Technical Report 2020-2

ADULT PACIFIC LAMPREY MIGRATION IN THE COLUMBIA AND SNAKE RIVERS: 2019 RADIOTELEMETRY AND HALF-DUPLEX PIT TAG STUDIES

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

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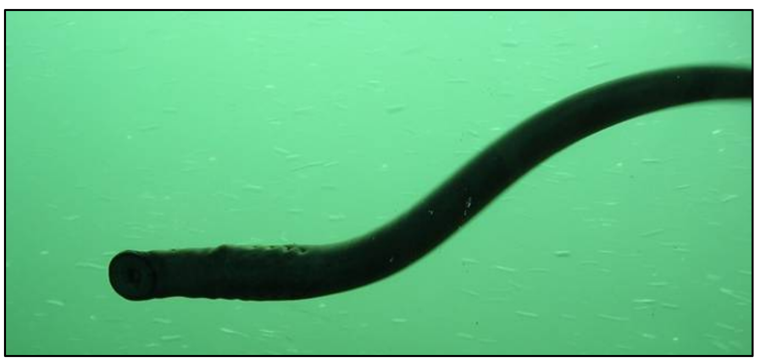

For

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

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Executive Summary

The 2019 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 2019 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. 2020), and results of experimental behavioral trials conducted in the Bonneville Adult Fish Facility (AFF) fishway flume (Hanchett and Caudill 2020). Our objectives here 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.

HD PIT-Tagged Samples

We HD PIT-tagged and released two samples of lampreys collected at Bonneville Dam: a group of 314 released downstream from the dam and 217 that were used in experiments at the Bonneville AFF 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 provided by cooperating agencies.

The 2019 escapement estimate for the downstream release group past Bonneville Dam was 52% (trap recaptures treated as not passing) to 58% (recaptures treated as passing), based on all data collected through October 2019. These escapements were near average estimates from the 2006-2014 and 2018 HD PIT studies (*range* = 41-61%) and would likely increase slightly (i.e., ≤3%) with inclusion of post-overwintering movements. Escapement from the top of Bonneville Dam to the top of The Dalles Dam (52%) from the top of The Dalles Dam to the top of John Day Dam (73%) and from the top of John Day Dam to the top of McNary Dam (25%) were similar to estimates in previous years.

Two traits of individual lampreys were associated with migration histories. The presence of the bacterial disease furunculosis was identified in 2019 and we assessed all tagged lampreys for symptoms (e.g., red hemorrhaging around the mouth). About 13% 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. As in previous years, large lampreys were substantially more likely than small lampreys to pass through most reaches; 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.

Passage times were similar to previous years. The median passage time in 2019 was 7.2 days (< 1 km•d^{-1}) from release to the top of Bonneville Dam, which was within the range (5.3-11.5 d) of prior study years. Median times between top-of-ladder antennas were 5.2 days between Bonneville and The Dalles dams (similar to previous years), 3.9 days between The Dalles and John Day dams (similar to previous years), and 9.0 days between John Day and McNary dams (relatively fast based on a small sample). Median passage time from release to the top of McNary Dam was 30.4 days. Lamprey

migration times were highly variable in 2019, as in all previous HD PIT study years, with dam-to-dam reach passage times ranging from a few days to more than two weeks.

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 early-run fish) and thus post-experiment behavior and distribution may not be representative of non-experimental fish. With these caveats, migration of these lampreys was similar to the other tag groups once accounting for differences in run timing and release location. Upstream escapement from release in the Bonneville forebay was 41% past The Dalles Dam, 40% past John Day Dam, and 9% past McNary Dam through October 2019. A little less than half (43%) of the flume study lampreys were not detected after release (similar to previous years).

Double-Tagged Sample

The 2019 escapement estimate from release past Bonneville Dam for radio and PIT tagged lampreys was ~39% (recaptures treated as passing) and ~33% (recaptures censored) through October 2019, which was similar to the highest estimates from comparable 2007-2014 radiotelemetry studies (*range* = 21-41%). Escapement estimates from release past The Dalles (17%) and John Day (9%) dams were both above average in 2019 whereas escapement from release past McNary Dam was slightly below average. 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 the pattern of negative radio-tagging effects reported in previous years.

Double-tagged lamprey migration rates were also highly variable but tended to be slow at dams and relatively rapid through reservoirs. Median passage times for double-tagged fish were 9.3 days from release to the top of Bonneville Dam, 3.1 days from tailrace to top-of-ladder antennas at The Dalles Dam, and 5.0 days between tailrace and top-of-ladder antennas at John Day Dam. Median passage times through reservoirs were 2.0 d (Bonneville) and 1.8 d (The Dalles).

