Technical Report 2019-2

ADULT PACIFIC LAMPREY MIGRATION IN THE COLUMBIA AND SNAKE RIVERS: 2018 RADIOTELEMETRY AND HALF-DUPLEX PIT TAG STUDIES

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

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T. J. Blubaugh, G. Brink, M. Hanks, C. T. Boggs, and C. C. Caudill
Department of Fish and Wildlife Sciences
University of Idaho, Moscow, ID 83844-1136

For

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

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Executive Summary

The 2018 adult Pacific Lamprey (*Entosphenus tridentatus*) studies assessed migration and behavior in the Columbia River Hydrosystem at a variety of scales. The results summarized in this report address reach-scale and system-wide migration using detection data from lampreys tagged with either half duplex (HD) passive integrated transponder (PIT) tags or an HD PIT tag and a radio transmitter. Companion 2018 study reports provide dam-specific fishway and dam passage metrics from the radio-tagged sample and behavioral summaries for the HD PIT-tagged fish in and near Bonneville lamprey passage structures (LPSs) (Clabough et al. 2019). Results of experimental behavioral trials conducted in the Bonneville Adult Fish Facility (AFF) fishway flume are reported in Hanchett and Caudill (2019).

HD PIT-Tagged Samples

We HD PIT-tagged and released two samples of lampreys collected at Bonneville Dam: a group of 578 released downstream from the dam and 309 that were used in artificial fishway experiments at the Bonneville Adult Fish Facility and then released upstream from Bonneville Dam near Stevenson, Washington. We monitored lamprey passage rates and escapement past Bonneville, The Dalles, John Day, and McNary dams. We also used PIT detection data from upper Columbia River dams, Lower Snake River dams, and some lower Columbia River tributaries that 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 2018 escapement estimate for the downstream release group past Bonneville Dam was 51% (trap recaptures treated as not passing) to 55% (recaptures treated as passing), based on all data collected through March 2019. These escapements were near average estimates from the 2006-2014 HD PIT studies (*range* = 41-61%) and will likely increase slightly once post-overwintering movements are included. Escapement from the top of Bonneville Dam to the top of The Dalles Dam (48%) and from the top of The Dalles Dam to the top of John Day Dam (68%) were similar to estimates in previous years. An outbreak of the bacterial disease furunculosis was identified in mid-migration, after which we assessed all lampreys for symptoms (e.g., red hemorrhaging around the mouth). About 22% of the PIT-tagged (and double-tagged) lampreys were symptomatic, and these fish had lower escapement than non-symptomatic fish past the four lower Columbia River dams.

Large lampreys were substantially more likely than small lampreys to pass through most 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.

Lamprey migration times were highly variable in 2018, as in all previous HD PIT study years. The median passage time was 5.3 days (< 1 km•d^{-1}) from release to the top of Bonneville Dam, which was the fastest median time reported across study years. Median times between top-of-ladder antennas were 4.0 days between Bonneville and The Dalles dams (relatively fast), 3.8 days between The Dalles and John Day dams (similar to previous years), and 8.9 days between John Day and McNary dams

(relatively fast). Each of these reaches included one reservoir and one dam. Faster than average times may have been related, in part, to above-average water temperatures.

We also monitored the upstream progression of HD PIT-tagged lampreys that were first used in fishway experiments (i.e., in flume studies at Bonneville Dam), but this sample was not collected in proportion to the run (it was comprised of primarily late-run fish) 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 39% past The Dalles Dam, 29% past John Day Dam, and 6% past McNary Dam through March 2019. Nearly half of the flume study lampreys were not detected after release.

Double-Tagged Sample

The 2018 escapement estimate from release past Bonneville Dam was 40% (recaptures treated as passing) through March 2019, which was similar to the highest estimates from comparable 2007-2014 radiotelemetry studies. Escapement estimates from release past The Dalles (18%), John Day (8%) and McNary (3%) dams were all above average in 2018. 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 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 6.3 days from release to the top of Bonneville Dam, 3.1 days from tailrace to top-of-ladder antennas at The Dalles Dam, and 1.3 days between tailrace and top-of-ladder antennas at John Day Dam. Median passage times through reservoirs were 2.7 d (Bonneville) and 1.7 d (The Dalles).

In contrast to previous radiotelemetry years, no tributaries were monitored with radio antennas in 2018. As expected, a lower percentage (~8%) of lampreys was last detected in tributaries through March 2019 than in previous years (13-25%); detections were at PIT antenna arrays. A majority (~61%) of the double-tagged sample was last detected at or downstream from Bonneville Dam. About 11% was last detected at top-of-fishway sites at Bonneville Dam, ~14% was last detected at The Dalles Dam, and ~8% was at John Day Dam. Final lamprey distributions are expected to change slightly after post-overwintering movements are completed; some lampreys tagged in 2018 continued to be detected moving upstream through August 2019.

Introduction

The Pacific Lamprey (*Entosphenus tridentatus*) is the largest lamprey species in the Columbia and Snake River basins. Pacific Lampreys are anadromous, and parasitic adults spend 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 substantially declined in the Columbia River basin and in other regional rivers starting in the early 1960's (Kostow 2002; Clemens et al. 2010, 2017; Luzier et al. 2011; Wang and Schaller 2015). Habitat loss, river impoundment, ocean conditions, ocean prey base (Murauskas et al. 2013), and water pollution have all likely contributed to the decline. Pacific 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). A range of research and management actions have been taken to understand and improve adult lamprey passage, including operational and structural changes at dam fishways (Andersen and Le 2010; Moser et al. 2011, *in press*; USACE 2014; Ackerman et al. 2019).

Radiotelemetry was used in an intermittent series of studies from 1997-2014 to identify lamprey problem passage areas at dams, 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 Lampreys in the Columbia River basin (e.g., Moser et al. 2002b, 2005; Johnson et al. 2012; Keefer et al. 2012, 2013a; Clabough et al. 2015). Starting in 2005, half duplex (HD) passive integrated transponder (PIT) tag monitoring sites were deployed at dams to monitor PIT-tagged adult lampreys. PIT tags are uniquely identifiable, allowing for individual fish monitoring. PIT tags are also relatively small and inexpensive and (unlike radio transmitters) are not limited by battery life; these are 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 (FD) PIT tags used to monitor salmonids in the basin and because HD PIT tags have longer read ranges. (Note: the prohibition on use of FD tags for Pacific Lamprey has ended.)

The objectives of the 2018 studies described in this report were 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; and (3) examine potential morphological and environmental correlates with upstream passage. This report also includes information on two unexpected study developments: (1) a group of small-bodied ('dwarf') Pacific Lampreys collected at Bonneville Dam in 2018; and (2) an outbreak of furunculosis during the 2018 run. Dwarf Pacific Lampreys have been reported to return to freshwater at lengths < 37 cm (Hess et al. 2015). They have been collected in western Washington, Oregon, and British Columbia in coastal streams as well as larger rivers like the Willamette and Fraser rivers (Beamish 1980; Beamish and Levings 1991; Kostow 2002; Hayes et al. 2013) but have been captured rarely at the Bonneville Dam Adult Fish Facility before 2018. Furunculosis, caused by *Aeromonas salmonicida*, is a bacterial disease that affects fishes worldwide (Austin and Austin 2012). Although the pathogen has been primarily known to infect salmonids, there are increasing reports of outbreaks in non-salmonids (see Faisal et al. 2007). *Aeromonas salmonicida* has been detected in Pacific Lamprey in the Columbia River Basin (Cummings et al. 2008). More spatially-detailed evaluations of tagged lamprey behaviors in and near lower Columbia River dam fishways in 2018, including their use of lamprey passage systems (LPSs) and summaries of their response to nighttime fishway velocity experiments at Bonneville and The Dalles dams, are presented in a separate report (Clabough et al. 2019).

Methods

Lamprey Collection and Tagging

In 2018, three samples of adult lampreys were collected at night in traps located in the fishway near the Bonneville Dam Adult Fish Facility (AFF). These fish were tagged in the AFF prior to release. The three groups were: 1) 578 lampreys tagged with only half-duplex passive integrated transponder (HD PIT) tags and released downstream from Bonneville Dam near Hamilton Island or Tanner Creek (rkm 232.0); 2) 309 lampreys tagged with HD PIT tags, used in experimental flume trials at the AFF, and then released upstream from Bonneville Dam at Stevenson boat ramp (rkm 242.7); and 3) 595 lampreys that were double-tagged with HD PIT tags and radio transmitters and released downstream from the dam near Hamilton Island or Tanner Creek. (Note: summaries of the flume experiments will be reported in Hanchett and Caudill 2019)

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 are less likely to enter fishways. Before tagging, all lampreys 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 lampreys 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 5.1-6 sec, tag life 69 d; model NTC-4-2L, Lotek Wireless Inc.) were surgically implanted in lampreys with a girth circumference > 9 cm (at the insertion of the dorsal fin) using the methods described in Moser et al. (2002a); a secondary HD PIT tag was inserted through the same incision. Collection and tagging protocols were reviewed and approved by the University of Idaho Institutional Animal Care and Use Committee.

Lampreys exhibiting symptons of furunculosis in 2018 were first identified in June (Ralph Lampman, Yakama Nation, *personal communication*). While diagnosis of furunculosis must be confirmed by biochemical testing, several clinical symptoms may be visible including furuncles (or boils) involving skin and/or muscle, bloody discharge from the vent and hemorrhages on the skin, fin bases and mouth. After furunculosis was identified in the run, we used a symptom severity index for all tagged lampreys based on the degree of red hemorrhaging around the mouth. We visually classified symptoms into four categories: (0) no red hemorrhaging around mouth; (1) low, <25% perimeter of mouth with red hemorrhages; (2) moderate, 25-50% perimeter of with red hemorrhages; and (3) heavy, >50% perimeter of mouth with red hemorrhages. Furunculosis symptoms were scored for all lampreys collected and tagged starting 3 July.

Monitoring Sites

Lamprey movements were monitored using an array of interrogation sites (Table 1). Underwater PIT antennas installed by the University of Idaho (UI) were located inside dam fishways at Bonneville, The Dalles, John Day, and McNary dams. 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, and in the flow-control section of the Cascades Island fishway. Antennas were also located at the south (east) top-of-ladder site at The Dalles Dam, at the lamprey trap in the south ladder at John Day Dam, and at the John Day north fishway entrance (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).

Dual PIT interrogation sites administered by Pacific States Marine Fisheries Commission (PSMFC) were turned on in 2017-2019 for half and full duplex monitoring at Lower Columbia and Snake River dams (site details at: www.ptagis.org). In fall of 2017, dual PIT sites were turned on at The Dalles count windows (29 August). Dual PIT sites were turned on in spring 2018 at the Bonneville Dam vertical slot weirs (30 March) and LPSs (15 June) and at the McNary dams count windows (2 April). In the fall of 2018, dual PIT sites were turned on at Ice Harbor Dam adult ladder orifices and slots (12 October), at Lower Monumental (17 September) and Little Goose Dam (18 September) count windows, and at Lower Granite Dam adult ladder orifices and slots (28 September). Adult ladder overflow and orifices were turned on at John Day Dam in January of 2019.

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 tailraces at Bonneville, The Dalles and John Day dams. Underwater antennas and some directed aerial antennas monitored radio-tagged fish as they approached, entered, and exited fishway openings, movements inside fishways, and exits from ladders into dam forebays.

Data Analyses

We used Pearson's χ^2 tests and logistic regression (Burnham and Anderson 2002) to assess whether lamprey passage at Bonneville, The Dalles, John Day, and McNary Dams was associated with symptoms of furunculosis. For both analyses, we combined the three categories of symptoms (see above) into a single category of any hemorrhaging around mouth and compared them to fish which were not symptomatic. In addition to the binary (y, n) furunculosis covariate, the logistic regression model included lamprey tag date and weight. Passage at each of the four dams (y, n; through March 2019) was the dependent variable. The full logistic regression model was: Passage at dam (y/n) = tagdate + weight + furunculosis.

Reach escapement estimates 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 estimates 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 in previous years, some lampreys released downstream were recaptured in Bonneville traps; through March 2019, 15 double-tagged lampreys and 22 HD PIT-tagged (only) lampreys were recaptured and these fish were transported upstream 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 or John Day dams were transported and released upstream. Recaptured fish were included or excluded from escapement and passage time analyses where appropriate (e.g., recaptured fish were not included in estimates of

Bonneville Dam passage times and escapement estimates were calculated with and without the recaptured sample).

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; post-overwintering detections were not included. Detection efficiencies for UI HD PIT, dual PIT (PTAGIS) and radiotelemetry sites were estimated by dividing the number of fish known to pass a site (based on upstream detections) 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 were evaluated at sites where radiotelemetry and PIT antennas were in close proximity, primarily at top-of-ladder fishway locations.

Table 1. Half-duplex PIT tag interrogation sites (antennas) used to monitor lamprey passage at lower Columbia River dams in 2018. Note: additional HD monitoring sites were operated at Priest Rapids, Wanapum, and Rocky Reach dams (Public Utility Districts), in Hood River, Mill Creek, Fifteenmile Creek, and Deschutes River (CTWSRO), and at Lower Columbia and Snake River dams (PTAGIS). PH = Powerhouse; LPS = lamprey passage structure; UMT = upstream migrant tunnel; UMTJ = upstream migrant tunnel junction.

