $P < 0.001$; 2009: Pearson's $\chi^2 = 8.5$, $P < 0.005$; Figure 2). In both years, the magnitude of reduced-velocity treatment effects was greater at the PH2 north entrances than at the PH2 south entrances. Entrance efficiencies during reduced-velocity periods were significantly higher (8.7–16.5%) than during control periods at the PH2 north entrances in 2007 (Pearson's $\chi^2 = 14.7$, $P < 0.001$) and 2009 (Pearson's $\chi^2 = 7.4$, $P < 0.05$) but not at the PH2 south entrances (Table 2). Total fishway exit rates also increased during the reduced-velocity treatments but were largely compensated for by increased entrance rates. Net entry ratio was significantly higher during control than standby conditions in two of three comparisons at PH2 north fishways (Table 2).

Pacific lampreys approached fishways at higher rates during standby operations than during reduced-velocity and control conditions (Figure 2). Entrance rates were also relatively high during standby conditions, though this effect was less than the effect on approach rate. Consequently, entrance efficiency was more than threefold higher during reduced-velocity conditions compared with standby conditions when considering PH2 north and south fishway entrances together (2007: Pearson's $\chi^2 = 25.3$, $P < 0.001$; 2009: Pearson's $\chi^2 = 65.3$, $P < 0.001$). Entrance efficiency was also significantly higher during control than standby conditions at both PH2 north and south fishway entrances in 2008 (Pearson's $\chi^2 = 34.9$, $P < 0.001$) and 2009 (Pearson's $\chi^2 = 25.4$, $P < 0.001$) but not in 2007 (Pearson's $\chi^2 = 2.2$, $P = 0.14$; Figure 2).