In contrast to previous radiotelemetry years, no tributaries were monitored with radio antennas during the 2018-2019 study years. As expected, a lower percentage (~4%) of lampreys was last detected in tributaries on PIT antenna arrays through October 2019 than in years with radiotelemetry monitoring in tributaries before 2018 (13-25%). A majority (~61%) of the double-tagged sample was last detected at or downstream from Bonneville Dam. About 9% was last detected at top-of-fishway sites at Bonneville Dam, ~14% was last detected at The Dalles Dam, ~10% was at John Day Dam, and ~2% where last detected at or upstream from McNary Dam. Final lamprey distributions are expected to change slightly after post-overwintering movements are completed in 2020.

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 4-7 years in the ocean before returning to spawn in freshwater rivers (Beamish 1980; Close et al. 2002; Moser and Close 2003; Porter et al. 2020). 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 and 2018 to identify passage areas at dams with low lamprey passage rates, 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) and 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 though use of HD PIT tags continued given the larger array of monitoring sites.)

The objectives of the 2019 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 study developments that began in 2018 and continued in 2019: (1) observations for a group of small-bodied ('dwarf') Pacific Lampreys collected at Bonneville Dam in 2019; and (2) the presence of lampreys exhibiting symptoms of furunculosis during the 2019 run. Dwarf Pacific Lampreys have been reported to return to freshwater in northern latitudes at lengths < 37 cm whereas non-dwarf adults range from 55 to 72 cm (Hess et al. 2015); body length can vary depending on location and time of measurement (Kostow 2002). Dwarf lampreys have been collected in western Washington, Oregon, and British Columbia in coastal streams as well as in 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 AFF 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). Detailed evaluations of tagged lamprey behaviors in and near lower Columbia River dam fishways in 2019, including their use of lamprey passage systems (LPSs) and summaries of their response to nighttime fishway reduced velocities at Bonneville and The Dalles dams, are presented in a separate report (Clabough et al. 2020).

Methods

Lamprey Collection and Tagging

In 2019, three samples of adult lampreys were collected at night in traps located in the fishway near the Bonneville Dam AFF. These fish were tagged in the AFF prior to release. The three groups were: 1) 314 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; location of release site was randomized by day); 2) 217 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) 449 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 are reported in Hanchett and Caudill 2020 and characterization of fishway use by HD PIT and double-tagged fish are reported in Clabough et al. 2020).

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 and thus our sample may have been biased toward larger lampreys. 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 the distance between dorsal fins [dorsal distance, dd; Clemens 2011, Moser et al *in press]* to the nearest mm), weighed (nearest g) and evaluated for muscle lipid content (% fat) with a non-invasive Distell fish fat meter (Distell Inc., West Lothian, Scotland). HD PIT lampreys were then outfitted with a uniquely-coded, glass-encapsulated HD PIT tag (BIO32.HDX.03V2, 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 signs of furunculosis in 2019 were identified and symptoms were recorded throughout the tagging season. 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 in June 2018, we used a symptom severity index in both years for all tagged lampreys based on the degree of red hemorrhaging around the mouth (Figure 1). 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 in 2019.

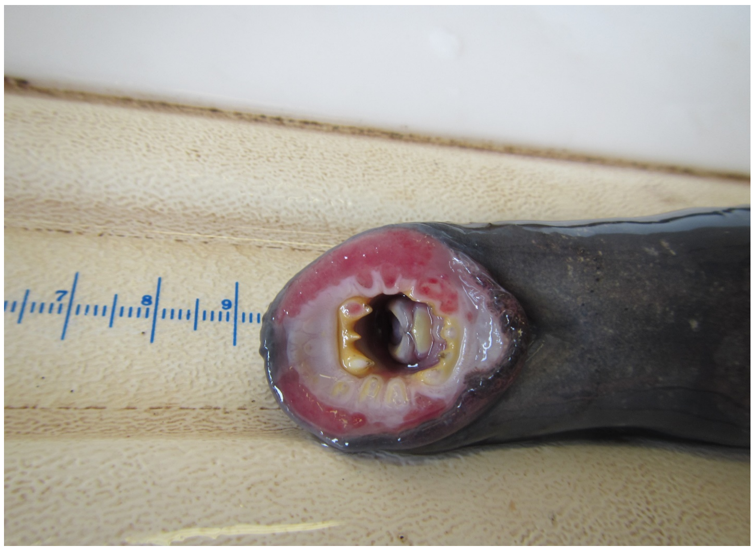

Figure 1. Photo of Pacific lamprey with severe (category 3) symptoms of furunculosis with >50% of the perimeter of the mouth having red hemorrhages.

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 (FD and HD) PIT interrogation sites administered by Pacific States Marine Fisheries Commission (PSMFC) were installed in 2017-2019 for 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 at the four lower Columbia River dams.