Dam	Location	Number of antenna(s)
Bonneville Dam	PH 2, WA-shore LFS	5
	PH 2, WA-shore ladder	4
	PH 2, WA-shore UMT Junction channel	1
	PH 2, WA-Shore UMTJ LPS	4
	PH 2, WA-Shore AWS LPS	2
	PH 2, WA-shore exit	1
	Cascades Island entrance	4
	Cascades Island lamprey LPS	1
	Cascades Island AWS	1
	PH 1, Bradford Island lamprey LPS	4
	PH 1, Bradford Island exit	1
The Dalles Dam	East ladder below count window	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

Table 2. Radiotelemetry antenna sites used to monitor lamprey passage at lower Columbia River dams in 2018.

Dam	Location	Type	Number of antenna(s)
Bonneville Dam	Tailrace	Aerial	2
	PH 2, South-shore entrances	Aerial	2
	PH 2, South-shore entrances	Underwater	4
	PH 2, North-shore entrances	Aerial	2
	PH 2, North-shore entrances	Underwater	4
	PH 2, WA-shore transition area	Underwater	9
	PH 2, WA-shore ladder / UMT junction	Underwater	3
	PH 2, WA-shore AWS	Underwater	3
	PH 2, WA-shore counting window	Underwater	2
	PH 2, WA-shore serpentine weirs	Underwater	5
	PH 2, WA-shore ladder exit	Underwater	1
	Cascades Island entrance	Aerial	1
	Cascades Island transition area	Underwater	5
	Cascades Island ladder / UMT junction	Underwater	3
	Cascades Island AWS	Underwater	2
	B-Branch entrance	Underwater	5
	B-Branch transition pool	Underwater	3
	PH 1, South-shore entrance	Aerial	1
	PH 1, South-shore entrance	Underwater	2
	PH 1, North-shore entrance	Aerial	1
	PH 1, North-shore entrance	Underwater	2
	PH 1, A-Branch transition area	Underwater	3
	PH 1, A- and B-Branch junction pool	Underwater	5
	PH 1, Bradford Island AWS	Underwater	3
	PH 1, Bradford Island count window	Underwater	2
	PH 1, Bradford Island serpentine weirs	Underwater	3
	PH 1, Bradford Island exit	Underwater	1
The Dalles Dam	Tailrace	Aerial	2
	North ladder entrance	Underwater	1
	North ladder transition area	Underwater	5
	North ladder exit	Underwater	1
	Spillway entrance	Underwater	3
	Powerhouse entrances	Underwater	5
	Collection channel	Underwater	2
	East ladder transition area	Underwater	8
	East ladder exit	Underwater	1
John Day Dam	Tailrace	Aerial	2
	North ladder entrance	Underwater	1
	North ladder transition area	Underwater	5
	North ladder exit	Underwater	1
	North powerhouse entrance	Underwater	4
	South-shore entrance	Underwater	4
	South-shore transition area	Underwater	6
	South ladder exit	Underwater	1

Table 2. Continued.

Dam	Location	Type	Number of antenna(s)
McNary Dam	North-shore entrance	Underwater	3
	North ladder exit	Underwater	1
	North powerhouse entrance	Underwater	4
	South-shore entrance	Underwater	3
	South ladder exit	Underwater	1

When lampreys were known to have passed a dam based on upstream detections but had no radiotelemetry (RT) or UI HD detections at the top of a fish ladder, detections at the dual PIT readers (located inside LPSs, vertical slot weirs, and near count stations) were used to denote lamprey passage. Using different antennas to denote dam passage reduced precision of reach passage time estimates. To evaluate the scope of this added variability, we compared travel times between dams using passage records at the top of the ladder from UI HD versus PTAGIS detection sites. Mean and median travel times (between dams) were longer when reach start times were detections at the PTAGIS sites (in vertical slot weirs or count windows) because they were located further downstream from the top of the fish ladders. For example, among lampreys with detections on both systems, the difference in detection times between UI HD top-of-fishway antennas and PTAGIS vertical slot antennas were 0.7 h (n = 22) at Bradford Island, 0.6 h (n = 15 at Washington shore, and 0.3 h (n = 39) at The Dalles Dam (count window vs UI HD top of ladder), on median. It is important to note that none of the double-tagged lamprey passage times were affected in this report since only two lampreys had top-of-fishway denoted by PTAGIS detections but they occurred at the PTAGIS LPS sites.

Results

Lamprey Collection and Tagging: Bonneville Dam

The total 'corrected' adult Pacific Lamprey count at Bonneville Dam including night and LPS passage estimates through 31 December 2018 was 131,268 (Zorich et al. 2019). A total of 1,482 lampreys were collected, tagged, and released or approximately 1.1% of the total corrected count (Figure 1). The tagged sample included three study groups. The first was 578 with HD PIT tags only that were released downstream from Bonneville Dam. The second was 309 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 595 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 given their use in experiments and upstream release location.

Sampling for the downstream release groups was generally proportional to daily counts, except under-sampling occurred during the unusually large period of peak abundance in mid- to late June

(Figure 1). Lamprey run timing, as indexed by the daytime count station counts, was 5 June (10% passage date), 21 June (25% date), 27 June (median date), 17 July (75% date), and 19 August (90% date). For comparison, the dates for the HD PIT group released downstream were 6 June, 23 June, 8 July, 27 July, and 23 August, respectively. Dates for the radiotelemetry group were 7 June, 23 June, 9 July, 26 July, and 9 August, respectively. The group used in the flume was collected much later in the run.

The four lamprey size metrics were all positively inter-correlated in the combined 2018 Bonneville samples (Figure 2). The coefficient of variation (CV) was 18% for dorsal distance, 22% for weight, 9% for girth, and 9% for length for the total sample (Table 3). Release date was weakly and negatively correlated with lamprey girth and weight ($-0.13 < r < -0.11$, $P \leq 0.05$).

Dwarf lampreys

During adult lamprey collection in 2018 at the AFF and lamprey flume structure (LFS) in the WA-shore ladder, 21 adult dwarf-sized lampreys (32.8 to 41.5 cm in length) were trapped and tagged with HD PIT tags. Eighteen were released downstream of Bonneville Dam and three were used in experimental flume and then released upstream. Dwarf lampreys were about half the length (*mean* = 37 cm), had 30% less girth (*mean* = 7.2 cm), weighed 80% less (*mean* = 104 g), and had half the dorsal distance (*mean* = 2.0) on average compared to all other HD PIT and double tagged lampreys (Table 3). The dwarf fish were included in analyses below, unless otherwise noted. The final detection locations of the 18 released downstream included 4 (22%) at the top of a Bonneville fishway ladder at Bonneville, 5 in a Bonneville fishway, 1 recapture at the AFF that was released upstream, and 8 that were not detected after release. The three used in flume trials were not detected after their release near Stevenson.

Table 3. Length, girth, weight, and dorsal distance of adult Pacific Lampreys collected and tagged in 2018 with HD PIT tags and released downstream from Bonneville Dam (near Hamilton Island or Tanner Creek) or upstream from the dam near Stevenson, WA (STE). The double-tagged group was released at the 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	575	64.8	6.9	577	10.9	1.2	578	443.4	115.2	577	3.6	0.7
PIT-STE[1]	307	67.7	5.7	309	11.3	1.0	308	498.9	108.1	309	3.8	0.6
Double-tag	595	69.2	3.7	592	11.7	0.7	595	534.7	79.2	594	3.9	0.7
Dwarf fish[2]	21	37.1	2.4	21	7.2	0.5	21	103.9	21.0	21	2.0	0.3
Non-dwarf fish[3]	1456	67.6	4.7	1457	11.4	0.9	1460	497.2	98.7	1459	3.8	0.7
All fish	1477	67.2	5.9	1478	11.3	1.0	1481	491.6	108.5	1480	3.8	0.7

[1] the Stevenson release group was used in flume studies and data not comparable to past years'
[2] includes HD PIT fish that were <50 cm in length
[3] includes HD PIT and double-tag fish that were ≥ 50 cm in length

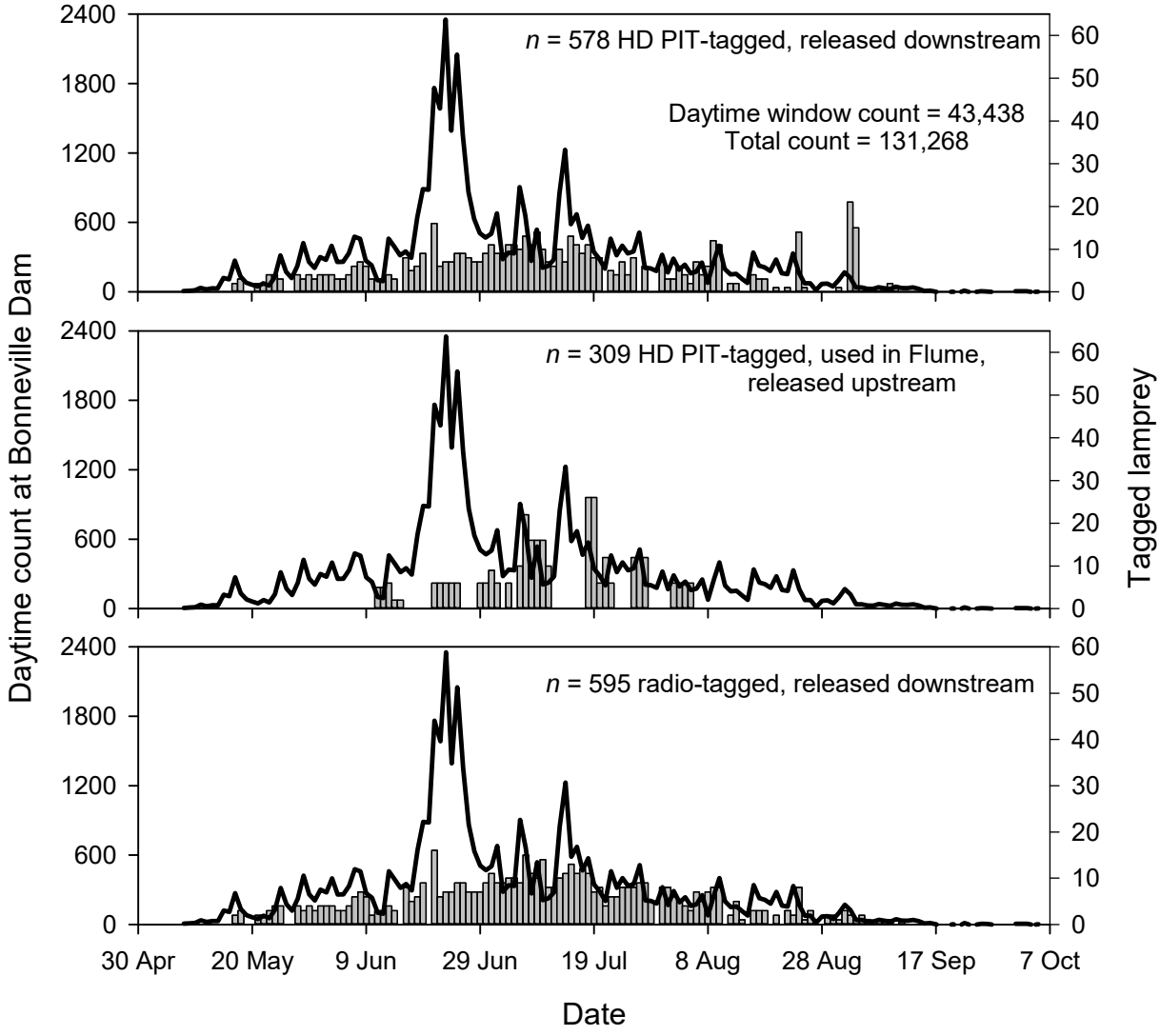

Figure 1. Number of adult Pacific Lampreys counted passing Bonneville Dam during the day (solid line) and the numbers that were collected and tagged (bars) in 2018. 'Total count' is the corrected total from daytime counts at windows, night video at windows, and LPS passage estimates through 31 December. Top panel shows fish released downstream from Bonneville Dam 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.

