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Fishway passage bottleneck identification and prioritization: a case study of Pacific lamprey at Bonneville Dam

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Abstract: Fishways designed for salmonids often restrict passage by non-salmonids, and effective tools are needed both to identify passage problems for nontarget species and to inform remediation planning. In this case study, we used migration histories from 2170 radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) to identify locations of poor passage (bottlenecks) at a large, multifishway dam. Over 10 years, 49% of tagged lamprey that entered fishways failed to pass the dam. Models accounting for repeated attempts by individual lamprey indicated successful passage strongly depended on attempted passage route. Success also varied with time of fishway entry, water temperature, and lamprey body size. Most failed passage attempts terminated in lower fishway segments, but extensive seasonal shifts in bottleneck locations were detected. Ranking metrics helped prioritize bottlenecks and identified sites where structural or operational modifications should improve lamprey passage. Our integration of spatially intensive monitoring with novel analytical techniques was critical to understanding the complex relationships among fishway features, environmental variation, and lamprey behavior. The prioritization framework can be applied to a wide range of fish passage assessments.

Résumé : Les passes migratoires conçues pour les salmonidés restreignent souvent le passage d'autres poissons, et des outils efficaces sont nécessaires pour cerner les problèmes associés au passage d'espèces non visées et éclairer la planification de mesures correctives. Dans la présente étude de cas, nous avons utilisé les historiques de migration de 2170 lamproies du Pacifique (*Entosphenus tridentatus*) adultes munies de radio-émetteurs pour cerner les lieux de passage difficiles (goulots d'étranglement) à un important barrage comptant plusieurs passes. Sur une période de 10 ans, 49 % des lamproies munies d'émetteurs qui entraient dans ces passes ne réussissaient pas à remonter le barrage. Des modèles tenant compte de tentatives multiples par les mêmes lamproies ont indiqué que le succès du passage dépendait fortement de la voie de passage employée. Le taux de succès variait également selon le moment de l'entrée dans la passe, la température de l'eau et la taille du corps de la lamproie. La plupart des tentatives de passage infructueuses prenaient fin dans des sections avals des passes, mais d'importantes variations saisonnières de l'emplacement des goulots d'étranglement ont été décelées. Le classement des différents paramètres a aidé à établir la priorité des goulets et à cerner les sites où des modifications structurales ou opérationnelles devraient améliorer le passage des lamproies. L'intégration d'une surveillance spatiale fine et de nouvelles techniques analytiques s'est avérée essentielle à une meilleure compréhension des liens complexes entre les caractéristiques des passes à poissons, les variations des conditions du milieu et le comportement des lamproies. Le cadre d'établissement de la priorité peut être appliqué à un vaste éventail d'évaluations de passes à poissons. [Traduit par la Rédaction]

Introduction

River systems worldwide have been fragmented by dams and other anthropogenic obstacles that restrict fish movements (Nilsson et al. 2005). A diverse array of fishways and other passage systems has facilitated upstream fish passage at such sites (Clay 1995; Odeh 1999). Unfortunately, many were designed solely to accommodate migratory species with high social or economic value, with little consideration for nontarget species, resulting in local extirpations (Winston et al. 1991), population fragmentation (Morita and Yamamoto 2002), and reduced abundance and diversity of riverine fauna (Pringle et al. 2000). These outcomes have been propagated by the export of fishways designed in one region — typically for a single species or group of related species — to regions with entirely different fish communities (e.g., Agostinho et al. 2007; Mallen-Cooper and Brand 2007).

Weir-and-pool and vertical slot fishways designed for anadromous salmonids (*Oncorhynchus* spp. and *Salmo* spp.) and clupeids (*Clupea* spp. and *Alosa* spp.) are among the most widely used fish passage systems. Performance testing for these fishway types historically included swim speed evaluations and velocity barrier experiments using the target species (e.g., Weaver 1963; Beamish 1978). Such designs effectively pass some species with high burst swim speeds, endurance, or motivation to pass upstream (e.g., Schwalme et al. 1985; Keefer et al. 2004; Noonan et al. 2012). However, they often present substantial challenges for nontarget species with limited ability to traverse turbulent or high velocity conditions (Agostinho et al. 2007; Pratt et al. 2009; Bunt et al. 2012). Even when structures are known to limit passage for a specific group of fishes, it can be difficult to identify causal mechanisms and specific locations associated with the poor performance.

In this paper, we apply passage metrics and statistical models novel to the fish passage literature to identify fishway bottlenecks

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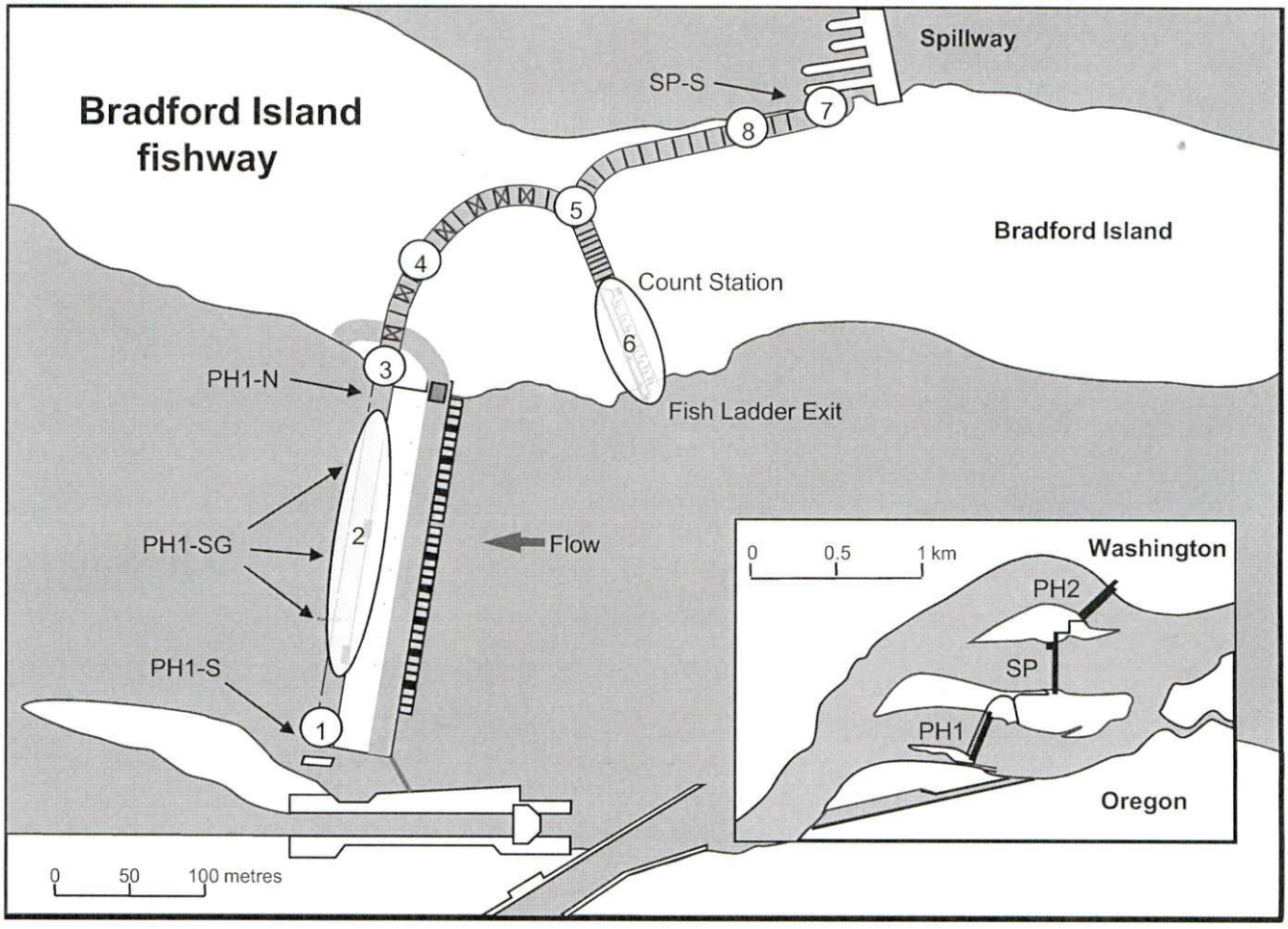
Fig. 1. Map of Powerhouse 1 and the Bradford Island fishway at Bonneville Dam on the Columbia River. Radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) were monitored as they entered fishway openings (arrows) and passed through the collection channel, transition area, and fish ladders. Circles and ellipses show locations inside the fishway where Pacific lamprey turn-around events were assigned. Inset shows the configuration of Bonneville Dam, including the two powerhouses and the spillway. PH1 = Powerhouse 1 (N = north; S = south); PH2 = Powerhouse 2; SP = spillway; SG = sluice gate.



for adult Pacific lamprey (*Entosphenus tridentatus*) at a large hydropower dam. The Pacific lamprey is an anadromous species in decline around the Pacific Rim, and poor dam passage success is a contributing factor (Luzier et al. 2011). We have conducted a series of studies of adult Pacific lamprey at Bonneville Dam (Columbia River, USA) to investigate mechanisms of passage failure. The research has included direct observation of lamprey behavior inside fishways (Clabough et al. 2012), performance challenges using an on-site experimental fishway (Keefer et al. 2010, 2011), construction of lamprey-specific passage structures (Moser et al. 2011), and on-site monitoring of passive integrated transponder- and radio-tagged lamprey (Moser et al. 2002a; Keefer et al. 2009; Johnson et al. 2012). Over 10 years, we generated a large radiotelemetry database of individual lamprey behaviors and fishway passage outcomes that is suitable for rigorous data exploration and analyses.

