Technical Report 2015-12

ADULT PACIFIC LAMPREY MIGRATION IN THE COLUMBIA AND SNAKE RIVERS: 2014 RADIOTELEMETRY AND HALF-DUPLEX PIT TAG STUDIES AND RETROSPECTIVE SUMMARIES

A Report for Study Code LMP-P-13-1

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For

U.S. Army Corps of Engineers
Portland and Walla Walla Districts, Portland OR

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Executive Summary

Our 2014 adult Pacific lamprey studies assessed adult Pacific lamprey (*Entosphenus tridentatus*) migration in the Columbia River Hydrosystem at a variety of scales. The results summarized in this report primarily address reach-scale and system-wide migration using detection data from lamprey tagged with either half duplex (HD) passive integrated transponder (PIT) tags or an HD PIT tag and a radio transmitter. Companion 2014 study reports provide dam-specific fishway passage metrics from the radio-tagged sample (Clabough et al. 2015), and behaviors of the HD PIT-tagged fish in and near Bonneville lamprey passage structures (LPSs), lamprey refuges (i.e., rest boxes), and in the Cascades Island auxiliary water supply channel (Corbett et al. 2015), and results of experimental behavioral trials conducted in the Bonneville Adult Fish Facility fishway flume (Kirk et al. 2015).

Bonneville HD PIT-Tagged Samples

We HD PIT-tagged two lamprey samples collected at Bonneville Dam: a group of 599 released downstream from the dam and 299 used in artificial fishway experiments and then released upstream from Bonneville Dam near Stevenson, Washington. We monitored lamprey passage rates and escapement past Bonneville, The Dalles, John Day, McNary, Ice Harbor, Lower Monumental, Lower Granite, and Priest Rapids dams. Additional HD PIT detection data from upper Columbia River dams and lower Columbia River tributaries were provided by cooperating agencies. Our objectives were to calculate lamprey passage times through various river reaches, to estimate escapement past the monitored sites, to evaluate potential associations between lamprey escapement and fish traits (i.e., size and migration timing), and to assess the final distributions of tagged fish.

The 2014 escapement estimate for the downstream release group past Bonneville Dam was 56% (trap recaptures treated as not passing) to 60% (recaptures treated as passing). These estimates were among the highest in the 2005-2014 HD PIT studies (41-61%). Escapement from the top of Bonneville Dam to the top of The Dalles Dam (58%) and from the top of The Dalles Dam to the top of John Day Dam (73%) was similar to previous years. Large lampreys were substantially more likely than small lampreys to pass through most dam-to-dam reaches. As in previous years, lampreys last detected at upriver sites were statistically larger than those last recorded closer to the release site, indicating size-dependent effects on migration distance and final distribution.

A total of 9% of the downstream-released sample was last detected at dams in the upper Columbia River (~1% at Priest Rapids, ~6% at Wanapum, and ~2% at Rock Island). Another 2% was last detected at Snake River dams, and 10% was detected in HD PIT-monitored tributaries to the Bonneville or The Dalles reservoirs (Hood River, Fifteenmile Creek, Deschutes River); we note that other unmonitored tributaries were presumably used by lamprey. Migration times were highly variable in 2014, as in all previous HD PIT study years. The median passage time was 7.2 days (< 1 $km \bullet d^{-1}$) from release to the top of Bonneville Dam, which was at the high end of the range reported across study years. Median times between top-of-ladder antennas were 7.0 days between Bonneville and The Dalles dams (relatively slow), 4.1 days between The Dalles and John Day dams (similar to previous years), and 12.9 days between John Day and McNary dams (relatively slow). Each of these reaches included one reservoir and one dam.

We monitored the upstream progression of HD PIT-tagged lampreys used in fishway experiments, but this sample was not collected in proportion to the run (early-run fish only) and post-experiment behavior and distribution may not be representative of non-experimental fish. With these caveats, upstream escapement from release in the Bonneville forebay was 49% past The Dalles Dam, 34% past John Day Dam, and 16% past McNary Dam. About 4% of the sample was last detected in Bonneville pool tributaries, 10% was in the Deschutes River, 10% was last detected at upper Columbia River dams, and 3% was in the Snake River.

Bonneville Double-Tagged Sample

The 2014 escapement estimate from release past Bonneville Dam was 41%, which was similar to the highest estimates from comparable 2007-2010 radiotelemetry studies. Escapement from the top of Bonneville Dam past The Dalles Dam (31%) was low relative to recent years, whereas escapement from the top of The Dalles Dam past John Day Dam (55%) was higher than in recent years. As with the HD PIT-tagged sample, large-bodied lampreys had consistently higher reach escapement than small lampreys. Importantly, however, double-tagged lampreys also had lower escapement than those with only HD PIT tags through all study reaches, continuing a pattern of apparent negative radio tagging effects reported in previous years.

Double-tagged lamprey migration rates were highly variable, but tended to be slow at dams and relatively rapid through reservoirs. Median passage times for radio-tagged fish were 5.4 days from release to the top of Bonneville Dam, 1.3 days from tailrace to top-of-ladder antennas at The Dalles Dam, and 1.6 days between tailrace and top-of-ladder antennas at John Day Dam. Median reservoir passage times were 2.2 d (Bonneville) and 1.5 d (The Dalles).

Five percent of double-tagged lampreys were detected in monitored tributaries, including 2% in the five monitored Bonneville reservoir tributaries, 2% in the Deschutes River, 1% in the John Day River, and 1% upstream from Priest Rapids Dam. Additional fish presumably entered smaller, unmonitored tributaries (*minimum* = ~10 small creeks plus the Umatilla River in the reach between Bonneville and McNary dams). Most lampreys that were last detected upstream from The Dalles Dam were in the largest size classes, indicating probable size effects on lamprey distribution. A large majority of the double-tagged sample was last detected at lower main stem dams or in dam tailraces.

John Day HD PIT-Tagged Sample

In 2014, we collected and HD PIT-tagged 100 lamprey from the trap at the terminus of the John Day north fishway LPS. These fish were released into the John Day forebay. Twenty-seven percent were not detected after release, 28% were last detected downstream from John Day Dam (including 12% in the Deschutes River), 4% were last at McNary Dam, 10% were at Snake River dams, and 31% were at upper Columbia River dams. On median, the largest fish in the sample entered the Snake River and the smallest were last detected at the release site and in the Deschutes River. We recommend moving the release site further upstream to reduce fallback behavior at John Day Dam.

Retrospective HD PIT Analyses

The 2005-2014 HD PIT dataset is an important time series for understanding migration-scale questions about adult Pacific lamprey. For this report, we tested the hypothesis that lamprey escapement past dams has increased through the study period. The weight of evidence from logistic regression analyses suggests that upstream escapement has statistically increased during the study period through most single- and multi-dam reaches and for all lamprey size classes. We think it is likely that operational and structural modifications at USACE dams intended to improve lamprey fishway passage efficiency have contributed to an increase in upstream escapement, though other unexplored explanations (i.e., changing ocean productivity) may also have been important.

Introduction

Pacific lamprey (*Entosphenus tridentatus*) is the largest lamprey species in the Columbia and Snake rivers. Pacific lampreys are anadromous, with parasitic adults spending 1-4 years in the ocean before returning to spawn in freshwater rivers (Beamish 1980; Close et al. 2002; Moser and Close 2003). Recent studies suggest that Pacific lamprey abundance has steadily declined in the Columbia River basin and in other regional rivers since the early 1960's (Kostow 2002; Clemens et al. 2010; Luzier et al. 2010). Habitat loss, river impoundment, ocean conditions, ocean prey base (Murauskas et al. 2013), and water pollution have all likely contributed to the decline. Lampreys also have difficulty locating and passing through Columbia and Snake River dam fishways designed for adult salmonids (see Luzier et al. 2011 and Keefer et al. 2012 for reviews).

Lamprey counts at dam fish ladders have been used as indicators of relative abundance and general run timing (e.g., Keefer et al. 2009a) because most historic counts were collected during the day (most lamprey pass at night), and most counting facilities were not designed to accurately enumerate lampreys (Moser et al. 2002a; Robinson and Bayer 2005; Clabough et al. 2012). Radiotelemetry was used in an intermittent series of studies from 1997-2010 to identify lamprey problem passage areas, evaluate structural and operational modifications to fishways (e.g., Clabough et al. 2011; Johnson et al. 2012; Keefer et al. 2013b), and estimate survival of adult Pacific lamprey in the basin (e.g., Moser et al. 2002b, 2005; Johnson et al. 2012; Keefer et al. 2012, 2013a). Starting in 2005, half duplex (HD) passive integrated transponder (PIT) tag monitoring sites were deployed at dams to monitor PIT-tagged adult lampreys. Like radio transmitters, PIT tags are uniquely identifiable, allowing individual fish monitoring. PIT tags are also relatively small and inexpensive and are not limited by battery life, useful features given that some adult lampreys overwinter in the Columbia River main stem and some lampreys are too small for radio transmitters. HD PIT tags were selected for Pacific lamprey passage evaluations to avoid potential tag collisions with the full-duplex (FDX) PIT tags used to monitor salmonids in the basin and because HD PIT tags have longer read ranges. (Note: the prohibition on use of FDX tags for Pacific lamprey has ended.)

The objectives of the 2014 studies described in this report were to use both radiotelemetry and PIT detection systems to: (1) calculate adult lamprey passage rates past multiple dams and reservoirs; (2) estimate lamprey escapement past multiple dams, through individual dam-to-dam reaches, and into tributaries; (3) examine potential morphological and environmental correlates with upstream passage; and (4) examine year-to-year patterns in lamprey escapement. A more detailed evaluation of HD PIT-tagged lamprey use of lamprey passage systems (LPS) and other structural modifications (i.e., lamprey refuges) at Bonneville Dam is presented in a separate report (Corbett et al. 2015). We also monitored a sample of HD PIT-tagged lamprey after experimental swimming trials in the Bonneville Dam Adult Fish Facility fishway flume and results of the flume trials are reported in Kirk et al. (2015). In addition, fine-scale behavioral summaries for the radio-tagged group at the lower Columbia River dams are presented in Clabough et al. (2015).

Methods

Lamprey Collection and Tagging

In 2014, three groups of adult lampreys were collected at night in traps located in the fishway near the Bonneville Dam Adult Fish Facility (AFF). These fish were assessed and tagged in the AFF prior to release. A fourth study group was collected at the top of the lamprey passage structure (LPS) located in the lower north fishway at John Day Dam. These four groups are summarized separately for most analyses in this report.

At Bonneville Dam, the three groups were: 1) 599 lampreys tagged with only half-duplex passive integrated transponder (HD PIT) tags and released downstream from Bonneville Dam near Hamilton Island (rkm 232.5); 2) 299 lampreys tagged with HD PIT tags, used in experimental flume trials at the AFF (see Kirk et al. 2015), and then released upstream from Bonneville Dam at Stevenson boat ramp (rkm 242.7); and 3) 599 lampreys that were double-tagged with HD PIT tags and radio transmitters and released downstream from the dam at Hamilton Island or Tanner Creek (rkm 232.0).

Lampreys were unselectively tagged (i.e., those that were tagged on any given day were a random sample of the fish that were collected the previous night). However, it was unknown whether lampreys collected inside Bonneville fishways were representative of the run at large. We have hypothesized that Pacific lamprey in the smallest adult size classes may be less likely to enter fishways. Before tagging, all fish were anaesthetized using 60 ppm (3 mL×50 L^{-1}) AQUI-S 20E (authorized under INAD protocol 11-741), measured (length, girth, and dorsal distance to the nearest mm), and weighed (nearest g). HD PIT fish were then outfitted with a uniquely-coded, glass-encapsulated HD PIT tag (Texas Instruments, 4×32 mm, 0.8 g). HD PIT tags were surgically implanted in the body cavity of anaesthetized fish through a small incision (< 1 cm) along the ventral midline and in line with the anterior insertion of the first dorsal fin as described in Moser et al. (2006). Uniquely-coded radio tags (18.3 mm length, 8.3 mm diameter, 2.1 g in water, burst rate 8 sec, tag life 130 d; model NTC-4-2L, Lotek Wireless Inc.) were surgically implanted using the methods described in Moser et al. (2002a), with an HD PIT tag inserted through the same incision. Collection and tagging protocols were reviewed and approved by the University of Idaho Institutional Animal Care and Use Committee.

Monitoring Sites

Lamprey movements were monitored using an array of interrogation sites (Table 1). Underwater antennas maintained by the UI and NOAA were located inside dam fishways at the four lower Columbia River dams, at Priest Rapids Dam on the Columbia River, and at Ice Harbor, Lower Monumental and Lower Granite dams on the lower Snake River. Antennas were located near top-of-ladder exits at all dams. At Bonneville Dam, additional sites were located at lamprey passage structures (LPSs), inside the Washington-shore and Cascades Island fishway entrances, in lamprey refuges, and in the flow-control section of the Cascades Island fishway. Antennas were also located near transition pools and/or the overflow weir portions of ladders at McNary and Ice Harbor dams and below the south (east) top-of-ladder site at The Dalles Dam, at a newly-installed lamprey trap in the south ladder at John Day Dam, and at the LPS in the John Day north fishway collection channel (Table 1). Additional antennas were maintained at upper Columbia River dams by the Chelan and Grant County PUDs and in several lower Columbia River tributaries by the Confederated Tribes of the Warm Springs Reservation of Oregon (CTWSRO). An instream multiplexing antenna array was also installed near the Deschutes River mouth in 2013 by CTWSRO and the Bonneville Power Administration (BPA). Mobile tracking of double-tagged fish was limited to two days of tracking downstream from Bonneville Dam.

Table 1. Half-duplex PIT tag interrogation sites (antennas) used by UI/NMFS to monitor lamprey passage at lower Columbia and Snake river dams in 2014. Note: additional HD monitoring sites were operated at Priest Rapids, Wanapum, Rock Island, and Rocky Reach dams (Public Utility Districts) and in Hood River, Fifteenmile Creek, Deschutes River, Warm Springs River, and Shitike Creek (CTWSRO).

Site	Location	Number of antenna(s)
Bonneville Dam	PH 1, Bradford Island lamprey bypass	4
	PH 1, Bradford Island exit	1
	PH 2, WA-shore entrance	4
	PH 2, WA-shore ladder	4
	PH 2, WA-shore exit	1
	PH 2, WA-shore lamprey bypass	2
	PH2, WA-shore lamprey refuge boxes	2
	Cascades Island entrance	1
	Cascades Island lamprey bypass	2
	Cascades Island flow-control	1
The Dalles Dam	Below East ladder count window	4
	East ladder exit (above count window)[1]	4
	North ladder exit	3
John Day Dam	South fish ladder trap near count station	1
	South ladder exit	1
	North ladder entrance	4
	North ladder exit	2
McNary Dam	South-shore transition pool / ladder	4
	South-shore exit	3
	South-shore juvenile channel near exit	2
	North-shore transition pool / ladder	4
	North-shore exit	1
Ice Harbor Dam	South-shore entrance	2
	South-shore transition pool / ladder	4
	South-shore exit	1
	North-shore transition pool / ladder	4
	North-shore exit	4
L. Monumental Dam	North-shore ladder	4
	North-shore exit	2
	South-shore ladder	4
	South-shore exit	2
Lower Granite Dam	Ladder	4
	Ladder exit	2
Priest Rapids Dam	East ladder exit	3
	West ladder exit	3

[1] did not operate in 2014

Table 2. Radiotelemetry antenna sites used to monitor lamprey passage at Columbia and Snake River dams, in reservoirs, and in tributaries in 2014.

		Antenna(s)	
Site	Location	Type	Number
Bonneville Dam	Tailrace	Aerial	2
	PH 1, South-shore entrance	Underwater	2
	PH 1, North-shore entrance	Underwater	3
	PH 1, A-Branch transition area	Underwater	3
	PH 1, A- and B-Branch junction pool	Underwater	5
	PH 1, Bradford Island makeup water channel	Underwater	3
	PH 1, Bradford Island exit	Underwater	1
	B-Branch entrance	Underwater	5
	B-Branch transition pool	Underwater	3
	Cascades Island entrance	Underwater	2
	Cascades Island transition area	Underwater	4
	Cascades Island makeup water channel	Underwater	5
	PH 2, South-shore entrances	Underwater	6
	PH 2, North-shore entrances	Underwater	6
	PH 2, WA-shore transition area	Underwater	5
	PH 2, WA-shore ladder and turnpool	Underwater	4
	PH 2, WA-shore ladder / UMT channel pool	Underwater	1
	PH 2, WA-shore ladder makeup water channel	Underwater	3
	PH 2, WA-shore counting window	Underwater	6
	PH 2, WA-shore ladder exit	Underwater	1
The Dalles Dam	Tailrace	Aerial	2
	South spillway entrance	Underwater	3
	Powerhouse entrances	Underwater	4
	Ice/Trash sluiceway outfall	Aerial	1
	East ladder entrance	Underwater	3
	East ladder entrance	Aerial	2
	East ladder transition area	Underwater	5
	East ladder exit	Underwater	1
	East powerhouse forebay	Aerial	1
	North ladder entrance	Underwater	1
	North ladder entrance	Aerial	1
	North ladder entrance / transition area	Underwater	5
	North ladder exit	Underwater	1
	North spillway forebay	Aerial	1
John Day Dam	Tailrace	Aerial	2
	South-shore entrance	Underwater	4
	South-shore transition area	Underwater	6
	North powerhouse entrance	Underwater	5
	South ladder exit	Underwater	1
	North ladder entrance / transition area	Underwater	6
	North ladder exit	Underwater	1
	North spillway tailrace	Aerial	1
	South spillway tailrace	Aerial	1
	South powerhouse tailrace	Aerial	1
	Juvenile fish outfall	Aerial	2

Table 2. Continued.

Site	Location	Antenna(s) Type	Number
John Day Dam (cont.)	Powerhouse forebay	Aerial	1
	Spillway forebay	Aerial	2
McNary Dam	Tailrace	Aerial	2
	South-shore entrance	Underwater	4
	South-shore transition pool / ladder	Underwater	7
	South ladder exit	Underwater	1
	North powerhouse entrance	Underwater	4
	North-shore entrance	Underwater	3
	North-shore transition area / ladder	Underwater	4
	North ladder exit	Underwater	3
	North powerhouse tailrace	Aerial	1
	North spillway tailrace	Aerial	1
	Ice / Trash sluiceway exit	Underwater	1
	North powerhouse forebay	Aerial	2
	South powerhouse forebay	Aerial	1
	North spillway forebay	Aerial	1
Priest Rapids Dam	East ladder exit	Underwater	1
	West ladder exit	Underwater	1
Ice Harbor Dam	Tailrace	Aerial	2
	South-shore entrance	Underwater	3
	South-shore transition pool / ladder	Underwater	6
	South ladder count window	Underwater	2
	South ladder trap / ladder exit	Underwater	3
	North powerhouse entrance	Underwater	3
	North-shore entrance	Underwater	2
	North-shore transition pool / ladder	Underwater	5
	North ladder count window / exit	Underwater	4
	South forebay	Aerial	1
	North forebay	Aerial	1
L. Monumental Dam	Tailrace	Aerial	2
	South powerhouse entrance	Underwater	4
	South ladder entrance / transition area	Underwater	7
	South ladder turnpool / exit	Underwater	4
	North ladder entrance	Underwater	4
	North ladder transition area	Underwater	4
	North ladder count window	Underwater	2
	North ladder exit	Underwater	3
	South forebay	Aerial	1
	North forebay	Aerial	1
L. Goose Dam	Tailrace	Aerial	2
	South ladder entrance	Underwater	4
	North powerhouse entrance / collection channel	Underwater	7
	North-shore entrance	Underwater	2

Table 2. Continued.

Site	Location	Antenna(s) Type	Number
L. Goose Dam	Ladder transition area	Underwater	4
(cont.)	Ladder count window / turnpool	Underwater	4
	Ladder exit	Underwater	2
	North spillway forebay	Aerial	1
	South forebay	Aerial	1
L. Granite Dam	Tailrace	Aerial	2
	South-shore entrance	Underwater	6
	North powerhouse entrance / collection channel	Underwater	5
	North entrance	Underwater	2
	Transition area	Underwater	5
	Count window / trap	Underwater	4
	Ladder serpentine weir / exit	Underwater	2
	South forebay	Aerial	1
	North spillway forebay	Aerial	1
Reservoir sites	Bridge of the Gods (rkm 238.6)	Aerial	1
	Viento State Park (rkm 258.8)	Aerial	1
	Cook-Underwood Rd (rkm 260.0)	Aerial	1
	Chamberlain Lake rest area (rkm 286.1)	Aerial	1
	Memaloose State Park (rkm 286.3)	Aerial	1
	Celilo Park (rkm 325.3)	Aerial	1
	Wishram-Celilo (rkm 325.3)	Aerial	1
	Big Flat HMU north end (rkm 549.6)	Aerial	1
	Fish Hook Park (rkm 549.7)	Aerial	1
Tributaries	Wind River	Aerial	1
	Little White Salmon River	Aerial	1
	White Salmon River	Aerial	2
	Hood River	Aerial	1
	Klickitat River	Aerial	1
	Deschutes River mouth	Aerial	1
	Deschutes River – Sherars Falls	Aerial	1
	John Day River	Aerial	1
	Tucannon River	Aerial	1
	Clearwater River	Aerial	1
	Snake River (> Clearwater confluence)	Aerial	1

Radio-tagged lamprey movements were additionally monitored using an array of fixed-site radiotelemetry antennas and receivers (Table 2). Aerial antennas were used to monitor dam tailraces and forebays, several Bonneville reservoir sites, and major tributary confluence areas. Underwater antennas and some directed aerial antennas detected radio-tagged fish as they approached, entered, and exited fishway openings, movements inside fishways and transition pools, and exits from ladders into dam forebays.