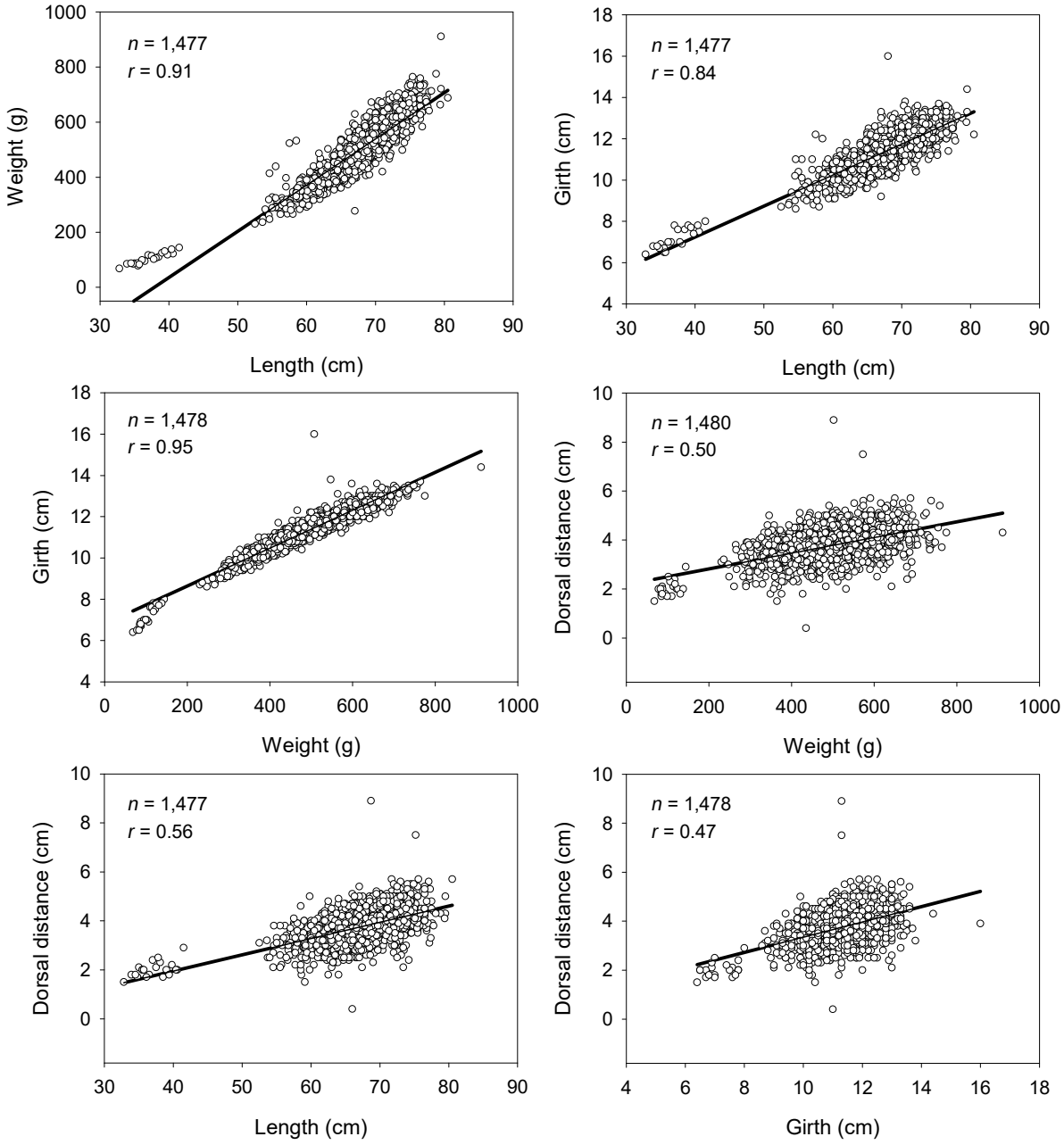

Figure 2. Linear relationships between length, weight, girth, and dorsal distance metrics for adult lampreys HD PIT- and radio-tagged in 2018. Note: all Bonneville release groups combined. All regression $P < 0.005$.

Furunculosis

We evaluated 371 (64%) of the 595 radio-tagged fish for symptoms of furunculosis. Of these, 78% (n = 288) had no symptoms, 20% (n = 74) had a low degree of red hemorrhaging, 2% (n = 7) had a moderate amount of red hemorrhaging and <1% (n = 2) had heavy red hemorrhaging. Of the 288 fish with no furunculosis symptoms, 38% passed Bonneville Dam compared to 30% for fish with any symptom (n = 83); the difference was not statistically significant in the Pearson's test (χ^2 = 1.8, P = 0.178, Table 4). However, furunculosis symptoms were associated (P = 0.048) with reduced passage at Bonneville Dam in the logistic regression model that included lamprey tag date and weight (Table 5). These patterns generally persisted upstream, with symptomatic fish less likely to be detected at The Dalles, John Day, and McNary dams compared to asymptomatic fish (Tables 4 and 5). Tag date was a significant predictor of reduced dam passage for radio-tagged lampreys in the logistic regression models for all four dams (Table 5)

We evaluated 354 of 578 (61%) of HD PIT-tagged fish for furunculosis symptoms. The symptomatic rates were similar to those of radio-tagged fish: 79% (n = 279) had no symptoms, 18% (n = 65) had a low degree of hemorrhaging, 2% (n = 8) had moderate hemorrhaging and <1% (n = 2) had heavy hemorrhaging. Of the 279 HD fish with no furunculosis symptoms, 50% passed Bonneville Dam compared to 45% for fish with symptoms (n = 75); as with the radio-tagged group, the difference was not statistically significant in a Pearson's test (χ^2 = 0.6, P = 0.456, Table 6) but was (P = 0.048) in the logistic regression model (Table 7). Upstream escapement was similarly lower for symptomatic fish at The Dalles, John Day and McNary dams. Tag date and weight were statistically significant in the logistic models for all four monitored dams for HD PIT-tagged fish (Table 7).

Table 4. The number of radio-tagged lampreys tagged at Bonneville Dam (n = 371) for symptoms of furunculosis and the percentage of fish with and without symptoms that passed Bonneville, The Dalles, John Day and McNary dams through March 2019.

			Pass Dam		
Dam	Symptomatic	Tagged	No	Yes	%Pass
Bonneville	No	288	178	110	38.2
	Yes	83	58	25	30.1
The Dalles	No	288	242	46	16.0
	Yes	83	73	10	12.0
John Day	No	288	268	20	6.9
	Yes	83	81	2	2.4
McNary	No	288	281	7	2.4
	Yes	83	82	1	1.2

Table 5. Results of logistic regression analyses to assess the association between tag date, weight and symptoms of furnuculosis and dam passage of radio-tagged lampreys at Bonneville, The Dalles, John Day and McNary dams through March 2019.

Dam	Parameter	Chi-square	P-value	Odds	95% CI
Bonneville	Date	13.3	0.0003	0.972	0.958-0.987
	Weight	2.6	0.1098	1.002	0.999-1.005
	Furunculosis	3.9	0.0477	1.737	1.006-3.001
	Intercept	4.3	0.0377		
The Dalles	Date	16.4	<0.0001	0.948	0.924-0.973
	Weight	3.3	0.069	1.004	1-1.008
	Furunculosis	2.9	0.091	1.939	0.9-4.177
	Intercept	5.9	0.0147		
John Day	Date	11	0.0009	0.918	0.873-0.966
	Weight	3.2	0.0734	1.005	0.999-1.011
	Furunculosis	4.4	0.0367	5.046	1.106-23.033
	Intercept	4.2	0.0398		
McNary	Date	5	0.0251	0.893	0.81-0.986
	Weight	2.1	0.1499	1.007	0.997-1.017
	Furunculosis	1.4	0.2346	3.721	0.426-32.494
	Intercept	2	0.1606		

Table 6. The number of HD PIT-tagged lamprey sampled at Bonneville Dam (n =354) for symptoms of furunculosis and the percentage of fish with and without symptoms that passed Bonneville, The Dalles, John Day and McNary dams through March 2019.

			Pass Dam		
Dam	Symptomatic	Tagged	No	Yes	%Pass
Bonneville	No	279	139	140	50.2
	Yes	75	41	34	45.3
The Dalles	No	279	204	75	26.9
	Yes	75	58	17	22.7
John Day	No	279	230	49	17.6
	Yes	75	63	12	16.0
McNary	No	279	265	14	5.0
	Yes	75	72	3	4.0

Table 7. Results of logistic regression analyses to assess the association between tag date, weight and symptoms of furnuculosis and dam passage of HD PIT-tagged lamprey at Bonneville, The Dalles, John Day and McNary dams through March 2019.

Dam	Parameter	Chi-square	P-value	Odds	95% CI
Bonneville	Date	28.4	<0.001	0.968	0.957-0.980
	Weight	7.2	0.0073	1.003	1.001-1.004
	Furunculosis	3.9	0.048	1.742	1.005-3.02
	Intercept	17.1	<0.001		
The Dalles	Date	14.6	0.0001	0.972	0.958-0986
	Weight	14.4	0.0001	1.004	1.002-1.007
	Furunculosis	3	0.0827	1.759	0.929-3.33
	Intercept	2.5	0.1117		
John Day	Date	12.9	0.0003	0.966	0.949-0985
	Weight	18.2	<0.0001	1.006	1.003-1.009
	Furunculosis	1.8	0.1847	1.647	0.788-3.444
	Intercept	1.3	0.2568		
McNary	Date	7.8	0.0051	0.924	0.824-0.977
	Weight	3.1	0.08	1.004	1.000-1.008
	Furunculosis	1	0.3125	1.961	1.961-7.241
	Intercept	3.6	0.0565		

Antenna Detection Efficiency Evaluations Using Double-Tagged Lampreys

We calculated detection efficiencies for radio and PIT antennas (UI HD and PTAGIS) at top-of-ladder sites at all four lower Columbia River dams using the double-tagged lampreys (Table 8). 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 UI HD and PTAGIS sites, reflecting differences in detection range between the two technologies and aging of the UI HD infrastructure. Detection efficiencies at individual radiotelemetry sites ranged from 92.3% at the John Day 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 45.8% at The Dalles north top-of-the-ladder to 97.9% at the Bonneville Washington-shore LPS (Table 8). Note that The Dalles east top-of-ladder HD site was inoperable in 2018, 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 2018.

The PTAGIS antenna detection efficiencies at individual sites ranged from 33.3% at McNary north to 98.2 % at Bonneville Bradford Island. Direct comparisons were not precise in this case because PTAGIS antenna sites in ladders were either in vertical slot weirs or near count windows that were slightly downstream of the radiotelemetry and UI HD top-of-the-ladder sites. Lampreys also have to swim through a vertical slot weir or orifice to be detected on the PTAGIS system while they only need

be in close proximity to a radiotelemetry antenna. In the LPSs, where PTAGIS and UI HD sites are in close proximity, 98.2 and 100% were recorded on PTAGIS antennas at the Bonneville Bradford Island and Washington-shore LPSs, respectively, compared to 87.3% and 97.9% on the older UI HD sites.

Table 8. Estimated detection efficiencies at top-of-ladder and LPS antennas calculated using double-tagged lampreys in 2018. Includes fish detected on at least one monitoring system.

			Detection efficiency		
Dam	Ladder	Total detected	Radiotelemetry	HD PIT	PTAGIS
Bonneville	South (Bradford)	55	100.0%	87.3%	98.2%
	South (LPS)	42	n/a	90.5%	92.9%
	North (WA-shore)	76	97.4%	53.9%	93.4%
	North LPS	48	n/a	97.9%	100.0%
The Dalles	South (East)	60	96.0%	n/a	65.0%
	North	48	97.9%	45.8%	93.8%
John Day	South	26	92.3%	69.2%	n/a
	North	17	100.0%	76.5%	n/a
McNary	South	12	100.0%	n/a	50.0%
	North	6	100.0%	n/a	33.3%

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, 209 lampreys from the downstream release group were detected at PIT antennas upstream from Bonneville Dam. Of these 209, 204 (97.6%) were recorded passing the dam via the following pathways: 143 (68.4%) were detected at top-of-ladder or top-of-LPS antennas, 42 (20%) were detected at one or more dual PIT vertical slot weir antennas, and 19 (9.1%) were recaptured at the AFF and transported upstream. There were 5 (2.4% of 209) that passed the dam without a top-of-ladder or top-of-LPS detection record. None of the 5 undetected fish were detected at any location at Bonneville Dam, only at upstream sites.

The Dalles Dam – A total of 241 lampreys (139 from the downstream release group and 102 from the upstream release group) were detected at antennas upstream from The Dalles Dam. Of these 241, 206 (85.5%) were recorded passing the dam via the following pathways: 162 (67.2%) were detected at one or more dual PIT count window antennas at The Dalles Dam, 43 (17.8%) were detected at the top of the north fishway (HD antenna) and one (0.4%) was recaptured and transported upstream. There were 35 (14.5% of 241) that passed the dam (based on upstream detections) without a top-of-ladder detection record. The top-of-ladder HD antenna at the east ladder was not operated in 2018 and consequently 28 (80.0% of 35) of the fish were last detected at the antenna inside the east fishway downstream from the east count station. The remaining 7 fish (20.0% of 35 and 2.9% of 241) were not detected at any location at The Dalles Dam.

John Day Dam – A total of 65 lampreys (both release groups) were detected at antennas upstream from John Day Dam. Of these 65, 52 (80.0%) were detected at the top-of-ladder antennas and 3 (4.6%) were recaptured and released upstream. Of the 10 fish not detected at top-of- ladder antennas, 9 were not detected at any John Day location and 1 was last detected only at the north entrance.

Migration Summaries for Downstream Release Group: HD PIT

Upstream Progression – Of the 578 lampreys released downstream from Bonneville Dam, 439 (75.9%) were subsequently recorded at one or more Bonneville Dam HD antennas inside fishways, at LPS systems, or at dams further upstream through March 2019 (Table 9). A total of 297 fish volitionally passed Bonneville Dam based on top-of-fishway or upstream detections (51.4% of the 578 released, and 67.7% of the 439 detected at one or more HD PIT sites after release). Importantly, another 22 (3.8% of 578) 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. Median recorded passage dates at top-of-ladder (or LPS) sites were 13 July at Bonneville Dam (n = 292), 19 July at The Dalles Dam (n = 135), 27 July at John Day Dam (n =89), 30 July at McNary Dam (n = 20), and 10 August at Wanapum Dam (n = 6). Additional fish passed each dam without detection at top-of-ladder (or LPS) antennas (i.e., passage date was uncertain). Top-of-fishway dates of detection for the HD PIT-tagged fish indicated some under-representation during peaks in the lamprey run at Bonneville Dam compared to the run at large and this carried over into the passage distributions at dams further upstream (Figure 3).

Point Estimates of Dam-to-Dam Escapement – Of 578 lampreys released, 55.2% (n = 319) were known to have passed Bonneville Dam (including the 22 that were recaptured and released upstream), 26.6% (n = 154) passed The Dalles Dam, 18.2% (n = 105) passed John Day Dam, 5.9% (n = 34) passed McNary Dam, 4.0% (n = 23) passed Priest Rapids Dam, 1.6% (n = 9) passed Wanapum Dam, and 0.7% passed Rocky Reach Dam (n = 4) (Tables 9 and 10). Escapement from the top of Bonneville Dam was 48.3% to the top of The Dalles Dam, 32.6% to the top of John Day Dam, and 10.7% to the top of McNary Dam. Escapements were 67.5% between ladder tops at The Dalles and John Day dams and 32.7% between ladder tops at John Day and McNary dams. Of 34 lampreys that passed McNary Dam, 2 (5.9%) passed Ice Harbor Dam and 23 (67.6%) passed Priest Rapids Dam (Tables 9 and 10).