Data Analyses

We used Pearson's χ^2 tests and logistic regression (Zar 1999) 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 the mouth and compared them to fish that were not symptomatic. In addition to the binary (y, n) furunculosis covariate, the logistic regression model included lamprey tag date and fish weight. Passage at each of the four dams through 31 October 2019 (y, n) 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 September 2019, 24 double-tagged lampreys and 18 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 conservative 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 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 2019. 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 LPS	1
	Cascades Island AWS	1
	PH 1, Bradford Island 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 2019. PH = Powerhouse; UMT= upstream migrant tunnel; AWS=Auxiliary water supply.

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	7
	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, in 2018 we compared travel times between dams using passage records at the top of the ladder from UI HD versus PTAGIS detection sites (Keefer et al. 2019). 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, in 2018 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; differences of this magnitude likely had limited biological relevance. We note that these antenna configuration differences did not affect passage time estimates for double-tagged fish.

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 2019, was 70,876 (N. McClain, USACE, *personal communication*). The lower-than-average run size limited collections and a total of 980 lampreys were collected, tagged, and released, or approximately 1.4% of the total corrected count (Figure 2). The tagged sample included three study groups. The first was 314 with HD PIT tags only that were released downstream from Bonneville Dam. The second was 217 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 449 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 release location upstream from Bonneville Dam.

Sampling for the downstream release groups was generally proportional to daily counts, except under-sampling occurred during the unusually large single-day increase in passage in mid-August (Figure 2). Lamprey run timing, as indexed by the daytime count station counts, was 10 June (10%

passage date), 23 June (25% date), 11 July (median date), 25 July (75% date), and 12 August (90% date). For comparison, the dates for the HD PIT group released downstream were 1 June, 16 June, 7 July, 16 July, and 27 July, respectively. Dates for the radiotelemetry group were 5 June, 22 June, 9 July, 24 July, and 14 August, respectively. The group used in the flume was collected only until mid-season.

The four lamprey size metrics (Table 3) were all positively inter-correlated in the combined 2019 Bonneville samples (Figure 3). The coefficient of variation (CV) was 20% for dorsal distance, 21% for weight, 10% for girth, and 8% for length for the total sample. Release date was weakly and negatively correlated with lamprey weight (r = -0.16, $P \leq 0.05$).

Dwarf lampreys

During adult lamprey collection in 2019 at the AFF in the WA-shore ladder, 6 adult dwarf-sized lampreys (31.9 to 41.0 cm in length) were trapped and tagged with HD PIT tags. All six lampreys were released downstream from Bonneville Dam. Dwarf lampreys were about half the length (*mean* = 35.8 cm), had 40% less girth (*mean* = 6.8 cm), weighed ~80% less (*mean* = 97.4 g), and had less than half the dorsal distance (*mean* = 1.7), on average, compared to all other HD PIT and double tagged lampreys (Table 3), though mean length-specific dorsal distance (DD/total length) was more similar (dwarf=0.048 cm and non-dwarf=0.056 cm) for the two groups. The dwarf fish were included in analyses below, unless otherwise noted. The final detection locations of the 6 dwarf lampreys released downstream included 1 (17%) at the top of a fishway at Bonneville, 1 (17%) recapture at the AFF that was released upstream, and 4 (66%) that were not detected after release.

Table 3. Length, girth, weight, and dorsal distance of adult Pacific Lampreys collected and tagged in 2019 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. Note: not all fish had size metric records.

	Length (cm)			Girth (cm)			Weight (g)			Dorsal distance (cm)		
Type	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*
PIT	314	65.2	6.3	313	11.1	1.2	313	452.1	110.3	314	3.7	0.8
PIT-STE[1]	217	66.5	4.7	217	11.2	0.9	217	483.5	99.2	217	3.7	0.7
Double-tag	446	69.4	3.9	449	12.0	0.9	448	541.6	87.1	448	4.0	0.8
Dwarf fish[2]	6	35.8	3.1	6	6.8	0.6	5	97.4	21.6	6	1.7	0.5
Non-dwarf fish[3]	971	67.6	4.7	973	11.6	1.0	973	502.1	101.6	973	3.8	0.7
All fish	977	67.4	5.3	979	11.3	1.1	978	500.0	105.4	979	3.8	0.8

[1] the Stevenson release group was used in flume studies and data are 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