Data Analyses

Reach escapement rates were calculated by dividing the number of lampreys known to pass an upstream HD PIT or radiotelemetry monitoring site by those known to pass a site downstream or by the number released. Lampreys were treated as having passed a site if they were detected at the site or at a location further upstream.

Escapement rates were calculated across all release dates. Lamprey sizes (length, weight, girth, dorsal distance) were compared for groups that passed through a reach and those that did not using generalized linear models (PROC GLM, SAS). As a result of additional trapping efforts at Bonneville Dam, 20 double-tagged lampreys and 49 HD PIT-tagged (only) lampreys were recaptured and these fish were transported to Stevenson, WA and released. Similarly, some lampreys tagged at Bonneville Dam were recaptured at The Dalles east fishway, at the John Day north LPS, or at the lamprey trap in the John Day south fishway. Those captured at The Dalles were transported and released at a nearby boat ramp or in The Dalles reservoir. Those captured in the John Day LPS were transported and released a short distance upstream from John Day Dam at the end of the navigation lock pier nose. Those captured in the John Day south trap were used in Tribal programs or released upstream. Recaptured fish were included or excluded from escapement and passage time analyses where appropriate.

Lamprey migration times (d) and passage rates ($km \bullet d^{-1}$) were calculated from release to top-of-ladder HD PIT or radio antennas at dams and between monitored sites. Detection efficiencies for both HD PIT and radiotelemetry sites were estimated by dividing the number of fish known to pass a site by the number that was detected at that site. These estimates were imprecise because fish could pass via unmonitored routes at many locations (e.g., navigation locks) and thus represent minimum estimates of detection efficiency. However, use of double-tagged fish allowed computation of somewhat more precise estimates of detection efficiencies. Detection efficiencies for both tag systems were evaluated at sites where radiotelemetry and PIT antennas were in close proximity, primarily at top-of-ladder fishway locations.

Experimental Group – The HD PIT-tagged sample that was used in the experimental fishway and then released upstream from Bonneville Dam was not appropriate for many of the migration-scale objectives addressed in this report. This group was collected only from the first ~50% of the 2014 migration and was used in experiments before transport and release. We provide some basic summaries for the group, including upstream escapement and final distribution. They were also used to estimate dam-wide HD PIT detection efficiencies. However, data from the experimental group should be compared cautiously (or not at all) to the downstream release group and to results from previous years.

Retrospective Summaries – The 2014 studies continued a multi-year integrated adult lamprey research program and marked the eleventh study year using radiotelemetry (1997-2002, 2007-2010, 2014) and the ninth HD PIT study year (2005-2009, 2011-2014). Results from most of these years have been summarized in several recent publications, including a synthesis of fishway, dam, and reservoir passage metrics for both radio- and PIT-tagged fish (Keefer et al. 2012), a 10-year evaluation of fishway passage bottlenecks at Bonneville Dam (radiotelemetry, Keefer et al. 2013a, 2014), and a multi-year evaluation of passage at McNary Dam (radiotelemetry, Keefer et al. 2013b).

In this report, we include an updated synthesis of reach escapement based on the HD PIT data. We used the >6,800 PIT-tagged lamprey released downstream from Bonneville Dam between 2006 and 2014 to test whether there have been year-to-year changes in lower Columbia River reach survival. Our hypothesis was that the many structural and operational changes at the lower Columbia River dams have resulted in incremental increases in dam passage success and therefore reach escapement by adult lamprey. We tested this hypothesis using logistic regression models for seven study reaches: from release past Bonneville, The Dalles, John Day, and McNary dams and between each pair of lower river dams. Covariates included lamprey size, release date, and year. Given the hypothesis of increased reach escapement through time, we treated year as a continuous variable.

Results

Lamprey Collection and Tagging: Bonneville Dam

The total 'corrected' adult Pacific lamprey count at Bonneville Dam including night and LPS passage estimates through 18 November 2014 was 120,099 (N. Zorich, USACE, *personal communication*). A total of 1,497 lampreys were collected, tagged, and released or approximately 1.2% of the total corrected count (Figure 1). The tagged sample included three study groups. The first was 599 with HD PIT tags only that were released downstream from Bonneville Dam. The second was 299 that were HD PIT-tagged, used in the experimental fishway ("flume") at Bonneville Dam, and then released upstream from the dam. The third group was 599 double-tagged (HD PIT tag and radio transmitter) released downstream from Bonneville Dam. The analyses in this report are focused on the two downstream release groups because they were tagged in proportion to the run for migration-scale evaluations. We include some summaries for the experimental group used in flume trials, but note that this group should not be considered equivalent to the downstream-release groups.

Sampling for the downstream release groups was generally proportional to daily counts (Figure 1). Lamprey run timing, as indexed by the daytime count station counts, was 4 June (10% date), 19 June (25% date), 10 July (median date), 25 July (75% date), and 14 August (90% date). For comparison, the dates for the HD PIT group released downstream were 9 June, 23 June, 8 July, 23 July, and 3 September, respectively. Dates for the radiotelemetry group were 10 June, 24 June, 7 July, 18 July, and 30 July, respectively. The group used in the flume were collected much earlier, with almost all fish tagged in June (median date = 15 June). We note that handling restrictions during a warm-water period in mid-August resulted in some under sampling during the late run.

The four lamprey size metrics were all positively inter-correlated in the combined 2014 Bonneville samples (Figure 2). The coefficient of variation (CV) was 22% for dorsal distance, 19% for weight, 8% for girth, and 7% for length for the total sample (Table 3). Release date was weakly, and negatively correlated with lamprey length, girth, and weight ($-0.26 < r < -0.23$, $P \leq 0.05$).

Table 3. Length, girth, weight, and dorsal distance of adult Pacific lampreys collected and tagged in 2014 with HD PIT tags and released downstream from Bonneville Dam near Hamilton Island (HAM) or upstream from the dam near Stevenson, WA (STE). The double-tagged group was released at two sites downstream from Bonneville Dam.

	Length (cm)			Girth (cm)			Weight (g)			Dorsal distance (cm)		
Type	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*
PIT-HAM	598	66.5	4.3	598	10.9	0.9	599	474.7	93.8	599	4.0	0.6
PIT-STE[1]	299	68.0	4.8	299	11.3	1.0	299	505.0	100.4	299	4.3	0.7
Double-tag	599	67.4	4.2	599	10.5	0.8	599	492.0	89.0	599	4.1	1.2
All fish	1497	67.1	4.4	1498	11.1	0.9	1497	487.7	94.0	1498	4.1	0.9

[1] the Stevenson release group was used in flume studies and data not comparable to past years'

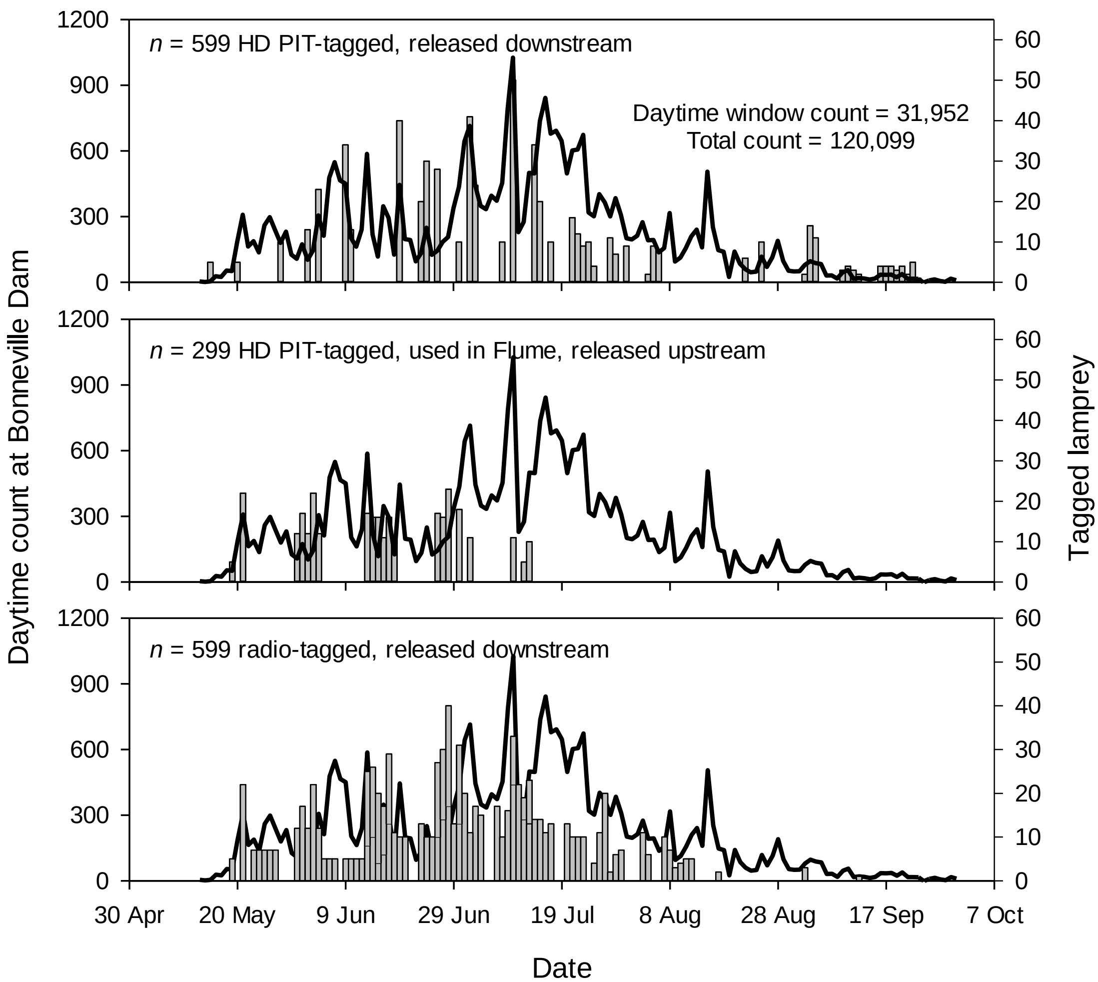

Figure 1. Number of adult Pacific lampreys counted passing Bonneville Dam during the day (solid line) and the numbers that were collected and tagged (bars) in 2014. 'Total count' is the corrected total from daytime counts at windows, night video at windows, and LPS passage estimates. Top panel shows fish released downstream from Bonneville Dam near Hamilton Island with HD PIT tags only. Middle panel shows fish that were HD PIT-tagged, used in experimental flume trials, and then released upstream from the dam near Stevenson, Washington. Bottom panel shows fish that were double-tagged (HD PIT and radio) and released downstream from the dam near Hamilton Island or Tanner Creek.

Antenna Detection Efficiency Evaluations Using Double-Tagged Lampreys

We calculated detection efficiencies for both radio and HD PIT antennas at top-of-ladder sites at all four lower Columbia River dams using the double-tagged lampreys (Table 4). These estimates represent the percentage of fish that passed an antenna that was detected. In general, detection efficiencies at top-of-ladder sites were higher for the radiotelemetry sites than for the HD sites, reflecting differences in detection range between the two technologies and also aging of the HD infrastructure. Detection efficiencies at individual radiotelemetry sites ranged from 77.8% at the McNary south ladder to 97.4% at the Bonneville Washington-shore ladder. Most missed passage events at the radiotelemetry antennas could be associated with power outages or damaged equipment.

The HD PIT antenna detection efficiencies at individual sites ranged from 72.2% at the Bonneville Washington-shore ladder top to 100% at The Dalles and John Day north ladder tops (Table 4). Note that The Dalles east top-of-ladder HD site was inoperable in 2014, but that most of the lampreys that used this fishway were recorded at the HD antenna installed downstream from the ladder top near the count window. The latter HD site did not have a radiotelemetry equivalent in 2014.

Dam-Wide Detection Efficiency: HD PIT-Tagged Fish

Dam-wide detection efficiencies described in this section were based on lamprey tagged with HD PIT tags only (i.e., no records from double-tagged fish).

Bonneville Dam – In total, 236 lampreys from the downstream release group were detected at antennas upstream from Bonneville Dam. Of these 236, 210 (89.0%) were detected at one or more Bonneville HD antennas, 164 (69.5%) were detected at top-of-ladder or top-of-LPS antennas, and 13 (5.5%) were recaptured at the AFF and transported upstream. There were 72 (30.5% of 236) that passed the dam without a top-of-ladder or top-of-LPS detection record. Of the undetected 72, 13 (18.1%) were recaptured and transported upstream, 24 (33%) were last recorded at Bonneville Dam on an antenna inside the Washington-shore fishway, 4 (6%) were at refuge boxes in the Washington-shore fishway, 4 (6%) were in the Cascades Island LPS, 3 (4%) were in the flow-control section of the Cascades Island fishway, 1 (1%) was in the Washington-shore LPS just downstream from the exit, and 23 (32%) were not detected at any Bonneville site (possible navigation lock passage).

The Dalles Dam – A total of 285 lampreys (167 from the downstream release group and 118 from the upstream release group) were detected at antennas upstream from The Dalles Dam. Of these 285, 206 (72.2%) were detected at one or more antennas at The Dalles Dam and 77 (27.0%) were detected at the top of the north fishway. The top-of-ladder antenna at the top of the east ladder was not operated in 2014 and consequently 129 (45.3%) of the fish were last detected at the antenna inside the east fishway near the east count station. The remaining 79 fish (27.7%) were not detected at any location at The Dalles Dam.

John Day Dam – A total of 136 lampreys (both release groups) were detected at antennas upstream from John Day Dam. Of these 136, 135 (99.3%) were detected at one or more antennas at John Day Dam, and 124 (91.2%) were detected at the top-of-ladder antennas. The 12 fish not detected at top-of-

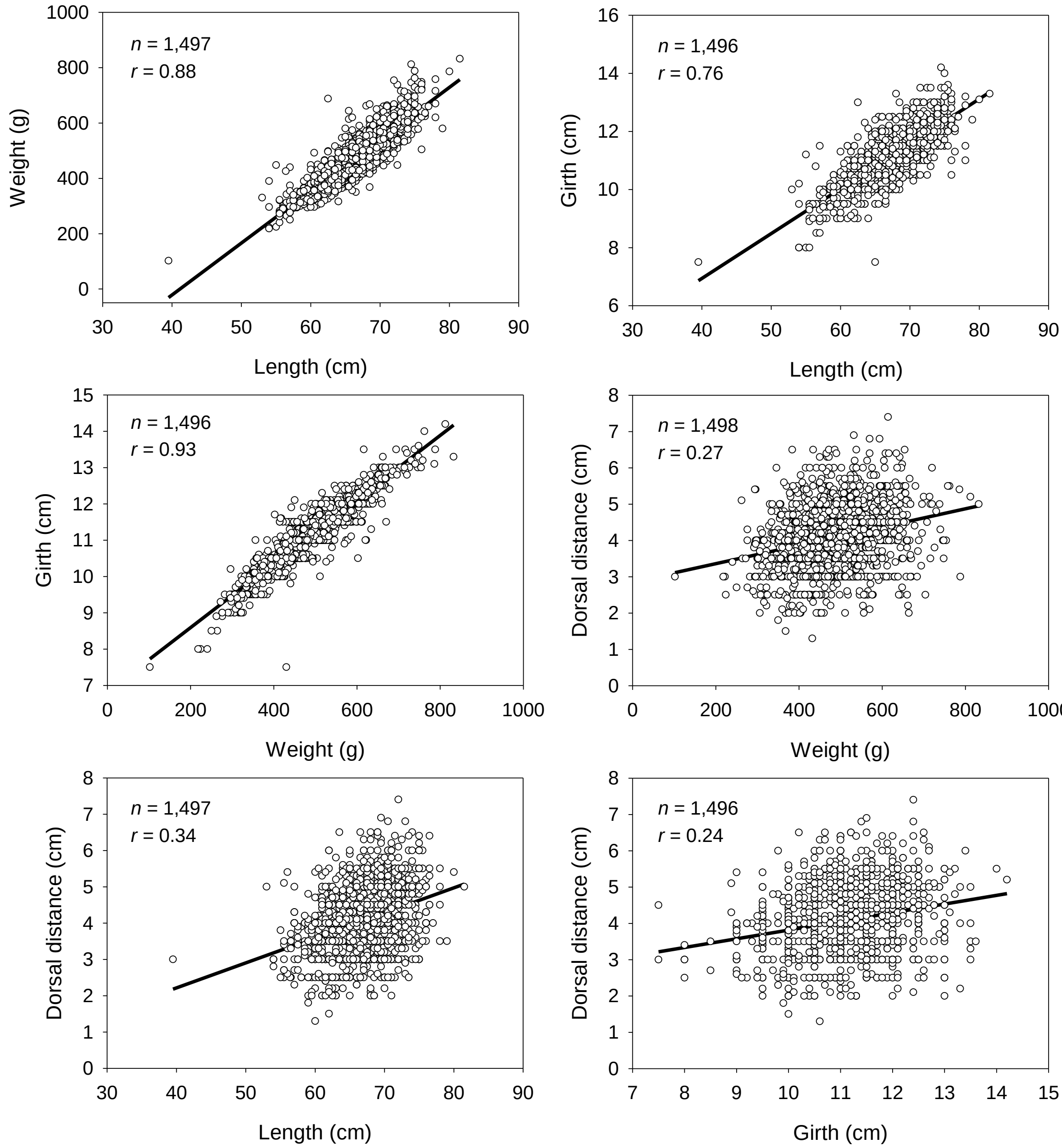

Figure 2. Linear relationships between length, weight, girth, and dorsal distance metrics for adult lampreys HD PIT- and radio-tagged in 2014. Note: all Bonneville release groups combined. All $P < 0.005$.

ladder antennas included 3 that were trapped at the north fishway LPS, 1 that was trapped in the north ladder, 7 that were detected at the north entrance antennas, and 1 that was not detected at any John Day location.

McNary Dam – A total of 104 lampreys (both release groups) were detected at antennas upstream from McNary Dam. Of these 104, 96 (99.3%) were detected at one or more antennas at McNary Dam, and 56 (53.8%) were detected at the top-of-ladder antennas. Of the 48 that passed top-of-ladder sites undetected, 37 (77%) were last detected at antennas inside the south fishway, 1 (2%) was last

Table 4. Detection efficiencies at top-of-ladder antennas calculated using double-tagged lampreys in 2014. Includes fish detected on at least one monitoring system.

Dam	Ladder	Total detected	Detection efficiency Radiotelemetry	HD PIT
Bonneville	South (Bradford)[1]	43	88.4%	86.0%
	North (WA-shore)	151	97.4%	72.2%
The Dalles	South (East)	50	96.0%	n/a
	North	24	100.0%	83.3%
John Day	South	21	95.2%	95.2%
	North	21	95.2%	100.0%
McNary	South	9	77.8%	77.8%
	North	-	-	-

[1] Does not include fish that passed through the AWS channel because there was no paired PIT antenna

detected on an antenna inside the south entrance lamprey structure, 2 (4%) were in the north fishway, and 8 (17%) were not detected at any McNary site.

Snake River Dams – Sample sizes at the Snake River dams were small (≤ 20) and there were limited upstream detection sites. Seventeen lampreys were detected upstream from Ice Harbor Dam, all of which (100%) were detected at an Ice Harbor antenna; 13 of the 17 (76.4%) were detected at top-of-ladder antennas. Eleven lampreys were detected at Lower Granite Dam, 7 (63.6%) of which were detected at Lower Monumental Dam; and 6 of the 11 (54.5%) were detected at top-of-ladder antennas at Lower Monumental Dam. No estimate was calculated for the Lower Granite antenna sites.

Upper Columbia River Dams – A total of 19 lampreys was detected at either University of Idaho or PUD antennas at Wanapum Dam, all of which (100%) were detected at Priest Rapids antennas; 16 of the 19 (84.2%) were detected at the uppermost sites at Priest Rapids Dam. We did not estimate efficiency for the Wanapum or Rock Island antenna arrays.

Downstream Release Group: HD PIT

Upstream Progression – Of the 599 lampreys released downstream from Bonneville Dam, 439 (73.3%) were subsequently recorded at one or more Bonneville Dam HD antennas inside fishways, at LPS systems, or at dams further upstream (Table 5). A total of 334 fish volitionally passed Bonneville Dam based on top-of-fishway or upstream detections (55.8% of the 599 released, and 76.1% of the 439 detected at one or more HD PIT sites after release). Importantly, another 27 (4.5%) were recaptured in traps at Bonneville Dam and were released upstream.