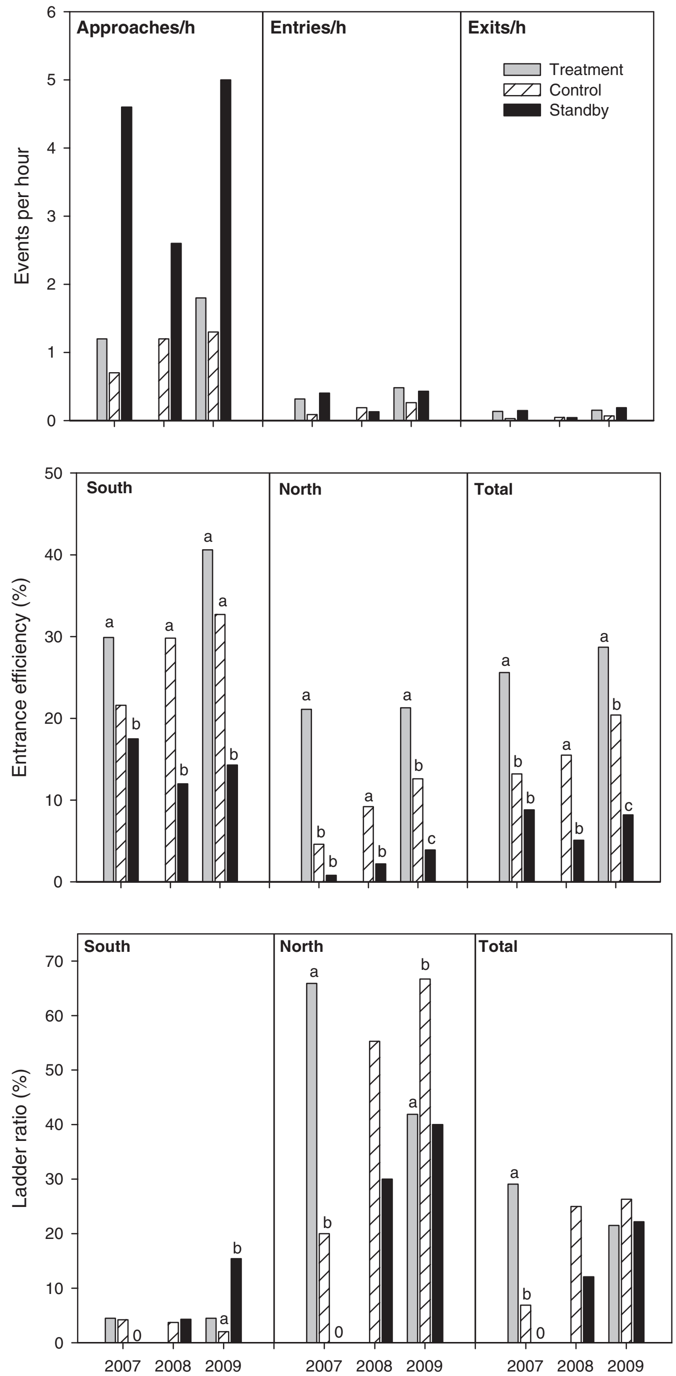

FIGURE 2. Number of Pacific lamprey approaches, entries, and exits recorded per hour at the Bonneville Dam Powerhouse 2 (PH2) fishway entrances (top panel); the entrance efficiencies (middle panel) and entry-to-lower-ladder ratios (bottom panel) at the PH2 north and south fishways are also shown. Gray bars represent the reduced-velocity treatment, cross-hatched bars represent the control, and black bars represent the standby velocity conditions. Entrance efficiencies and ladder ratios were compared among velocity treatments by using Pearson's χ^2 tests; treatments with different letters were significantly different at $\alpha = 0.05$.

Passage through the Lower Powerhouse 2 Fishway

Few fishway approaches resulted in Pacific lamprey passage through the lower fishway to the lower ladder (approach-to-lower-ladder ratio) during any treatment, and the ratio was nearly four times lower at PH2 south (interannual mean = 1.3%) than at PH2 north (interannual mean = 5.1%; Pearson's $\chi^2 = 32.0$, $P < 0.001$; Table 2). Telemetry records indicated that after Pacific lampreys entered the PH2 south fishway, most exited to the tailrace before reaching the transition pool area, either via

TABLE 2. Estimated entrance efficiencies at Bonneville Dam Powerhouse 2 (PH2; south and north fishway entrances) for Pacific lampreys that approached and entered the same site during the same treatment ([total number of entries]/[total number of approaches]) and the net entry ratio ([total number of entries]/[total number of exits]) that occurred during each treatment. Also included are the approach-to-lower-ladder ratio and entry-to-lower-ladder ratio ([number that reached the ladder]/[number that approached or entered]) at each fishway entrance site. For a given year and location, treatment values with different letters were significantly different at $\alpha = 0.05$. Sample sizes are shown in parentheses.

Year	PH2 entrance location	Condition	Efficiency (%)	Net entry ratio (%)	Approach-to-ladder ratio (%)	Entry-to-ladder ratio (%)
2007	South	Treatment	29.9 (221) z	50.0 (66)	1.4 (221)	4.5 (66)
		Control	21.6 (111)	58.3 (24)	0.9 (111)	4.2 (24)
		Standby	17.5 (103) y	61.1 (18)	0.0 (103)	0.0 (18)
		Total	24.8 (435)	53.7 (108)	0.9 (435)	3.7 (108)
	North	Treatment	21.1 (209) z	68.2 (44)	13.9 (209) z	65.9 (44) z
		Control	4.6 (108) y	100.0 (5)	0.9 (108) y	20.0 (5) y
		Standby	0.8 (113) y	100.0 (1)	0.0 (113) y	0.0 (1)
		Total	11.6 (430)	72.0 (50)	7.0 (430)	60.0 (50)
2008	South	Treatment				
		Control	29.8 (178) z	69.8 (53)	1.1 (178)	3.7 (53)
		Standby	12.0 (192) y	78.3 (23)	0.5 (192)	4.3 (23)
		Total	20.5 (270)	72.4 (76)	0.8 (270)	3.9 (76)
	North	Treatment				
		Control	9.2 (404) z	81.1 (37) z	5.2 (404) z	55.3 (37)
		Standby	2.2 (450) y	40.0 (10) y	0.7 (450) y	30.0 (10)
		Total	5.5 (854)	72.3 (47)	2.8 (854)	50.0 (47)
2009	South	Treatment	40.6 (219) z	65.2 (89)	1.8 (219)	4.5 (89)
		Control	32.7 (153) z	64.0 (50)	0.7 (153)	2.0 (50) z
		Standby	14.3 (182) y	57.7 (26)	2.2 (182)	15.4 (26) y
		Total	29.8 (554)	63.6 (165)	1.6 (554)	5.5 (165)
	North	Treatment	21.3 (348) z	73.0 (74)	8.9 (348) z	41.9 (74) z
		Control	12.6 (239) y	90.0 (30) z	8.4 (239) z	66.7 (30) y
		Standby	3.9 (255) x	50.0 (10) y	1.6 (255) y	40.0 (10)
		Total	13.5 (842)	75.4 (114)	6.5 (842)	48.2 (114)