Our overarching objectives here were to (*i*) use the radiotelemetry data to estimate dam-wide and route-specific Pacific lamprey passage efficiency at Bonneville Dam; (*ii*) investigate relationships between lamprey passage efficiency and biologically meaningful covariates; (*iii*) identify lamprey passage bottlenecks within fishways; and (*iv*) develop a general set of quantitative tools to help prioritize sites for fishway remediation. To evaluate the efficiency relationships, we used generalized linear models, both assuming independence among passage attempts and accounting for repeated attempts by individual lamprey. Likely bottlenecks were identified by assigning failed passage attempts to specific fishway segments. We then used multinomial logistic regression models to investigate spatial and temporal shifts in bottleneck locations. Several bottleneck-specific metrics were used to rank fishway segments with respect to Pacific lamprey passage failure. This integrated, quantitative approach could help diagnose and rank fish passage problems at a variety of existing barriers.

Materials and methods

Study site

Bonneville Dam is located 235 river kilometres from the Columbia River mouth on the Washington–Oregon border (45°N, 121°W). The dam spans three channels separated by islands and has multiple fishways that merge into two primary routes past the dam: the Bradford Island fishway to the south (Fig. 1) and the Washington-shore fishway to the north (Fig. 2). These fishways were designed for adult Pacific salmonids (*Oncorhynchus* spp.) and have physical and hydraulic features that are common at the large hydropower projects on the Columbia and Snake rivers and to weir-and-pool fishways worldwide.

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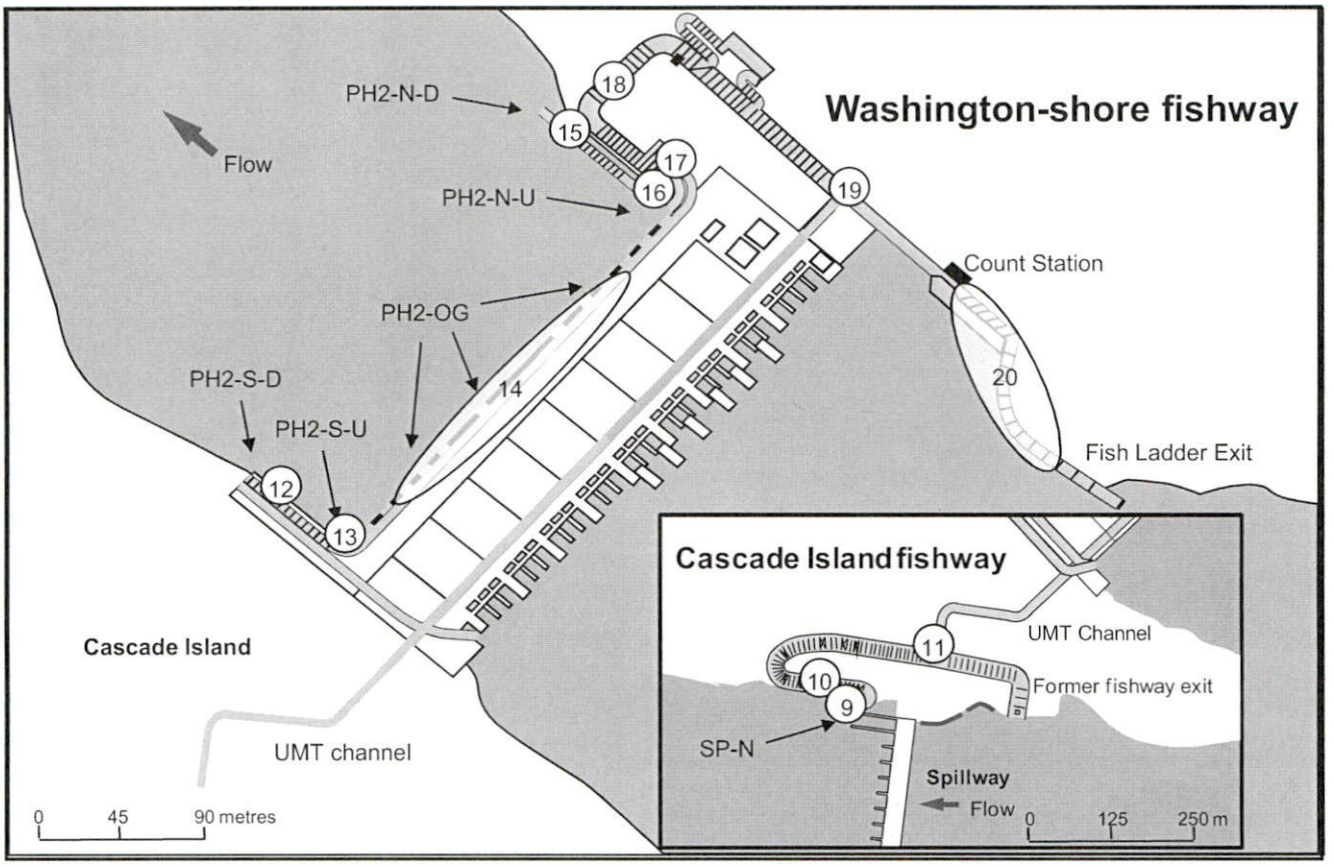
Fig. 2. Map of Powerhouse 2 and the Washington-shore fishway at Bonneville Dam on the Columbia River. Radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) were monitored as they entered fishway openings (arrows) and passed through the collection channel, transition area, and fish ladder. Circles and ellipses show locations inside the fishway where Pacific lamprey turn-around events were assigned. Inset shows the Cascades Island fishway, which has one entrance (SP-N) and joins the Washington-shore fishway at the terminus of the upstream migrant tunnel (UMT). PH2 = Powerhouse 2 (N = north; S = south; D = downstream; U = upstream); SP = spillway; OG = orifice gate.



The Bradford Island fishway has three primary openings, one each adjacent to the north and south ends of Powerhouse 1 and one adjacent to the south end of the spillway. The fishway also has a series of smaller sluice gate openings along the face of Powerhouse 1. The Washington-shore fishway has five primary openings, two each at the north and south ends of Powerhouse 2 and one adjacent to the north end of the spillway. The north spillway opening leads to the Cascades Island fish ladder, which historically exited directly into the Bonneville forebay. That exit was closed during our study; instead, fish using the Cascades Island ladder were diverted through the upstream migrant tunnel (UMT) and entered the upper Washington-shore fish ladder (Fig. 2). The Washington-shore fishway also has a series of floating orifice gate openings along the face of Powerhouse 2.

Collection channels inside all Bonneville fishway openings guide fish to transition areas at the base of each fish ladder where some weirs are fully inundated. All ladders at the dam have combination submerged-orifice and overflow weirs that rise 0.3 m per pool on a 10% slope, plus sections of vertical slot (i.e., serpentine) weirs upstream from the two fish counting stations. There are junction pools where two or more fishway passage routes merge at the north end of Powerhouse 2 and downstream from the count stations. The elevation gain of all fishways is ~18.3 m.

Lamprey collection and tagging

Adult Pacific lamprey were captured at Bonneville Dam at night using passive traps from mid-May or early June through August or early September. Differences in tagging timing among years were largely a function of run timing variability plus some temperature-related fish handling restrictions. Moser et al. (2002*a*, 2002*b*) and Johnson et al. (2012) provide details on lamprey collection, anesthesia, and radio-tagging methods. Surgical and handling protocols were reviewed and approved by the University of Idaho Animal Care and Use Committee. Briefly, each lamprey was anesthetized using either tricaine methanesulfonate or eugenol. A small (~1.2–3.0 cm) incision was made along the ventral midline and below the anterior edge of the first dorsal fin fold. A uniquely coded radio transmitter was placed inside the body cavity with its trailing antenna threaded through the body wall using a cannula or catheter. Incisions were closed with a minimum of two simple, interrupted sutures.

Different radio transmitters were used as a result of increased miniaturization in later years. In 1997–2002, most transmitters were 11 mm × 43 mm and weighed 7.7 g in air (Model MCFT-3BM, Lotek Wireless, Newmarket, Ontario). Starting in 2000, smaller lamprey received a 9 mm × 29 mm, 4.5 g transmitter (Model NTC-6). In 2007, transmitters were 9 mm × 30 mm and 4.5 g (Model NTC-6-2), and in 2008–2010 they were 8 mm × 18 mm and 2.1 g (Model NTC-4-2L). Only lamprey from larger size classes were radio-tagged in the 1997–2000 study years to accommodate larger transmitters. Samples in 2007–2010 were more representative of the runs at large, with only the smallest lamprey (girth at incision <9 cm) excluded from tagging. Tagged lamprey were released from both sides of the river at sites ~10 km (1997) and ~3 km (all other years) downstream from Bonneville Dam.

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Table 1. Dam passage efficiency metrics and fishway bottleneck metrics used to evaluate passage behavior and success of radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) at Bonneville Dam.