The median tag date for HD PIT-tagged lampreys released downstream was 8 July (*mean* = 10 July). Median recorded passage dates at top-of-ladder sites were 18 July at Bonneville Dam (*n* = 273), 31 July at The Dalles Dam (*n* = 82), 31 July at John Day Dam (*n* = 145), 17 August at McNary Dam (*n* = 43), 17 August at Priest Rapids Dam (*n* = 36), 19 August at Wanapum Dam (*n* = 28), and 26 August at Rock Island Dam (*n* = 9). In the Snake River, median passage dates were 21 July at Ice Harbor Dam (*n* = 7), 23 July at Lower Monumental Dam (*n* = 5), and 2 August at Lower Granite Dam (*n* = 5). Additional fish passed each dam without detection at top-of-ladder (or LPS) antennas (i.e., passage date was uncertain). Top-of-ladder dates of detection for the HD PIT-tagged fish indicated some under-representation during peaks in the lamprey run at Bonneville Dam (Figure 3) compared to the run at large and this carried over into the distributions at dams further upstream (Figure 3).

Table 5. Minimum numbers of adult lampreys that passed each site estimated as the number of adult tagged lampreys detected at dam antennas or inferred to pass sites based on upstream detections in 2014. HD PIT-tagged lampreys were released downstream from Bonneville Dam near Hamilton Island (HAM) or upstream from the dam near Stevenson, WA (STE); the latter group was used in experiments before release. The double-tagged group was released at two sites downstream from Bonneville Dam. See Table 1 for antenna locations. Note: does not include some summer 2015 detections.

	Release group		
Site	PIT-HAM Minimum past (*n*)	PIT-STE Minimum past (*n*)	Double-tagged Minimum past (*n*)
Release	599	299	599
Bonneville[1]	439	-	477
Bonneville top[2]	334-361[4]	-	224-243[4]
The Dalles[1]	236	165	159
The Dalles top[2]	210	145	76
John Day[1]	167	118	50
John Day top[2]	154	101	42
McNary[1]	83	53	10
McNary top[2]	75	47	9
Ice Harbor[1]	10	10	-
Ice Harbor top[2]	9	10	-
L. Monumental[1]	8	9	-
L. Monument top[2,3]	7	9	-
L. Granite[1]	5	6	-
L. Granite top[2,3]	5	6	-
Priest Rapids[5]	51	33	5
Priest Rapids top[5]	47	30	5
Wanapum[5]	46	30	5
Wanapum top[5]	30	19	4
Rock Island[5]	11	8	1
Rock Island top[5]	11	8	1
Rocky Reach[5]	n/a	n/a	n/a
Rocky Reach top[5]	n/a	n/a	n/a

[1] all fishway antennas, including LPS at Bonneville
[2] top-of-ladder antennas, including LPS at Bonneville
[3] no or limited upstream sites to assess missed detections
[4] higher numbers include fish recaptured in Bonneville traps and released upstream
[5] combined detections at UI and PUD antennas

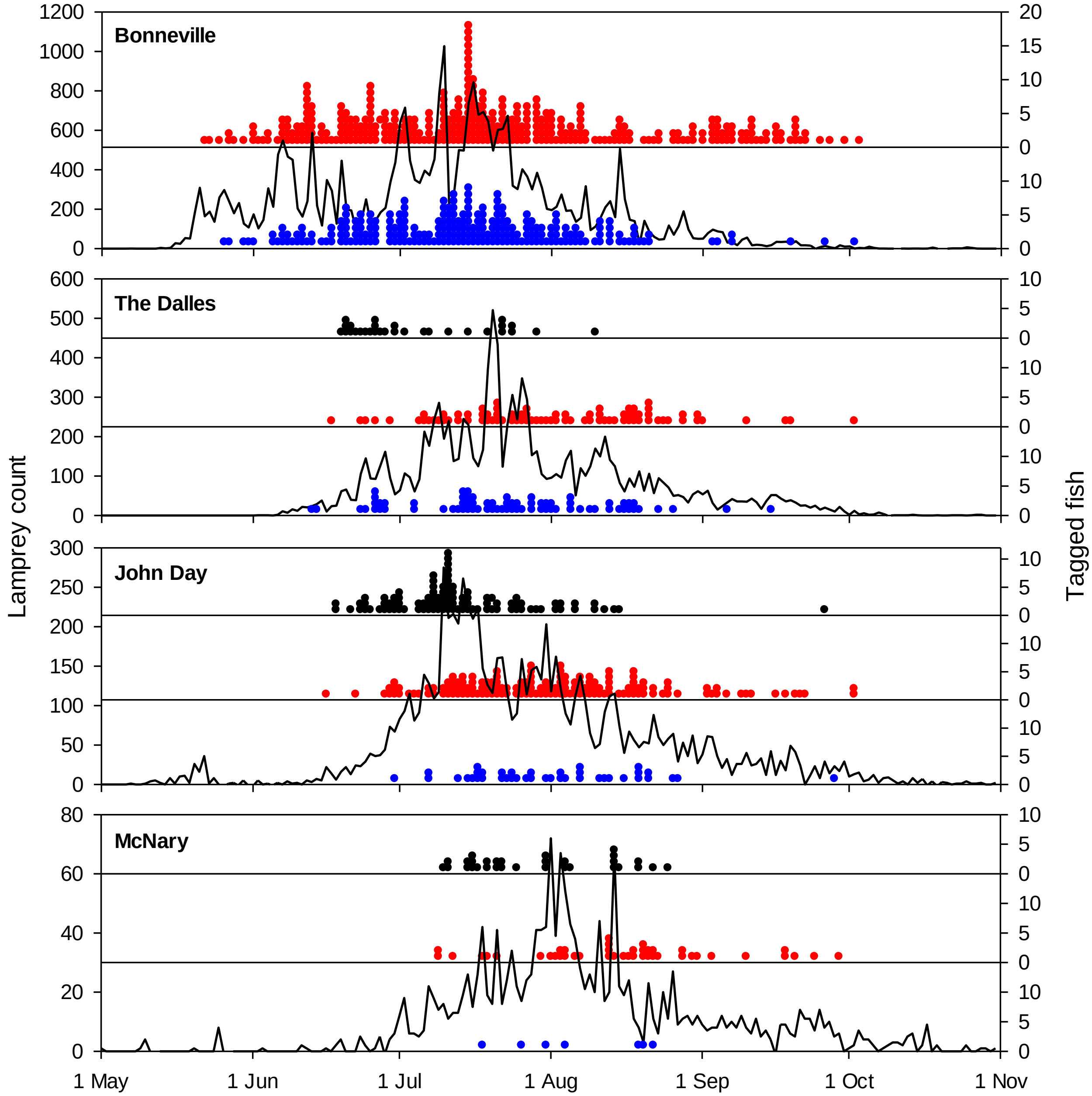

Figure 3. Daily numbers of adult Pacific lampreys counted passing lower Columbia and Snake River dams via fish ladders (black lines) and the numbers of tagged fish that were detected at top-of-ladder antennas (blue circles = double-tagged fish; red circles = HD PIT-tagged fish released downstream from Bonneville; black circles = HD PIT-tagged fish released upstream from Bonneville) in 2014. Notes: many tagged lampreys passed dams undetected, particularly at The Dalles and McNary dams; counts are daytime window counts only. Note scale differences.

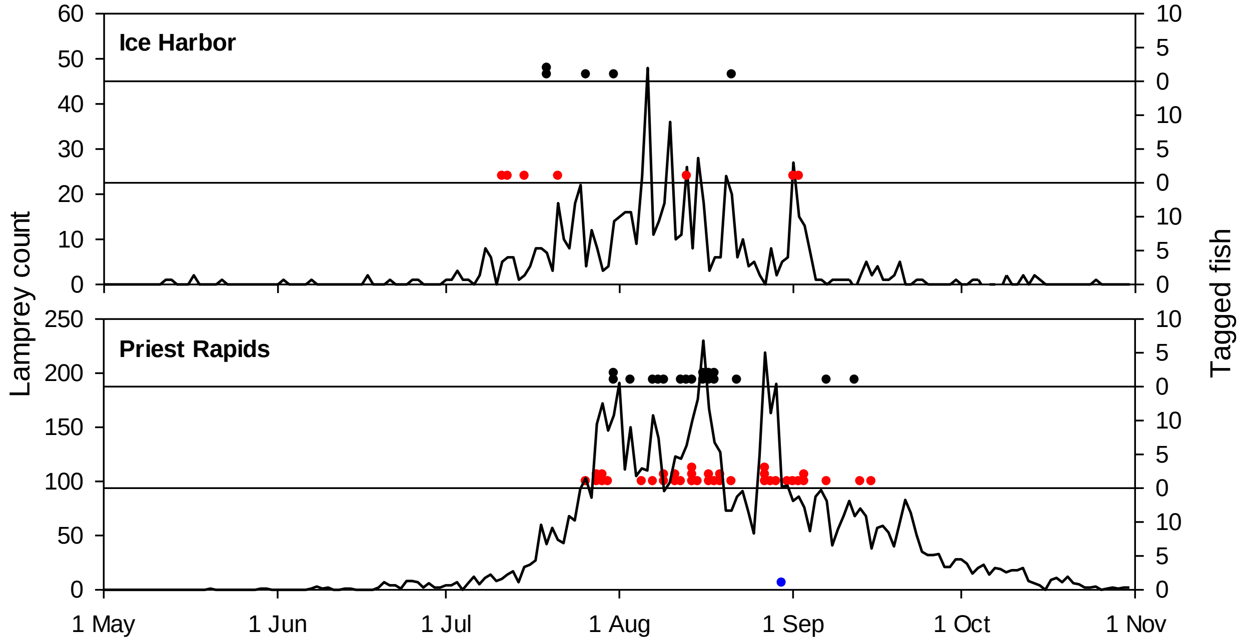

Figure 3. Continued.

Point Estimates of Dam-to-Dam Escapement – Of 599 lampreys released, 60.3% (*n* = 361) were known to have passed Bonneville Dam (including the 27 that were recaptured and released upstream), 35.1% (*n* = 210) passed The Dalles Dam, 25.7% (*n* = 154) passed John Day Dam, 12.5% (*n* = 75) passed McNary Dam, 7.8% (*n* = 47) passed Priest Rapids Dam, 5.0% (*n* = 30) passed Wanapum Dam, and 1.8% passed Rock Island Dam (*n* = 11) (Tables 5 and 6). A total of 1.5% (*n* = 9) passed Ice Harbor Dam, 1.2% (*n* = 7) passed Lower Monumental Dam, and 0.8% (*n* = 5) passed Lower Granite Dam. Escapement from the top of Bonneville Dam was 58.2% to the top of The Dalles Dam, 42.7% to the top of John Day Dam, and 20.8% to the top of McNary Dam. Escapements were 73.3% between ladder tops at The Dalles and John Day dams and 48.7% between ladder tops at John Day and McNary dams. Of 75 lampreys that passed McNary Dam, 9 (12.0%) passed Ice Harbor Dam and 47 (62.7%) passed Priest Rapids Dam (Tables 5 and 6).

In single variable logistic regression models, lampreys that passed upstream sites were longer, heavier, and had larger girth and dorsal distance than those that did not pass in almost all reaches (Figure 4). The relationship between size metrics and reach escapement was similar whether trap-recaptured fish were included or excluded, though sample sizes were reduced somewhat by excluding recaptured fish which reduced statistical power. In addition, the odds ratios increased (i.e., the effect size was larger) as the distance from release to the upstream dam increased, indicating that the largest lampreys migrated the furthest, on average.

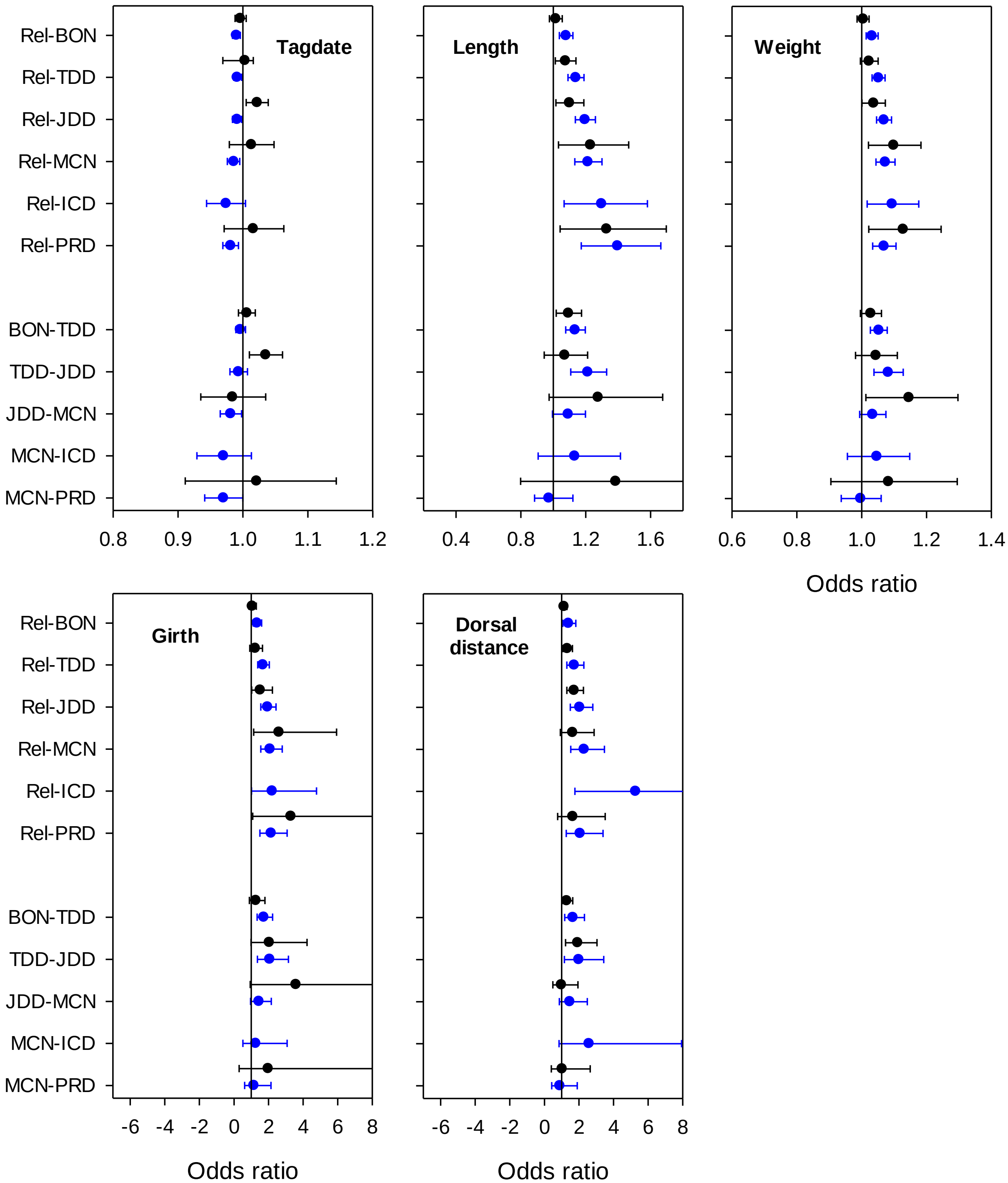

Figure 4. Odds ratios (+/- 95% ci) estimated from logistic regression models of upstream escapement by HD PIT-tagged lampreys (blue circles) and double-tagged lampreys (black circles) released downstream from Bonneville Dam in 2014. Odds ratios were scaled to the independent variables: release date (1 d) and lamprey length (1 cm), weight (10 g), girth (1 cm), and dorsal distance (1 cm). Fish recaptured at Bonneville Dam and released upstream were treated as passing; excluding recaptured fish produced similar results.

Lampreys that were tagged early in migration escaped from release past the four lower Columbia River dams at slightly higher rates than those released later in the summer (Figure 4). This effect was less evident in dam-to-dam reaches, except for the John Day-McNary reach.

Passage Times and Rates – Median HD PIT-tagged lamprey passage times were 7.2 d from the release site to the top of Bonneville Dam, 7.0 d between Bonneville and The Dalles dams, 4.1 d between The Dalles and John Day dams, and 12.9 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 7). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 10.5 km•d^{-1} (Bonneville-The Dalles), 9.4 km•d^{-1} (The Dalles-John Day), and 9.5 km•d^{-1} (John Day-McNary). Above McNary Dam, median passage times were 9.9 d (17.1 km•d^{-1}) between McNary and Priest Rapids dams, 7.1 d (4.3 km•d^{-1}) between Priest Rapids and Wanapum dams, and 5.8 d (10.5 km•d^{-1}) between Wanapum and Rock Island dams. Small sample sizes at the Snake River dams precluded meaningful summaries for reaches that included those sites.

Last Detection Summary – A total of 156 (26.0%) of the 599 lampreys released near Hamilton Island were not subsequently detected (Table 8). Another 86 (14.4%) were last recorded at HD antennas inside Bonneville Dam fishways, and 102 (17.0%) were last at top-of-ladder exit sites or LPS sites. Ten fish (1.7%) were last recorded in Fifteenmile Creek or its tributaries and 1 (0.2%) was recorded in the Hood River. A total of 38 (6.3%) was last detected at The Dalles Dam, and 47 (7.8%) were recorded in the Deschutes River. Above the Deschutes River, 76 (11.7%) were at John Day Dam, 22 (3.7%) were at McNary Dam, 10 (1.7%) were at Snake River dams, and 51 (8.5%) were at dams in the upper Columbia River (Priest Rapids through Rock Island dams) (Table 8).

When lampreys were grouped based on final recorded location, median release dates varied only slightly among groups with adequate sample size (Figure 5). Fish last recorded in the Snake and upper Columbia Rivers were tagged earlier by about 1-2 weeks, on median, than most other groups. In contrast, there were clear among-group differences in lamprey size (Figure 6). On median, lampreys were largest in the groups last detected in the Snake River (560 g) and at McNary Dam (550 g). Lampreys were smallest in the groups last recorded in Bonneville tributaries (*median* = 366 g) and at the release site (*median* = 448 g).

Downstream Release Group: Double-Tagged

Upstream Progression – Of the 599 double-tagged lampreys released downstream from Bonneville Dam, 477 (79.6%) were subsequently recorded at one or more Bonneville Dam antennas or at dams further upstream (Table 5). A total of 224 fish volitionally passed Bonneville Dam based on top-of-fishway or LPS detections or upstream detections (37.4% of the 599 released, and 47.0% of the 477 detected at one or more sites after release). Importantly, another 19 (3.2%) were recaptured in traps at Bonneville Dam and were released upstream; a single fish was recaptured and released downstream.

The median tag date for double-tagged lampreys released downstream was 7 July (*mean* = 5 July). Median recorded passage dates at top-of-ladder sites were 14 July at Bonneville Dam (*n* = 191), 23 July at The Dalles Dam (*n* = 71), 29 July at John Day Dam (*n* = 40), and 4 August at McNary Dam (*n* = 7). Sample sizes were in the single digits at Snake and upper Columbia River dams. Additional fish passed each dam without detection at top-of-ladder (or LPS) antennas (i.e., passage date was uncertain). Top-of-ladder dates of detection for the double-tagged fish indicated some under-sampling early in the run and during peak counts.