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 most 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. 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; effects of release date were similar in dam-to-dam reaches, though were generally not statistically significant (Figure 4). The association between furunculosis symptoms and upstream escapement was described above.

Table 9. Minimum numbers of adult lampreys that passed each site through March 2019 estimated as the number of adult tagged lampreys detected at dam antennas or inferred to pass sites based on upstream detections in 2018. HD PIT-tagged lampreys were released downstream from Bonneville Dam (PIT) 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.

	Release group		
	PIT	PIT-STE	Double-tagged
	Minimum	Minimum	Minimum
Site	past (*n*)	past (*n*)	past (*n*)
Release	578	309	595
Bonneville[1]	439	n/a	534
Bonneville top[2]	297-319[4]	n/a	222-237[4]
The Dalles[1]	200	165	152
The Dalles top[2]	152-154[4]	115-116[4]	108-109[4]
John Day[1]	112	94	68
John Day top[2]	99-105[4]	82-86[4]	43-47[4]
McNary[1]	41	23	23
McNary top[2]	34	19	20
Ice Harbor[3]	2	1	2
Ice Harbor top[3]	2	1	2
L. Monumental[3]	2	1	2
L. Monument top[3]	2	1	2
L. Goose[3]	2	1	-
L. Goose top[3]	2	1	-
L. Granite[3]	2	-	2
L. Granite top[3]	1	-	-
Priest Rapids[5]	32	18	8
Priest Rapids top[5]	23	18	7-8[4]
Wanapum[5]	22	18	6
Wanapum top[5]	9	5	2
Rocky Reach[5]	5	3	-
Rocky Reach top[5]	4	2	-

[1] all fishway antennas, including LPSs at Bonneville
[2] top-of-ladder antennas, including LPSs at Bonneville
[3] no UI HD or RT monitoring only PTAGIS detections
[4] higher numbers include fish recaptured in traps and released upstream
[5] detections at PUD or PTAGIS antennas

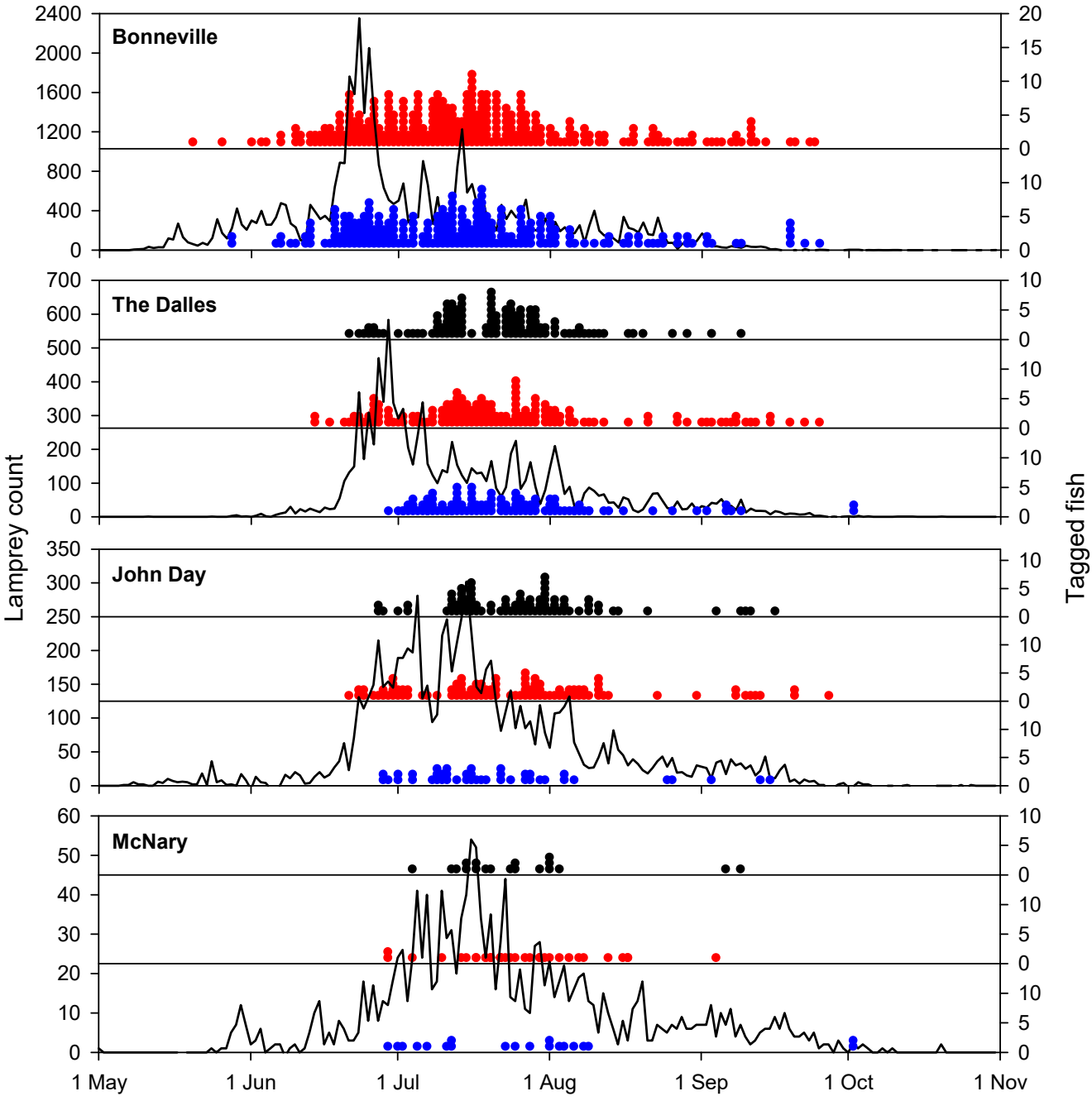

Figure 3. Daily numbers of adult Pacific Lampreys counted passing lower Columbia River dams via fish ladders (black lines) and the numbers of tagged fish that were detected at top-of-fishway antennas (blue circles = double-tagged fish; red circles = HD PIT-tagged fish released downstream from Bonneville; black circles = HD PIT-tagged fish released upstream from Bonneville, in 2018. Notes: many tagged lampreys passed dams undetected, particularly at The Dalles and McNary dams; counts are daytime window counts only; y-axis scales differ.

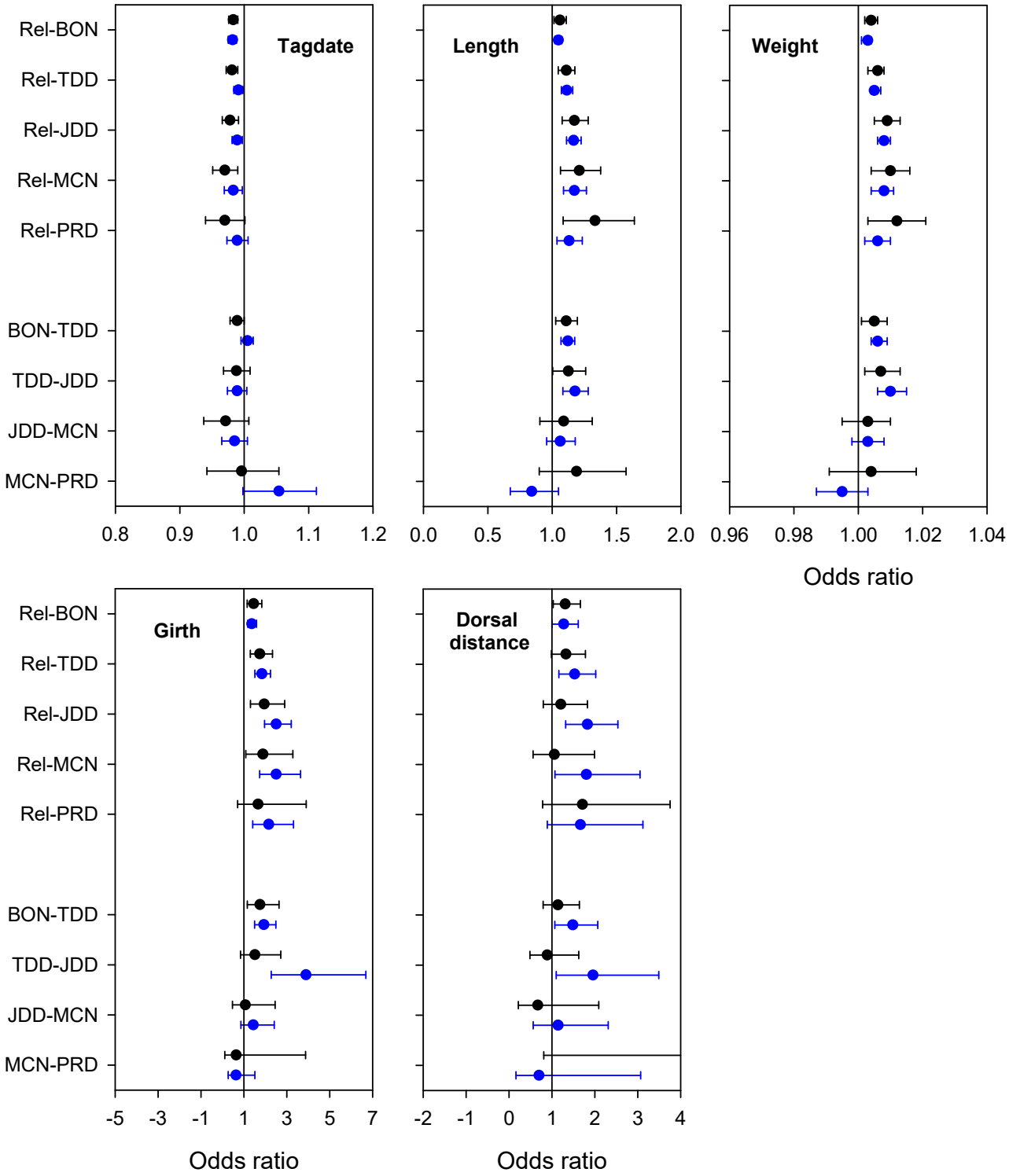

Figure 4. Odds ratios (+/- 95% ci) estimated from logistic regression models of upstream escapement through March 2019 by HD PIT-tagged lampreys (blue circles) and double-tagged lampreys (black circles) released downstream from Bonneville Dam in 2018. Odds ratios were scaled to the independent variables: release date (1 d) and lamprey length (1 cm), weight (1 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.

Passage Times and Rates – Median HD PIT-tagged lamprey passage times were 5.3 d from the release site to the top of Bonneville Dam, 4.0 d between Bonneville and The Dalles dams, 3.8 d between The Dalles and John Day dams, and 8.9 d between John Day and McNary dams (top-of-ladder or LPS sites at all dams, Table 11). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 18.3 km•d^{-1} (Bonneville-The Dalles), 10.2 km•d^{-1} (The Dalles-John Day), and 13.8 km•d^{-1} (John Day-McNary). Small sample sizes between McNary and the upper Columbia River dams and at the Snake River dams precluded meaningful summaries for reaches that included those sites.

Last Detection Summary – A total of 157 (27.2%) of the 578 lampreys released downstream of Bonneville Dam were not subsequently detected through March 2019 (Table 8). Another 100 (17.3%) were last recorded at HD antennas inside Bonneville Dam fishways, and 105 (18.2%) were last at Bonneville top-of-ladder or LPS exit antennas. Three fish (0.5%) were last recorded in Fifteenmile Creek or its tributaries and 6 (1.0%) were recorded in the Hood River. A total of 60 (10.4%) was last detected at The Dalles Dam, and 27 (4.7%) were recorded in the Deschutes River (note: at least 9 additional lampreys entered the Deschutes River in 2019 for a total of at least 36 [6.1%]). Above the Deschutes River, 70 (12.1%) were at John Day Dam, 7 (1.2%) were at McNary Dam, 2 (0.3%) were at Snake River dams, and 32 (5.5%) were at dams in the upper Columbia River (Priest Rapids through Rocky Reach dams) (Table 12).

When lampreys were grouped based on final recorded location, median release dates varied considerably among groups (Figure 5). Fish last recorded in Bonneville tributaries were tagged earlier by about 1-2 weeks, on median, than most other groups, and fish last detected at release had the latest median date. There were clearer among-group differences in lamprey size (Figure 6). On median, lampreys were largest in the groups last detected at John Day (522 g) and McNary (531 g) dams followed by the upper Columbia River (508 g) and Snake River (498 g) dams. Lampreys were smallest in the groups last recorded in Bonneville tributaries (*median* = 365 g) and in the Deschutes River (*median* = 401 g).