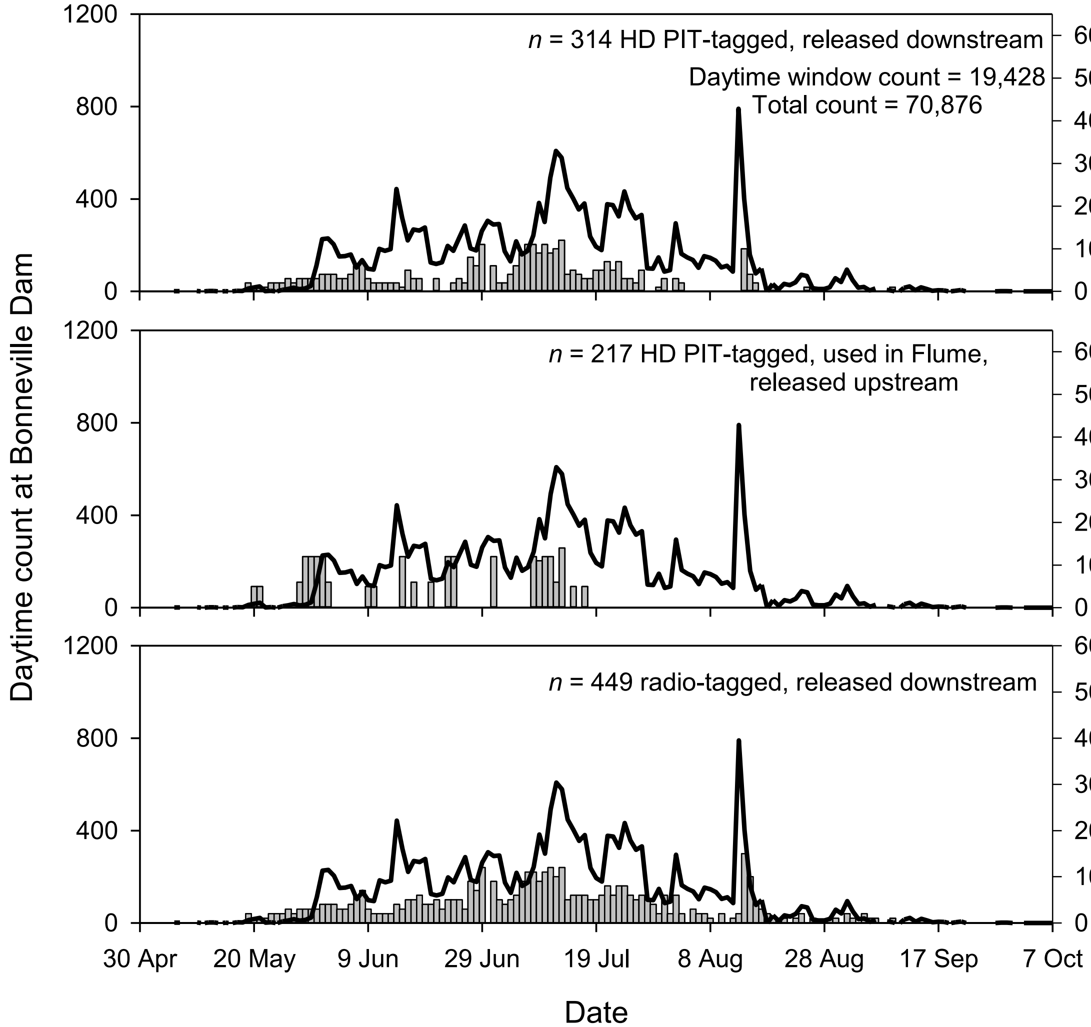

Figure 2. Number of adult Pacific Lampreys counted passing Bonneville Dam during the day (solid line) and the numbers that were collected and tagged (bars) in 2019. 'Total count' is the corrected total from daytime counts at windows, night video at windows, and LPS passage estimates through 31 December. 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.