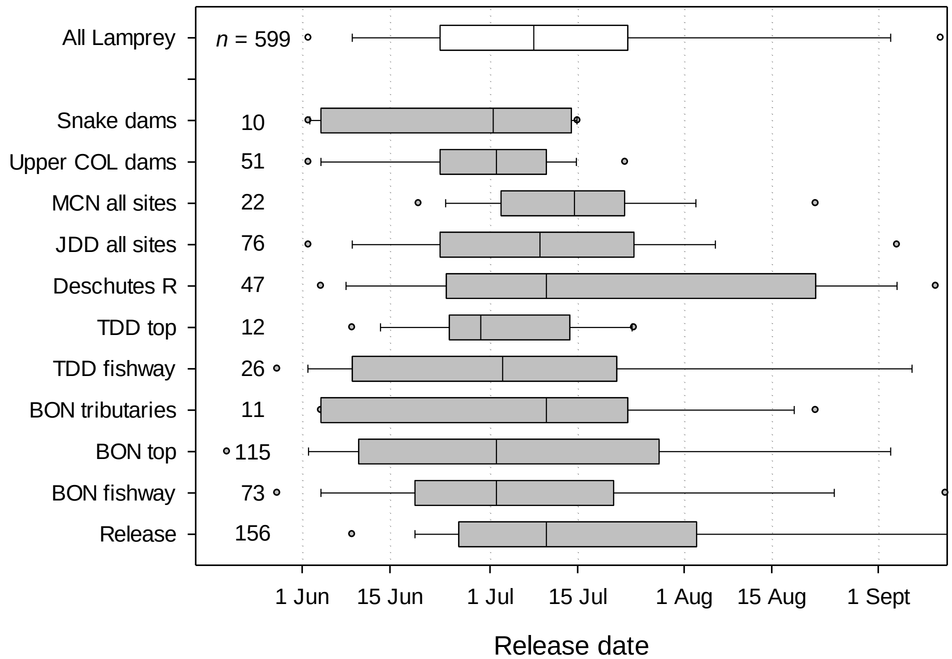

Figure 5. Distributions of HD PIT-tagged lamprey release dates by the final recorded locations for each fish. Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Note: updated to include some summer 2015 detections**.**

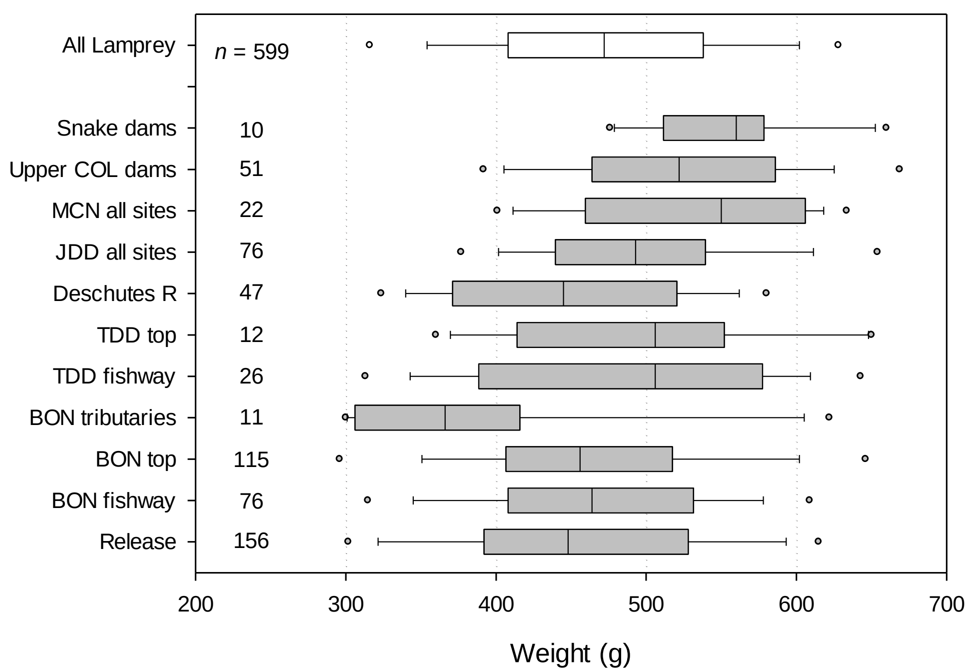

Figure 6. Distributions of HD PIT-tagged lamprey weights (g) by the final recorded locations for each fish (grey boxes). Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Note: updated to include some summer 2015 detections

Table 6. Lamprey escapement estimates for fish HD PIT-tagged and released downstream from Bonneville Dam near Hamilton Island or upstream from the dam near Stevenson, WA and for double-tagged fish released at two sites downstream from Bonneville Dam 2014. See Table 5 for sample sizes. Note: does not include some summer 2015 detections.

Reach	PIT-HAM Escapement	PIT-STE Escapement	Double-tagged Escapement
Release-Bonneville	73.3%	n/a	79.6%
Release-Bonneville top[1]	55.8-60.3%	n/a	37.4-40.6%
Release-The Dalles	39.4%	55.2%	26.5%
Release-The Dalles top	35.1%	48.5%	12.7%
Release-John Day	27.9%	39.5%	8.3%
Release-John Day top	25.7%	33.8%	7.0%
Release-McNary	13.9%	17.7%	1.7%
Release-McNary top	12.5%	15.7%	1.5%
Release-Ice Harbor top	1.5%	3.3%	-
Release-Lower Monumental top	1.2%	3.0%	-
Release-Lower Granite top	0.8%	2.0%	-
Release-Priest Rapids top	7.8%	10.0%	0.8%
Release-Wanapum top	5.0%	6.4%	0.7%
Release-Rock Island top	1.8%	2.7%	0.2%
Release-Rocky Reach top	n/a	n/a	n/a
Bonneville-Bonneville top[1]	81.1-82.2%	-	48.9-50.9%
Bonneville top-The Dalles top	58.2%	n/a	31.3%
Bonneville top-John Day top	42.7%	n/a	17.3%
Bonneville top-McNary top	20.8%	n/a	3.3%
Bonneville top-Ice Harbor top	2.5%	n/a	-
Bonneville top-L. Monum. top	1.9%	n/a	-
Bonneville top-L. Granite top	1.4%	n/a	-
Bonneville top-Pr. Rapids top	13.0%	n/a	2.1%
Bonneville top-Wanapum top	8.3%	n/a	1.6%
Bonneville top-Rock Island top	3.0%	n/a	0.4%
Bonneville top-Rocky Reach top	n/a	n/a	n/a
The Dalles top-John Day top	73.3%	69.7%	55.3%
The Dalles top-McNary top	35.7%	32.4%	10.5%
The Dalles top-Ice Harbor top	4.3%	6.9%	-
The Dalles top-L. Monum. top	3.3%	6.2%	-
The Dalles top-L. Granite top	2.4%	4.1%	-
The Dalles top-Pr. Rapids top	22.4%	20.7%	6.6%
The Dalles top-Wanapum top	14.3%	13.1%	5.3%
The Dalles top-Rock Island top	5.2%	5.5%	1.4%
The Dalles top-Rocky Reach top	n/a	n/a	n/a

[1] lower estimate treats recaptured fish as not passing Bonneville; higher estimate treats them as passed

Table 6 (cont).

Reach	PIT-HAM Escapement	PIT-STE Escapement	Double-tagged Escapement
John Day top-McNary top	48.7%	46.5%	19.0%
John Day top-Ice Harbor top	5.8%	9.9%	-
John Day top-L. Monum. top	4.5%	8.9%	-
John Day top-L. Granite top	3.2%	5.9%	-
John Day top-Priest Rapids top	30.5%	29.7%	11.9%
John Day top-Wanapum top	19.5%	18.8%	9.5%
John Day top-Rock Island top	7.1%	7.9%	2.4%
John Day top-Rocky Reach top	n/a	n/a	n/a
McNary top-Ice Harbor top	12.0%	21.3%	-
McNary top-L. Monum. top	9.3%	19.1%	-
McNary top-L. Granite top	6.7%	12.8%	-
McNary top-Priest Rapids top	62.7%	63.8%	55.6%
McNary top-Wanapum top	40.0%	40.4%	44.4%
McNary top-Rock Island top	14.7%	17.0%	11.1%
McNary top-Rocky Reach top	n/a	n/a	n/a
Priest Rapids top-Wanapum top	63.8%	63.3%	80.0%
Priest Rapids top-Rock Island top	23.4%	26.7%	20.0%
Priest Rapids top-Rocky Reach top	n/a	n/a	n/a
Wanapum top-Rock Island top	36.7%	42.1%	25.0%
Wanapum top-Rocky Reach top	n/a	n/a	n/a
Rock Island top-Rocky Reach top	n/a	n/a	n/a
Ice Harbor top-L. Monum. Top	77.8%	90.0%	-
Ice Harbor top-L. Granite top	55.6%	60.0%	-
L. Monum. top-L. Granite top	71.4%	66.7%	-

[1] lower estimate treats recaptured fish as censored; higher estimate treats them as passed

Table 7. Summary of HD PIT-tagged adult lamprey passage times (d) through monitored reaches of the lower Columbia River, for fish released downstream from Bonneville Dam in 2014.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to pass Bonneville Dam	272	7.22	12.86	2.43	16.06
Release to pass The Dalles Dam	75	22.27	26.95	11.22	35.17
Release to pass John Day Dam	137	25.12	27.23	17.03	35.08
Release to pass McNary Dam	41	46.88	42.88	25.29	53.04
Release to pass Priest Rapids Dam	34	48.27	50.96	42.00	58.03
Release to pass Wanapum Dam	27	50.47	52.68	39.08	61.60
Release to pass Rock Island Dam	9	60.21	59.56	45.19	61.29
Release to pass Ice Harbor Dam	7	40.36	39.23	33.09	48.32
Release to pass L. Monumental Dam	5	5.28	44.20	42.43	50.54
Release to pass L. Granite Dam	5	62.17	63.56	60.33	67.40
Bonneville top to pass The Dalles Dam	58	6.97	10.20	3.10	11.73
Bonneville top to pass John Day Dam	97	13.67	15.84	7.90	19.77
Bonneville top to pass McNary Dam	30	29.57	31.28	19.01	40.03
Bonneville top to pass Priest Rapids Dam	24	37.34	39.76	28.68	46.95
Bonneville top to pass Wanapum Dam	20	46.81	45.50	40.53	49.75
Bonneville top to pass Ice Harbor Dam	8	36.32	35.78	28.78	40.70
Bonneville top to pass L. Monumental	5	40.04	37.22	30.31	40.23
The Dalles top to pass John Day Dam	47	4.11	6.43	2.73	8.02
The Dalles top to pass McNary Dam	9	23.35	25.98	10.85	28.97
The Dalles top to pass Priest Rapids Dam	9	29.01	32.61	20.96	35.23
The Dalles top to pass Wanapum Dam	8	38.60	37.73	34.66	40.66
The Dalles top to pass Ice Harbor Dam	5	24.90	27.52	22.23	26.06
John Day top to pass McNary Dam	39	12.91	16.34	7.48	20.56
John Day top to pass Priest Rapids Dam	35	20.57	23.79	15.62	28.76
John Day top to pass Wanapum Dam	27	29.62	30.18	22.84	34.12
John Day top to pass Rock Island Dam	11	35.20	37.34	26.62	40.57
John Day top to pass Ice Harbor Dam	6	18.60	20.79	16.50	22.42
McNary top to pass Priest Rapids Dam	19	9.89	9.62	7.83	10.93
McNary top to pass Wanapum Dam	12	16.07	17.76	13.94	17.27
McNary top to pass Rock Island Dam	6	20.08	30.71	19.04	34.57
Priest Rapids top to pass Wanapum Dam	22	7.06	8.66	5.29	10.56
Priest Rapids top to pass Rock Island Dam	10	13.95	20.84	11.95	24.79
Wanapum top to pass Rock Island Dam	9	5.77	9.00	3.97	10.06

Note: overwintering fish not included; recaptured fish included

Table 8. Last recorded locations for lampreys HD PIT-tagged and released downstream from Bonneville Dam near Hamilton Island or upstream from the dam near Stevenson, WA and for double-tagged fish released at two sites downstream from Bonneville Dam 2014. WA = Washington shore fishway; LPS = lamprey passage structure. Notes: Hood River, Fifteenmile Creek, and Warm Springs River sites were maintained by the CTWRSO; some Wanapum sites and all Rock Island sites were maintained by Chelan and Grant county PUDs; 2015 detections through mid-June were used to assign some fates.

	PIT-HAM (n = 599)		PIT-STE (n = 299)		Double-tagged (n = 599)	
Last recorded location	*n*	%	*n*	%	*n*	%
Release site	156	26.0%	116	38.8%	16	2.7%
Bonneville tailrace	-	-	-	-	109	18.2%
Bonneville – Brad. Is. fishway	-	-	-	-	82	13.7%
Bonneville – WA-shore fishway	-	-	-	-	152	25.4%
Bonneville – LFS[1]	3	0.5%	-	-	-	-
Bonneville – Casc. Is. flow cont.	22	3.7%	1	0.3%	-	-
Bonneville – lamprey refuges	8	1.3%	-	-	-	-
Bonneville – WA ladder	40	6.7%	-	-	-	-
Bonneville – recapture[2]	13	2.2%	-	-	-	-
Bonneville – WA ladder exit / LPS[3]	81	13.5%	-	-	32	5.3%
Bonneville – Bradford exit / LPS[3]	21	3.5%	-	-	18	3.0%
Bonneville pool	-	-	-	-	25	4.2%
Little White Salmon River	-	-	-	-	1	0.2%
Hood River	1	0.2%	-	-	4	0.7%
Mill Creek	-	-	-	-	1	0.2%
Fifteenmile Creek	10	1.7%	12	4.0%	4	0.7%
The Dalles tailrace	-	-	-	-	24	4.0%
The Dalles Dam fishways	26	4.3%	16	5.4%	55	9.2%
The Dalles ladder exits	12	2.0%	4	1.3%	13	2.2%
The Dalles pool	-	-	-	-	2	0.3%
Deschutes River + tributaries	47	7.8%	32	10.7%	13	2.2%
John Day tailrace	-	-	-	-	1	0.2%
John Day Dam fishways	[5]8	1.3%	11	3.7%	13	2.2%
John Day LPS or traps[4]	4	0.7%	9	3.0%	-	-
John Day ladder exits	64	10.7%	45	15.1%	21	3.5%
John Day River	-	-	-	-	5	0.8%
McNary Dam fishways	9	1.5%	6	2.0%	-	-
McNary Dam ladder exits	13	2.2%	4	1.3%	5	0.8%
Ice Harbor Dam	2	0.3%	2	0.7%	-	-
Lower Monumental Dam	3	0.5%	2	0.7%	-	-
Lower Granite Dam	5	0.8%	6	2.0%	-	-
Priest Rapids Dam	5	0.8%	3	1.0%	-	-
Wanapum Dam	35	5.8%	22	7.4%	4	0.7%
Rock Island Dam	11	1.8%	8	2.7%	-	-

[1] recaptured fish, released upstream; [2] released upstream
[3] includes small number not recorded at uppermost LPS site
[4] presumed released upstream from John Day Dam

Point Estimates of Dam-to-Dam Escapement – Of 599 fish released, 40.6% (n = 243) were known to have passed Bonneville Dam (including the 19 that were recaptured and released upstream), 12.7% (n = 76) passed The Dalles Dam, 7.0% (n = 42) passed John Day Dam, 1.5% (n = 9) passed McNary Dam, 0.8% (n = 5) passed Priest Rapids Dam, 0.7% (n = 4) passed Wanapum Dam, and 0.2% passed Rock Island Dam (n = 1) (Tables 5 and 6). None of the double-tagged fish was recorded passing a Snake River dam. Escapement from the top of Bonneville Dam was 31.3% to the top of The Dalles Dam, 17.3% to the top of John Day Dam, and 3.7% to the top of McNary Dam. Escapements were 55.3% between ladder tops at The Dalles and John Day dams and 21.4% between ladder tops at John Day and McNary dams. Of 9 lampreys that passed McNary Dam, 5 (55.6%) subsequently passed Priest Rapids Dam (Tables 5 and 6).

In single variable logistic regression models, lampreys that passed upstream sites were longer, heavier, and had larger girth and dorsal distance than those that did not pass in almost all reaches (Figure 4). The relationship between size metrics and reach escapement was generally similar whether recaptured fish were included or excluded. In addition, the odds ratios increased (i.e., the effect size was larger) as the distance to the upstream dam increased, indicating that the largest lampreys migrated the furthest. There was little evidence for a migration timing effect on escapement.

Passage Times and Rates – Median HD PIT-tagged lamprey passage times were 5.4 d from the release site to the top of Bonneville Dam, 5.7 d between Bonneville and The Dalles dams, 3.0 d between The Dalles and John Day dams, and 10.8 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 9). Median passage rates in these reaches were < 1 km●d^{-1} (release-Bonneville top), 12.8 km•d^{-1} (Bonneville-The Dalles), 13.1 km•d^{-1} (The Dalles-John Day), and 11.3 km•d^{-1} (John Day-McNary). Sample sizes were limiting upstream from McNary Dam.

Last Detection Summary – A total of 16 (2.77%) of the 599 lampreys released below Bonneville Dam were not subsequently detected (Table 8). Another 109 (18.2%) were last recorded at tailrace radiotelemetry antennas and 234 (39.1%) were last detected at Bonneville Dam fishways and 50 (8.3%) were at top-of-ladder exit sites or LPS sites. Twenty-five fish (4.2%) were last detected at antennas in the Bonneville reservoir and 10 (1.7%) were at tributaries to the reservoir (Little White Salmon and Hood rivers, Mill Creek, Fifteenmile Creek). A total of 24 (4.0%) were last detected at The Dalles tailrace, 55 (9.2%) were at The Dalles fishways, and 13 (2.2%) were last recorded at The Dalles exit antenna. Thirteen (2.2%) were in the Deschutes River. Above the Deschutes River, 35 (5.8%) were at John Day Dam, 5 (0.8%) were at McNary Dam, and 4 (0.7%) were at Wanapum Dam (Table 8).

When double-tagged lampreys were grouped based on final recorded location, median release dates varied only slightly among groups with adequate sample size (Figure 7). As with the HD PIT-tagged group, there were clear among-group differences in double-tagged lamprey size (Figure 8). On median, lampreys were largest in the groups last detected in the upper Columbia River (582 g), at McNary Dam (544 g) and at John Day Dam or in the John Day River (529 g). Lampreys were smallest in the groups last recorded in Bonneville reservoir tributaries (*median* = 426 g).

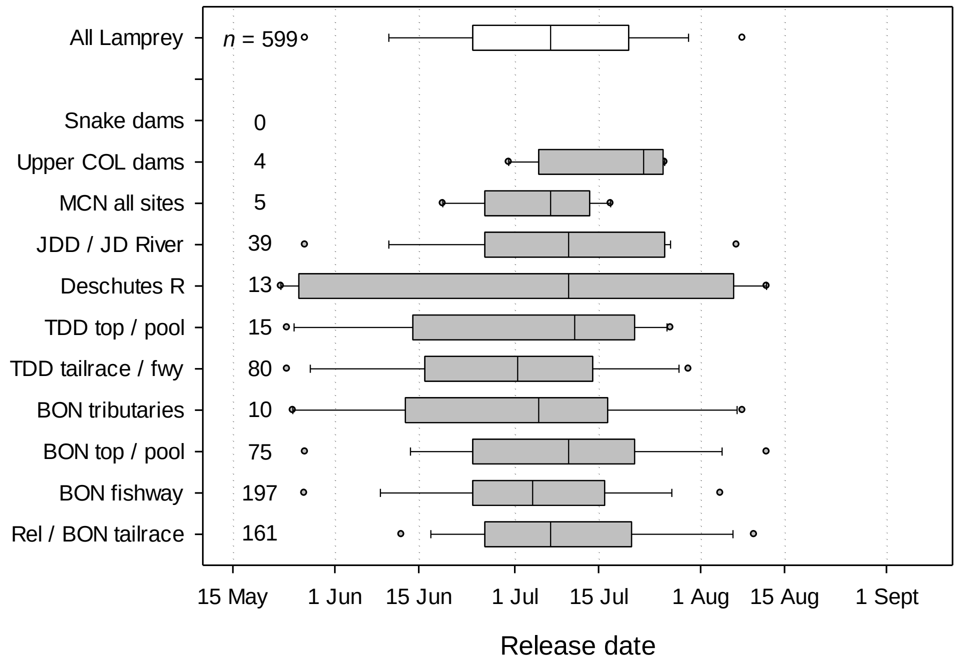

Figure 7. Distributions of double-tagged lamprey release dates by the final recorded locations for each fish. Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Note: updated to include some summer 2015 detections.

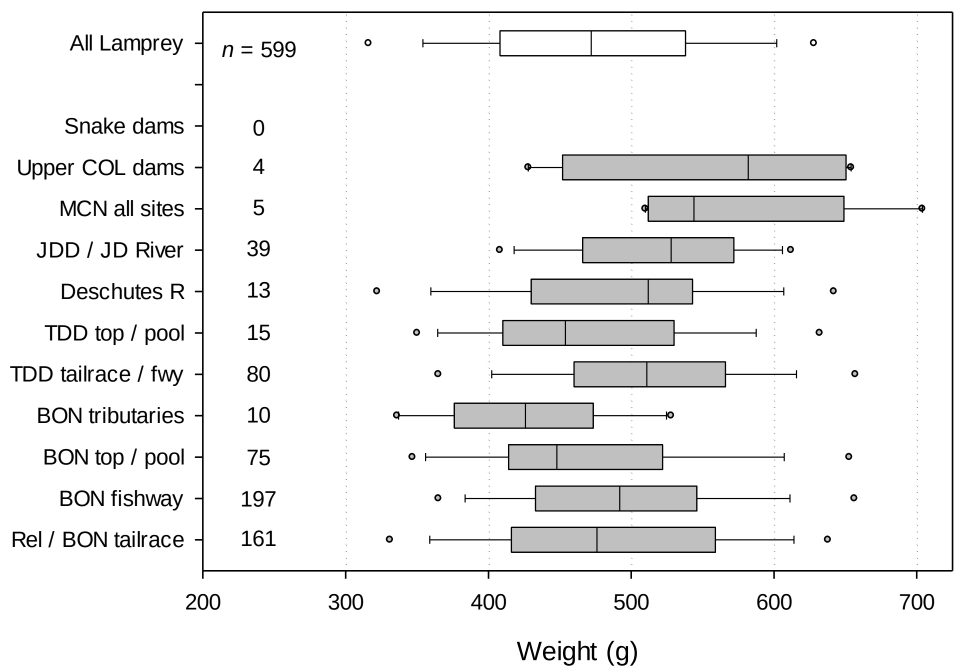

Figure 8. Distributions of double-tagged lamprey weights (g) by the final recorded locations for each fish (grey boxes). Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Note: updated to include some summer 2015 detections.