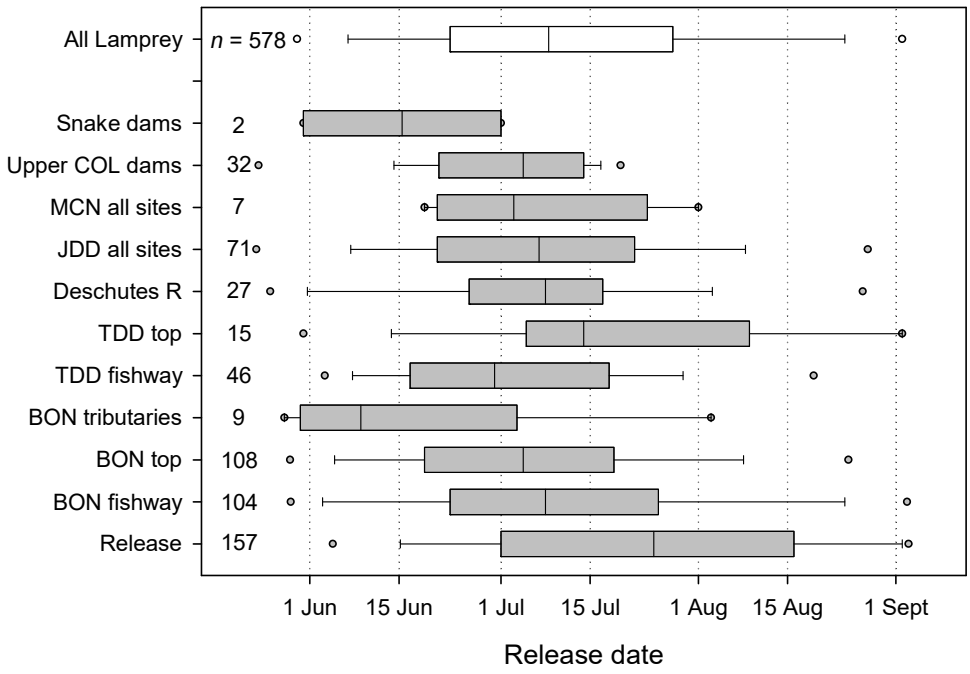

Figure 5. Distributions of HD PIT-tagged lamprey release dates by the final recorded locations for each fish through March 2019. Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

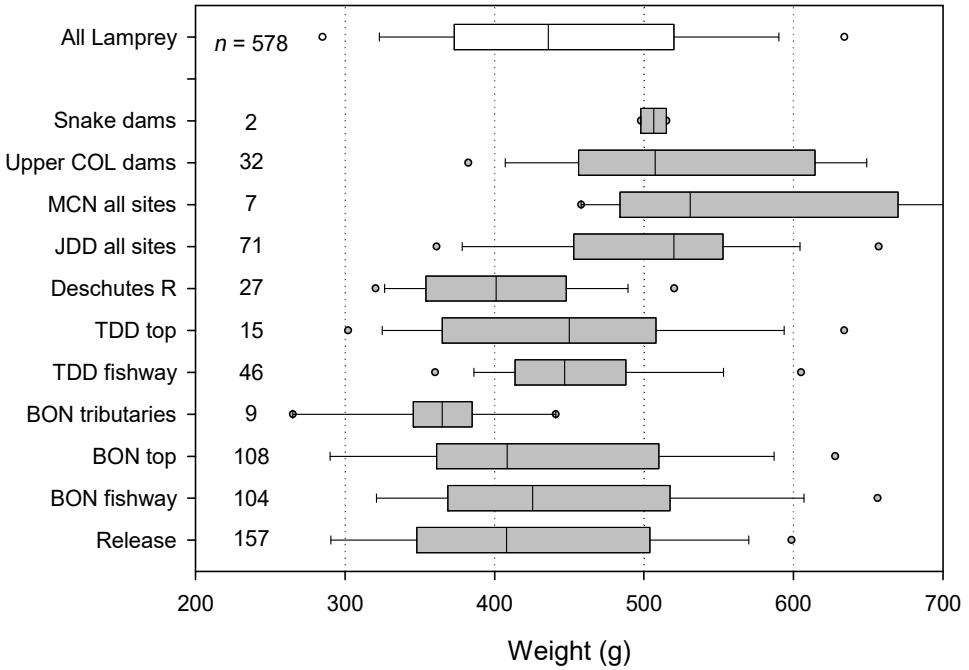

Figure 6. Distributions of HD PIT-tagged lamprey weights (g) by the final recorded locations for each fish (grey boxes) through March 2019. Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

Table 10. Lamprey escapement estimates for fish HD PIT-tagged and released downstream from Bonneville Dam or upstream from the dam near Stevenson, WA and for double-tagged fish released at two sites downstream from Bonneville Dam 2018, including all detections through March 2019. See Table 5 for sample sizes.

Reach	PIT Escapement	PIT-STE Escapement	Double-tagged Escapement
Release-Bonneville	76.0%	n/a	89.7%
Release-Bonneville top	51.4-55.2%	n/a	37.3-39.8%
Release-The Dalles	34.6%	55.9%	25.5%
Release-The Dalles top	26.3-26.6%	38.8%	18.2-18.3%
Release-John Day	19.4%	31.4%	11.3%
Release-John Day top	17.1-18.2%	28.8%	7.2-7.9%
Release-McNary	7.1%	7.7%	3.9%
Release-McNary top	5.9%	6.4%	3.4%
Release-Ice Harbor top	0.3%	0.3%	0.3%
Release-Lower Monumental top	0.3%	0.3%	0.3%
Release-Lower Granite top	0.2%	-	0.0%
Release-Priest Rapids top	4.0%	6.0%	1.2-1.3%
Release-Wanapum top	1.6%	1.7%	0.3%
Release-Rock Island top	n/a	n/a	n/a
Release-Rocky Reach top	0.7%	0.7%	n/a
Bonneville-Bonneville top[1]	67.6-72.7%	n/a	42.8-44.4%
Bonneville top-The Dalles top	48.3%	n/a	46.0-48.6%
Bonneville top-John Day top	32.6%	n/a	19.4-19.8%
Bonneville top-McNary top	10.7%	n/a	8.4-9.0%
Bonneville top-Ice Harbor top	0.6%	n/a	0.8-0.9%
Bonneville top-L. Monum. top	0.6%	n/a	0.8-0.9%
Bonneville top-L. Granite top	0.3%	n/a	0.0%
Bonneville top-Pr. Rapids top	7.2%	n/a	3.4%
Bonneville top-Wanapum top	2.8%	n/a	0.8%
Bonneville top-Rock Island top	n/a	n/a	n/a
Bonneville top-Rocky Reach top	1.3%	n/a	n/a
The Dalles top-John Day top	67.5%	74.1%	39.8-43.1%
The Dalles top-McNary top	22.1%	16.4%	18.5%
The Dalles top-Ice Harbor top	1.3%	0.9%	1.9%
The Dalles top-L. Monum. top	1.3%	0.9%	1.9%
The Dalles top-L. Granite top	0.6%	-	0.0%
The Dalles top-Pr. Rapids top	14.9%	15.5%	6.5-7.3%
The Dalles top-Wanapum top	5.8%	4.3%	1.9%
The Dalles top-Rock Island top	n/a	n/a	n/a
The Dalles top-Rocky Reach top	2.6%	1.7%	n/a

Note: lower estimate treats recaptured fish as not passing Bonneville The Dalles or John Day; higher estimate treats them as passed

Table 10 (cont).

Reach	PIT Escapement	PIT-STE Escapement	Double-tagged Escapement
John Day top-McNary top	32.7%	22.1%	42.6-46.5%
John Day top-Ice Harbor top	1.9%	1.2%	4.3-4.7%
John Day top-L. Monum. top	1.9%	1.2%	4.3-4.7%
John Day top-L. Granite top	1.0%	-	-
John Day top-Priest Rapids top	22.1%	20.9%	16.3-17.0%
John Day top-Wanapum top	8.7%	5.8%	1.8-1.9%
John Day top-Rock Island top	n/a	n/a	n/a
John Day top-Rocky Reach top	3.8%	2.3%	n/a
McNary top-Ice Harbor top	5.9%	5.3%	10.0%
McNary top-L. Monum. top	5.9%	5.3%	10.0%
McNary top-L. Granite top	2.9%	-	-
McNary top-Priest Rapids top	67.6%	94.7%	35.0-40.0%
McNary top-Wanapum top	26.5%	26.3%	10.0%
McNary top-Rock Island top	n/a	n/a	n/a
McNary top-Rocky Reach top	11.8%	10.5%	n/a
Priest Rapids top-Wanapum top	39.1%	27.8%	25.0-28.6%
Priest Rapids top-Rock Island top	n/a	n/a	n/a
Priest Rapids top-Rocky Reach top	17.4%	11.1	n/a
Wanapum top-Rock Island top	n/a	n/a	n/a
Wanapum top-Rocky Reach top	44.4%	40.0%	n/a
Rock Island top-Rocky Reach top	n/a	n/a	n/a
Ice Harbor top-L. Monum. Top	100%	100.0%	100.0%
Ice Harbor top-L. Granite top	50.0%	-	-
L. Monum. top-L. Granite top	50.0%	-	-

Note: lower estimate treats recaptured fish as not passing Bonneville The Dalles or John Day; higher estimate treats them as passed

Table 11. 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 2018.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to pass Bonneville Dam	292	5.28	9.73	2.22	12.15
Release to pass The Dalles Dam	135	11.15	15.41	6.44	19.78
Release to pass John Day Dam	88	17.64	20.13	11.11	26.37
Release to pass McNary Dam[1]	19	30.35	30.73	19.57	38.66
Release to pass Priest Rapids Dam	2	66.70	66.70	66.52	66.87
Release to pass Wanapum Dam	6	45.16	43.07	35.72	47.31
Release to pass L. Granite Dam[2]	1	38.42	38.42	-	-
Bonneville top to pass The Dalles Dam	124	3.99	6.51	2.48	7.43
Bonneville top to pass John Day Dam	80	9.94	12.01	6.05	16.78
Bonneville top to pass McNary Dam[1]	19	20.24	22.82	14.65	30.96
Bonneville top to pass Priest Rapids Dam	2	65.55	66.55	65.39	65.71
Bonneville top to pass Wanapum Dam	5	34.01	38.63	32.65	45.22
The Dalles top to pass John Day Dam	76	3.82	6.14	2.78	6.95
The Dalles top to pass McNary Dam[1]	18	12.33	17.42	10.85	25.02
The Dalles top to pass Priest Rapids Dam	2	56.48	56.48	52.78	60.19
The Dalles top to pass Wanapum Dam	6	30.53	34.14	29.83	37.08
John Day top to pass McNary Dam[1]	13	8.92	12.75	8.17	16.93
John Day top to pass Priest Rapids Dam	2	51.99	51.99	47.04	56.95
John Day top to pass Wanapum Dam	5	27.10	26.70	23.85	28.14
McNary top[1] to pass Priest Rapids Dam	1	8.13	8.13	-	-
McNary top[1] to pass Wanapum Dam	2	18.08	18.08	18.03	18.13

[1]No UI HD antennas installed at McNary Dam in 2018. Passage times were calculated from dual PIT detectors (PTAGIS) at McNary north or south count window. Not directly comparable to estimates from previous years.
[2] No UI HD antennas installed at Lower Granite Dam in 2018. Passage times were calculated from dual PIT detectors (PTAGIS) at Lower Granite Dam fish ladder exit. Not directly comparable to estimates from previous years.
Note: overwintering fish not included, recaptured fish included, and passage times at Bonneville and The Dalles Dam include some PTAGIS detections at vertical slot weirs and count windows that slightly increased dam-to-dam passage times compared to estimates from previous years.

Table 12. Last recorded locations for lampreys HD PIT-tagged and released downstream from Bonneville Dam or upstream from the dam near Stevenson, WA and for double-tagged fish released downstream from Bonneville Dam in 2018; includes all detections through March 2019. WA = Washington-shore fishway; LPS = lamprey passage structure. Notes: Hood River, Fifteenmile Creek, and Warm Springs River sites were maintained by the CTWRSO; Wanapum and Rocky Reach sites were maintained by Chelan and Grant county PUDs. McNary (PIT) and lower Snake River dams PIT detections were from PTAGIS.

	PIT (n = 578)		PIT-STE (n = 309)		Double-tagged (n = 595)	
Last recorded location	n	%	n	%	n	%
Release site	157	27.2%	141	45.6%	8	1.3%
Bonneville tailrace	4	0.7%	-	-	101	17.0%
Bonneville – Brad. Is. fishway	-	-	-	-	126	21.2%
Bonneville – WA-shore fishway	-	-	-	-	87	14.6%
Bonneville – LFS[1]	2	0.4%	-	-	-	-
Bonneville – Casc. Is.fishway	12	2.1%	-	-	35	5.9%
Bonneville – WA ladder	55	9.5%	-	-	2	0.3%
Bonneville – Brad. Is. ladder	31	5.4%	-	-	1	0.2%
Bonneville – recapture[2]	3	0.5%	-	-	4	0.7%
Bonneville – WA ladder exit / LPS[3]	60	10.4%	-	-	38	6.4%
Bonneville – Casc. Is. LPS	2	0.4%	-	-	-	-
Bonneville – Bradford exit / LPS[3]	43	7.4%	-	-	30	5.0%
Hood River	6	1.0%	1	0.3%	-	-
Fifteenmile Creek	3	0.5%	-	-	-	-
The Dalles tailrace	-	-	-	-	22	3.7%
The Dalles Dam fishways	46	7.9%	52	16.8%	36	6.1%
The Dalles ladder exits	15	2.6%	13	4.2%	26	4.4%
Deschutes River + tributaries	27	4.7%	8	2.6%	10	1.7%
John Day tailrace	-	-	-	-	12	2.0%
John Day Dam fishways	8	1.4%	9	2.9%	12	2.0%
John Day north LPS[4]	-	-	-	-	1	0.2%
John Day ladder exits	62	10.7%	62	20.1%	21	3.5%
McNary Dam fishways	7	1.2%	4	1.3%	3	0.5%
McNary Dam ladder exits	-	-	-	-	10	1.7%
Ice Harbor Dam	-	-	-	-	-	-
Lower Monumental Dam	-	-	-	-	-	-
Little Goose Dam	-	-	1	0.3%	-	-
Lower Granite Dam	2	0.3%	-	-	2	0.3%
Snake River tributaries[5]	1	0.2%	-	-	-	-
Priest Rapids Dam	10	1.7%	-	-	2	0.3%
Wanapum Dam	17	2.9%	15	4.9%	6	1.0%
Rocky Reach Dam	5	0.9%	3	1.0%	-	-

[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
[5] presumed recaptured at John Day Dam and released in Grande Ronde River

Migration Summaries for Downstream Release Group: Double-Tagged

Upstream Progression – Of the 595 double-tagged lampreys released downstream from Bonneville Dam, 534 (89.7%) were subsequently recorded at one or more Bonneville Dam antennas or at dams further upstream through March 2019 (Table 9). A total of 222 fish volitionally passed Bonneville Dam based on top-of-fishway or LPS detections or upstream detections (37.0% of the 595 released, and 41.6% of the 534 detected at one or more sites after release). Fifteen lampreys (2.5% of the 595 released) were recaptured in traps at Bonneville Dam and were released upstream.