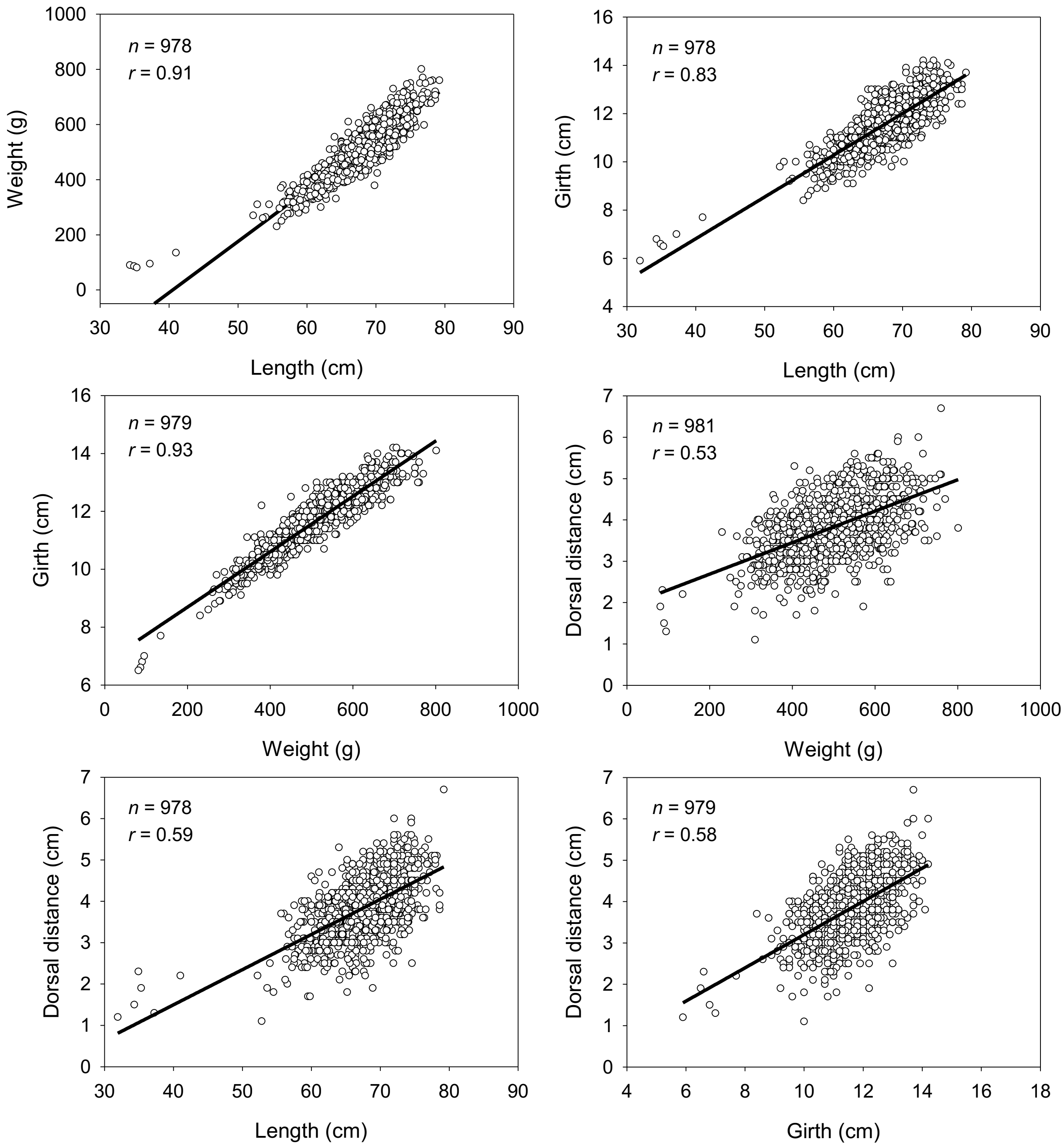

Figure 3. Linear relationships between length, weight, girth, and dorsal distance metrics for adult lampreys HD PIT- and double-tagged in 2019, including six dwarf lampreys. Note: all Bonneville release groups combined. All regression $P < 0.005$.

Lamprey Condition

Fish 'condition' has long been used to assess the relative size and potential energetic reserves or 'fatness'of fishes based on the relationship between fish length and weight (Ricker 1975; Anderson and Neumann 1996). Condition (K) it is commonly calculated as $10^5 \times$weight/FL^3, but has recently been re-parameterized for Pacific lamprey as $10^5 \times$weight/FL$^{2.6}$ (Lampman et al. *in press*). We calculated condition (K) for the downstream release groups in 2019. Mean condition was 2.21 (*sd* = 0.16, *range* =1.82-2.66) for double-tagged fish and 2.13 (*sd* = 0.18, *range* =1.53-2.66) for PIT-tagged fish. As expected, K was positively correlated with most of the lamprey size metrics in both samples (Table 4), but especially weight and girth ($0.43 \leq r \leq 0.51$). K was also negatively correlated ($-0.18 \leq r \leq -0.33$) with tag date, indicating that lamprey condition declined over the course of the migration period. In multiple regression models, the size metrics alone accounted for 84% (PIT-tagged) and 97% (double-tagged) of the variation in K. For this reason, condition factor was not included as a predictor variable in lamprey passage or escapement models.

Table 4. Correlation coefficients (*r*) between adult Pacific lamprey body size metrics and tag date at Bonneville Dam and fish condition (K) as defined by Lampman et al. (*In press*). Bold text indicates statistical significance at $P < 0.001$.