Table 9. Summary of double-tagged adult lamprey passage times through dam-to-dam and multi-dam reaches of the lower Columbia River in 2014. Fish recaptured at Bonneville Dam were excluded from reaches starting at release and ending at sites upstream from Bonneville Dam.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to approach Bonneville fishway	337	1.04	2.55	0.13	3.12
Release to enter Bonneville fishway	231	1.17	3.25	0.18	4.12
Release to pass Bonneville Dam	191	5.41	8.20	2.18	10.66
Release to The Dalles tailrace	28	8.93	10.49	4.29	15.20
Release to pass The Dalles Dam	66	13.17	15.54	7.47	19.80
Release to John Day tailrace	9	20.43	20.23	11.18	21.24
Release to pass John Day Dam	36	12.91	16.22	9.91	22.07
Release to McNary tailrace	-	-	-	-	-
Release to pass McNary Dam	7	23.31	27.03	19.23	31.05
Bonneville top to The Dalles tailrace	23	2.21	3.51	1.94	3.81
Bonneville top to pass The Dalles Dam	57	5.69	8.08	3.89	9.79
Bonneville top to John Day tailrace	8	8.20	12.83	6.11	15.18
Bonneville top to pass John Day Dam	33	8.21	10.41	6.93	11.79
Bonneville top to McNary tailrace	-	-	-	-	-
Bonneville top to pass McNary Dam	6	18.92	20.81	17.34	22.25
The Dalles tailrace to pass The Dalles Dam	9	1.27	5.05	1.12	5.08
The Dalles top to John Day tailrace	12	1.50	5.35	1.17	5.40
The Dalles top to pass John Day Dam	39	2.97	3.28	2.22	3.81
The Dalles top to McNary tailrace	-	-	-	-	-
The Dalles top to pass McNary Dam	7	13.05	14.70	10.39	16.96
John Day tailrace to pass John Day Dam	5	1.56	3.37	1.24	3.13
John Day top to McNary tailrace	-	-	-	-	-
John Day top to pass McNary Dam	7	10.84	11.93	7.51	13.80
McNary tailrace to pass McNary Dam	-	-	-	-	-

Negative Effects of Double Tagging: Comparison of Downstream Release Groups

Double-tagging with an HD PIT tag and a radio transmitter has been associated with reduced escapement past dams in previous study years and this pattern continued in 2014. We tested whether reach escapement differed for the two tag groups after statistically controlling for release date and lamprey size (weight) using a series of logistic regression models (Table 10). In all reaches, double-tagged fish had a lower probability of upstream detection than those with HD PIT tags only (tagtype effect: $7.7 \leq \chi^2 \leq 85.6$, $P \leq 0.005$). Lamprey size effects were also evident in each model, with larger fish escaping at higher rates than smaller fish ($P \leq 0.044$). Tagdate was a statistically significant effect in two of seven reaches, with lower likelihood of reach passage later in the migration (Table 10).

Double-tagged lamprey had reach escapement probabilities that were 7-15% lower than those for HD PIT-tagged lamprey, based on point estimates for fish with median tagdate and median weight (Figure 9). The largest absolute differences were for the Release-TDD reach, where double-tagged fish had 14.1% lower probability to pass then HD only fish and the BON-TDD reach (14.7% lower escapement probability for double-tagged fish).

Table 10. Results of logistic regression models of reach escapement by HD PIT-tagged and double-tagged lampreys released downstream from Bonneville Dam in 2014. The models were: reach escapement = tagtype (HD only, double) + tagdate + lamprey weight.

	HD PIT	Double	Tagtype		Tagdate		Weight	
Reach	*n*	*n*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Release-BON	599	599	51.75	<0.001	7.34	0.007	4.12	0.042
Release-TDD	599	599	85.63	<0.001	0.78	0.377	23.70	<0.001
Release-JDD	599	599	76.60	<0.001	0.06	0.803	38.07	<0.001
Release-MCN	599	599	44.51	<0.001	1.82	0.178	25.72	<0.001
BON-TDD	361	243	43.75	<0.001	0.87	0.350	19.18	<0.001
TDD-JDD	210	76	10.12	0.002	3.22	0.073	17.13	<0.001
JDD-MCN	154	42	7.74	0.005	3.91	0.048	4.06	0.044

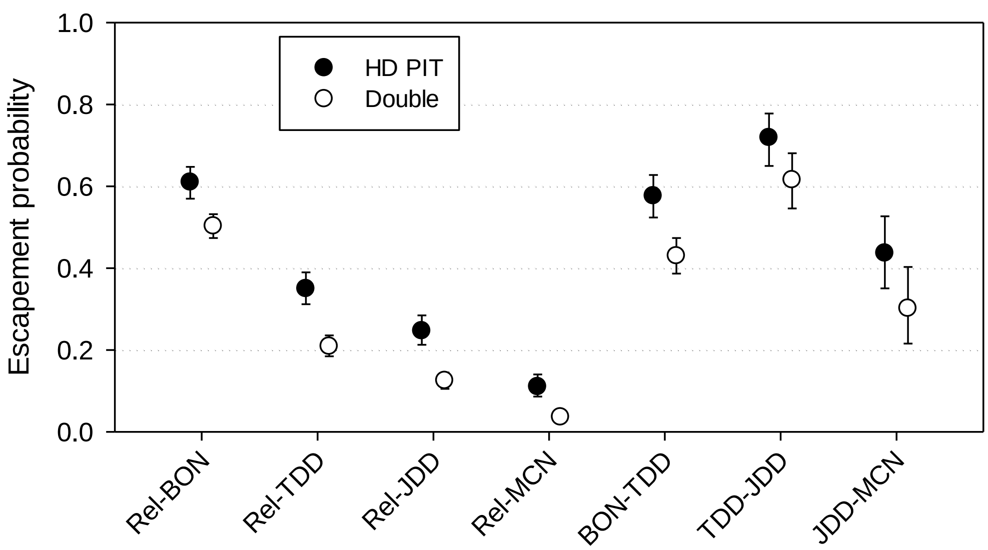

Figure 9. Estimated reach escapement probabilities (+/- 95% ci) of HD PIT-tagged (●) and double-tagged (○) lampreys released downstream from Bonneville Dam in 2014. Point estimates are from logistic regression models where: escapement = tagtype + tagdate + lamprey weight. Estimates were for the median lamprey weight (478 g) and the median release date (8 July) for the combined HD PIT- and double-tagged samples.

Stevenson Release Group: HD PIT (used in experimental fishway)

The 299 HD PIT-tagged lampreys released near Stevenson, WA were not tagged in proportion to the lamprey run (Figure 1). This subsample was collected only between 19 May and 13 July (*mean* = 15 June) and was used in experiments prior to release. Mean size metrics for the group were slightly higher than those for the downstream HD PIT- and double-tagged release groups (Table 3), consistent with the observation that early-run lampreys were slightly larger, on average, than later-run fish across tag groups.

The Stevenson release group was experimental and we therefore did not estimate passage times and migration timing (i.e., upstream progress) and we did not model covariate effects on escapement. However, we do provide summaries of upstream escapement and final detection locations.

Point Estimates of Dam-to-Dam Escapement – For the 299 HD PIT-tagged lampreys released near Stevenson, escapement from release was, 48.5% (n = 145) past The Dalles Dam, 33.8% (n = 101) past John Day Dam, 15.7% (n = 47) past McNary Dam, 10.0% (n = 30) past Priest Rapids Dam, and 3.3% (n = 10) past Ice Harbor Dam (Tables 5 and 6). Escapements were 69.7% between ladder tops at The Dalles and John Day dams and 46.5% between ladder tops at John Day and McNary dams. Of 47 lampreys that passed McNary Dam, 30 (63.8%) passed Priest Rapids Dam and 10 (21.3%) passed Ice Harbor Dam (Tables 5 and 6).

Last Detection Summary – A total of 116 (38.8%) of the 299 lampreys released near Stevenson were not subsequently detected (Table 8). Twelve fish (4.0%) were last recorded in Fifteenmile Creek or its tributaries. A total of 20 (6.7%) were last detected at The Dalles Dam, and 32 (10.7%) were recorded in the Deschutes River. Above the Deschutes River, 65 (21.7%) were at John Day Dam, 10 (3.3%) were at McNary Dam, 10 (3.3%) were at Snake River dams, and 33 (11.0%) were at dams in the upper Columbia River (Priest Rapids through Rock Island dams) (Table 8).

John Day LPS Release Group

We collected and HD PIT-tagged 100 lampreys from the John Day north fishway LPS and released them in the John Day forebay in 2014. These fish were tagged opportunistically on seven days in July during the peak of the run and before water temperatures were too warm for tagging (Figure 10). The sample was ~1.2% of the daytime count at John Day Dam and was not representative of the run at large.

Passage Times and Rates – Median HD PIT-tagged lamprey passage times were 11.2 d from the release site to the top of McNary Dam, 21.7 d from release past Priest Rapids Dam, and 11.5 d from release past Ice Harbor Dam (Table 12). Above McNary Dam, median passage times were 10.2 d between McNary and Priest Rapids dams and 4.2 d between McNary and Ice Harbor dams. Median passage rates in these reaches were 10.9 km•d^{-1} (release-McNary top), 13.4 km•d^{-1} (release-Priest Rapids top), 16.5 km•d^{-1} (release-Ice Harbor top), 16.6 km•d^{-1} (McNary-Priest Rapids) and 16.2 km•d^{-1} (McNary-Ice Harbor).

Last Detection Summary – Final detections locations for the 100 fish included 27 (27%) at the John Day forebay release site, 28 (28%) at sites downstream from the release site including the Deschutes

River, 4 (4%) at McNary Dam, 10 (10%) at Snake River dams, and 31 (31%) at upper Columbia River dams (Table 11).

Fallback at John Day Dam – Forty one lampreys had downstream detections that indicated that they fell back at John Day Dam or moved from the forebay into a fishway. At least 30 of the 41 (73%) subsequently were recorded at top-of-ladder PIT antennas at John Day Dam, suggesting they reascended a fishway after falling back via spillway, adult fishway, juvenile bypass system or navigation lock; limited monitoring made interpretation of these records ambiguous in some cases, though it appeared likely that some of these fish fell back at the dam a second time. In total, 16 had final detections at sites downstream from John Day Dam, including 12 that were last detected in the Deschutes River, one was at a PIT antenna in the north fishway entrance area, and three were in the John Day LPS and were transported and released upstream.

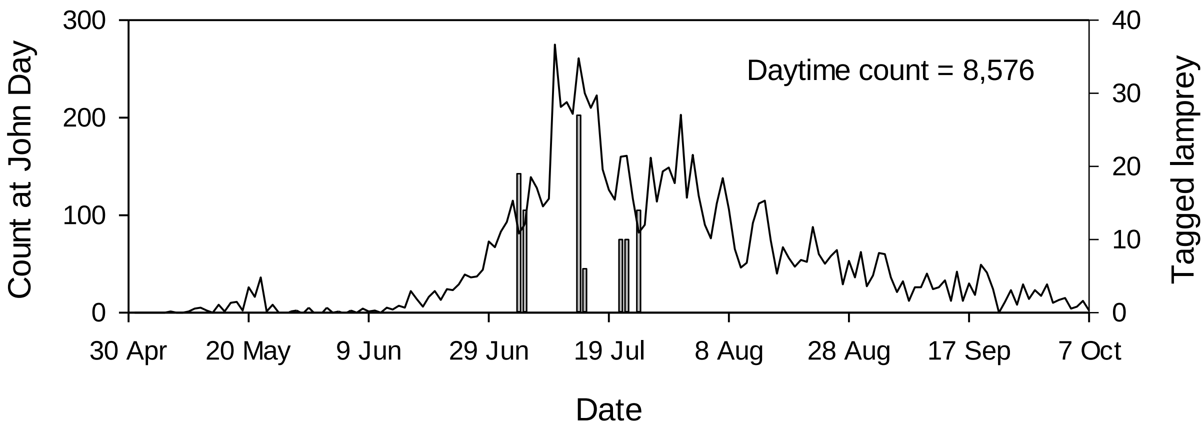

Figure 10. Number of adult Pacific lamprey counted passing John Day Dam during the day (solid line) and the numbers that were collected in the John Day north fishway LPS and HD PIT-tagged (bars, *n* = 100) in 2014. Tagged fish were transported a short distance upstream from John Day Dam and released at the end of the navigation lock pier nose.

Table 11. Last recorded locations for 100 lampreys collected in the John Day LPS (north fishway), HD PIT-tagged and released in the John Day forebay in 2014. LPS = lamprey passage structure. Note: some Wanapum Dam sites and all Rock Island Dam sites were maintained by Chelan and Grant county PUDs.

Last recorded location	*n*	%		*n*	%
Release site	27	27%			
			Ice Harbor south fishway	2	2%
Deschutes River mouth	[1]*12*	*12%*	Ice Harbor ladder exits	3	3%
John Day north fishway entrance	[1]*1*	*1%*	Lower Monumental ladder exits	2	2%
John Day north LPS	[1]*3*	*3%*	Lower Granite ladder exit	3	3%
John Day ladder exits	[1]*12*	*12%*			
			Priest Rapids Dam	4	4%
McNary south fishway	3	3%	Wanapum Dam	19	19%
McNary ladder exits	1	1%	Rock Island Dam	8	8%

[1] downstream from release site – fish fell back at John Day Dam

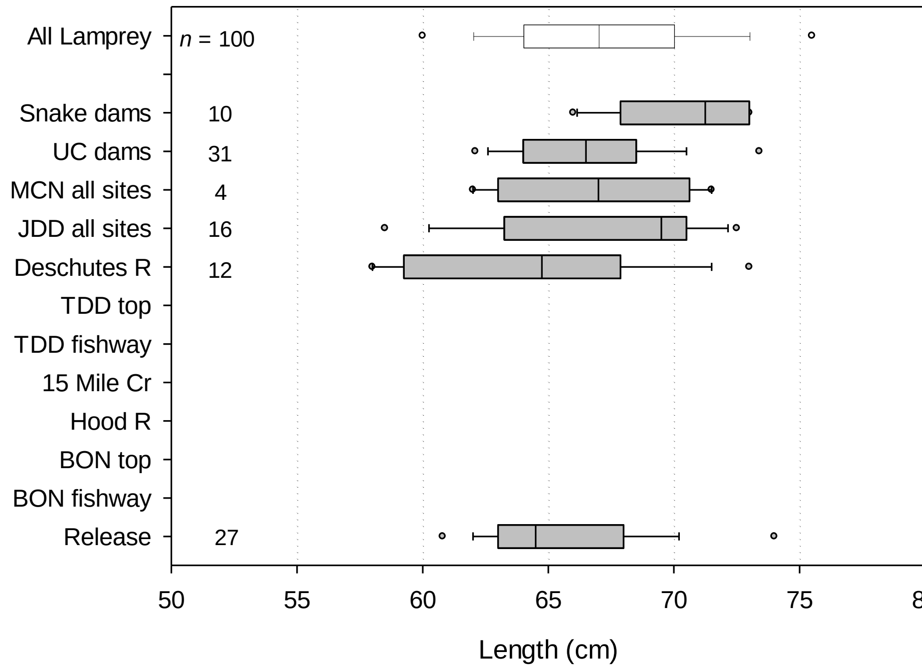

Figure 11. Distributions of HD PIT-tagged lamprey lengths (cm) by the final recorded locations for each fish (grey boxes). Data shown are for lamprey released downstream upstream from John Day Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Note: updated to include some summer 2015 detections.

Table 12. Summary of HD PIT-tagged adult lamprey passage times (d) through monitored reaches, for fish released upstream from John Day Dam in 2014. Only includes reaches with 5 or more fish.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to pass McNary Dam	28	11.24	13.46	5.49	20.52
Release to pass Priest Rapids Dam	21	21.72	27.59	18.57	33.62
Release to pass Wanapum Dam	14	38.94	38.87	27.82	47.40
Release to pass Rock Island Dam	5	31.50	35.72	30.87	44.39
Release to pass Ice Harbor Dam	7	11.54	17.17	10.51	20.13
McNary top to pass Priest Rapids Dam	15	10.20	11.29	9.61	13.59
McNary top to pass Wanapum Dam	14	22.09	23.20	18.06	25.90
McNary top to pass Rock Island Dam	5	25.24	24.72	24.04	25.38
McNary top to pass Ice Harbor Dam	6	4.20	5.01	3.37	7.01
Priest Rapids top to pass Wanapum Dam	12	7.02	8.60	5.10	12.20
Priest Rapids top to pass Rock Island Dam	5	14.89	14.46	12.29	14.95
Wanapum top to pass Rocky Reach Dam	5	5.91	6.27	4.00	7.92

Note: overwintering fish not included; recaptured fish included

Detection of Lampreys Tagged in 2013

A total of 115 (8.3%) of the 1,393 lampreys tagged in 2013 (all release groups) were detected at one or more HD antennas in 2014. These included 76 (9.3%) of the 819 HD PIT-only fish released near Bonneville Dam, 2 (4.0%) of the 50 double-tagged (radio + HD PIT) fish released at Bonneville Dam, and 37 (9.3%) of 400 double-tagged (JSATS + HD PIT) fish released at Bonneville Dam.

Final recorded locations for the 115 overwintering fish included: 60 (52%) at the Deschutes River mouth, 20 (17%) at Bonneville Dam, 2 (2%) at The Dalles Dam, 29 (25%) at John Day Dam, 2 (2%) in the Umatilla River, and 1 (1%) each at McNary and Wanapum dams. We note that additional detections were likely at dams upstream from Priest Rapids Dam, but those data were not available at this writing. The last 2014 records for 2013-tagged lampreys were in April (3%), May (53%), June (36%), and July (8%).

Multi-Year Summary: Bonneville HD PIT-Tagged Lampreys

Reach escapement point estimates for the HD PIT samples varied among years (Table 13), and differences can likely be attributed to a variety of factors. Important considerations when interpreting the multi-year assessments include: 1) environmental differences both among and within years; 2) increased lamprey trapping effort at Bonneville, The Dalles, and John Day dams; 3) changing monitoring effort through time (i.e., added HD antenna monitoring sites at Bonneville and John Day LPSs, the John Day south fishway trap, the McNary south entrance structure, at upper Columbia and Snake River dams, and at Hood River, Fifteenmile Creek, and Deschutes River sites); 4) deteriorating HD monitoring infrastructure at lower Columbia River dams (i.e., many antennas were originally installed ten years ago and detection capabilities have declined). In our opinion, the increased trapping and monitoring effort probably has more than offset the negative accounting effects of infrastructure aging in terms of identifying lamprey passage at dams.

Release to Pass Bonneville Dam – Escapement estimates for lampreys released downstream from Bonneville Dam ranged from 0.41-0.56 (*mean* = 0.51, CV = 10.3%) past Bonneville Dam when trap recaptures were censored and from 0.41-0.61 (*mean* = 0.53, CV = 7.9%) when trapped fish were treated as successfully passing (Table 13). (Note: 2005 data were excluded because fish were released into the Bradford Island fishway and 2010 data excluded due to a small sample of recaptures (n = 13).

In all subsequent summaries, lampreys that were trapped at Bonneville and released upstream were included in the ‘passed Bonneville’ category and they were included in upstream reach escapement estimates. Our rationale for treating these fish as successful was three-fold: 1) about 80% of radio-tagged lamprey that reach the vicinity of AFF trap site / Washington-shore count station eventually pass Bonneville Dam (Clabough et al. 2011; Keefer et al. 2013a); censoring these fish would exclude many likely successful migrants, which would bias escapement estimates low; and 3) lamprey trap and haul has been part of the general passage plan at Bonneville Dam, including at the experimental collection structures (i.e., the Cascades Island LPS and the Washington-shore LPS) and in the Cascades Island auxiliary water supply channel.

Table 13. Summary of release to top-of ladder and dam-to-dam reach escapement estimates for HD PIT-tagged (only) lampreys released in the Bradford Island fishway (2005) or downstream from Bonneville Dam (2006-2014) and recorded at or known to pass top-of-ladder sites at monitored dams. Numbers in parentheses are the number past the upstream dam for the reaches starting at release and the number at the downstream dam for the dam-to-dam estimates.