The median tag date for double-tagged lampreys released downstream was 10 July (*mean* = 10 July). Median recorded passage dates at top-of-ladder sites were 12 July at Bonneville Dam (n = 218), 16 July at The Dalles Dam (n = 107), 16 July at John Day Dam (n = 43), and 3 August at McNary Dam (n = 18). 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.

Point Estimates of Dam-to-Dam Escapement – Of 595 lampreys released downstream from Bonneville Dam, 39.8% (n = 237) were known to have passed it through March 2019 (including 15 that were recaptured and released upstream), 18.3% (n = 109 with 1 recapture) passed The Dalles Dam, 7.9% (n = 47 with 4 recaptures) passed John Day Dam, 3.4% (n = 20) passed McNary Dam, 1.3% (n = 8 with 1 recapture) passed Priest Rapids Dam, and 0.3% (n = 2) passed Wanapum Dam (Tables 9 and 10). Two double-tagged lampreys (0.3% of the 595 released) were detected in the adult fishway at Lower Granite Dam after having passed Ice Harbor, Lower Monumental, and Little Goose dams. No double-tagged lampreys were detected upstream from Lower Granite Dam. Escapement from the top of Bonneville Dam was 46.0% to the top of The Dalles Dam, 19.8% to the top of John Day Dam, and 8.4% to the top of McNary Dam. Inter-dam escapements were 43.1% between ladder tops at The Dalles and John Day dams and 42.6% between ladder tops at John Day and McNary dams. Of 20 lampreys that passed McNary Dam, 2 (10.0%) passed Ice Harbor Dam and 8 (40.0%) passed Priest Rapids Dam (Tables 9 and 10).

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 most 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 for length and weight (i.e., the effect size was larger) as the distance to the upstream dam increased, indicating that the largest lampreys migrated the furthest. Early migrants were more likely than late migrants to pass most dams (Figure 4).

Passage Times and Rates – Median double-tagged lamprey passage times were 6.3 d from the release site to the top of Bonneville Dam, 6.3 d between Bonneville and The Dalles dams, 2.9 d between The Dalles and John Day dams, and 6.8 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 13). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 11.6 km•d^{-1} (Bonneville-The Dalles), 13.6 km•d^{-1} (The Dalles-John Day), and 18.0 km•d^{-1} (John Day-McNary). Sample sizes were limited upstream from McNary Dam. Passage rates through reservoirs were much faster than through reaches that included dams (Table 13).

Table 13. Summary of double-tagged adult lamprey passage times through dam-to-dam and multi-dam reaches of the lower Columbia River in 2018. Fish recaptured at Bonneville Dam were excluded from reaches starting at release and ending at sites upstream from Bonneville Dam. Fish recaptured at The Dalles or John Day dams were excluded at the point of recapture through all upstream/subsequent detections.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to approach Bonneville fishway	503	0.18	2.40	0.13	2.02
Release to enter Bonneville fishway	358	1.08	3.16	0.17	3.34
Release to pass Bonneville Dam	218	6.28	9.43	2.41	14.21
Release to The Dalles tailrace	62	8.60	11.93	5.23	13.72
Release to pass The Dalles Dam	98	13.96	17.14	8.11	23.02
Release to John Day tailrace	22	12.93	17.22	9.34	22.45
Release to pass John Day Dam	36	16.58	19.22	10.59	22.20
Release to McNary tailrace	-	-	-	-	-
Release to pass McNary Dam	13	27.11	37.10	14.38	39.52
Bonneville top to The Dalles tailrace	61	2.66	3.25	1.86	3.61
Bonneville top to pass The Dalles Dam	96	6.29	7.69	4.04	9.89
Bonneville top to John Day tailrace	22	9.15	10.37	5.91	14.40
Bonneville top to pass John Day Dam	35	9.07	10.93	6.83	12.36
Bonneville top to McNary tailrace	-	-	-	-	-
Bonneville top to pass McNary Dam	13	14.81	28.84	12.56	33.20
The Dalles tailrace to pass The Dalles Dam	36	3.07	4.14	1.88	4.68
The Dalles top to John Day tailrace	22	1.65	2.24	1.16	2.15
The Dalles top to pass John Day Dam	36	2.86	4.52	2.01	3.86
The Dalles top to McNary tailrace	-	-	-	-	-
The Dalles top to pass McNary Dam	13	10.13	22.97	7.32	23.38
John Day tailrace to pass John Day Dam	10	1.26	1.50	0.69	2.08
John Day top to McNary tailrace	-	-	-	-	-
John Day top to pass McNary Dam	13	6.84	16.08	5.82	20.46
McNary tailrace to pass McNary Dam	-	-	-	-	-

Last Detection Summary – A total of 8 (1.3%) of the 595 lampreys released below Bonneville Dam were not subsequently detected through March 2019 (Table 12). Another 101 (17.0%) were last recorded at tailrace radiotelemetry antennas, 265 (44.5%) were last detected at Bonneville Dam fishways, and 68 (11.4%) were at top-of-ladder exit sites or LPS sites. No fish were last detected in tributaries to the Bonneville reservoir. A total of 22 (3.7%) were last detected at The Dalles tailrace, 36 (6.1%) were at The Dalles fishways, and 26 (4.4%) were last recorded at The Dalles exit antennas. Ten (1.7%) were in the Deschutes River. Upstream from the Deschutes River, 46 (7.7%) were at John Day Dam, 13 (2.2%) were at McNary Dam, 2 (0.3%) were at Priest Rapids Dam, and 6 (1.0%) were at Wanapum Dam. Two lamprey (0.3%) were last detected at Lower Granite Dam (Table 12).

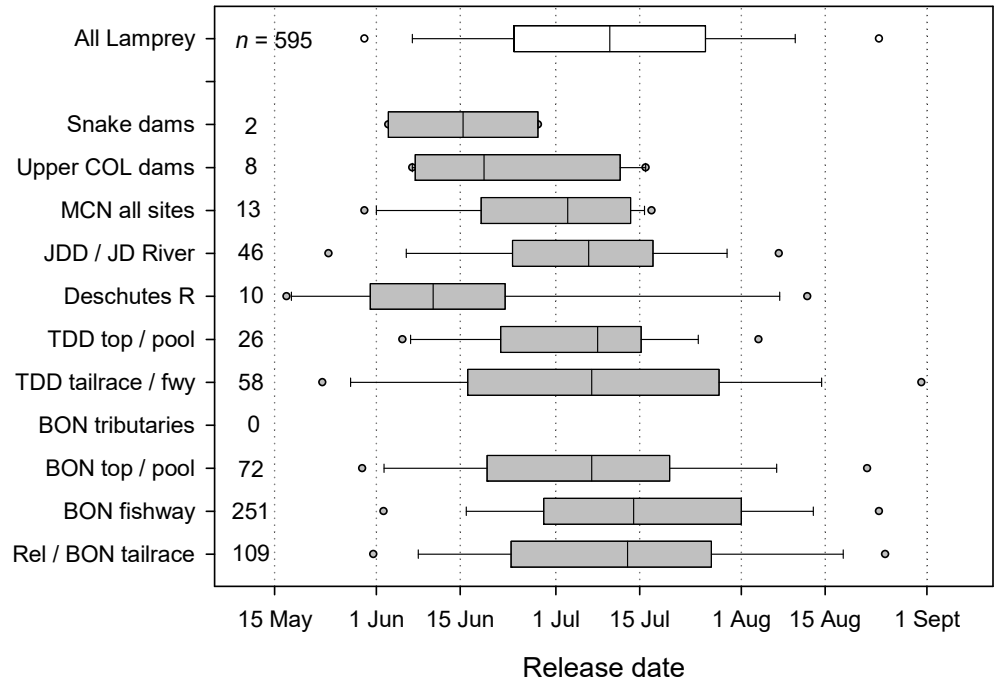

Figure 7. Distributions of double-tagged lamprey release dates by the final recorded locations for each fish through March 2019. Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

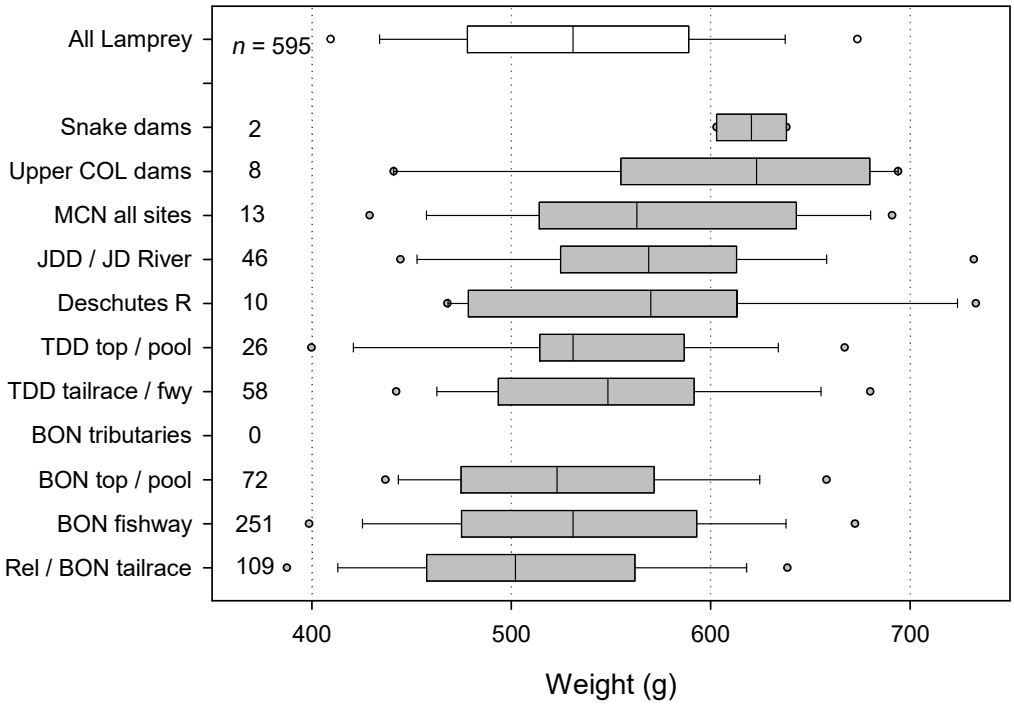

Figure 8. Distributions of double-tagged lamprey weights (g) by the final recorded locations for each fish through March 2019. Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

When double-tagged lampreys were grouped based on final recorded location, median release dates varied by about one month (Figure 7). The earliest-timed group was last detected in the Deschutes River and the latest median dates were for fish last detected in the Bonneville tailrace or at Bonneville Dam. There were also 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 (623 g), at McNary Dam (563 g) and at John Day Dam r (569 g). Lampreys were smallest in the groups last recorded in Bonneville reservoir tributaries (*median* = 502 g).

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 2018. 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 14). In six of seven reaches, double-tagged fish had a lower probability of upstream detection than those with HD PIT tags only (tagtype effect: $9.73 \leq \chi^2 \leq 59.76$, $P \leq 0.002$). Lamprey size effects were also evident in six of the reaches, with larger fish escaping at higher rates than smaller fish ($P \leq 0.001$). Tagdate was a statistically significant effect in four of seven reaches, with lower likelihood of reach passage later in the migration (Table 14).

Double-tagged lamprey had reach escapement probabilities that averaged 9% 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 difference was for the TDD-JDD reach, where double-tagged fish had 21.9% lower probability to pass than HD only fish.

Table 14. Results of logistic regression models of reach escapement by HD PIT-tagged and double-tagged lampreys released downstream from Bonneville Dam in 2018. The models were: reach escapement = tagtype (HD only, double) + tagdate + lamprey weight. Includes all detections through March 2019.