Metric	Objective	Equation
Dam-wide passage efficiency	Unique fish; route- and event-independent	(Unique N_{Pass})·(Unique N_{Enter})$^{-1}$
	Total attempts; route-independent	(N_{Pass})·(Attempt N_{Enter})$^{-1}$
Route-specific passage efficiency	Unique fish at each route *i*	(Unique $N_{Pass\ i}$)·(Unique $N_{Enter\ i}$)$^{-1}$
	Total attempts at each route *i*	($N_{Pass\ i}$)·(Attempt $N_{Enter\ i}$)$^{-1}$
Turn-around rate	Number of turn-around events in each fishway segment *j* per unique fish detected	(turn-arounds *j*)·(unique lamprey *j*)$^{-1}$
Additional attempt rate	Proportion of turn-around events in each fishway segment *j* that were followed by additional passage attempt	(additional attempts)·(turn-around event *j*)$^{-1}$
Failure rate	Proportion of turn-around events in each fishway segment *j* that were not followed by additional passage attempt	(unsuccessful final entry *j*)·(unique lamprey)$^{-1}$

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Monitoring

Fishways at Bonneville Dam were intensively monitored using underwater coaxial cable antennas. There were ~80–100 unique antennas per year, with detection ranges of approximately 10 m. Detection efficiencies were >95% at most sites, and antenna redundancy in most fishway segments increased detection efficiency to near 100% at the fishway segment scale; missed detections were primarily associated with power outages. Detection ranges for the different transmitter types used did not differ markedly. Transmissions were logged by ~20–25 receivers with digital spectrum processors to detect transmissions on multiple frequencies simultaneously. Monitored sites included fishway openings, collection channels, transition areas, junction pools, ladders, count stations, serpentine weirs, top-of-ladder exits, and auxiliary water supply (AWS) channels adjacent to count stations that lamprey could access but salmonids could not.

There were important year-to-year differences in monitoring effort owing to resource availability and evolving objectives. The most important changes were as follows: (*i*) floating orifice gate openings at Powerhouse 2 were monitored in 1997–1999 only; (*ii*) sluice gate openings at Powerhouse 1 were monitored in 1997–2002 only; and (*iii*) monitoring in the upper fishways from fish count stations to top-of-ladder exits was limited to exit antennas in 1997–1999, but included additional antennas near count stations, AWS channels, and in serpentine weir sections in 2000–2002 and 2007–2010. We accounted for these changes by separating some analyses by specific monitoring eras (Phase 1 = 1997–1999; Phase 2 = 2000–2002; Phase 3 = 2007–2010).

Passage efficiency analyses

Likely "noise" records were excluded using filters that identified signal collisions (i.e., two or more codes at the same receiver at the same time) and by experienced technicians who identified records that did not have corroborating support from detections at nearby antennas. For example, near-continuous blocks of detections along the presumed route used by a fish were occasionally interspersed with single records at distant receiver sites, and the latter were censored. A detection history for each radio-tagged lamprey was generated using an automated program that assigned activity codes (e.g., fishway entry, fishway exit to tailrace, transition area entry, dam passage, etc.) to the time-stamped detections at each antenna using a set of vetted decision rules. There were minor year-to-year changes in coding rules, but these had little effect on interpretation of results because there was very little change in how fishway entry or exit events were identified.

Several fishway passage efficiency metrics were used to evaluate lamprey passage success at Bonneville Dam (Table 1). The first was a dam-wide metric for unique lamprey, defined as the number of tagged fish that passed Bonneville Dam (Unique N_{Pass}) divided by the number that entered a fishway (Unique N_{Enter}). This is a widely used metric that provided a measure of dam-scale fishway passage success, aggregating over all passage routes and ignoring the number of passage attempts by individual lamprey. The second was a dam-wide metric that used all passage attempts, regardless of lamprey identification or route. This metric was defined as the number of dam passage events (N_{Pass}) divided by the number of attempts (Attempt N_{Enter}) and was used to incorporate a penalty for multiple attempts. Each passage attempt was manually reviewed, and outcomes were assigned as either a success (i.e., dam passage) or failure (i.e., exit to tailrace). We note that "failure" was only in reference to dam passage and not to motivation, migration success, or reproductive success (e.g., Cooke and Hinch 2013).

The third and fourth fishway passage efficiency metrics were defined at individual passage routes, rather than dam-wide. Analogous to the dam-wide metrics, the third was calculated using unique lamprey and the fourth used total attempts. Twelve routes were identified using fishway entry location (see Figs. 1 and 2). Some lamprey entered fishways without being detected at opening antennas, especially when sluice and orifice gates were unmonitored, and these attempts were assigned as unknown.

We also used logistic regression models with a binary response variable (success or failure) to assess relationships between the probability of fishway passage success and chosen covariates. The attempt-level covariates were fishway entry time of day, site of fishway entry, lamprey body length (cm), date of fishway entry, and mean daily values of water temperature (°C) and tailwater elevation (m). We included quadratic terms for the seasonal and time-of-day effects based on what we expected to be biologically reasonable (confirmed in exploratory analyses). The seasonal variables (date, water temperature, and tailwater elevation) were collinear, as expected, but had different potential mechanistic associations with lamprey behavior. Date was a proxy for photoperiod and was likely associated with lamprey migration motivation. Water temperature was also related to migration motivation as well as scope for activity. Tailwater elevation determined inundation depth of the lower fishways.

Four logistic regression analyses were used to align with the previously described metrics and were used to assess evidence for relationships between the probability of successful passage and covariates at both the dam-wide and route-specific scales. For example, the first dam-wide model used only data for unique lamprey (route assigned to the first passage attempt), and the second dam-wide model used all attempts. The model using unique lamprey was fit using standard logistic regression assuming independence among observations because there was only one observation per lamprey. For the all attempts analyses, where multiple attempts from the same lamprey were included, the assumption of independence was violated. Therefore, we chose to account for the dependence of observations from the same fish using generalized estimating equations (GEE) (Liang and Zeger 1986; Agresti 2012), with an exchangeable correlation structure. We chose the marginal method (GEE) over the common conditional method of generalized linear mixed models because we were explicitly interested in "population-averaged" rather than

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Table 2. Annual and total numbers of adult Pacific lamprey (*Entosphenus tridentatus*) that were radio-tagged and that entered fishways at Bonneville Dam, numbers of fishway entry events, and mean events·fish^{-1} recorded in the 10 study years.

		Lamprey that entered fishways			Dam passage efficiency	
Year	Lamprey tagged	Unique fish	Total events	Events·fish^{-1}	Unique fish	Total events
1997	147	102	326	3.2	0.46	0.14
1998	205	154	452	2.9	0.46	0.16
1999	199	161	501	3.1	0.50	0.16
2000	299	212	361	1.7	0.57	0.34
2001	298	238	708	3.0	0.53	0.18
2002	201	167	503	3.0	0.55	0.18
2007	398	199	375	1.9	0.41	0.22
2008	595	317	588	1.9	0.47	0.26
2009	596	384	815	2.1	0.52	0.24
2010	312	236	598	2.5	0.51	0.22
Total	3250	2170	5227	2.4	0.51	0.21

Note: Dam passage efficiencies were defined as follows: Unique fish: (Unique lamprey$_{passed}$)·(Unique lamprey$_{entered}$)$^{-1}$; and Total events: (Events$_{passed}$)·(Events$_{entered}$)$^{-1}$.

"subject-specific" relationships (Agresti 2012). We also compared these results with those obtained under the independence model (GLM) to investigate how different the results would have been had we naively used the standard logistic regression approach, ignoring the repeated observations.

Given the large association between successful passage and fishway passage route (see Results), additional route-specific models were used to investigate relationships with covariates at the route-specific scale. All GLM and GEE models were run with a binomial distribution and a logit link function using PROC GENMOD in SAS (SAS Institute, Inc. 2000) and the geepack package in R (Halekoh et al. 2006; R Development Core Team 2012).

Passage bottleneck analyses

To identify potential fishway bottlenecks for Pacific lamprey, each passage failure was assigned to a specific turn-around location inside a fishway. The location was identified as the most upstream antenna where a lamprey was detected prior to exiting to the Bonneville tailrace. To simplify analyses and interpretation, turn-around events at some adjacent antennas were then aggregated within fishway segments. In total, 20 fishway segments were used in the passage bottleneck analyses (see Figs. 1 and 2).

Three bottleneck metrics were used to help identify potential priority sites for remediation. The first was segment-specific turn-around rate, defined as the number of turn-around events in a fishway segment divided by the number of unique lamprey that were detected in the segment (i.e., turn-arounds·unique lamprey^{-1}). This metric provided a measure of where fish were more or less likely to turn around inside the fishways. The second was the proportion of turn-around events in each segment that were followed by additional dam passage attempts (i.e., additional attempt·turn-around event^{-1}). Sites where fish had high re-attempt rates potentially had favorable passage cues (i.e., attraction flow) relative to sites with low re-attempt rates, but also higher apparent passage difficulty. The third metric was the proportion of turn-around events that resulted in no additional passage attempts by unique lamprey (i.e., the "failure rate"; unsuccessful final entry·unique lamprey^{-1}). This provided potential information about where unfavorable conditions prompted fish to abandon passage altogether. Because each bottleneck metric was a ratio based on the number of unique lamprey or turn-around events detected in each fishway segment, relative magnitudes could be used to rank segments, and changes in monitoring effort did not substantively affect interpretation.