the PH2 south entrances or via the unmonitored orifice gates along the PH2 collection channel. At PH2 north, the percentages of lampreys that reached the lower ladder after approaching varied across treatments, with means of less than 1.0% during standby operations, 5.6% during control conditions, and 10.8% during the reduced-velocity treatment (Pearson's $\chi^2 = 65.4$, $P < 0.001$). There was no consistent effect of treatment condition on entry-to-lower-ladder ratios, though there was a trend toward lower overall entry-to-lower-ladder ratios during standby periods: means were 13.6% (standby), 24.5% (reduced velocity), and 22.9% (control; Pearson's $\chi^2 = 0.1$, $P = 0.10$; Table 2). There was more than a 10-fold increase in the entry-to-lower-ladder ratio between Pacific lampreys entering at PH2 north (interannual mean = 51.4%) and those entering at PH2 south (4.6%; Pearson's $\chi^2 = 164.8$, $P < 0.001$), consistent with the location effect on approach-to-lower-ladder ratios.

Notably, the magnitude of treatment effects on entrance efficiency and entry-to-lower-ladder ratios was not consistent between PH2 south and PH2 north entrances. Specifically, entrance efficiency increased by the greatest magnitude at PH2 north, which also had very high overall approach-to-lower-ladder and entry-to-lower-ladder ratios during the reduced-velocity treatment (Table 2). The pattern was reversed at PH2 south.

Fishway Entrance Velocity Test: Passage Times

Across years, point estimates of median fishway approach-to-entry times at PH2 north and south entrances were longer during control treatments than during reduced-velocity treatments. At PH2 south fishways, the median fishway approach to entry times ranged from 3.3 to 3.7 min (reduced velocity) and from 5.7 to 104.3 min (control). At PH2 north, the median approach to entry time ranged from 6 to 18 min (reduced velocity) and from 2.2 to 40.1 h (control). Sample sizes for standby treatments were low in most cases ($n < 6$), with point estimates similar to or longer than those during reduced-velocity periods. Median entry-to-lower-ladder passage times were generally longer during the control velocity treatments. Passage times to the lower ladder for fish that entered PH2 south fishways ranged from 1.7 to 1.8 h (reduced-velocity treatment) and from 7.4 to 20.0 h (control velocity treatment). Median entry-to-lower-ladder passage times at PH2 north fishways were considerably shorter (median, <10 min) than those at PH2 south (median, 1.1–1.7 h) during any treatment and were generally longer during the control treatments, particularly for fish that entered PH2 south.

DISCUSSION

Species-specific differences in diel migratory activity provided an opportunity to test whether modified fishway operations would improve passage for adult Pacific lampreys at night while maintaining fishway criteria for adult salmonids during the day. Several lines of evidence indicated that reducing fishway entrance velocity improved adult Pacific lamprey passage into and through the lower PH2 fishway at Bonneville Dam. The benefit was most evident at the fishway openings, but in some cases the effect extended upstream, with more fish reaching the lower ladder during reduced-velocity treatments. This experiment demonstrated how a cost-effective operational modification can accommodate behavioral differences and improve fishway function for multiple species.

Benefits to Pacific lampreys of reducing entrance velocity were site-specific. This operational change clearly improved Pacific lamprey entrance efficiency at the north end of the fishway but not at the south fishway entrances. It is likely that differences in tailrace conditions near fishway entrances or structural differences among entrances themselves affected Pacific lamprey guidance or entrance behavior. For example, reducing the velocity emanating from fishway entrances adjacent to the Bonneville Dam spillway had no positive effect on Pacific lamprey passage (Moser et al. 2002a), suggesting that the design of spillway entrances or the turbulent conditions surrounding these entrances negated the potential benefits we observed in experiments at PH2 north.

Reducing the fishway entrance velocity resulted in improvements in entrance efficiency and in the numbers of fish that reached the lower ladder; however, these results did not translate to notable improvements in overall passage efficiency at the dam. Instead, additional passage bottlenecks upstream from the fishway entrances apparently limited total passage success through the PH2 fishway. A critical result from these analyses was that Pacific lamprey passage efficiency from the PH2 south entrances through the collection channel and transition pool were very low (i.e., 3–6% across treatments), especially when compared with Pacific lampreys that entered at PH2 north (48–60%). Treatment effects at the base of the fish ladder were diminished for lampreys that entered the PH2 south entrances because many fish exited the fishway (possibly through open orifice gates) prior to ladder ascension or turned around in the approximately 250-m-long collection channel that spans the length of PH2.