		Release to ladder exit			
Year	Rel	BO	TD	JD	MN
2005	841	0.53 (446)	-	-	0.05 (40)
2006	2000	0.41 (822)	0.28 (558)	0.19 (382)	0.04 (80)
2007	757	0.52 (393)	0.33 (246)	0.17 (129)	0.05 (35)
2008	608	0.52 (318)	0.27 (166)	0.18 (109)	0.05 (28)
2009	368	0.47 (172)	0.25 (90)	0.14 (50)	0.02 (8)
2010	13	[1]0.58 (7)	0.23 (3)	0.15 (2)	-
2011	800	[2]0.56 (451)	0.30 (238)	0.24 (190)	0.08 (65)
2012	823	[3]0.50 (414)	0.26 (212)	0.22 (177)	0.08 (69)
2013	876	[4]0.56 (491)	0.32 (276)	0.21 (180)	0.09 (79)
2014	599	[5]0.56 (334)	0.35 (210)	0.26 (154)	0.13 (75)

	Ladder exit to ladder exit				
	BO - TD	TD - JD	JD - MN	MN - IH	MN - PR
2005	n/a	n/a	n/a	0.05 (40)	n/a
2006	0.67 (840)	0.69 (565)	0.21 (387)	0.06 (82)	n/a
2007	0.63 (393)	0.52 (247)	0.27 (129)	0.14 (35)	n/a
2008	0.52 (318)	0.66 (166)	0.26 (109)	0.18 (28)	0.11 (28)
2009	0.52 (172)	0.56 (90)	0.16 (50)	0.0 (8)	0.50 (8)
2010	0.38 (8)	0.67 (3)	-	-	-
2011	0.52 (462)	0.80 (238)	0.34 (190)	0.23 (65)	0.54 (65)
2012	0.47 (447)	0.83 (212)	0.39 (177)	0.16 (69)	0.49 (69)
2013	0.52 (531)	0.65 (276)	0.44 (180)	0.18 (79)	0.56 (79)
2014	0.58 (361)	0.73 (210)	0.49 (154)	0.12 (75)	0.63 (75)

[1] 0.62 (n = 8); [2] 0.58 (n = 460); [3] 0.54 (n = 447); [4] 0.61 (n = 531); [5] 0.60 (n = 361) when recaptures were treated as passing the dam

In the multi-year logistic regression model for the release-Bonneville reach, escapement increased through the study period (odds ratio year^{-1} = 1.103, *ci* = 1.084-1.122) and increased with lamprey length (odds ratio cm^{-1} = 1.068, *ci* = 1.56-1.080) (Table 14). Lamprey release date was not statistically important (χ^2 = 0.2, P = 0.663). Within each year, longer lampreys were consistently more likely to pass Bonneville Dam than were shorter lampreys (Figure 12). Point estimates of escapement probability from the annual logistic regression models indicated that escapement increased through time for fish of median length (linear regression r^2 = 0.63, P = 0.019) length and for those in the 90th percentile for length (r^2 =0.80, P = 0.003).

Release to Pass The Dalles Dam – Annual escapement estimates from release below Bonneville Dam to past The Dalles Dam ranged from 0.23-0.35 (*mean* = 0.30, CV = 12.7%) (Table 13). The multi-year model indicated a positive year effect (odds ratio = 1.033, *ci* =1.014-1.052), a positive lamprey size effect (odds ratio = 1.122, *ci* =1.108-1.137), and no release date effect (Table 14).

Within each year, longer lampreys were consistently more likely to pass The Dalles Dam than were smaller lampreys: estimated probabilities ranged from <10% for the smallest fish to >60% for the largest fish (Figure 13). The linear regression relationships between year and point estimates of escapement probability from the annual logistic regression models suggested that there was little year-to-year change in escapement past The Dalles Dam at the 10th, 50th, or 90th percentiles of lamprey length (all $P > 0.05$).

Table 14. Reach-specific logistic regression results from models that were used to test whether HD PIT-tagged lamprey escapement was associated with migration year, release date, or Pacific lamprey length in 2006-2009 and 2011-2014. Year was treated as a continuous variable to test the hypothesis that escapement increased through time. Recaptured lamprey were included in all models.

Reach (*n*)	Covariate	χ^2	*P*	Odds ratio	95% ci
Release-Bonneville (6,665)	Year	123.4	<0.001	1.103	1.084-1.122
	Date	0.2	0.663	0.999	0.997-1.002
	Length	137.1	<0.001	1.068	1.056-1.080
Release-The Dalles (6,665)	Year	11.7	<0.001	1.033	1.014-1.052
	Date	0.0	0.987	1.000	0.997-1.003
	Length	314.5	<0.001	1.122	1.108-1.137
Release-John Day (6,665)	Year	33.1	<0.001	1.064	1.042-1.086
	Date	0.1	0.763	1.000	0.998-1.003
	Length	359.4	<0.001	1.156	1.139-1.173
Release-McNary (6,665)	Year	98.1	<0.001	1.188	1.148-1.229
	Date	0.4	0.511	0.998	0.994-1.003
	Length	148.2	<0.001	1.163	1.135-1.191
Bonneville-The Dalles (3,429)	Year	21.8	<0.001	0.943	0.821-0.967
	Date	0.3	0.602	1.001	0.998-1.004
	Length	191.1	<0.001	1.127	1.108-1.147
The Dalles-John Day (1,955)	Year	21.8	<0.001	1.086	1.049-1.124
	Date	0.3	0.610	1.001	0.996-1.007
	Length	88.7	<0.001	1.129	1.101-1.158
John Day-McNary (1,339)	Year	68.3	<0.001	1.189	1.141-1.239
	Date	1.3	0.254	0.996	0.990-1.003
	Length	12.3	<0.001	1.060	1.026-1.095

Release to Pass John Day Dam – Annual escapement estimates from release below Bonneville Dam ranged from 0.14-0.26 (*mean* = 0.20, CV = 19.4%). The multi-year model indicated a positive year effect (odds ratio = 1.064, *ci* =1.042-1.086), a positive lamprey size effect (odds ratio = 1.156, *ci* =1.139-1.173), and no release date effect (Table 14).

Within each year, longer lampreys were sharply more likely to pass John Day Dam than were smaller lampreys: estimated probabilities ranged from <5% for the smallest fish to ≥60% for the largest fish (Figure 14). The regression relationships between year and point estimates of escapement probability from the annual logistic regression models indicated positive slopes (i.e., increasing escapement through time), but no statistically significant effects at the 10th, 50th, or 90th percentiles (all linear regression $P > 0.05$).

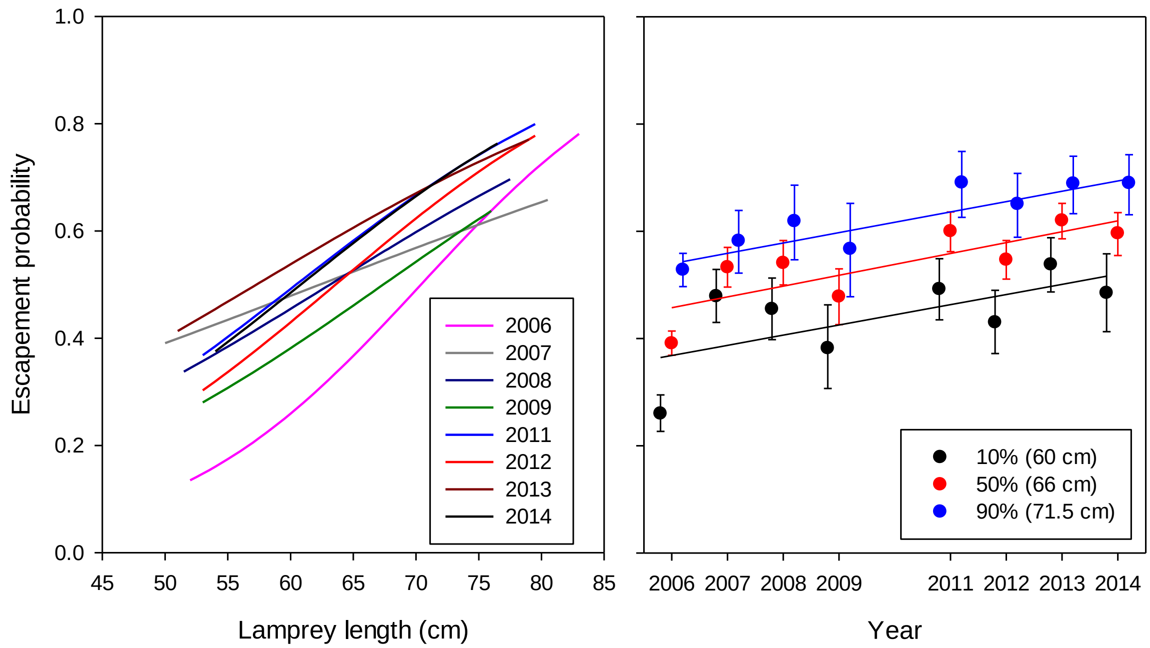

Figure 12. Left: Probability of HD PIT-tagged Pacific lamprey escapement from release past Bonneville Dam in relation to lamprey length (cm) as predicted by annual logistic regression models (2006-2009, 2011-2014). Right: Point estimates (+/- 95% ci) of escapement for lamprey sized at the 10th, 50th, and 90th percentiles of the sample population across all years; lines are linear regression results.

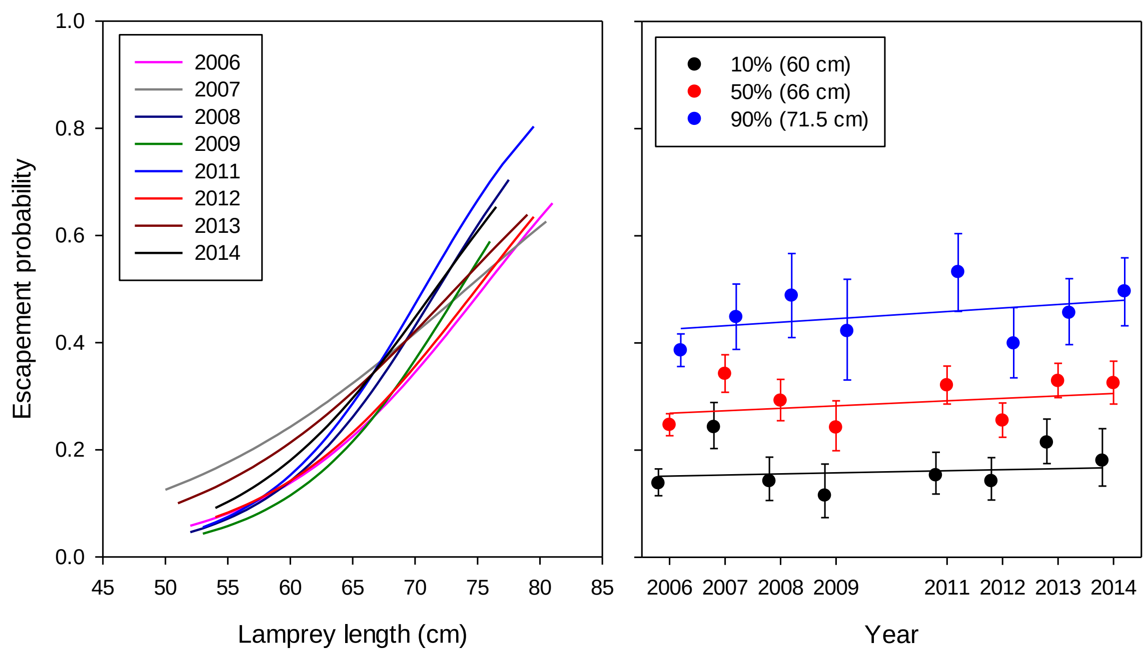

Figure 13. Left: Probability of HD PIT-tagged Pacific lamprey escapement from release past The Dalles Dam in relation to lamprey length (cm) as predicted by annual logistic regression models (2006-2009, 2011-2014). Right: Point estimates (+/- 95% ci) of escapement for lamprey sized at the 10th, 50th, and 90th percentiles of the sample population across all years; lines are linear regression results.

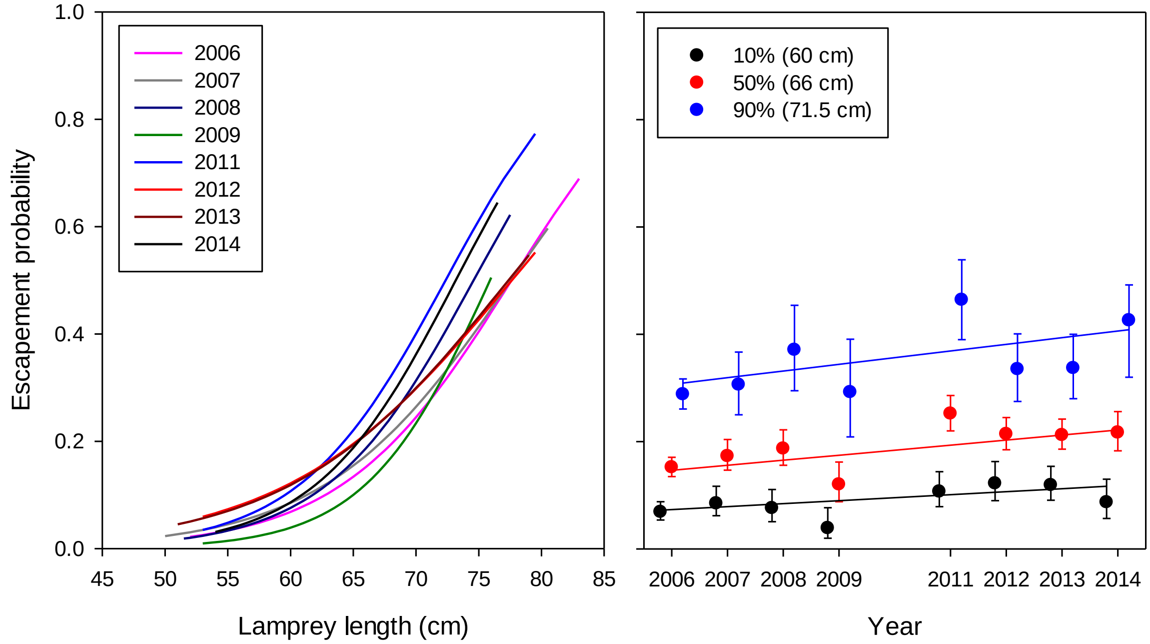

Figure 14. Left: Probability of HD PIT-tagged Pacific lamprey escapement from release past John Day Dam in relation to lamprey length (cm) as predicted by annual logistic regression models (2006-2009, 2011-2014). Right: Point estimates (+/- 95% ci) of escapement for lamprey sized at the 10^{th}, 50^{th}, and 90^{th} percentiles of the sample population across all years; lines are linear regression results.

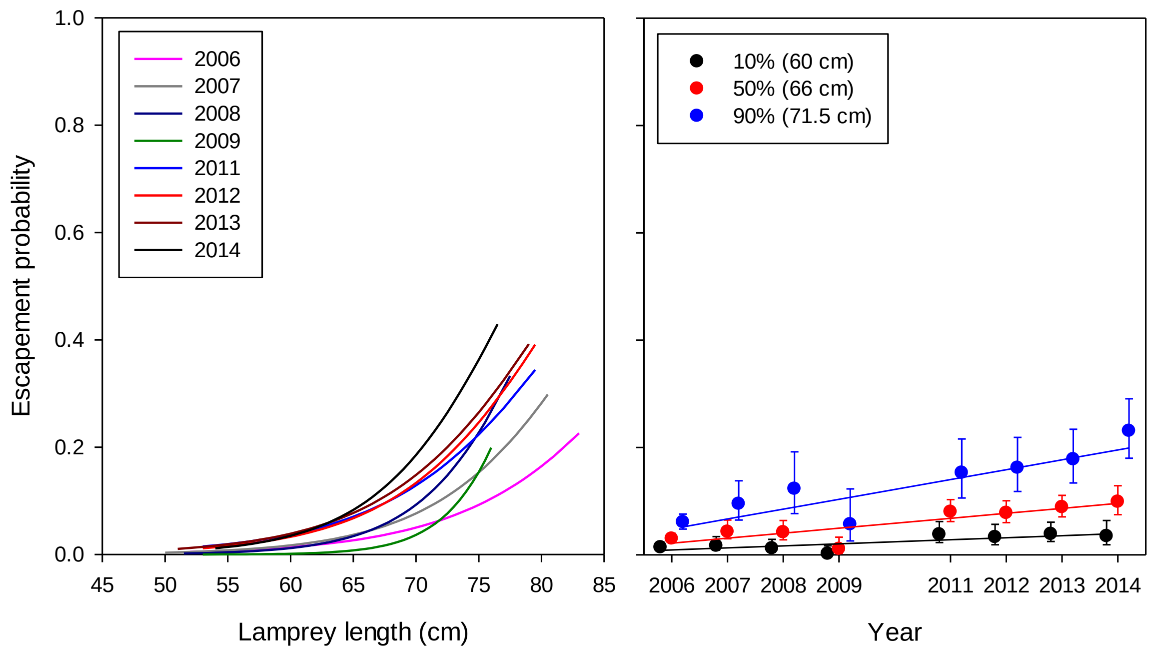

Figure 15. Left: Probability of HD PIT-tagged Pacific lamprey escapement from release past McNary Dam in relation to lamprey length (cm) as predicted by annual logistic regression models (2006-2009, 2011-2014). Right: Point estimates (+/- 95% ci) of escapement for lamprey sized at the 10^{th}, 50^{th}, and 90^{th} percentiles of the sample population across all years; lines are linear regression results.

Release to Pass McNary Dam – Annual escapement estimates from release below Bonneville Dam ranged from 0.02-0.13 (*mean* = 0.07, CV = 51.2%). The multi-year model indicated the largest positive year effect among reaches (odds ratio = 1.163, *ci* =1.135-1.191), a large positive lamprey size effect (odds ratio = 1.188, *ci* =1.148-1.229), and no release date effect (Table 14).

Within each year, longer lampreys were more likely to pass McNary Dam than were smaller lampreys: estimated probabilities ranged from <5% for the smallest fish to ≥30% for the largest fish (Figure 15). The regression relationships between year and point estimates of escapement probability from the annual logistic regression models indicated positive slopes (i.e., increasing escapement through time) for fish in the 10^{th} percentile ($r^2 = 0.62$, $P = 0.021$), 50^{th} percentile ($r^2 = 0.74$, $P = 0.006$), and 90^{th} percentile ($r^2 = 0.80$, $P = 0.003$). The increased monitoring effort in the upper Columbia and Snake rivers may have increased identification of lamprey that passed McNary Dam (i.e., the escapement effect size may have been larger due to increased effort in addition to increased passage).

Top of Bonneville Dam to Pass The Dalles Dam – Annual escapement estimates from the top of Bonneville Dam past The Dalles Dam ranged from 0.47-0.67 (*mean* = 0.55, CV = 12.1%). The multi-year model indicated that the Bonneville-The Dalles reach was the only reach with a negative year effect, with lower escapement in recent years (odds ratio = 0.943, *ci* =0.821-0.967). The model also identified a positive lamprey size effect (odds ratio = 1.127, *ci* = 1.108-1.147) and no release date effect (Table 14).

Within each year, longer lampreys were more likely to pass The Dalles Dam than were smaller lampreys: estimated probabilities were quite variable across years, ranging from ~10-35% for the smallest fish to ≥75% for the largest fish (Figure 16). The regression relationships between year and point estimates of escapement probability from the annual logistic regression models indicated negative slopes (i.e., decreasing escapement through time). None of the regressions was statistically significant ($0.25 \leq r^2 \leq 0.45$, $P \geq 0.069$). We note that reduced detection efficiency, and then non-operation (2013-2014), of the top-of-fishway antenna in The Dalles east fishway may have resulted in passage underestimates in recent years.

Top of The Dalles Dam to pass John Day Dam – Annual escapement estimates through this reach were the highest among all reaches, and ranged from 0.52-0.83 (*mean* = 0.68, CV = 15.8%). The multi-year model indicated a positive year effect, with higher escapement in recent years (odds ratio = 1.129, *ci* = 1.101-1.158), a positive lamprey size effect (odds ratio = 1.129, *ci* =1.101-1.158), and no release date effect (Table 14).

Within almost every year, longer lampreys were more likely to pass John Day Dam than were smaller lampreys: estimated probabilities were variable across years, but were ≥75% for the largest fish in all years (Figure 17). The regression relationships between year and point estimates of escapement probability from the annual logistic regression models had positive slopes (i.e., increasing escapement through time) but none of the regressions was statistically significant ($0.17 \leq r^2 \leq 0.37$, $P \geq 0.110$).

Top of John Day Dam to pass McNary Dam – Annual escapement estimates through this reach were among the most variable across reaches, and ranged from 0.16-0.49 (*mean* = 0.32, CV = 35.9%). The multi-year model indicated a strong positive year effect, with higher escapement in recent years (odds ratio = 1.189, *ci* = 1.141-1.239), a positive lamprey size effect (odds ratio = 1.060, *ci* =1.026-1.095), and no release date effect (Table 14).