In preliminary analyses, it was evident that the spatial distribution of Pacific lamprey turn-around events varied within and among years. We hypothesized that these "moving bottlenecks" resulted from lamprey responding to changing environmental conditions at Bonneville Dam and inside the fishways. We used turn-around locations to define a nominal categorical variable (i.e., the 20 fishway segments were mutually exclusive categories), thus defining a multinomial response for each attempt. Multinomial logistic regression (Allison 2010; Agresti 2012) was then used to investigate relationships between the probability that a turn-around occurred in a specific fishway segment in relation to water temperature and tailwater elevation. Separate models were run for the two fishways, with eight categories (i.e., the fishway segments) for the Bradford Island fishway and 12 categories for the Washington-shore fishway.

Results

Lamprey samples

A total of 3250 adult Pacific lamprey was collected, radio-tagged, and released downstream from Bonneville Dam over 10 years. Annual sample sizes ranged from 147 to 596 (mean = 325; Table 2). Mean annual collection dates ranged from 27 June to 21 July (Fig. 3*a*). Across years, lamprey body length ranged from 49 to 86 cm (mean = 68.2 cm, SD = 4.6 cm). Annual mean lengths ranged from 69.7 to 72.1 cm in 1997–2002 and from 65.8 to 67.0 cm in 2007–2010 (Fig. 3*b*). Among-year body length differences were due to tagging smaller lamprey as smaller transmitters became available (i.e., selection of larger lamprey through 2002).

River environment

Columbia River water temperature during the Pacific lamprey runs typically warmed from June through late August or early September and then began to cool. Peak annual temperatures were between 21.0 °C in 1999 and 23.5 °C in 2009 (Fig. 3*c*). Annual means from 15 June to 15 September ranged from 17.4 to 18.9 °C. Within a year, water temperatures were lowest during periods of high tailwater elevation ($0.71 \leq r \leq 0.93$) and early in the migration (date; $0.85 \leq r \leq 0.95$). Tailwater elevation was highest and most variable in June and early July in most years and then steadily decreased through late summer and early fall. Mean tailwater elevation differed widely among years, reflecting differences in winter snowpack and spring–summer precipitation. The highest seasonal means were in 1997 and 1999 and lowest were in 2001 and 2007 (Fig. 3*d*).

Dam-wide fishway passage efficiency

A total of 2170 radio-tagged Pacific lamprey entered fishways at Bonneville Dam 5227 times (2.4 entry events·fish^{-1}) over the 10 study years (Table 2). The numbers of events·fish^{-1} were higher, on average, in the early and middle study years when more fishway openings were monitored and mean lamprey size was higher

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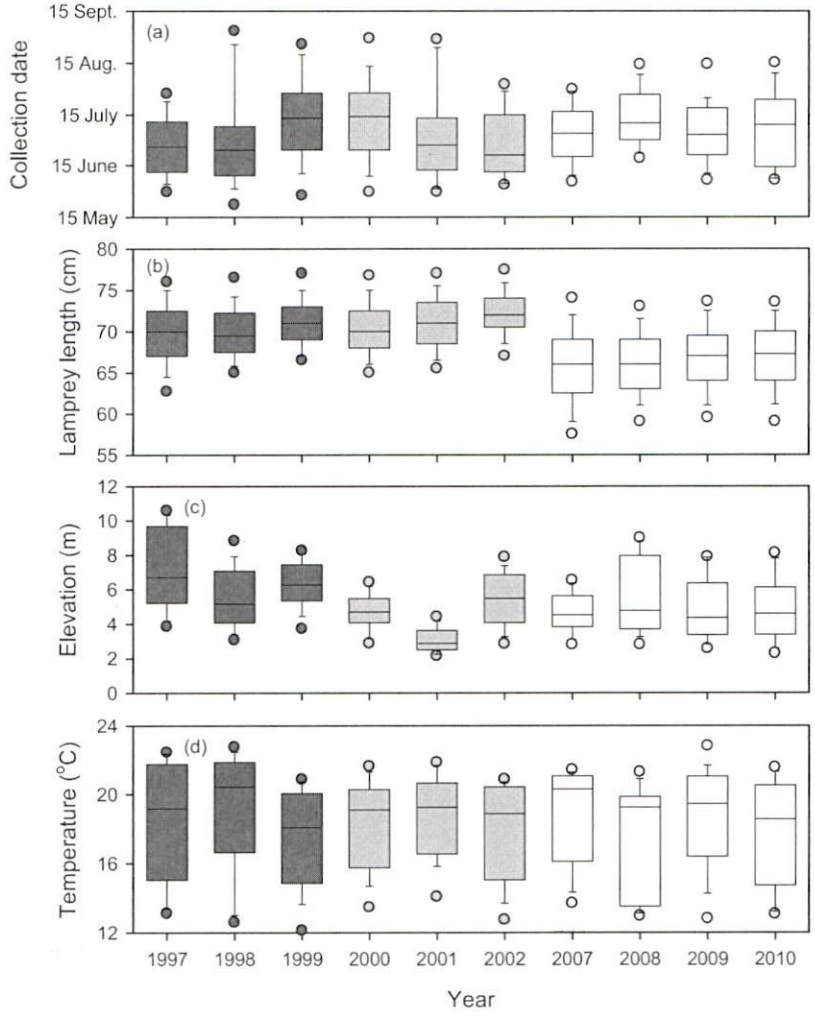
Fig. 3. Annual distributions of (*a*) collection date and (*b*) length (cm) of adult Pacific lamprey (*Entosphenus tridentatus*) collected and radio-tagged at Bonneville Dam and of (*c*) Bonneville tailwater elevation (m) and (*d*) Columbia River water temperature (°C). Elevation and temperature data are from 15 May to 15 September. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Three monitoring eras are indicated by different shading.



(Fig. 3*b*). Annual observed fishway passage efficiency estimates ranged from 0.41 to 0.57 when considering only unique fish and from 0.14 to 0.34 when considering all attempts.

With all years combined, passage efficiency for unique fish increased with lamprey size (Fig. 4*a*), decreased with tailwater elevation beyond about 4.5 m (Fig. 4*c*), and was higher at night than during the day (Fig. 4*e*). Efficiency increased as water temperature rose from ~13 to ~21 °C and then decreased at higher temperatures (Fig. 4*d*). Unique fish passage efficiency differed dramatically among fishway entry sites (Fig. 4*f*), ranging from <0.04 for lamprey that entered the PH2-south (PH2-S) fishway openings to 0.48 for those that entered at PH1-north (PH1-N). Attempt-based dam passage efficiency estimates paralleled the unique fish patterns, but varied less with fish length and time-of-day of fishway entry (Fig. 4).

In the GLM model treating all fishway passage attempts as independent, the probability of successful passage was associated with entry site, entry time, water temperature, and body length (all $P \leq 0.001$) as well as year ($P = 0.020$), when all were included in the same model (see online Supplementary Material,Table S1[1]). Little evidence existed for relationships between tailwater elevation and migration date after accounting for the other variables ($P \geq 0.141$). The comparable GEE model, which accounted for repeated attempts by individual lamprey, had very similar results in terms of estimates (as expected) and standard errors (Table S1[1]). Because date, water temperature, and tailwater elevation were collinear within year, we compared GLM models that excluded each of these terms. All three models indicated a clear seasonal effect.

Route-specific fishway passage efficiency

The relationship between dam passage probability and measured covariates differed by route of attempted passage. For example, in separate route-specific logistic regression models with tailwater elevation as the sole covariate, elevation was associated with dam passage success at five of 12 routes (Figs. 5*d*–5*f*). Passage probabilities were generally highest at these routes when tailwater elevation was in the 3–6 m range and were lowest at high (>9 m) tailwater elevations. Similarly, when water temperature

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0164.