	Correlation (*r*) with lamprey condition factor (K)				
	Length	Weight	Girth	DD	Tagdate
PIT	0.146	**0.483**	**0.497**	-0.020	**-0.329**
Double-tag	-0.030	**0.430**	**0.512**	0.042	**-0.186**

Furunculosis

We evaluated 449 double-tagged fish for symptoms of furunculosis. Of these, 86% (*n* = 387) had no symptoms, 12% (*n* = 53) had a low degree of red hemorrhaging and 2% (*n* = 9) had a moderate amount of red hemorrhaging. None of the double-tagged fish had heavy hemorrhaging. Of the 387 fish with no furunculosis symptoms, 42% passed Bonneville Dam compared to 16% for fish with any symptom (*n* = 62); a difference that was statistically significant in the Pearson's test ($\chi^2 = 15.0$, $P = 0.0001$, Table 5). Furunculosis symptoms were also associated ($P = 0.0002$) with reduced passage at Bonneville Dam ($P < 0.001$) and The Dalles Dam ($P = 0.0241$) in the logistic regression models that included lamprey tag date and weight (Table 6). These patterns generally persisted upstream with reduced sample sizes, with symptomatic fish less likely to be detected at John Day and McNary dams compared to asymptomatic fish (Tables 5 and 6). Passage probability also significantly declined during the passage season for double-tagged lampreys in the logistic regression models of passage past Bonneville, The Dalles and John Day dams (Table 6).

We evaluated 314 HD PIT-tagged fish (released below Bonneville Dam) for furunculosis symptoms (Table 7). The symptomatic rates were similar to those of double-tagged fish: 88% (*n* = 276) had no symptoms, 11% (*n* = 33) had a low degree of hemorrhaging and < 2% (*n* = 5) had moderate hemorrhaging. None of the fish showed signs of heavy hemorrhaging. Of the HD fish with no furunculosis symptoms, 61% (*n* = 276) passed Bonneville Dam compared to 29% of fish with symptoms (*n* = 38). As with the double-tagged group, the difference was statistically significant in a Pearson's test ($\chi^2 = 14.6$, $P = 0.0001$, Table 7) and ($P = 0.0002$) in the logistic regression model (Table 8). Upstream escapement was similarly lower for symptomatic fish in the passage models at The Dalles, John Day and McNary dams. Weight was statistically significant in the logistic models for all four monitored dams for HD PIT-tagged fish (Table 8). Tag date was only significant past Bonneville Dam.

Table 5. The number of double-tagged lampreys tagged at Bonneville Dam (*n* = 449) for symptoms of furunculosis and the percentage of fish with and without symptoms that passed Bonneville, The Dalles, John Day and McNary dams.

Dam	Symptomatic	Tagged	Pass Dam No	Pass Dam Yes	%Pass
Bonneville	No	387	225	162	41.9
	Yes	62	52	10	16.1
The Dalles	No	387	314	73	18.9
	Yes	62	58	4	6.5
John Day	No	387	350	37	9.6
	Yes	62	59	3	4.8
McNary	No	387	382	5	1.3
	Yes	62	62	0	0.0

Table 6. Results of logistic regression analyses to assess the association between tag date, weight and symptoms of furunculosis and dam passage of double-tagged lampreys at Bonneville, The Dalles, John Day and McNary dams. Note: the reference value for the Furunculosis term was for asymptomatic fish (i.e., the odds ratio for Furunculosis in the Bonneville model results indicate that asymptomatic fish were ~4 times more likely than symptomatic fish to pass Bonneville Dam).

Dam	Parameter	Chi-square	P-value	Odds	95% CI
Bonneville	Date	26.0723	<0.0001	0.976	0.968-0.986
	Weight	1.6271	0.2021	1.002	0.999-1.004
	Furunculosis	14.2181	0.0002	3.994	1.944-8.204
	Intercept	4.657	0.0309		
The Dalles	Date	4.2323	0.0397	0.988	0.978-0.999
	Weight	6.6822	0.0097	1.004	1.001-1.007
	Furunculosis	5.0851	0.0241	3.351	1.171-9.585
	Intercept	1.8817	0.1701		
John Day	Date	6.5322	0.0106	0.980	0.964-0.995
	Weight	13.4179	0.0002	1.008	1.003-1.012
	Furunculosis	1.0968	0.295	1.927	0.565-6.578
	Intercept	2.3212	0.1276		
McNary[1]	Date	0.0776	0.7806	0.994	0.956-1.034
	Weight	1.3329	0.2483	1.006	0.996-1.016
	Furunculosis	0.0016	0.9681	>999.999	<0.001->999.99
	Intercept	0.0079	0.929		

[1] no double-tagged lampreys with Furunculosis passed McNary Dam.

Table 7. The number of HD PIT-tagged lampreys sampled at Bonneville Dam (n =314) for symptoms of furunculosis and the percentage of fish with and without symptoms that passed Bonneville, The Dalles, John Day and McNary dams in 2019.