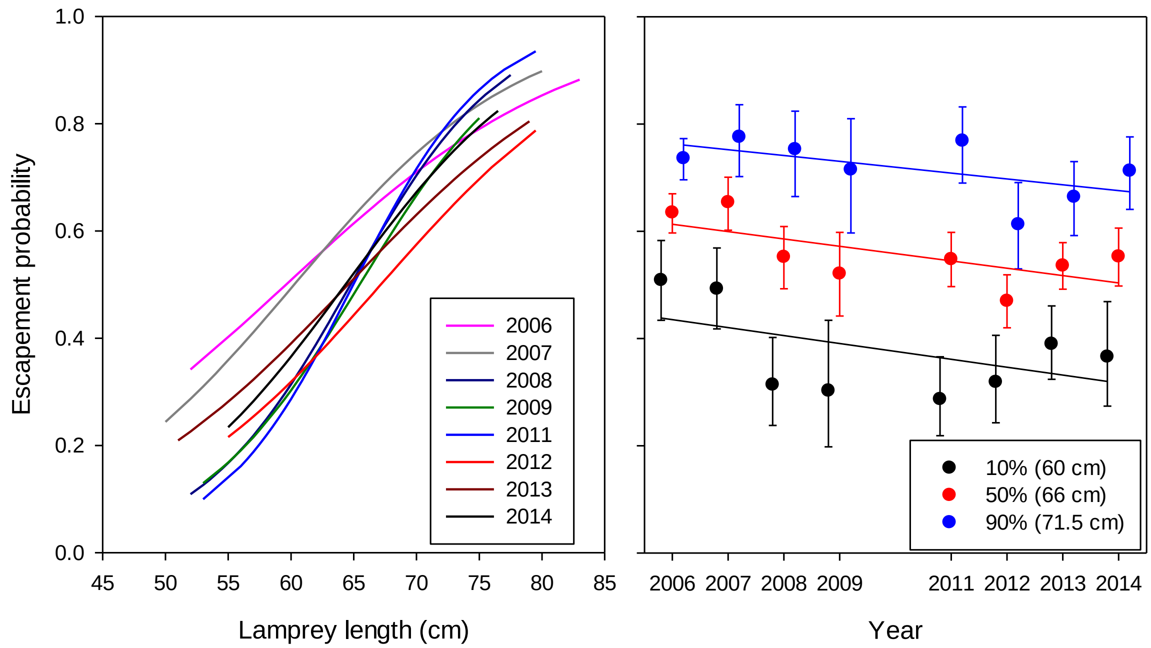

Figure 16. Left: Probability of HD PIT-tagged Pacific lamprey escapement from the top of Bonneville Dam past The Dalles Dam in relation to lamprey length (cm) as predicted by annual logistic regression models (2006-2009, 2011-2014). Right: Point estimates (+/- 95% ci) of escapement for lamprey sized at the 10th, 50th, and 90th percentiles of the sample population across all years; lines are linear regression results.

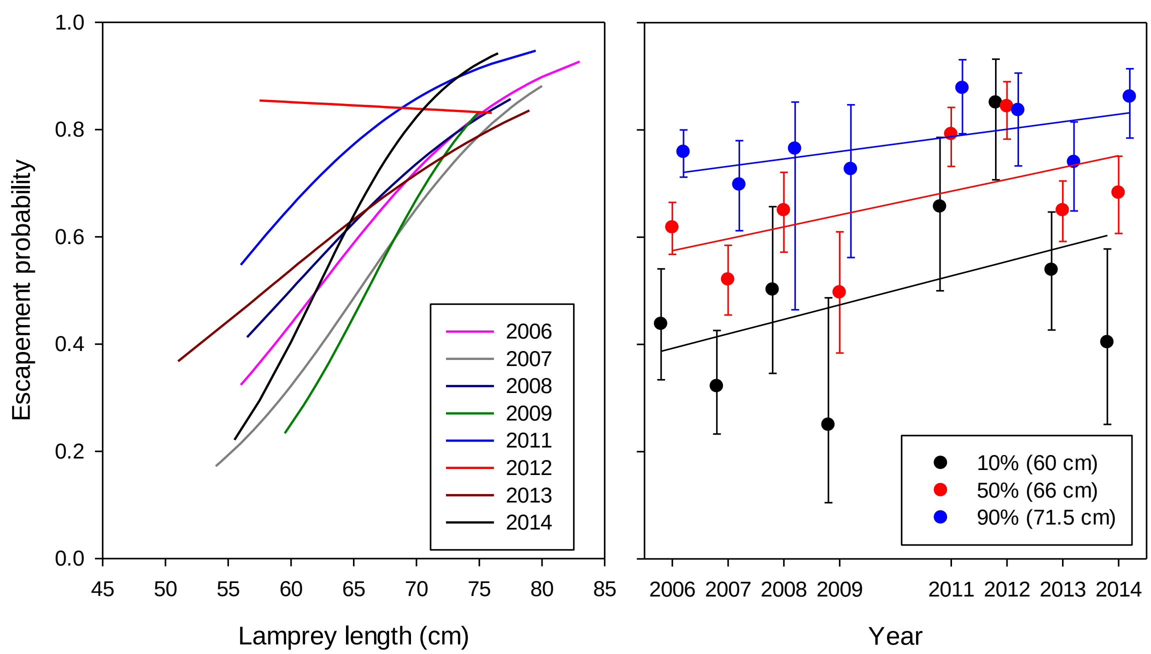

Figure 17. Left: Probability of HD PIT-tagged Pacific lamprey escapement the top of The Dalles Dam past John Day Dam in relation to lamprey length (cm) as predicted by annual logistic regression models (2006-2009, 2011-2014). Right: Point estimates (+/- 95% ci) of escapement for lamprey sized at the 10th, 50th, and 90th percentiles of the sample population across all years; lines are linear regression results.

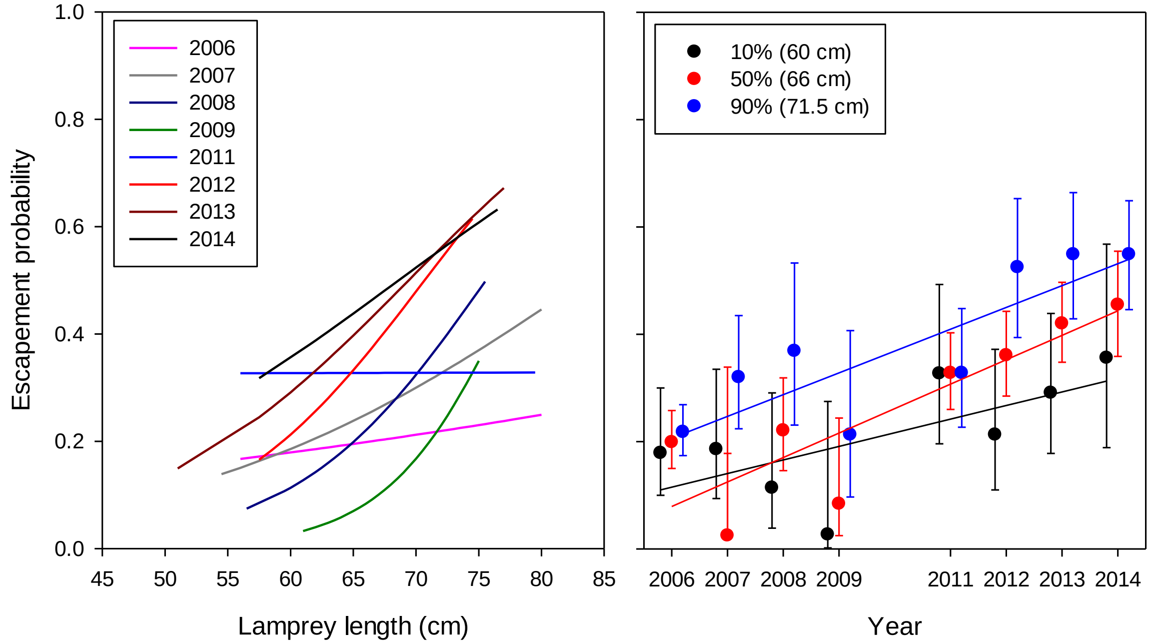

Figure 18. Left: Probability of HD PIT-tagged Pacific lamprey escapement from the top of John Day Dam past McNary Dam in relation to lamprey length (cm) as predicted by annual logistic regression models (2006-2009, 2011-2014). Right: Point estimates (+/- 95% ci) of escapement for lamprey sized at the 10th, 50th, and 90th percentiles of the sample population across all years; lines are linear regression results.

Within almost every year, longer lampreys were more likely to pass McNary Dam than were smaller lampreys (Figure 18). The regression relationships between year and point estimates of escapement probability from the annual logistic regression models had significant positive slopes (i.e., increasing escapement through time) for the 50th (r^2 = 0.73, P = 0.007) and 90th (r^2 = 0.71, P = 0.008) length percentiles.

Reach Passage Times – Calculation of passage times for HD PIT-tagged lampreys required detection at top-of-fishway antennas and they therefore were estimable for only a portion of the fish that passed dams in each study year. Median passage times from release past Bonneville ranged from 6.3-11.5 d (*mean* of medians = 8.8 d, CV = 24.1%), with no evidence for a temporal trend (Table 15). Median times ranged from 4.0-7.0 d (*mean* = 5.1 d, CV – 22.8%) from the top of Bonneville past The Dalles Dam, from 3.3-4.3 d (*mean* = 3.9 d, CV = 10.1%) from the top of The Dalles past John Day Dam, and from 5.4-12.9 d (*mean* = 9.4 d, CV = 26.6%). There was no evidence of a shift in median passage time through the study years in any of these reaches. Importantly, there was a very large amount of variation in lamprey passage times within years. Individual fish passage times were likely sensitive to a variety of environmental factors in the reservoirs, variation in fishway passage efficiency, and lamprey traits in these combined reaches.

Table 15. Numbers of HD PIT-tagged lampreys released in the Bradford Island fishway (2005) or downstream from Bonneville Dam (2006-2014), mean lamprey length, weight, and girth and the median time (days) to pass selected reaches in the lower Columbia River. Note: weight was not collected for all fish in all years.

					Median passage times (d)			
Year	Released	Mean Length	Mean Weight	Mean Girth	Release - Top BO	Top BO - Top TD	Top TD - Top JD	Top JD - Top MN
2005[1]	841	67.9	500	11.5	n/a	n/a	n/a	n/a
2006	2000	67.0	482	11.2	9.6 d	5.1 d	4.1 d	12.8 d
2007	757	64.8	445	10.9	6.5 d	4.0 d	4.3 d	8.8 d
2008	608	64.7	434	10.6	7.7 d	4.9 d	3.7 d	5.4 d
2009	368	65.3	443	10.8	11.5 d	6.7 d	4.1 d	9.8 d
2010	13	63.0	-	-	-	-	-	-
2011	800	64.8	437	10.8	10.2 d	4.3 d	3.4 d	9.1 d
2012	823	65.3	449	10.9	11.3 d	4.7 d	3.3 d	7.5 d
2013	876	65.0	444	10.8	6.3 d	4.0 d	4.3 d	9.2 d
2014	599	67.0	472	11.0	7.2 d	[2]7.0 d	[2]4.1 d	12.9 d

[1] released into the Bradford Island fishway
[2] top of East fishway not monitored in 2013-2014

Multi-Year Summary: Bonneville Double-Tagged Lamprey

The reach escapement time series for double-tagged (radio + HD PIT) lampreys is more difficult to assess due to methodological and technological changes. In the late 1990s to early 2000s, radio transmitters were considerably larger than those available in recent study years. Consequently, only lampreys from larger size classes were radio-tagged early in the time series, whereas a wider spectrum of size classes were tagged starting in 2007 (see Keefer et al. 2013a for transmitter details).

Release to pass Bonneville Dam – Escapement estimates for lampreys released downstream from Bonneville Dam ranged from 0.21-0.46 (*mean* = 0.36, CV = 21.7%) past Bonneville Dam when trap recaptures were censored and from 0.21-0.46 (*mean* = 0.37, CV = 21.0%) when trapped fish were treated as successfully passing (Table 16). Annual Bonneville escapement estimates were positively correlated ($r^2 = 0.57$, $P < 0.05$) with mean lamprey weight across years (Figure 19). Escapement estimates in the two most recent study years (2010, 2014) were well above the regression line, providing indirect support for a size-adjusted increase in lamprey passage in recent years, though this is a speculative conclusion.

Release to Pass Upstream Dams – Annual escapement estimates from release below Bonneville Dam ranged from 0.05-0.23 (*mean* = 0.15, CV = 42.0%) past The Dalles Dam (Table 14). Estimates were 0.01-0.11 (*mean* = 0.05, CV = 63.7%) past John Day Dam and were 0.01-0.02 (*mean* = 0.01, CV = 40%) past McNary Dam. These patterns are consistent with the lower passage success for radio-tagged lampreys versus HD PIT-tagged lamprey described previously of this report and in other study years.

Table 16. Summary of release to top-of ladder and dam-to-dam reach escapement estimates for radio-tagged lampreys released downstream from Bonneville Dam from 1997-2002, 2007-2010 and 2014 and recorded at or known to pass top-of-ladder sites at monitored dams. Numbers in parentheses are the number past the upstream dam for the reaches starting at release and the number at the downstream dam for the dam-to-dam estimates. Note: increased HD PIT monitoring increased the likelihood of detection in later study years.

		Release to ladder exit			
Year	Rel	BO	TD	JD	MN
1997	147	0.33 (49)	0.11 (16)	0.02 (3)	n/a
1998	205	0.36 (73)	0.12 (24)	0.01 (3)	n/a
1999	199	0.41 (82)	0.13 (25)	0.02 (3)	n/a
2000	299	0.41 (123)	0.23 (70)	0.09 (27)	n/a
2001	298	0.43 (129)	0.23 (68)	0.08 (17)	n/a
2002	201	0.46 (92)	0.23 (46)	0.08 (17)	n/a
2007	398	0.21 (83)	0.05 (21)	0.02 (9)	n/a
2008	595	[1]0.25 (146)	0.11 (63)	0.05 (27)	0.01 (7)
2009	596	[2]0.31 (177)	0.11 (68)	0.04 (22)	0.01 (3)
2010	312	[3]0.41 (126)	0.22 (70)	0.11 (34)	0.02 (6)
2014	599	[4]0.37 (224)	0.13 (76)	0.07 (42)	0.01 (8)

[1] 0.26 (*n* = 156); [2] 0.33 (*n* = 198); [3] 0.41 (*n* = 128); [4] 0.41 (*n* = 243); when recaptures were treated as passing the dam

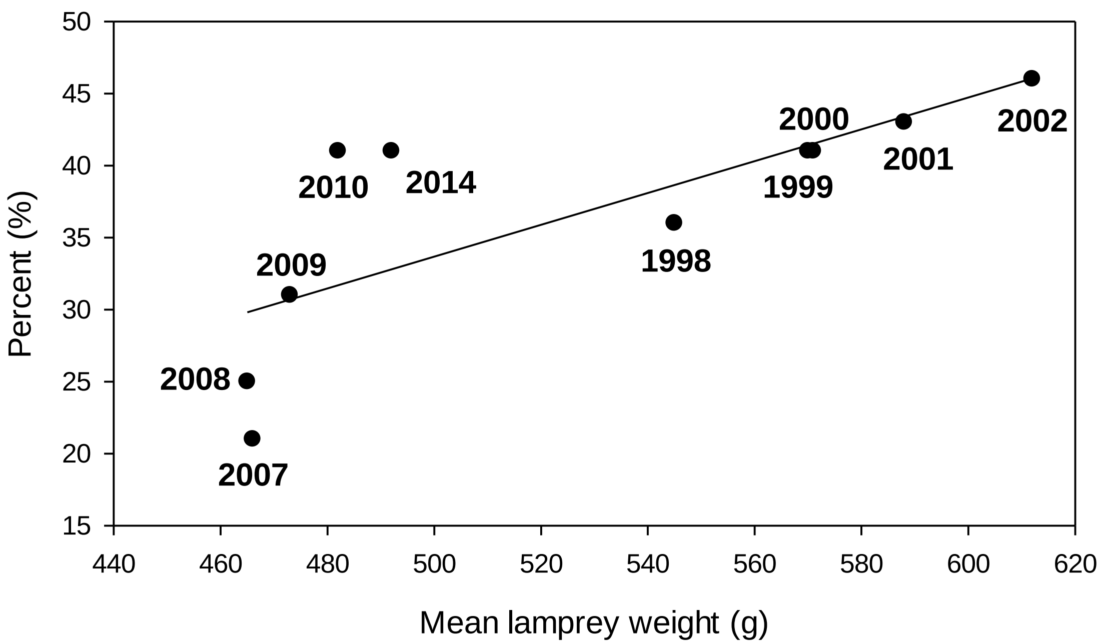

Figure 19. Relationship between annual mean radio-tagged Pacific lamprey weights and the percentage that passed Bonneville Dam of those released (linear regression, r^2 = 0.57). Note: weight data were not collected in 1997.

Table 17. Numbers of radio-tagged lampreys (including double-tagged fish) released below Bonneville Dam from 1997-2002, 2007-2010, and 2014, mean lamprey length (cm) and weight (g), percent detected approaching fishway antennas at Bonneville Dam, percent of tagged fish recorded passing the dam (escapement rate or passage efficiency of fish detected at fishways = passing / approached), and the median passage time (days) to pass the dam after release. Pre-2010 data are from Moser et al. (2002a, 2003, 2004 and 2005) and Keefer et al. (2009a, 2009b, 2010. 2011). The navigation lock was unmonitored in 2007-2010.

Year	Released	Mean Length	Length range	Mean Weight	Weight range	Detected at BON	Escapement Rate[1]	Median BO pass
1997	147	70	60-80	-	>450	88%	38%	4.9 d
1998	205	70	59-79	545	420-830	89%	40%	5.7 d
1999	199	71	65-78	571	475-755	92%	45%	5.5 d
2000	299	70	62-80	570	405-825	87%	47%	4.4 d
2001	298	77	62-82	588	380-880	93%	46%	11.0 d
2002	201	72	60-80	612	440-790	96%	48%	9.0 d
2007	398	66	53-86	466	256-810	68%	31%	3.0 d
2008	595	66	49-79	465	284-706	75%	34%	5.6 d
2009	596	67	56-79	473	276-860	79%	39%	7.5 d
2010	312	67	55-77	482	272-722	88%	46%	12.6 d
2014	599	67	53-79	492	262-788	80%	49%	5.4 d

[1] 'passage efficiency' in previous years; [2] excludes 10 (2008), 21 (2009), 3 (2010), and 19 (2014) lampreys recaptured at a trap and released upstream or in LPS

Discussion

Bonneville HD PIT-Tagged Samples

Downstream Release Group – The migration-scale escapement data generated by the 2005-2014 HD PIT studies provide the most consistently collected baseline monitoring information for adult Pacific lamprey in the Columbia River Basin. In 2014, lamprey escapement for the downstream release group from release past Bonneville Dam (60%) was at the upper end of the distribution of estimates in HD PIT samples from 2005-2013 (41-61%). Furthermore, the relatively low top-of-fishway detection efficiency at the Bonneville HD antenna array suggests that additional lampreys likely passed the dam undetected. The estimate is therefore conservative, as in past years.

The percentage of lampreys that passed John Day Dam (26%) and McNary Dam (13%) in 2014 was higher than previous estimates of 14-24% past John Day Dam and 2-9% past McNary Dam. Dam-to-dam estimates in 2014 were also higher than in previous years for the John Day-McNary (49%) and McNary-Priest Rapids (63%) reaches and estimates for The Dalles-John Day and McNary-Ice Harbor reaches were in the range of previous. HD PIT detection efficiency >90% at the John Day top-of-ladder sites make this dam among the best locations for year-to-year comparisons.

The multi-year analyses of HD PIT-tagged lamprey indicated that reach escapement has increased over the course of the nine study years. In the logistic regression models that controlled for lamprey body size and release date effects, increasing migration year was associated with increasing escapement in six of the seven lower Columbia River study reaches. In several reaches, escapement increased for all lamprey size classes. We think this is indicative – at least in part – of improved passage conditions at the dam fishways. At Bonneville Dam, operations-related improvements implemented specifically for adult lamprey passage include night-time fishway velocity reductions at Powerhouse 2 to increase fishway entrance efficiency (Johnson et al. 2012a); addition of Bonneville LPSs and lifting of picket leads at auxiliary water supply channels in the Washington-shore and Bradford Island fishways (Moser et al. 2011; Corbett et al. 2013). Numerous structural improvements (i.e., pier nose rounding, elimination of steps inside weir orifices, plating over diffuser grating, installation of velocity-reducing bollards in the Cascades Island entrance area, etc.) also presumably contribute to the escapement improvement through time. We think it is possible, if not likely, that changes made at Bonneville Dam have had a 'trickle up' effect on higher escapement through multi-dam and upstream dam-to-dam reaches given that lamprey passage success at Bonneville Dam was historically among the lowest in the FCRPS (e.g., Moser et al. 2002a; Keefer et al. 2012). Structural and operational changes at upstream dams (e.g., orifice rounding, addition of diffuser plating, weir modifications, addition of ramps to raised orifices, blocking access to routes without exits, etc.) presumably also have contributed to the observed changes.

It is important to note that other factors, including river environment and ocean conditions, may have affected the observed escapement pattern. Our analysis did not directly include environmental covariates. From 2005-2014, there was a slight trend (r^2 =0.19) of increasing Columbia River June-August discharge and decreasing June-August water temperature (r^2 =0.07). It is possible that temperature and flow patterns contributed to the year-to-year differences in escapement, though these modest trends are not likely enough to explain all of the differences. Similarly, changes in ocean environment or productivity of Pacific lamprey prey species (e.g., Murauskas et al. 2013) have the potential to affect lamprey condition upon arrival at Bonneville Dam and consequently on upstream migration behavior or distance. Testing for these types of relationships, however, was beyond the scope of our analyses.