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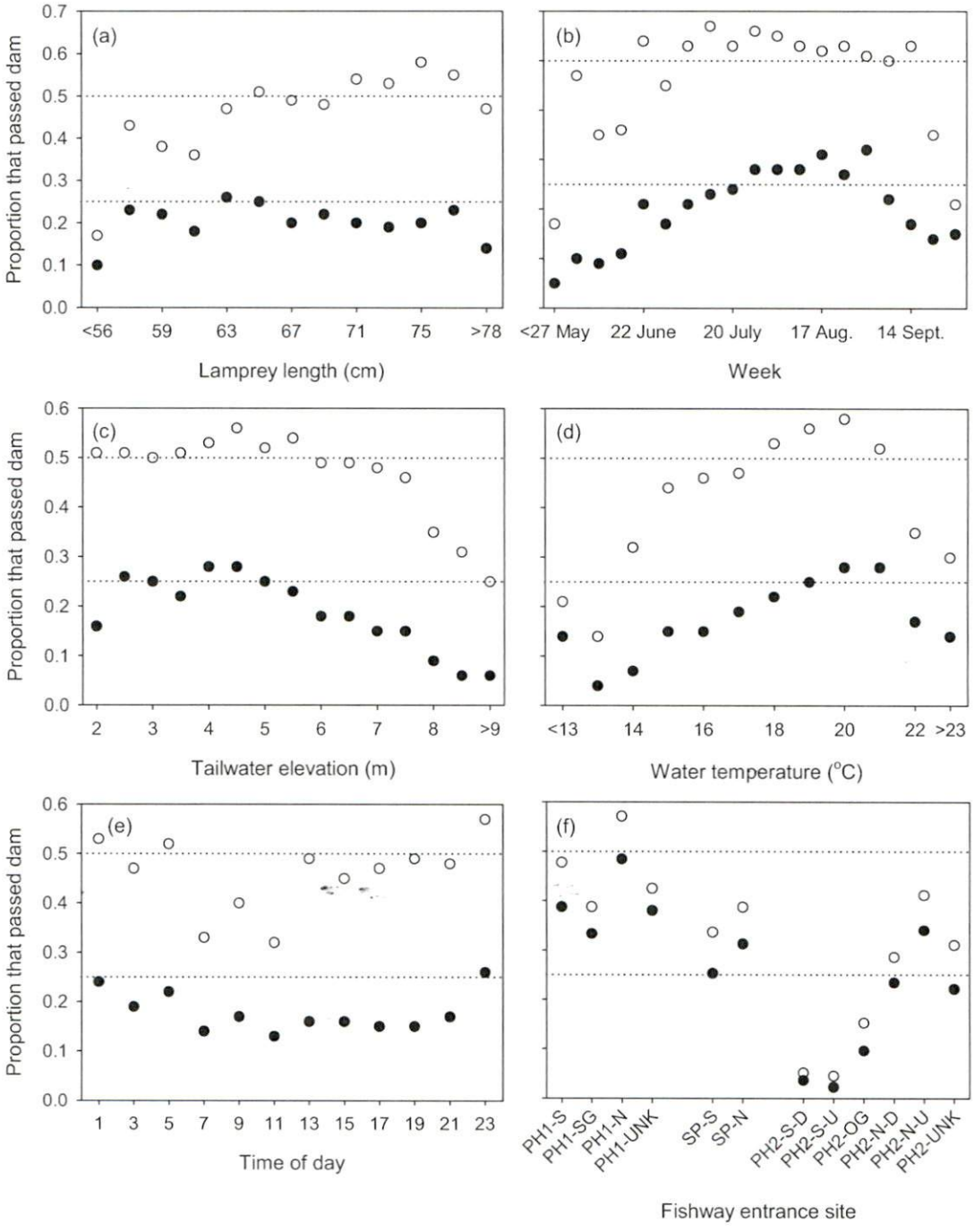
Fig. 4. Observed Bonneville Dam passage efficiency estimates for radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) calculated for unique fish (open circles) (Unique $\text{lamprey}_{\text{passed}}$)·(Unique $\text{lamprey}_{\text{entered}}$)$^{-1}$ and for all fishway entry events (solid circles) ($\text{Events}_{\text{passed}}$)·($\text{Events}_{\text{entered}}$)$^{-1}$, all years combined. Data were grouped by (*a*) Pacific lamprey length (cm), (*b*) date of fishway entry, (*c*) tailwater elevation (m), (*d*) water temperature (°C), (*e*) time of fishway entry (h), and (*f*) fishway entry site. In panels *a*–*e*, only the final entry event was included in the unique lamprey estimates (i.e., the event that resulted in either dam passage or failure to pass); in panel (*f*), the first event for each unique fish at each fishway opening was included. Dotted lines at 0.25 and 0.50 are for reference. See Fig. 1 for entry site locations.



was the sole covariate there was evidence for a temperature–efficiency relationship for five of 12 routes (Figs. 5*g*–5*i*). In these cases, passage probabilities increased with water temperature up to approximately 19–20 °C and then declined. There was also evidence of a time of day effect for four of the 12 routes (Figs. 5*j*–5*l*), but no evidence that larger Pacific lamprey were more (or less) likely to pass (Figs. 5*a*–5*c*). In route-specific models that included all covariates, there was evidence at one or more routes of relationships between passage success and tailwater elevation, water temperature, time of day, and Pacific lamprey length.

Bottleneck identification

Pacific lamprey turned around inside fishways and then exited to the Bonneville Dam tailrace a total of 4127 times. Across years,

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Fig. 5. Route-specific estimated probabilities that radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) would pass Bonneville Dam relative to single covariates. Relationships were estimated using separate generalized linear models (GLMs) for each fishway entry route ($n = 12$). Explanatory variables were fish length (cm), tailwater elevation (m), water temperature (°C), and time of fishway entry (h); quadratic terms were included in all models except for Pacific lamprey length. Routes for which the covariate $P < 0.05$ are indicated by entry site labels (see Fig. 1), and sample sizes for each route are in Table 3. Dotted lines at 0.25 and 0.50 are for reference. PH1-UNK and PH2-UNK indicate that the specific fishway entrance location was unknown.

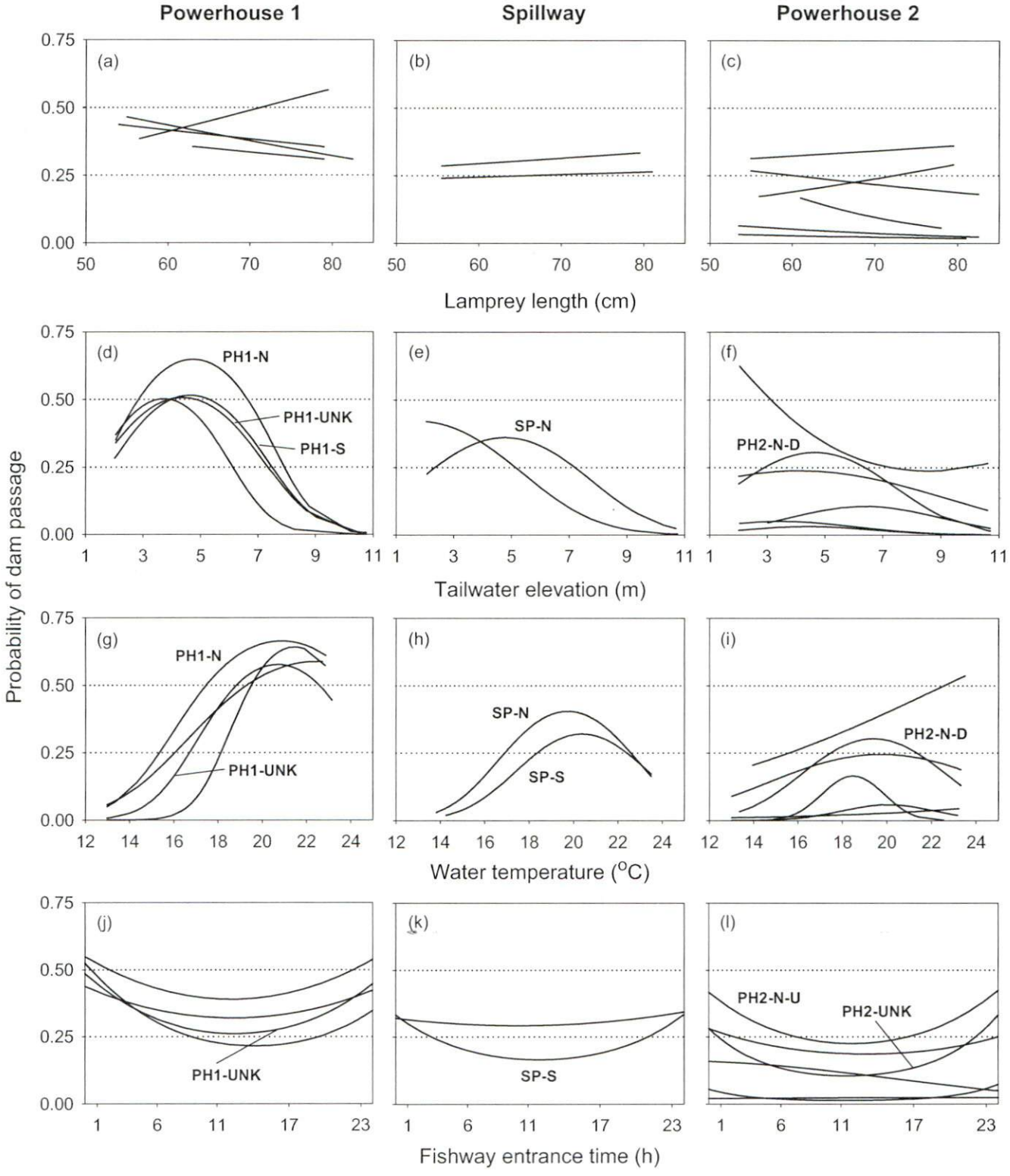

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Table 3. Numbers of fishway entry events recorded for radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) and estimated turn-around locations inside fishways for those events that did not result in Bonneville Dam passage.

(*a*) Bradford Island fishway.

		Turn-around segment							
Entry location	Entry *n*	1	2	3	4	5	6	7	8
PH1-S	361	111	19	22	24	10	35		
PH1-SG	114		36	20	9	6	5		
PH1-N	264			61	32	16	27		
PH1-UNK	255	11	51	44	20	11	21		
SP-S	541					4	39	263	59
Total	1535	122	106	147	85	47	127	263	59

(*b*) Washington-shore fishway.

		Turn-around segment											
Entry location	Entry *n*	9	10	11	12	13[a]	14	15	16	17	18	19	20
SP-N	355	111	74	6								3	50
PH2-S-D	438				61	289	51			11	3		6
PH2-S-U	1242					1084	93			27	4		5
PH2-OG	134					3	103			9	3	3	
PH2-N-D	303							82	52	67	16	4	10
PH2-N-U	418									210	32	9	24
PH2-UNK	802				24	282	39	8	7	171	32	1	69
Total	3692	111	74	6	85	1658	286	100	59	495	90	20	164

Note: Turn-around locations were inferred from underwater antenna sites inside fishways. Bradford Island and Washington-shore fishway segments are shown in Fig. 1. PH1, Powerhouse 1; S, south; SG, sluice gate; N, north; UNK, unknown; SP, spillway; PH2, Powerhouse 2; D, downstream; U, upstream; OG, orifice gate.