			Pass Dam		
Dam	Symptomatic	Tagged	No	Yes	%Pass
Bonneville	No	276	107	169	61.2
	Yes	38	27	11	28.9
The Dalles	No	276	186	90	32.6
	Yes	38	33	5	13.2
John Day	No	276	211	65	23.6
	Yes	38	34	4	10.5
McNary	No	276	261	15	5.4
	Yes	38	37	1	2.6

Table 8. Results of logistic regression analyses to assess the association between tag date, weight and symptoms of furunculosis and dam passage of HD PIT-tagged lampreys at Bonneville, The Dalles, John Day and McNary dams in 2019. Note: the reference value for the Furunculosis term was for asymptomatic fish (i.e., the odds ratio for Furunculosis in the Bonneville model results indicate that asymptomatic fish were ~4.3 times more likely than symptomatic fish to pass Bonneville Dam).

Dam	Parameter	Chi-square	P-value	Odds	95% CI
Bonneville	Date	4.4526	0.0348	0.988	0.977-0.999
	Weight	10.3265	0.0013	1.004	1.001-1.006
	Furunculosis	13.9984	0.0002	4.309	2.005-9.261
	Intercept	0.3472	0.5557		
The Dalles	Date	0.0198	0.8882	0.999	0.987-1.012
	Weight	27.0826	<0.0001	1.007	1.004-1.01
	Furunculosis	6.8855	0.0087	3.961	1.417-11.074
	Intercept	9.695	0.0018		
John Day	Date	0.1203	0.7288	0.998	0.984-1.011
	Weight	25.7118	<0.0001	1.008	1.005-1.011
	Furunculosis	4.0658	0.0438	3.200	1.033-9.915
	Intercept	9.1474	0.0025		
McNary	Date	0.5916	0.4418	0.99	0.966-1.015
	Weight	7.695	0.0055	1.007	1.002-1.012
	Furunculosis	0.5828	0.4452	2.260	0.279-18.32
	Intercept	2.7728	0.0959		

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 9). 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. Detection efficiencies at individual radiotelemetry sites ranged from 88.9% at the John Day north ladder to 100% at the ladder tops of the Bonneville WA-shore and Bradford Island ladders, the east ladder top at The Dalles Dam, and the south ladder top at McNary Dam. 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 41.8% at the WA-shore top-of-the-ladder site at Bonneville Dam to 100% at the south and north ladder tops of John Day Dam (Table 9); efficiencies at the WA-shore site have declined from 72.2% in 2014 and 53.9% in 2018. The Dalles east top-of-ladder HD site was inoperable in 2019, but most (69%) 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 2019.

The PTAGIS antenna detection efficiencies at individual sites ranged from 65.6% at The Dalles east ladder top to 100.0% at Bonneville Bradford Island. Direct comparisons were not precise because PTAGIS antenna sites in ladders were either in vertical slot weirs or near count windows that were slightly downstream from the radiotelemetry and UI HD top-of-the-ladder sites. Lampreys also had to swim through a vertical slot weir or orifice to be detected on the PTAGIS system whereas they only needed be in close proximity to a radiotelemetry antenna. In the LPSs, where PTAGIS and UI HD sites are in close proximity, 86.7 and 100% were recorded on PTAGIS antennas at the Bonneville Bradford Island and WA-shore LPSs, respectively, compared to 86.7% and 96.0% on the older UI HD sites.

Table 9. Estimated detection efficiencies at top-of-ladder and LPS antennas calculated using double-tagged lampreys in 2019. Includes fish detected on at least one monitoring system.

			Detection efficiency		
Dam	Ladder	Total detected	Radiotelemetry	HD PIT	PTAGIS
Bonneville	South (Bradford)	42	100.0%	97.6%	100.0%
	South (LPS)	15	n/a	86.7%	86.7%
	North (WA-shore)	67	100.0%	41.8%	98.5%
	North LPS	25	n/a	96.0%	100.0%
The Dalles	South (East)	32	100.0%	[1]n/a	65.6%
	North	42	97.6%	83.3%	95.2%
John Day	South	21	90.5%	100.0%	n/a
	North	18	88.9%	100.0%	n/a
McNary	South	5	100.0%	[2]n/a	100.0%
	North	0	-	[2]n/a	-

[1] Not functional in 2019.
[2] Not monitored in 2019.

Dam-Wide Detection Efficiency: HD PIT-Tagged Fish

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

Bonneville Dam – In total, 123 lampreys from the downstream release group were detected at PIT antennas upstream from Bonneville Dam. Of these, 120 (97.6%) were recorded passing the dam via the following pathways: 81 (65.9%) were detected at top-of-ladder or top-of-LPS antennas, 29 (23.6%) were detected at one or more dual PIT vertical slot weir antennas, and 10 (8.1%) were recaptured at the AFF and transported upstream. There were 3 (2.4% of 123) that passed Bonneville Dam without a top-of-ladder or top-of-LPS detection record. Two of the three were detected at a Bonneville fishway entrance or inside a fishway and the other lampreys had no detections after release.