	HD PIT	Double	Tagtype		Tagdate		Weight	
Reach	*n*	*n*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Release-BON	578	595	44.71	<0.001	45.91	<0.001	16.92	<0.001
Release-TDD	578	595	35.56	<0.001	13.55	<0.001	45.06	<0.001
Release-JDD	578	595	59.76	<0.001	9.28	0.002	60.50	<0.001
Release-MCN	578	595	14.24	<0.001	8.79	0.003	27.25	<0.001
BON-TDD	319	237	9.73	0.002	0.02	0.884	32.64	<0.001
TDD-JDD	154	109	31.54	<0.001	0.98	0.322	24.14	<0.001
JDD-MCN	105	47	0.27	0.604	3.26	0.071	1.00	0.317

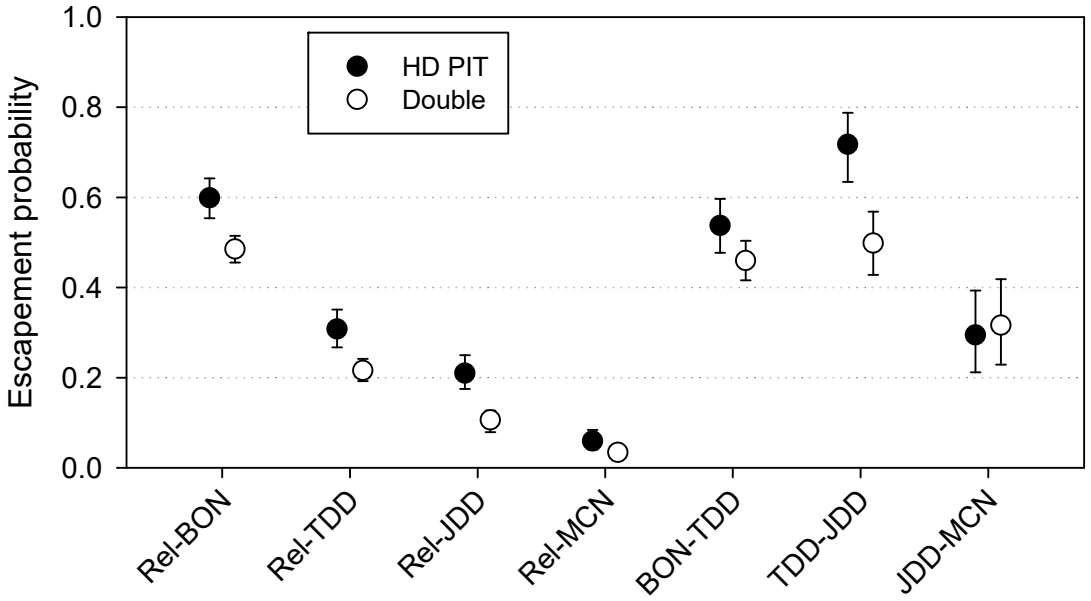

Figure 9. Estimated reach escapement probabilities (+/- 95% ci) of HD PIT-tagged (●) and double-tagged (○) lampreys released downstream from Bonneville Dam in 2018. Point estimates are from logistic regression models where: escapement = tagtype + tagdate + lamprey weight. Estimates were for the median lamprey weight (497 g) and the median release date (9 July) for the combined HD PIT- and double-tagged samples. Includes all detections through March 2019.

Migration Summaries for Stevenson Release Group: HD PIT

The 309 HD PIT-tagged lampreys released near Stevenson, WA, were not tagged in proportion to the lamprey run (Figure 1). This subsample was collected between 11 June and 5 August (*mean* = 10 July) and was used in experiments prior to release. Mean size metrics for the group were slightly higher than those for the downstream HD PIT group and slightly lower than those for the double-tagged release group (Table 3). The Stevenson group was experimental and was not representative of the run at large. We therefore did not summarize passage times or migration timing and did not model covariate effects on escapement. We do report summaries of upstream escapement and final detection locations to show basic post-experiment behaviors.

Point Estimates of Dam-to-Dam Escapement – Escapement for the 309 lampreys from release was 38.8% (*n* = 116) past The Dalles Dam, 28.8% (*n* = 86) past John Day Dam, 6.4% (*n* = 19) past McNary Dam, 6.0% (*n* = 18) past Priest Rapids Dam, and 0.3% (*n* = 1) past Ice Harbor Dam (Tables 9 and 10). Escapement estimates were 74.1% between ladder tops at The Dalles and John Day dams and 22.1% between John Day and McNary dams. Of the 19 lampreys that passed McNary Dam, 18 (94.7%) passed Priest Rapids Dam and 1 (5.3%) passed Ice Harbor Dam (Tables 9 and 10).

Last Detection Summary – A total of 141 (45.6%) of the 309 lampreys released near Stevenson were not subsequently detected through March 2019 (Table 12). One fish (0.3%) was last recorded in the Hood River. A total of 65 (21.0%) were last detected at The Dalles Dam, and 8 (2.6%) were

recorded in the Deschutes River. Upstream from the Deschutes River, 71 (23.0%) were at John Day Dam, 4 (1.3%) were at McNary Dam, 1 (0.3%) was at a Snake River dam, and 18 (5.8%) were at dams in the upper Columbia River (Priest Rapids through Rocky Reach dams) (Table 12).

Discussion

The migration-scale data generated in the multi-year HD PIT and radiotelemetry studies provide the most consistently collected baseline monitoring information for individual adult Pacific Lampreys in the Columbia River Basin. The 2018 migration was unusual in three important ways. First, we identified furunculosis symptoms in about 22% of the fish collected from July to September. The symptomatic rate was unknown for early-run fish and it was also unknown when or how adult lampreys became infected with *Aeromonas salmonicida*. Symptomatic fish were less likely to pass Bonneville Dam after release and their distribution in the basin was truncated relative to non-symptomatic fish. Symptoms of furunculosis have been present in other run-years (Ralph Lampman, *personal communication*) but the incidence of the disease and its potential effects on upstream escapement and distribution have not been previously evaluated. Consequently, we are uncertain whether the apparent increased prevalence of the disease in 2018 affected study results.

The second unusual factor was the collection of small-bodied 'dwarf' Pacific Lampreys at the AFF trap at Bonneville Dam. Dwarfs comprised <2% of the adults collected, 2018 was the first time our research group has collected this life history type during routine trapping at the AFF, and most records of the life history type in Washington and Oregon have been closer to the Pacific Ocean (Kostow 2002; Hess et al. 2015). It is unknown whether dwarfs were simply more prevalent in 2018, if changes to Bonneville fishways allowed more dwarfs to enter and ascend to the AFF, or whether the redesigned adult trap facilitated their collection. We included dwarfs in the migration summaries, but their effect on escapement and distribution metrics was likely limited given the small sample size.

The third notable difference in 2018 was the incorporation of PIT antennas that were capable of reading both HD and FD PIT tags. The dual-reader antennas at dams expanded our monitoring scope, added redundancy to some locations, and reduced the likelihood of missed lamprey passage events. Data from the new sites added some analytical complexity, as well as some comparability issues with previous results. On balance, however, the new sites improved monitoring effectiveness and reduced uncertainty.

HD PIT-Tagged Samples

Downstream Release Group – In 2018, HD PIT-tagged lamprey escapement for the downstream release group from release past Bonneville Dam (53%) was near the mean and median of estimates for HD PIT samples from 2006-2014 (*range* = 41-61%, Table 15). The percentages of lampreys that passed The Dalles Dam (29%), John Day Dam (18%), and McNary Dam (6%) in 2018 were similar to or slightly lower than the means and medians of previous estimates of 29-30% past The Dalles Dam, ~20% past John Day Dam and 6-7% past McNary Dam. Dam-to-dam estimates in 2018 were similar to mean and median estimates in previous years for the Dalles-John Day (65%) and John Day-McNary (32%) reaches; the estimate for the Bonneville-The Dalles reach (51%) was slightly lower than the previous mean and median values.

Table 15. 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 (2006-2018) 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. Two sets of estimates for 2018 include detections through March 2019 and 1 August 2019, respectively.

		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)
2018[a]	*578*	*[6]0.51 (297)*	*[7]0.26 (152)*	*[8]0.17 (99)*	*0.06 (34)*
2018[b]	*578*	*[c]0.53 (306)*	*[d]0.29 (165)*	*[e]0.18 (102)*	*0.06 (35)*

	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)
2018[a]	*0.48 (319)*	*0.68 (154)*	*0.33 (105)*	*0.06 (34)*	*0.68 (34)*
2018[b]	*0.51 (329)*	*0.65 (167)*	*0.32 (108)*	*0.09 (35)*	*0.66 (35)*

[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); [6]0.55 (n = 319); [7] 0.27 (n = 154); [8] 0.18 (n = 105); [c]0.57 (n = 329); [d] 0.29 (n = 167); [e] 0.19 (n = 108) when recaptures were treated as passing the dam

[a] Detections through March 2019; [b] Detections through 1 August 2019

Following the 2014 study, we concluded that reach escapement for HD PIT-tagged lampreys had increased over the course of nine study years (Keefer et al. 2015). That evaluation included a group of statistical models that controlled for lamprey body size and release date effects and indicated that lamprey escapement increased with year in six of the seven lower Columbia River study reaches. In several reaches, escapement increased for all lamprey size classes. We concluded that operational and structural improvements implemented specifically for adult lamprey passage (e.g., USACE 2014) contributed, at least in part, to the increased escapement (Keefer et al. 2015). The mostly near-average escapement estimates in 2018 could be interpreted as a discontinuation of the positive trends in escapement. However, HD PIT-tagged lampreys in 2018 were somewhat smaller than in several previous years (Table 16), and the furunculosis outbreak was a unique event that may have reduced

escapement. Quantifying the total impact was not possible because only later migrants were evaluated for symptoms.

The 2018 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, 2015). 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., PIT vs. JSATS vs. radiotelemetry). There is also evidence that the relationship between migration distance and lamprey body size has a genetic basis. Using genetic data collected from lampreys in this series of HD PIT and radiotelemetry studies, Hess et al. (2014) identified markers that link Pacific Lamprey phenotype (e.g., body size) with migration distance in the Columbia River basin.

Table 16. Numbers of HD PIT-tagged lampreys released in the Bradford Island fishway (2005) or downstream from Bonneville Dam (2006-2018), 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. Summary does not include post-overwintering movements.

					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
[1]2005	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
2018	[3]578	64.8	443	10.9	5.3 d	[2]4.0 d	[2]3.8 d	8.9 d

[1] released into the Bradford Island fishway
[2] top of East fishway not monitored in 2013-2014 and 2018
[3] includes dwarf lamprey (n = 18)

Lamprey migration times through dam-to-dam study reaches generally fell within the ranges reported in previous HD PIT study years (Table 16). An exception was that the 2018 median time in the release-Bonneville reach (5.3 d) was the fastest in the time series and more than 3 d faster than the mean and median values from previous years. Above-average water temperatures and below-average discharge (Appendix A) may have contributed to relatively rapid passage, though operational (i.e, reduced nighttime velocity) and structural changes at Bonneville fishways may also have played a role. 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 10-18 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).

About 27% of downstream-released HD PIT-tagged lampreys were not detected after release in 2018. This matched the lowest non-detected percentage in the multi-year study (it was also 27% in 2014), but continues to be cause for concern. The underlying reasons for failed upstream movement 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, moved into downstream tributaries, and/or used main stem sites downstream from Bonneville Dam for spawning.

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 primarily from the later portion of the 2018 migration and therefore encountered different environmental conditions than the downstream-released sample. Release upstream from Bonneville also eliminated the significant barrier to dispersal presented by Bonneville Dam.

About 46% of the flume fish were never detected after release, a rate that was higher than the 27% undetected from the downstream release group and higher than the 39% for Stevenson-released flume fish in 2014 (an early-timed sample). The nearest upstream PIT antennas from the Bonneville forebay were in the Hood River, followed by Fifteenmile Creek and at The Dalles Dam. All of these sites 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 Stevenson release group may have entered unmonitored tributaries, fallen back downstream past Bonneville Dam, spawned in the Bonneville reservoir, or died after release.

Escapement from Stevenson release past The Dalles Dam was 39%, which was somewhat lower than the most comparable estimate for the downstream release group: 48% from the top of Bonneville Dam past the Dalles Dam. Differences in escapement estimates between The Dalles and John Day dams were broadly similar at 65% (downstream release) and 74% (Stevenson release), but the downstream release group had higher escapement for the John Day-McNary reach (32% versus 22% for the Stevenson group). Despite the potentially confounding effects of sample timing and size-selective pressures that favor escapement by larger fish from the downstream group, these result do suggest 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.

Double-Tagged Sample

The 2018 escapement estimate for radio-tagged lampreys from release to top-of-ladder and LPS sites at Bonneville Dam was 39%, within the range of the estimates in the 1997-2002, 2007-2010, and 2014 radiotelemetry studies (33-46%, Table 17). The most directly comparable study years were 2007-2010 and 2014, when smaller transmitters allowed more representative tagging. The 2018 escapement past Bonneville was substantially higher than the 2007-2009 estimates (21-31%) and was just ~2% lower than the 2010 and 2014 estimates. Two countervailing effects are important for interpreting this result. First, mean body size of radio-tagged fish in 2018 was slightly higher than in recent years (Figure 10) because we elected to tag slightly larger fish to maximize the number

available for the nighttime fishway velocity experiments (see Clabough et al. 2019); this selection criterion would tend to increase escapement. Second, furunculosis effects on escapement were more consequential for radio-tagged fish than for PIT-tagged fish (compare tables 4 and 6). Furunculosis potentially reduced escapement past Bonneville Dam by several percentage points.

About 90% of the radio-tagged lampreys were detected near fishway openings at Bonneville Dam, a rate of post-release upstream movement that was slightly higher than the mean and median values (85-88%) in all previous radiotelemetry study years (Table 18). Dam passage efficiency, calculated as the number that passed Bonneville Dam divided by the number that approached fishway openings, was 42% in 2018; this value was slightly lower than the multi-year median (45%) and the same as the multi-year mean (42%). A greatly expanded summary of lamprey behaviors and passage metrics at all four lower Columbia River dams is presented in a companion report (Clabough et al. 2019).

Multi-dam escapement estimates for radio-tagged lampreys in 2018 were 19% (past The Dalles), 8% (past John Day), and 3% (past McNary, Table 17). These estimates were above average and median values from the full series of radiotelemetry years and were higher than estimates from the more representative studies starting in 2007.