[a]Some segment 13 events likely occurred in unmonitored segment 14 in 2000–2002 and 2007–2010.

956 (23%) exits were from the Bradford Island fishway and 3171 (77%) were from the Washington-shore fishway (Table 3). Turn-arounds were most likely in the first or second fishway segment encountered after fishway entry (Fig. 6). This behavior was consistent across entry sites and monitoring phases, although the proportions that turned around close to the tailrace varied considerably among routes. Smaller numbers of lamprey turned around in fishway segments upstream from transition areas.

Dam-wide, four fishway segments accounted for 65% of all turn-around events across years: segment 13 (n = 1658), segment 17 (n = 495), segment 14 (n = 286), and segment 7 (n = 263). Independent of monitoring effort, segment-specific turn-around rates (turn-arounds·unique lamprey^{-1}) were highest at these same four sites: 1.98 (segment 13), 1.11 (segment 14), 0.65, (segment 7), and 0.57 (segment 17) (Fig. 7*a*). Turn-around rates were lowest in mid-elevation areas (<0.10 in segments 5, 11, and 19).

Pacific lamprey were least likely to make additional dam passage attempts after turning around in middle and upper ladder segments (additional attempt·turn-around event^{-1}; Fig. 7*b*). These included segment 11 (0.17), segment 6 (0.24), segment 20 (0.25), segment 8 (0.25), and segment 5 (0.28). Additional passage attempts were most likely following turn-arounds in lower fishway segments at both PH1 and PH2 fishways (all >0.75).

Failure rates (unsuccessful final entry·unique lamprey^{-1}) were highest at the southern end of the PH2 collection channel (0.30, segment 13), in segments 7 and 8 of the south spillway fishway (0.18–0.29), and at the tops of both fishways (0.15–0.18). Failure rates were <0.05 for turn-arounds at most mid-elevation fishway segments (Fig. 7*c*).

Seasonal variability in bottleneck locations

The results from the multinomial logistic regression model indicated important seasonal differences in where Pacific lamprey turned around inside fishways (i.e., moving bottlenecks; Fig. 8). At the Bradford Island fishway, turn-around probabilities in each monitoring phase (i.e., 1997–1999, 2000–2002, 2007–2010) were highest at PH1 fishway openings and collection channels (segments 1–4) when water temperature was low and were highest at the SP-S opening (segment 7) and the top-of-ladder (segment 6) when water temperature was high ($28.6 \le \chi^2 \le 91.5$, df = 6–7, $P < 0.001$). Bottlenecks also shifted seasonally among fishway segments in the Washington-shore fishway in each phase ($22.7 \le \chi^2 \le 79.3$, df = 8–10, $P < 0.001$). Predicted probabilities increased with temperature at the top-of-ladder (segment 20; Figs. 8*d* and 8*f*) and decreased with temperature in the south end of the collection channel (segment 13; Fig. 8*b*), the PH2-S-D fishway opening (segment 12; Fig. 6*d*), and the transition area above the junction pool (segment 18; Fig. 8*f*). Substituting tailwater elevation for water temperature produced qualitatively similar results at both fishways; turn-arounds were more likely in lower fishway segments at high tailwater elevation and in upper fishway segments when elevation was low.

Discussion

Pacific lamprey passage efficiency

Nearly half of the radio-tagged Pacific lamprey that entered a Bonneville fishway failed to pass the dam and were thus prevented from reaching upstream spawning habitats. This high attrition is compounded by similar passage problems at upstream dams and has been widely cited as an important driver of the "high risk" status of Pacific lamprey in the mid-Columbia, upper Columbia, and Snake River basins (Luzier et al. 2011). In contrast, full-dam passage efficiency for *Oncorhynchus* species adults for which these fishways were designed routinely exceeds 95% (e.g., Keefer et al. 2005). The individual Pacific lamprey behavior histories in our study suggest that mechanisms of lamprey passage failure were complex and route-specific. No routes had consistently high success rates, indicating systemic hydraulic or structural challenges for lamprey. Furthermore, the relative frequency of passage failures shifted in space and time (i.e., moving bottlenecks) in response to changing proximate conditions. Such spatially explicit route and bottleneck associations have rarely been identified in the fishway passage literature and present novel opportunities and challenges for designing effective fish passage improvements.

The dam-wide logistic regression models showed that fishway passage route was the most important predictor of Pacific lam-

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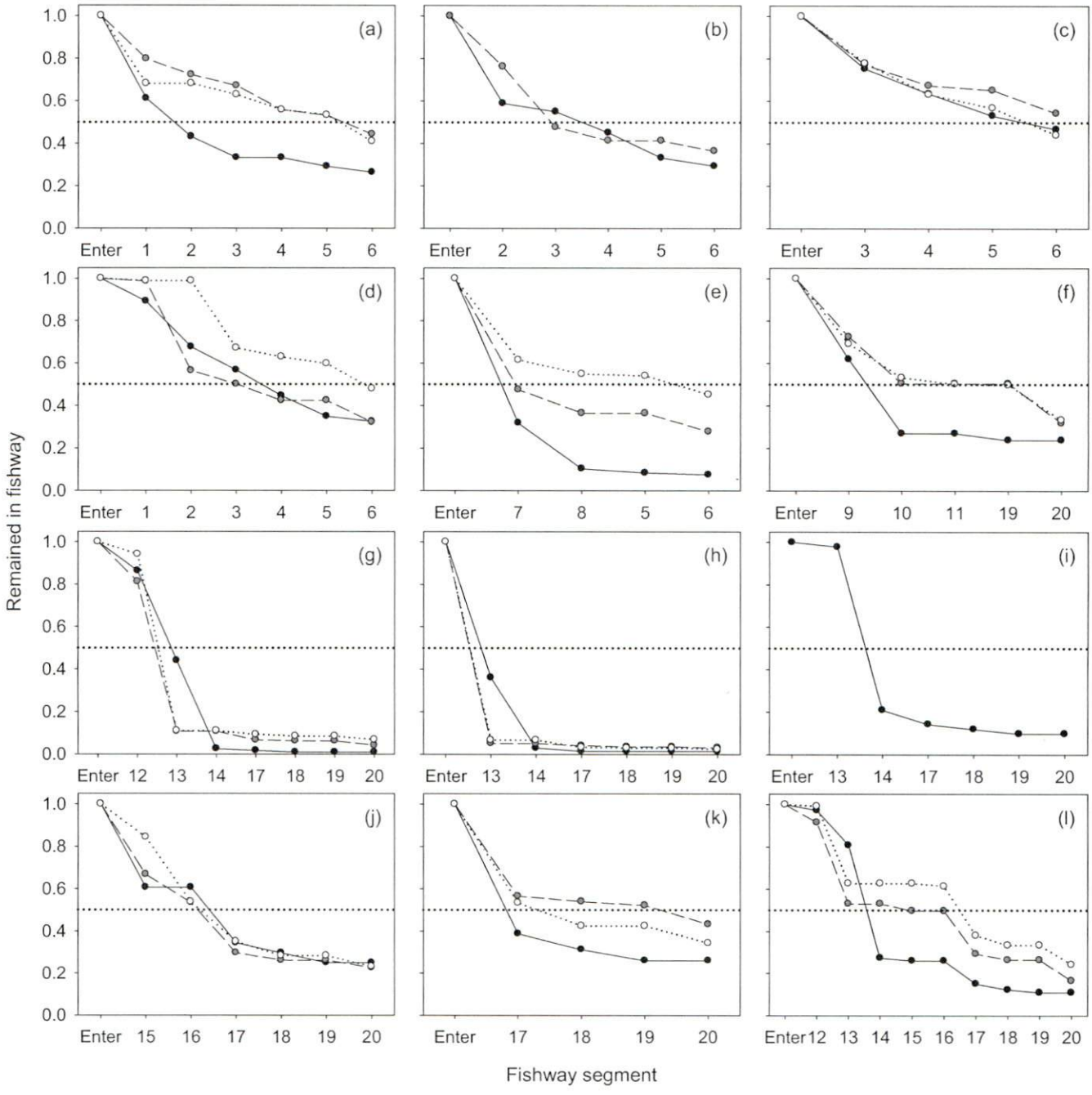
Fig. 6. Route-specific relationships among fishway entrance location, fishway segment, and the observed proportions of radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) that remained inside Bonneville Dam fishways in relation to those that entered. Symbols represent study years with different antenna arrays: black circles = 1997–1999; grey circles = 2000–2002; open circles = 2007–2010. Panels represent the 12 fishway entrance routes: (*a*) PH1-S, (*b*) PH1-SG, (*c*) PH1-N, (*d*) PH1-UNK, (*e*) SP-S, (*f*) SP-N, (*g*) PH2-S-D, (*h*) PH2-S-U, (*i*) PH2-OG, (*j*) PH2-N-D, (*k*) PH2-N-U, and (l) PH2-UNK. Dotted line at 0.50 is for reference. See Figs. 1 and 2 for entrance locations and Table 3 for total sample sizes.



prey dam passage, even after accounting for other covariates we expected to influence passage success. Route selection at barriers is a function of attraction cues from dominant discharge sources (e.g., Thorstad et al. 2008; Lucas et al. 2009), olfactory or behavioral cues from conspecifics, and the effectiveness of individual fishway openings (e.g., Bunt 2001; Noonan et al. 2012). In the Bonneville tailrace, bulk flow patterns strongly influence the distribution of adult salmonids among fishways (Keefer et al. 2006). In general, migrants (salmonids and Pacific lamprey) first approach and enter Bonneville fishways in proportion to discharge volume from the two powerhouses. Proportionately fewer migrants first use spillway openings (SP-S and SP-N), presumably because high turbulence and water velocity deter some fish and because many migrants favor shoreline-oriented approaches (e.g., Johnson et al. 2007). The initial assortive distribution in the tailrace is followed by additional filtering at fishway openings, where Pacific lamprey entrance efficiency can vary several-fold among sites (Moser et al. 2002*a*; Johnson et al. 2012).