The above results demonstrate that fishway components should be considered independently to optimize functionality. At complex, multicomponent fishways like those at Bonneville Dam, a series of operational or structural modifications (or both) will almost certainly be needed to alleviate the major passage bottlenecks for Pacific lampreys. Indeed, the reduced entrance velocity experiment was just one of several changes (e.g., construction of lamprey passage structures, rounding of sharp fishway edges, removal of vertical steps inside weir orifices, installation of plating over metal diffuser grating) that have been tested or implemented at known Pacific lamprey passage bottlenecks at lower Columbia River dams (Keefer et al. 2009, 2010; Moser et al. 2011). In combination, these changes have incrementally improved dam passage efficiency for adult Pacific lampreys and presumably have increased escapement to spawning areas. At less-complex sites with fewer bottlenecks, a single operational change such as a reduced fishway entrance velocity may immediately and cost-effectively improve overall dam passage efficiency for this species.

To be effective, fishway velocity manipulations must maintain enough head to attract and guide Pacific lampreys without creating a velocity barrier. As illustrated in this study, high entrance velocities encountered during the control condition resulted in passage failure or delay, while the standby condition resulted in low entrance efficiency and high fishway exit ratios. Point estimates of Pacific lamprey passage time indicated that lampreys moved from fishway approach to fishway entry faster during reduced-velocity conditions, although this effect was limited to the entrance area. During standby conditions, Pacific lampreys readily approached the fishways, but entrance efficiency was low, indicating poor attraction. Moreover, point estimates of fishway exit ratios were highest during standby in 2007 and 2009, perhaps because rheotactic orientation cues were reduced inside the fishway. Importantly, our approach rate and entrance efficiency estimates assumed that approach records were actually attempts at fishway entry, and it is plausible that at least some approaches, particularly during standby operations, were the result of "swim-bys" as fish passed along the face of the powerhouse and passed fishway openings. Regardless, the overall results indicated that Pacific lamprey passage success was poor during standby conditions compared with reduced-velocity conditions and was as low as (or lower than) the passage success observed during control conditions in most fishway segments. Consequently, reducing total standby time or shifting standby operations to nonpeak passage times would probably benefit Pacific lamprey passage at Bonneville Dam.

This experiment demonstrated how a change in fishway operations can increase fishway effectiveness for species that were not considered during the fishway design process. Our approach exploited behavioral differences among species so that there was little or no effect on adult salmonids, but there were clear local-scale benefits for adult Pacific lampreys. Among radio-tagged adult Pacific salmon, few approached or entered during the nighttime experimental periods (1.6% of total approach attempts, 6.6% of all adults tagged in 2007 and 2009). This result is consistent with previous observations of reduced nighttime passage rates for adult salmonids at Columbia River and Snake River dams (Hatch et al. 1998; Naughton et al. 2005; Caudill et al. 2007). Additionally, dam passage times at Bonneville Dam for summer Chinook salmon *O. tshawytscha* that approached PH2 during the treatment period in 2007 and 2009 were similar (reduced-velocity conditions: median = 8.8 h, $n = 19$; control conditions: median = 8.7 h, $n = 26$), with all of these fish successfully passing Bonneville Dam. However, fishway entrance areas (even with reduced velocities) continued to be a passage challenge for Pacific lampreys and there were clearly additional passage bottlenecks that remained inside the collection channel and in upstream fishway segments. Challenges analogous to those for Pacific lampreys at Bonneville Dam exist at other fish passage structures worldwide, as many existing fishways were built to accommodate single species or populations, often to the detriment or exclusion of other native species. Species-specific behavioral and ecological data are needed at these sites so that fishways can be designed and operated to most efficiently pass the full complement of native species. For existing fishways, we recommend assessing species-specific behavior and swimming capabilities, quantitatively assessing fish passage constraints, and then modifying structural or operational criteria to accommodate each species. In the future, planning for new fishways should consider the passage requirements of the full complement of species present, provide a range of suitable hydraulic conditions, and strive to include features that allow operational flexibility in an effort to minimize fishway selection against specific species, size-classes, or ages (Agostinho et al. 2002, 2007; Mallen-Cooper and Brand 2007; Naughton et al. 2007; Moser et al. 2011).

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