The 2014 escapement data for the downstream release group indicated higher dam passage for larger fish at a variety of spatial scales, consistent with many previous studies (e.g., Keefer et al. 2009b, 2013a, 2013b). We have hypothesized that this pattern is related to swimming ability, energetic reserves, and/or to more negative handling effects for smaller fish (e.g., Moser et al. 2007). However, handling effects almost certainly cannot fully account for the size effects reported across recent studies because the effect has been evident regardless of tag type and size (i.e., HD vs. JSATS vs. radiotelemetry) and handling time (i.e., longest for radiotelemetry) and there has been no evidence of an interaction between size and tag effects. There is also evidence that the relationship between migration distance and lamprey body size has a genetic basis. Using data collected in this series of HD PIT and radiotelemetry studies, Hess et al. (2014) identified genetic markers that link Pacific lamprey phenotype (e.g., body size) with migration distance in the Columbia River basin.

Lamprey migration times through dam-to-dam study reaches generally fell within the ranges reported in previous HD PIT study years (Release-Bonneville, The Dalles-John Day) or were slightly slower than in the past (Bonneville-The Dalles, John Day-McNary). The slower median times in the latter two reaches were slower than in the year with the next-longest passage times by about 5%, which translates to a few hours. Although we do not have an explanation for the slightly slower passage in 2014, it was not likely a biologically important effect for most fish. Because HD PIT monitoring was primarily limited to upper fishway sites, it was not possible to separate the time lampreys spent passing dams versus migrating through reservoirs (but see comments below regarding double-tagged fish). Median migration rates of HD PIT fish from ladder top to ladder top (i.e., past one reservoir + one dam) were mostly 11-13 km•d^{-1} but maximum rates exceeded 50 km•d^{-1}. The median rates were similar to the median values recorded for radio-tagged lampreys in the unimpounded John Day, Snake, and Clearwater rivers (Robinson and Bayer 2005; McIlraith et al. 2015) and were faster than rates recorded for radio-tagged lampreys in the Willamette River (Clemens et al. 2012).

As mentioned previously, several new HD PIT monitoring sites have been installed in recent years, including at upper Columbia River and Snake River dams, and in the Hood River, Fifteenmile Creek, Deschutes River, and Umatilla River. These sites help with a final accounting for fish that would not have been possible previously. The addition of new monitoring sites complicates direct inter-annual comparisons of reach escapement and final distribution estimates. The antenna near the Deschutes River mouth has provided particularly informative data, as relatively large numbers of lampreys from all release groups (including those PIT tagged at John Day Dam) were last detected in the Deschutes River. Fifteenmile Creek continued, in 2014, to be used by more lamprey than the Hood River, indicating that it is an important spawning tributary to the Bonneville reservoir and illustrates that lamprey use is not directly associated with tributary size. Monitoring tributary entry remains a critical challenge for adult lamprey tagging studies. Gaps persist at many other tributaries potentially used by adult lamprey (e.g., tributaries below Bonneville Dam, the Wind, Klickitat, and White Salmon rivers, Willow and Rock creeks, the John Day and Walla Walla rivers, etc.).

About 27% of downstream-released HD PIT-tagged lampreys were not detected after release in 2014. This was the lowest non-detected percentage in the multi-year study, but continues to be cause for concern. The underlying reasons for failed passage and the ultimate fate of these adults remain unknown: they may have been lost to the reproductive population (true migration and reproductive failure), moved upstream without detection, and/or they may have moved into downstream tributaries or used main stem sites downstream from Bonneville Dam for spawning. The observation of high fallback at John Day Dam and entry to the Deschutes River among the sample of HD PIT tagged lamprey in 2014-2015 suggests some undetected lampreys released below Bonneville Dam moved downstream and entered tributaries.

Stevenson Release Group – Lampreys used in Bonneville flume experiments and then released upstream from Bonneville Dam had migration outcomes that were broadly similar to those in the downstream-released sample, despite important differences in the samples. The flume group was selected from the first half of the 2014 migration and therefore encountered cooler water temperatures and lower discharge than the downstream sample. Release into the Bonneville forebay also eliminated the significant barrier to dispersal presented by Bonneville Dam and adults released a Stevenson had a smaller size distribution than the group entering Bonneville Reservoir after downstream release.

About 39% of the flume fish were never detected after release, a rate that was higher than the 27% undetected from the downstream release group. However, the nearest upstream HD PIT antennas from the Bonneville forebay were in the Hood River, followed by Fifteenmile Creek and at The Dalles Dam – all of which were 10s of kilometers further upstream than the nearest sites for the downstream release group (i.e., the antennas inside the Bonneville fishways). Undetected lampreys from the forebay release group may have entered unmonitored tributaries, fallen back downstream past Bonneville Dam, spawned in the Bonneville reservoir, or died after release. Smaller size was associated with tributary entry compared to upstream passage of The Dalles Dam (Figure 6) and thus, the differences in size between the Stevenson release group and adults passing Bonneville Dam and entry into unmonitored tributaries likely contributed to the difference in detection rate.

Escapement from forebay release past The Dalles Dam was 49%, which was lower than the most comparable estimate for the downstream release group: 58% from the top of Bonneville Dam past the Dalles Dam. This may indicate a negative effect of handling for the flume group, or may have been related to earlier release timing for the flume group. Lampreys from the downstream release group that volitionally passed Bonneville Dam also may have had traits that favored upstream migration (i.e., they were larger or more motivated, on average). Escapement estimates between The Dalles and John Day dams were more similar for the two release groups at 73% (downstream release) and 69% (forebay release) as were estimates for the John Day-McNary reach (49% and 47%, respectively). These similarities may reflect the higher probability of dam passage by the largest lampreys in the samples as the fish progressed upstream. There may also have been other unmonitored processes that affected the convergence in estimates for the two release groups. The data do suggest, however, that the use of lampreys in short-duration fishway experiments did not have large negative consequences on post-release migration and distribution relative to the non-experimental group (see Kirk et al. 2015 for additional details regarding the experimental sample).

Bonneville Double-Tagged Sample

The 2014 escapement estimate for radio-tagged lamprey from release to top-of-ladder sites at Bonneville Dam was 41%, within the range of the estimates in the 1997-2002 and 2007-2010 radiotelemetry studies (33-46%) but lower than all but one of the HD PIT estimates from 2006-2014 (41-61%). Perhaps more importantly, the radiotelemetry result for 2014 was substantially higher than the 2007-2009 radiotelemetry estimates (21-31%) and was the same as the 2010 estimate; these four years were the most directly comparable radiotelemetry study years because smaller transmitters were available and lampreys from all size classes were tagged. Multi-dam escapement estimates for radio-tagged lampreys in 2014 were in the middle of the ranges of estimates from the 1997-2002 and 2007-2010 studies. Thirteen percent of the radio-tagged fish released eventually passed The Dalles Dam and 7% passed John Day Dam in 2014.

Metrics used to evaluate radio-tagged lamprey use of fishways at Bonneville, The Dalles, and John Day dams (i.e., approach and entry times, entrance and fishway passage efficiencies, etc.) indicated that dam passage efficiency was ~47% at The Dalles Dam in 2014 (Clabough et al. 2015). This was low compared to the 10-year median of 68% (range 55-79%) (Keefer et al. 2012). Fishway entrance efficiency at The Dalles Dam was also relatively low in 2014 compared to previous years, particularly at the east fishway. We are continuing to investigate potential operational and environmental explanations for the lower passage.

In 2014, a relatively low percentage of the radio-tagged lampreys were last recorded in tributaries or at upper basin sites. Only about 13% of the fish that passed Bonneville Dam entered lower Columbia River tributaries, the Snake River, or passed Priest Rapids Dam. This was at the low end of the 13-25% recorded with similar monitoring effort in 2008-2010. Relatively few lampreys were detected in Bonneville reservoir tributaries in 2014 (n = 10, 4% of those that passed Bonneville Dam) compared to some previous years (Keefer et al. 2009c, 2010). Similarly, the five fish in the John Day River (12% of those that passed John Day Dam) in 2014 was proportionately lower than in some previous years (Keefer et al. 2011). We do not currently have a hypothesis to explain these year-to-year differences.

Two additional important escapement results from this study were consistent with those from previous studies. Specifically, a majority (59%) of tagged adults did not pass Bonneville Dam in 2014 and a large portion (~65%) of adults that passed Bonneville Dam were not detected in Bonneville reservoir spawning tributaries and did not appear to have passed The Dalles Dam. The underlying reasons for failed passage and the ultimate fate of these adults remain unknown. Whether the lampreys were lost to the reproductive population (true migration and reproductive failure) or whether these adults used main stem Columbia River sites for spawning remains an important question. Results of acoustic telemetry studies in the Bonneville Reservoir indicate that adults move quickly through the reservoir with low mortality or enter tributaries. Among JSATS-tagged lamprey not passing The Dalles Dam in the fall, most have final records in the tailrace of the dam and a small proportion has been recorded moving downstream to tributaries in the spring (Noyes et al. 2015). Whether adults last recorded in the tailrace and upper reservoir were able to spawn in the tailrace, were predated, were prespawn mortalities, or entered tributaries undetected remains unknown. Noyes et al. (2015) provides a summary of tributary entry, including a simulation of potential lamprey use of unmonitored tributaries. HD-PIT data from recent years indicate that a small proportion overwinter below Bonneville Dam or in the Bonneville reservoir, move upstream in the spring, and may move into spawning tributaries above Bonneville Dam.

The 2014 radio-tagged lamprey passed quickly through reservoirs as compared to past dams, as has been reported in previous studies (e.g., Keefer et al. 2012; Moser et al. 2013). Median times in 2010 were ~2.2 d through the Bonneville reservoir and ~1.5 d through The Dalles reservoir. These times were approximately twice as long as those recorded for summer Chinook salmon and sockeye (Keefer et al. 2004; Naughton et al. 2005), and faster than or within the range of times calculated for radio-tagged lampreys in 2007-2010. Median lamprey passage rates through the Bonneville and The Dalles reservoirs were 32 and 26 $km\bullet d^{-1}$, respectively. These rates were similar to or faster than the passage rates recorded for radio-tagged lampreys in the unimpounded John Day and Snake rivers (Robinson and Bayer 2005; McIlraith et al. 2015) and were consistent with those for radio- and PIT-tagged lampreys in the Columbia River in previous years (e.g., Keefer et al. 2009b).

John Day HD PIT-Tagged Sample

This sample was collected and tagged opportunistically during the peak of the run and there were no previous data collected under similar circumstances for making comparisons. Nonetheless, there were several important results worth noting. First, the John Day north LPS was effective for collecting upstream migrating lampreys. The 100 HD PIT-tagged fish were 8.1% of the 1,228 lampreys collected from the LPS in 2014 during 99 days of operation. Second, the release site near the end of the navigation lock pier nose was apparently too close to John Day Dam as 41% of the sample had HD PIT detections that suggested the fish moved downstream of the dam. Lamprey fallback has historically been relatively high at John Day Dam versus at other lower Columbia River dams (unpublished radiotelemetry results), but the 41% estimate in 2014 was among the highest reported. It was not possible to determine fallback routes from the HD PIT data, but some fish likely passed over the spillway or through turbines, while others may have moved down the adult fishways. Continued trap-and-haul of lampreys collected at the John Day north LPS is likely in the short term and we recommend that the release site for transported fish be moved further upstream or to a location more distant from the John Day spillway.

A third important result was that HD PIT tagged lampreys that moved upstream after release appeared to behave similarly to tagged fish from the Bonneville-tagged samples. Ten percent of the John Day sample eventually entered the Snake River and 31% were last detected at or upstream from Priest Rapids Dam. The 3:1 Snake River to Upper Columbia River ratio was similar to results in tagging studies conducted in previous years (Keefer et al. 2013b). About a quarter (26%) of the John Day sample was not detected after release, which was lower than the non-detection rate for the 2014 Stevenson HD PIT group (39%) and the non-detection rate for the HD PIT group released below Bonneville Dam (27%). Some of the undetected fish from the John Day release likely entered the unmonitored John Day River, a tributary with considerable known spawning by Pacific lamprey, or Rock Creek (less is known regarding lamprey use).

Finally, we note that ~1:8 lamprey from the sample moved downstream and was detected entering the Deschutes River and that these lamprey were among the smallest of the 100 (Figure 11). This result suggests the potential for a size-dependent threshold that induced downstream movement and tributary entry, perhaps caused by capture and handling or the exertion of entering the John Day North Fishway and LPS. Downstream movement by many fish from the John Day tag group also appears to be consistent with results from other release sites; the degree to which the behavior is associated with handling is unknown.

Negative Effects of Radio Tagging

An ongoing concern in the adult lamprey tagging program has been that radio-tagged fish have significantly lower escapement than HD PIT-tagged fish in almost all study reaches. In contrast, passage times for the two groups have generally been similar, with radio-tagged fish passing more rapidly in some reaches and HD PIT-tagged fish passing faster in others. Higher escapement by larger fish has also been consistent across tag types. One obvious explanation for the escapement differences is that the additional tag burden of radio tagging and associated handling negatively affects survival relative to HD PIT tagging. Total handling time (including anesthetized time) for radio-tagged lampreys has averaged about ten minutes versus about three minutes for HD-PIT tagging. In addition, the incision has been larger for radio transmitter insertion, sutures are required, and the diameter of the transmitter is about double that of the HD-PIT tag (8 mm versus 4 mm, respectively). The external trailing radio antenna may be a concern for lamprey given their swimming behavior and attachment to surfaces. Qualitative observations also suggest some negative behavioral reaction to the antennas, which lampreys may perceive as an ectoparasite. Sutures required to hold transmitters inside the body cavity may also pose a problem as they come in contact with benthic substrates (Mesa et al. 2003) or if they fail to dissolve (Mesa et al., *unpublished data*).

Radio tagging was associated with a ~7-15% reduced probability of reach escapement in 2014 relative to HD PIT tagging. This difference was similar in scale to results from 2009, the most recent year with adequate samples of both HD PIT and double-tagged fish (Keefer et al. 2010). Given the lamprey handling and tagging experience of most of the technicians at Bonneville Dam in 2014, we think it is unlikely that additional training or minor modifications to the radio tagging protocols can substantively improve escapement outcomes, though review of procedures may be beneficial. To what degree the difference in escapement represents mortality vs. shorter migration distance and undetected movement into tributaries (i.e., after overwintering in reservoirs and tag failure) remains unknown. Regardless, the informational value of radiotelemetry data for any future studies must be weighed against the reduced upstream escapement associated with the radiotelemetry.

Antenna Detection Efficiency

Understanding detection efficiencies for the HD PIT and radiotelemetry arrays is a challenge with important implications for study results. We used the double-tagged sample to evaluate detection efficiency of both systems and also used HD PIT detections at all sites to estimate minimum efficiency for the dam-wide arrays. In the double-tagged evaluation, the reliability of estimates is constrained by the number of lampreys detected at any given antenna. In the HD PIT-only evaluation, there is an additional risk of underestimating detection efficiency when fish pass a dam via unmonitored routes (e.g., navigation locks or off-fishway routes that do not pass through antennas) but are subsequently detected upstream. For example, 141 HD PIT-tagged lampreys were detected upstream from John Day Dam and were used to estimate detection efficiency, but at least 255 passed John Day Dam based on exit antennas and upstream records (i.e., 114 fish detected at John Day antennas were excluded from efficiency estimates at the dam because they were not detected upstream).

Top-of-ladder detection efficiency estimates from the double-tagged group ranged from 78-100% for the radiotelemetry sites and from 72-100% for the HD PIT sites. However, the radiotelemetry antennas had notably higher efficiency at the Bonneville Washington-shore fishway (97% versus 72%) and at The Dalles north fishway (100% versus 83%). Better detection performance for the radiotelemetry system was expected, was consistent with results from previous years, and was largely a function of differences in read range for active radio transmitters (up to 10s of meters for underwater antennas) versus passive tags (often < 1 meter).

As in past years, the highest detection efficiencies at HD PIT antennas (based on HD data only) were at the top-of-ladder sites at John Day Dam. The fishways at these sites have relatively small cross-sections and there are no alternative routes past the antennas. Efficiencies were also high at the combined antenna sites at Ice Harbor, Lower Monumental, and Priest Rapids dams. Efficiency continues to be well below preferred levels at Bonneville, The Dalles and McNary dams. In part, this is due to aging antenna infrastructure, as many individual antennas have been in place since 2005 and opportunities to repair or replace these sites are intermittent. Additionally, these sites consist of single antennas at each location rather than a series of antennas (as are used at the Bonneville Dam FD PIT antennas at the Bradford Island and Washington Shore fishway exits). Improving efficiency for the HD PIT system can be achieved by building antenna redundancy into the most important monitoring sites (e.g., Bonneville Dam exits), as has been done for the highly efficient full duplex (FD) arrays. In the meantime, detection efficiencies for HD PIT antenna sites will remain lower than preferred and result in some underestimation of dam passage and reach escapement rates. Antenna redundancy at upriver locations reduces the underestimation bias (i.e., some fish that pass undetected can be counted as passing a site based on upstream detections), but low efficiency at some sites remains a challenge.

Conclusions

The multi-year HD PIT and radiotelemetry studies have provided a wealth of information about lamprey behavior at reach and full-migration scales. The resulting multi-year datasets are by far the best baseline data for evaluating changes in lamprey passage performance at dams and in the FCRPS hydrosystem as improvements are implemented. The HD PIT and radiotelemetry monitoring complement experimental testing and the JSATS study results from recent years (Naughton et al. 2011; Noyes et al. 2014, 2015), and we think this type of integrated, multi-scale approach will continue to advance our understanding of lamprey passage at dams and their distribution in the basin.

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Appendix A. 2014 Columbia River discharge and temperature profiles.

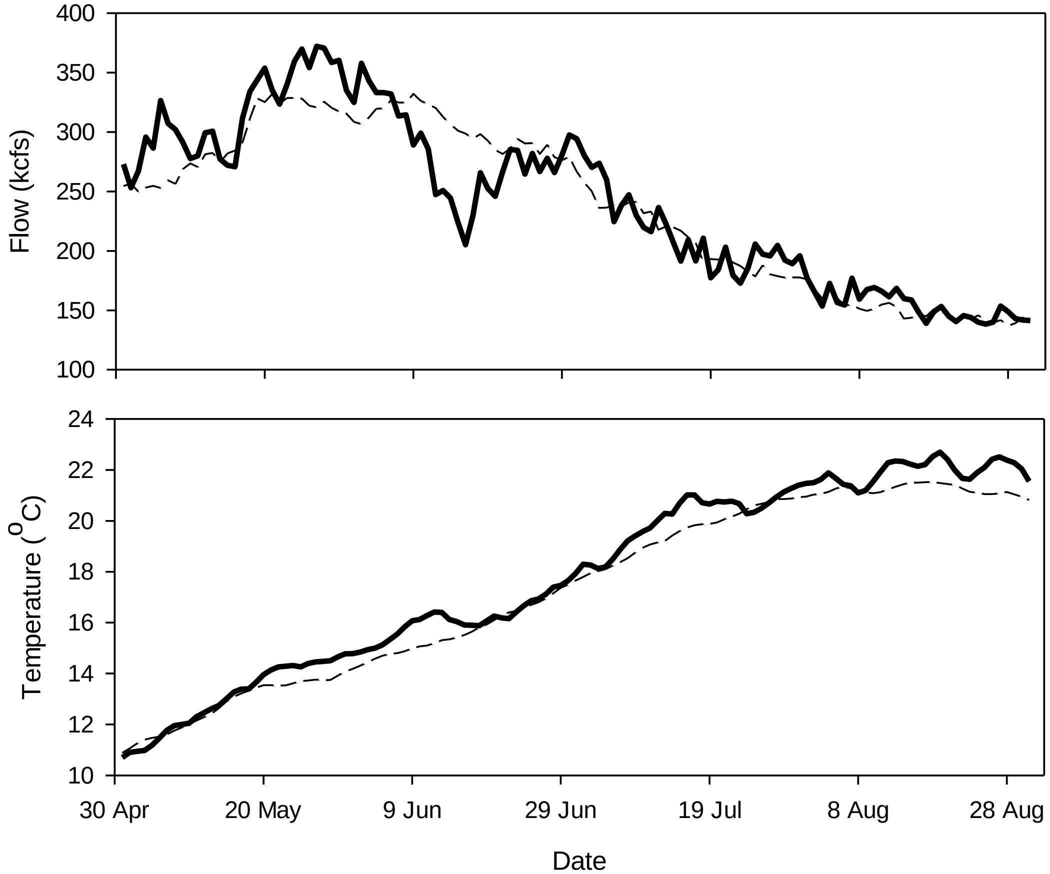

Figure A1. Mean daily Columbia River flow (kcfs) and temperature (°C) at Bonneville Dam in 2014 (solid line) and the 2004-2013 average (dashed line).