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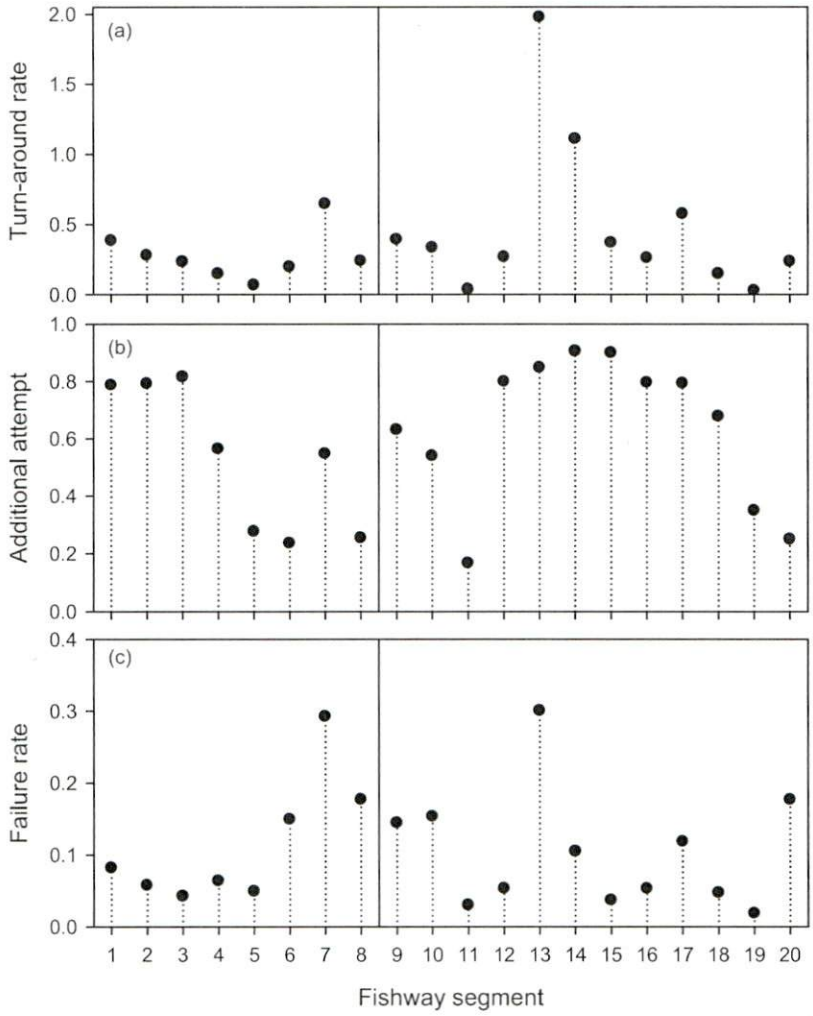
Fig. 7. Fishway bottleneck metrics estimated for radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) at 20 fishway segments at Bonneville Dam. Metrics include (*a*) proportion of unique lamprey recorded at each segment that turned around and exited to the tailrace (turn-arounds·unique lamprey^{-1}); (*b*) proportion of turn-around events that were followed by an additional dam passage attempt (additional attempt·turn-around event^{-1}); and (*c*) proportion of unique lamprey that never made an additional dam passage attempt (unsuccessful final entry·unique lamprey^{-1}). See Figs. 1 and 2 for fishway segments.



Even after filtering in the tailrace and at fishway openings, the likelihood that radio-tagged Pacific lamprey passed the dam varied among routes by an order of magnitude. Those that entered via openings at the southern end of Powerhouse 2 or at floating orifice gates were the least likely — by far — to pass the dam. This was true for unique fish and for attempt-based analyses. The least efficient routes each included at least a portion of the ~250 m long collection channel that spans the length of Powerhouse 2. Passage efficiency for these routes was not associated with any of the covariates we investigated, indicating that underlying structural, hydraulic, or other factors (e.g., presence of predators or fishway length) prompted Pacific lamprey to abandon these routes and exit to the tailrace.

In contrast, there were clear diel and seasonal associations with passage success at the more efficient Powerhouse 1, spillway, and Powerhouse 2 north routes. Lamprey that entered these routes at night had higher passage efficiency, presumably because adult migrants are most active at night, especially in hydraulically challenging environments (Keefer et al. 2013*b*). The lower efficiency for daytime entries also may reflect light-avoidant retreat from the relatively exposed fishways to tailrace refuge habitats (e.g., Binder and McDonald 2007). The seasonal relationships with fishway passage efficiency have at least two possible explanations. First, as tailwater elevation increases, additional weirs in the lower Bonneville fish ladders become submerged. Hydraulic head is consequently reduced, and limited attraction flow passes through the weir orifices (e.g., Naughton et al. 2007). In the absence of suitable rheotactic cues, Pacific lamprey have difficulty identifying upstream pathways (Keefer et al. 2011; Johnson et al. 2012) and consequently may abandon the submerged weir sections in search of more attractive routes. Second, increasing water temperature stimulates migratory activity for many lamprey species (Binder and McDonald 2008; Clemens et al. 2010). The generally positive relationship between Bonneville passage efficiency and temperature may have been a function of performance physiology (e.g., increased burst or sustained swim speed; Starrs et al. 2011) or of increased motivation to reach spawning sites later in the run. Separating tailwater elevation from temperature effects was difficult given their relationship, but we expect that both influenced Pacific lamprey behaviors and that their relative effects varied across routes.

The role of Pacific lamprey size on fishway passage efficiency was mixed. Larger fish were more likely to pass Bonneville Dam in the dam-wide logistic regression results. This parallels previous

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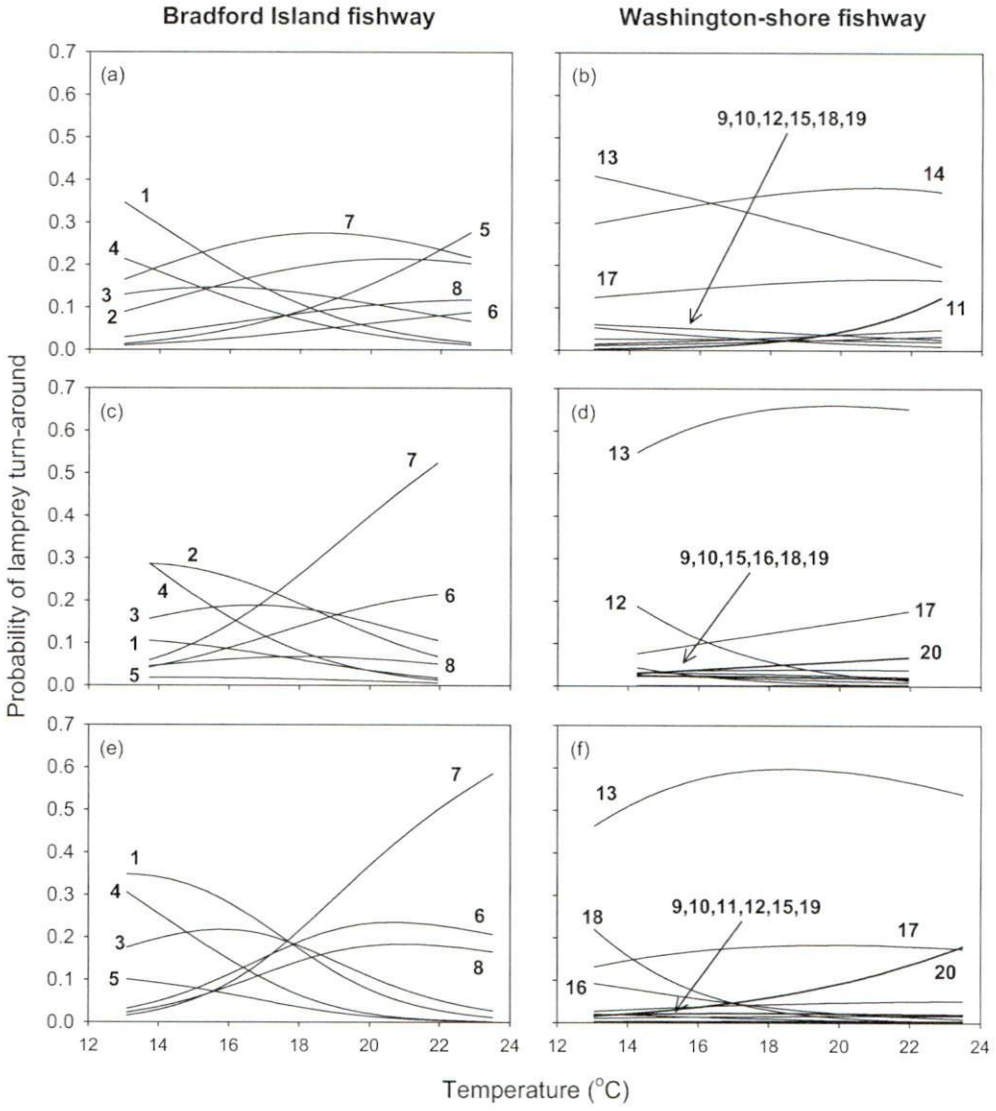
Fig. 8. Predicted probabilities that radio-tagged adult Pacific lamprey (*Entosphenus tridentatus*) would turn around at specific fishway segments within the Bradford Island or Washington-shore fishway and exit to the Bonneville Dam tailrace relative to Columbia River water temperature (°C). Probabilities were estimated using separate multinomial logistic regression models for each fishway ($n = 2$) and monitoring era ($n = 3$). Fishway segments are indicated by numbers (see Figs. 1 and 2 for locations). Monitoring eras were (*a*–*b*) 1997–1999; (*c*–*d*) 2000–2002; and (*e*–*f*) 2007–2010.