Table 17. 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, 2014, and 2018 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. Two sets of estimates for 2018 include detections through March 2019 and 1 August 2019, respectively.

		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)
2018[a]	*595*	*[5]0.37 (222)*	*[6]0.18 (108)*	*[7]0.07 (43)*	*0.03 (20)*
2018[b]	*595*	*[8]0.39 (230)*	*[9]0.19 (112)*	*[c]0.08 (46)*	*0.03 (20)*

[1] 0.26 (n = 156); [2] 0.33 (n = 198); [3] 0.41 (n = 128); [4] 0.41 (n = 243); [5] 0.40 (n = 237); [6] 0.18 (n = 109); [7] 0.08 (n = 47); [8] 0.41 (n = 245); [9] 0.19 (n = 113); [c] 0.09 (n = 51) when recaptures were treated as passing the dam

[a] Detections through March 2019; [b] Detections through 1 August 2019

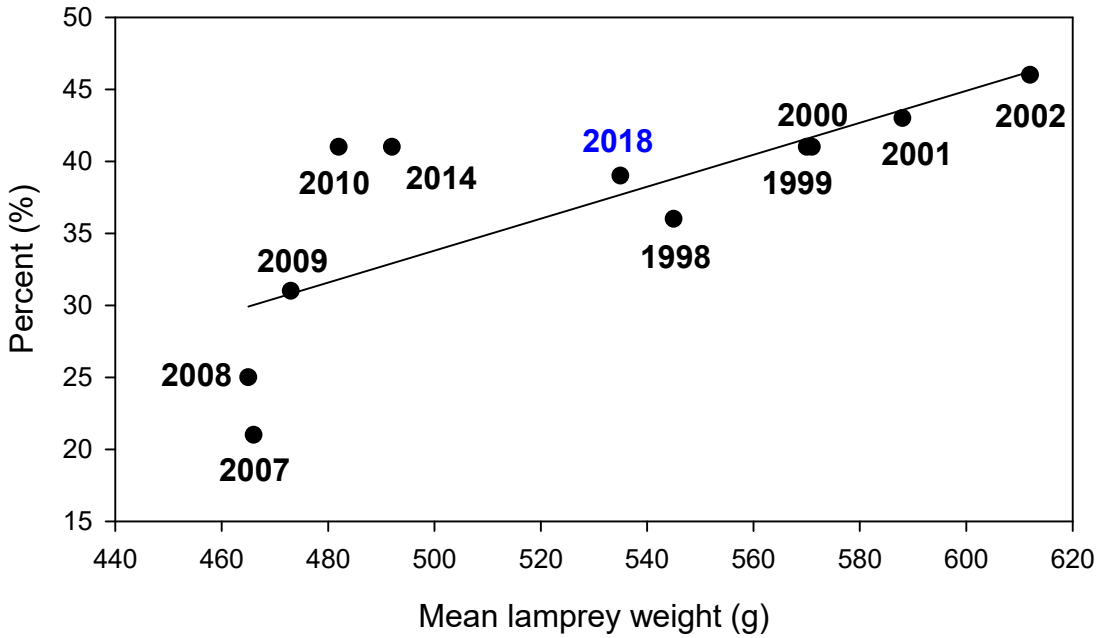

Figure 10. Linear regression relationship between annual mean radio-tagged Pacific Lamprey weights and the percentage that passed Bonneville Dam of those released (linear regression, $r^2 = 0.57$, $P < 0.05$). Lampreys recaptured at the Bonneville AFF were treated as not passing. Note: weight data were not collected in 1997.

Table 18. Numbers of radio-tagged lampreys released below Bonneville Dam from 1997-2002, 2007-2010, 2014, and 2018 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, 2014 and 2018.

Year	Released	Mean Length	Length range	Mean Weight	Weight range	Detected at BON	Passage Efficiency[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
2018	595	69	55-81	535	330-775	90%	42%	6.3 d

[1] Differs from Table 17 because limited to fish that approached a fishway; [2] excludes 10 (2008), 21 (2009), 3 (2010), 19 (2014), and 15 (2018) lampreys recaptured at a trap and released upstream or in LPS

A notable departure from previous study years was that we did not use radiotelemetry in any tributaries in 2018. We were able to identify some lamprey use of tributaries by detections at instream PIT detection arrays, but only about 8% of the fish that passed Bonneville Dam were detected in lower Columbia River tributaries, the Snake River, or passed Priest Rapids Dam through March 2019. This was well below the 13-25% recorded in 2008-2010 and 2014, when radio antennas were in many lower river tributaries (Keefer et al. 2010, 2015). Notably, no radio-tagged lampreys were detected in Fifteenmile Creek or in the Hood, Klickitat, or John Day rivers in 2018, although some fish entered these sites in almost all prior years. (Note: 2 radio-tagged lampreys were detected in the Klickitat River in summer 2019.)

Two additional important escapement results from the radiotelemetry study were consistent with those from previous studies. Specifically, a majority (~60%) of tagged adults did not pass Bonneville Dam in 2018 and about a third (~36%) 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 non-passage and the ultimate fate of these adults remain unknown. Results of acoustic telemetry studies in the Bonneville Reservoir indicate that adult lampreys moved quickly through the reservoir with high survival (Noyes et al. 2015). Most JSATS-tagged lamprey that did not pass The Dalles Dam in the fall had final records in the tailrace of the dam and a small proportion was recorded moving downstream to tributaries in the spring. Whether adults last recorded in tailraces or reservoirs spawned, were predated, were prespawn mortalities, or entered tributaries undetected remains unknown.

The 2018 radio-tagged lampreys passed quickly through reservoirs as compared to past dams, as has been reported in previous studies (e.g., Moser et al. 2013; Keefer et al. 2015). Median times in 2018 were ~2.7 d through the Bonneville reservoir and ~1.7 d through The Dalles reservoir. These times were faster than or within the range of times calculated for radio-tagged lampreys in 2007-2010 (Table 18). Median lamprey passage rates through the Bonneville and The Dalles reservoirs were 27 and 24 $km \bullet d^{-1}$, respectively. These rates were similar to or faster than the 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, 2015).

Negative Effects of Radio Tagging

An ongoing concern in the adult lamprey research program has been that radio-tagged fish have significantly lower escapement than HD PIT-tagged fish in most study reaches. Higher escapement by larger fish has also been consistent across tag types. One potential 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 six minutes versus about three minutes for HD-PIT tagging. In addition, the incision has been larger for radio transmitter insertion, more 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 also be a concern for lampreys given their swimming behavior and attachment to surfaces. Qualitative observations 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*).

In 2018, radio-tagged lamprey reach escapement was ~9% lower, on average, than estimates for HD PIT-tagged lampreys. This difference was similar in scale to results from 2009 and 2014, recent years with adequate samples of both HD PIT and double-tagged fish (Keefer et al. 2010, 2015). As noted in previous reports, the informational value of radiotelemetry data for future studies must be weighed against reduced upstream escapement. Year two of the current study (2019) includes radiotelemetry because there will be an additional experimental evaluation of reduced fishway entrance velocity. Monitoring adults in the tailrace and at fishway openings cannot currently be achieved using PIT telemetry.

The Monitoring Array and Lamprey Detection Efficiency

The multi-year evolution of the arrays used to monitor adult lampreys is important for interpreting study results across years and tag types. Monitoring effort has definitely changed through time. In the radiotelemetry system, antenna coverage has depended on lamprey study objectives as well as whether there were concurrent adult salmonid studies, which typically included monitoring at more fishway, reservoir, and tributary sites. In the HD PIT system, antennas have been sequentially added at LPS sites (Bonneville and John Day dams), at lamprey traps (e.g., John Day Dam), at upper Columbia and Snake River dams, and in some tributaries. The increased HD footprint has been partially offset by deteriorating HD infrastructure at some fishway sites. The deterioration is due to aging, as most antennas were installed more than a decade ago and their capacity has declined; the most egregious decline is the non-functioning top-of-fishway antenna at The Dalles east. Fortunately, the recent addition of PIT antennas that can read both FD and HD tags has partially compensated for the HD system decline. As noted above, the dual-reader antennas at dams (and in some tributaries) has expanded our monitoring scope and added redundancy.

Calculating detection efficiencies for the PIT and radiotelemetry arrays is a challenge with important implications for study results. The top-of-fishway arrays are critical for estimating the escapement and system-wide metrics in this report. Using the double-tagged sample, the estimated detection efficiencies at top-of-fishway sites averaged 98% (radiotelemetry), 74% (HD PIT), and 78% (PTAGIS dual readers). There was considerable among-site variability in the PIT antennas that was related to site configuration. For example, lampreys could avoid detection on some PTAGIS antennas in vertical slots or orifices by using alternate passage routes and could avoid detection at some very large swim-through HD antennas simply by swimming in mid-water column. In the double-tagged method, the reliability of detection efficiency estimates was constrained by the number of lampreys detected at any given antenna. There was an additional risk of underestimating detection efficiency when fish passed a dam via unmonitored routes (e.g., navigation locks or off-fishway routes that did not pass through antennas) but are subsequently detected upstream.

The second efficiency estimation method was for PIT-tagged lampreys only and focused on top-of-fishway detections at all sites at each dam. Our intention was to understand what proportion of PIT-tagged fish were potentially passing undetected. Our estimates of non-detection were ~2% (Bonneville), ~15% (The Dalles), and ~17% (John Day), with recaptured fish as detected. Importantly, most lampreys that passed undetected at The Dalles Dam passed via the east fishway where the top-of-

ladder HD site was non-functioning; a large majority of these fish were detected at antennas near the east count station. The 17% missed at John Day Dam was higher than in previous years and may indicate some new deterioration at one or both top-of-ladder sites at the dam.

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Appendix A. 2018 Columbia River discharge and temperature profiles.

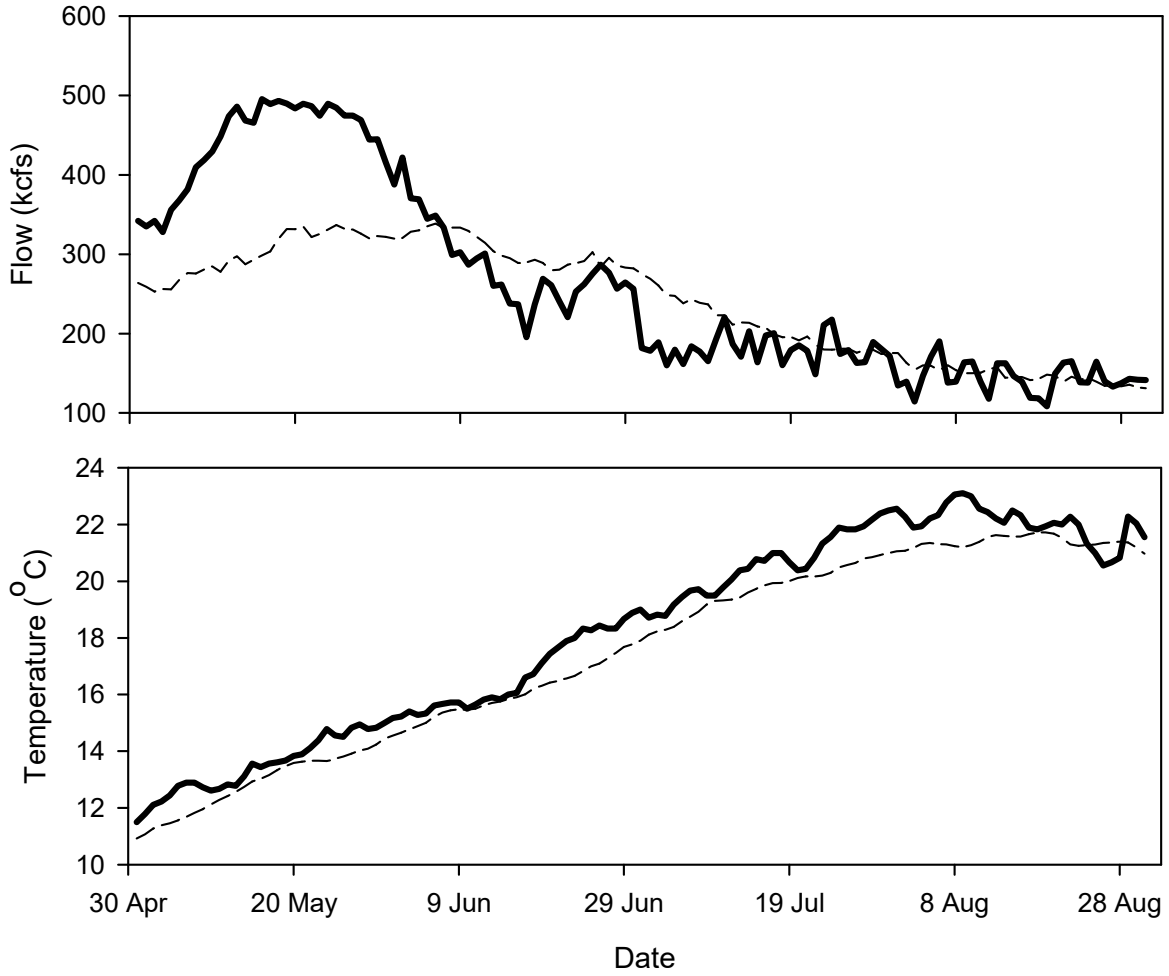

Figure A1. Mean daily Columbia River flow (kcfs) and WQM temperature (°C) at Bonneville Dam in 2018 (solid line) and the 2008-2017 average (dashed line).