observations of size-dependent Pacific lamprey migration distance (Keefer et al. 2009) and dam passage efficiency (Keefer et al. 2013*a*). However, body size was not associated with success at any of the 12 individual Bonneville routes. This was unexpected and was driven, at least in part, by more frequent passage attempts by larger Pacific lamprey. Fish size effects on passage success and attempt rates have been demonstrated experimentally for several other species (e.g., Bunt et al. 1999; Castro-Santos 2004; Haro et al. 2004). These authors attributed the patterns to possible size- or sex-related differences in swim capacity or to among-individual differences in motivation, and similar effects were likely in our study.

Fishway passage bottlenecks

Fishway remediation decisions will ultimately be determined by feasibility and cost, but our results suggest that multitiered and incremental solutions may be most effective. For example, the bottleneck metrics provided some clear guidance on where improvements will be most beneficial. At the broadest scale, Pacific lamprey passage failures fell into two categories: (1) frequent turnaround events in low-elevation segments that were relatively likely to be followed by additional passage attempts; and (2) turnarounds in high-elevation segments that often resulted in loss from the upstream population (i.e., no additional attempts). An adaptive management approach could potentially test remediation actions in both low- and high-elevation fishway segments, preferably using experiments to investigate the mechanisms of passage failure (and success).

The propensity for lamprey to turn around and exit at low-elevation fishway segments may be attributed to a variety of factors, including collection channel length, hydraulic conditions, white sturgeon (*Acipenser transmontanus*) abundance, or a combination of these and other factors. Upwelling turbulence created by flow diffusers on the collection channel floor, for example, may have produced insufficient rheotactic cues or confusing orienta-

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tion cues in this low velocity area. Alternately, aggregation of white sturgeon in the channel may have been an important deterrent to upstream movement. These large (up to ~4 m) predators reside for extended periods inside lower fishway segments at Columbia River dams (Parsley et al. 2007). High sturgeon density has been reported in Bonneville powerhouse collection channels, in the Washington-shore junction pool, and in the spillway entrance and transition areas (US Army Corps of Engineers, unpublished data). An adaptive, hypothesis-testing approach could inform remediation decisions for these segments, building upon our finding that high turn-around rates were not linked to diel or seasonal effects or to Pacific lamprey size in these areas.

A different set of hydraulic conditions has been associated with bottlenecks in upper fishway segments. High velocity and turbulence in the serpentine weirs (segments 6, 20) likely explained the poor passage performance in these sections. Clabough et al. (2012) reported that Pacific lamprey averaged five to nine attempts·fish^{-1} to pass serpentine weirs and frequently retreated downstream past count stations between attempts. We suspect that turbulence and water velocity in the serpentine weir segments presented a partial or intermittent passage barrier, as has been reported for other species at vertical-slot type fishways (e.g., Schwalme et al. 1985; Laine et al. 1998; Rodríguez et al. 2006). Furthermore, our results showed that lamprey that moved the ~18 m elevation from serpentine weirs to the tailrace were very unlikely to re-enter fishways. Those that turned around near the obsolete Cascades Island fishway exit (segment 11) or the Bradford Island junction pool (segment 5) surrendered similar elevation gains and were also unlikely to make additional attempts.

The inverse relationship between the fishway elevation where lamprey turned around and re-attempt rate is consistent with fish passage behaviors at other high-head dams (e.g., Agostinho et al. 2007; Mallen-Cooper and Brand 2007) and may reflect physical limitations or perhaps life history traits. For example, it is possible that individuals that fail high in fishways surpass a threshold in time or energy investment (e.g., Castro-Santos and Letcher 2010) relative to those that turn around closer to the tailrace. Alternately, when the cost of barrier passage is high, a migratory but nonphilopatric species like Pacific lamprey (Spice et al. 2012) may simply seek alternate spawning sites downstream (e.g., Cooke and Hinch 2013). This may be especially likely when pheromone cues used to select spawning locations (Yun et al. 2011) are sufficiently available downstream. This is probable below Bonneville Dam, where there are numerous suitable Pacific lamprey spawning tributaries.

Lastly, the "moving bottleneck" result speaks to the potentially ephemeral nature of some fishway passage problems and highlights the importance of identifying causal mechanisms before attempting to implement solutions. At the Bradford Island fishway, for example, the multinomial models indicated large seasonal shifts in where radio-tagged lamprey turned around inside fishways. Early in the migration when tailwater elevation was typically high and water temperature was low, turn-arounds were concentrated in low-elevation segments of the Powerhouse 1 fishway. By late summer, turn-around probabilities were much higher along the south spillway route and at the top-of-fishway segments. These patterns reflect both assortive processes in the tailrace (e.g., lamprey were attracted to different fishways at different seasons) and relaxation of the lower fishway bottlenecks later in the summer (see Figs. 5*d* and 5*g*), perhaps as a result of changing hydraulic conditions. Understanding the mechanisms behind this type of spatiotemporal variability should lead to more informed implementation decisions. For instance, temporary operational changes designed to benefit fish passage, such as reduced nighttime velocity (Johnson et al. 2012) or seasonal changes to accommodate different species should be considered at sites and times where they are most likely to be effective. Similarly, site selection for permanent structural improvements should consider the likely benefit across the range of expected environmental and operational conditions.

Quantitative research framework

Improvements to existing fishways are costly and ideally should be undertaken only after passage bottlenecks have been clearly identified and passage failure mechanisms are known. Such information is rarely available, however, because logistic or cost constraints inhibit the necessary data collection (Castro-Santos et al. 2009; Bunt et al. 2012) or because funds are available for retrofits but not monitoring. Therefore, we suggest that fish passage problems resulting from multiple mechanisms or that vary in space or time may require iterative, integrated approaches before solutions can be confidently implemented. Ultimately, upfront investments in preremediation research (e.g., performance experiments), monitoring, or behavioral simulations (e.g., Goodwin et al. 2006) can be cost-effective by resolving specific spatial, temporal, and mechanistic questions about problem areas.

The combination of fishway passage efficiency estimates, bottleneck metrics, GLMs, GEEs, and multinomial logistic regression analyses we used provided a quantitative foundation for making fishway improvement decisions for Pacific lamprey. The dam-wide and route-specific efficiency estimates are critical benchmarks for postremediation effectiveness monitoring. The GEE models allowed us to appropriately account for the repeated measures on individual lamprey, a common analytical challenge. In this case, the similarity of standard errors and parameter estimates between the GLM and GEE indicated that inference from either approach was reasonable and the effects of the violation of independence was minimal. Consequently, we could confidently include all passage attempts available in the multiyear dataset (rather than just first or last attempts). The attempt-based analyses captured more of the individual behavioral variation in tagged samples and resulted in more nuanced conclusions about the relationships between passage success and the tested covariates. For example, this approach helped parse out the relationship between lamprey size and passage success (i.e., size was not predictive of success at the route scale, but larger lamprey made more attempts and were thus more likely to pass the dam). Similarly, the multinomial analyses provided evidence that bottlenecks varied in space and time. This raises testable, location- and time-specific hypotheses concerning factors that most affect behavior.

In combination, these analyses lay the groundwork for identifying the mechanisms driving low Pacific lamprey passage efficiency at many barriers with salmonid-style fishways (e.g., Mesa et al. 2010; Jackson and Moser 2012; Keefer et al. 2013*a*). In particular, understanding the conditions experienced by lamprey at the times and locations that bottlenecks occur can help focus remediation efforts at other dams. The seasonal effects of fishway inundation, potential light avoidance in upper fishway segments, and apparent hydraulic barriers we identified at Bonneville Dam, for example, likely apply to many fishways in the Columbia River basin and elsewhere. Our analyses also suggest likely avenues for future research that may redirect remediation efforts at Columbia River basin dams. For example, exclusion of lamprey predators from lower fishway segments may be an important consideration in addition to hydraulic, structural, or operational changes to fishways.

The analytical techniques described here could be applied whenever there is spatially explicit monitoring of tagged fish at passage barriers. This includes studies where multiple monitoring sites are arranged in sequence along a single passage route (e.g., Stuart et al. 2008; Roscoe et al. 2011; Thiem et al. 2012), when there are multiple barriers in sequence (e.g., Gowans et al. 2003; Caudill et al. 2007) or when there are multiple routes at a single obstacle (i.e., fishways with many openings or dams with more than one fishway). The inferential value derived from these types

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of monitoring arrays depends, in part, on the spatial arrangement of sites relative to the scale and location(s) of specific bottlenecks. We suggest that effective fish passage evaluations should include hypothesis-driven selection of monitoring sites as well as robust postmonitoring analytical methods to maximize the value of collected data.

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