The Dalles Dam – A total of 157 lampreys (77 from the downstream release group and 80 from the upstream release group) were detected at antennas upstream from The Dalles Dam. Of these 157, 137 (87.3%) were recorded passing The Dalles Dam via the following pathways: 75 (47.8%) were detected at one or more dual PIT count window antennas, 61 (38.9%) were detected at the top of the north fishway (HD antenna) and one (0.6%) was recaptured and transported upstream. There were 20 (12.7% of 157) 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 2019 and consequently 14 (70.0% of 20) of the fish were last detected at the antenna inside the east fishway downstream from the east count station. The remaining 6 fish (30.0% of 20 and 3.8% of 157) were not detected at any location at The Dalles Dam.

John Day Dam – A total of 48 lampreys (both release groups) were detected at antennas upstream from John Day Dam. Of these 48, 46 (96.0%) were detected at the top-of-ladder antennas and 2 (4.0%) were detected at one or more dual PIT count window antennas.

Migration Summaries for Downstream Release Group: HD PIT

Upstream Progression – Of the 314 lampreys released downstream from Bonneville Dam, 238 (75.8%) were subsequently recorded at one or more Bonneville Dam HD antennas inside fishways, at LPS systems, or at dams further upstream through October 2019 (Table 10). A total of 164 fish volitionally passed Bonneville Dam based on top-of-fishway or upstream detections (52.2% of the 314 released, and 68.9% of the 238 detected at one or more HD PIT sites after release). Importantly, another 18 (5.7% of 314) were recaptured in traps at Bonneville Dam and were released upstream.

The median tag date for HD PIT-tagged lampreys released downstream was 7 July. Median recorded passage dates at top-of-ladder (or LPS) sites were 13 July at Bonneville Dam (n = 161), 19 July at The Dalles Dam (n = 83), 24 July at John Day Dam (n =69), 1 August at McNary Dam (n = 15), 10 August at Priest Rapids Dam (n = 4) and 17 August at Wanapum Dam (n = 7). Additional fish passed each dam without detection at top-of-ladder (or LPS) antennas (i.e., passage date was uncertain; Table 10). 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 4).

Point Estimates of Dam-to-Dam Escapement – Of 314 lampreys released downstream, 57.9% (*n* = 182) were known to have passed Bonneville Dam (including the 18 that were recaptured and released upstream), 30.3% (*n* = 95) passed The Dalles Dam, 22.0% (*n* = 69) passed John Day Dam, 5.4% (*n* = 17) passed McNary Dam, 3.2% (*n* = 10) passed Priest Rapids Dam, and 2.5% (*n* = 8) passed Wanapum Dam (Tables 10 and 11). Escapement from the top of Bonneville Dam was 57.9% to the top of The Dalles Dam, 42.1% to the top of John Day Dam, and 13.4% to the top of McNary Dam. Escapements were 72.6% between ladder tops at The Dalles and John Day dams and 24.6% between ladder tops at John Day and McNary dams as of 31 October 2019. Of 17 lampreys that passed McNary Dam, 4 (23.5%) passed Ice Harbor Dam and 10 (58.8%) passed Priest Rapids Dam (Tables 10 and 11).

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 5). 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 passed the four lower Columbia River dams before 31 October 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 5).

Table 10. Minimum numbers of adult lampreys that passed each site in 2019 estimated as the number of adult tagged lampreys detected at dam antennas or inferred to pass sites based on upstream detections through October 2019. 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		
Site	PIT Minimum past (*n*)	PIT-STE Minimum past (*n*)	Double-tagged Minimum past (*n*)
Release	314	217	449
Bonneville[1]	238	n/a	379
Bonneville top[2]	164-182[4]	n/a	149-173[4]
The Dalles[1]	114	115	116
The Dalles top[2]	94-95[4]	86-89[4]	74-77[4]
John Day[1]	73	64	52
John Day top[2]	68-69[4]	56-57[4]	40
McNary[1]	22	26	11
McNary top[2]	17	19	5
Ice Harbor[3]	4	5	2
Ice Harbor top[3]	4	4	2
L. Monumental[3]	4	4	2
L. Monument top[3]	3	3	-
L. Goose[3]	3	3	-
L. Goose top[3]	2	2	-
L. Granite[3]	2	2	-
L. Granite top[3]	1	-	-
Priest Rapids[5]	13	15	2
Priest Rapids top[5]	10	12	1
Wanapum[5]	9	13	1
Wanapum top[5]	8	12	1
Rocky Reach[5]	4	2	1
Rocky Reach top[5]	n/a	n/a	n/a

[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

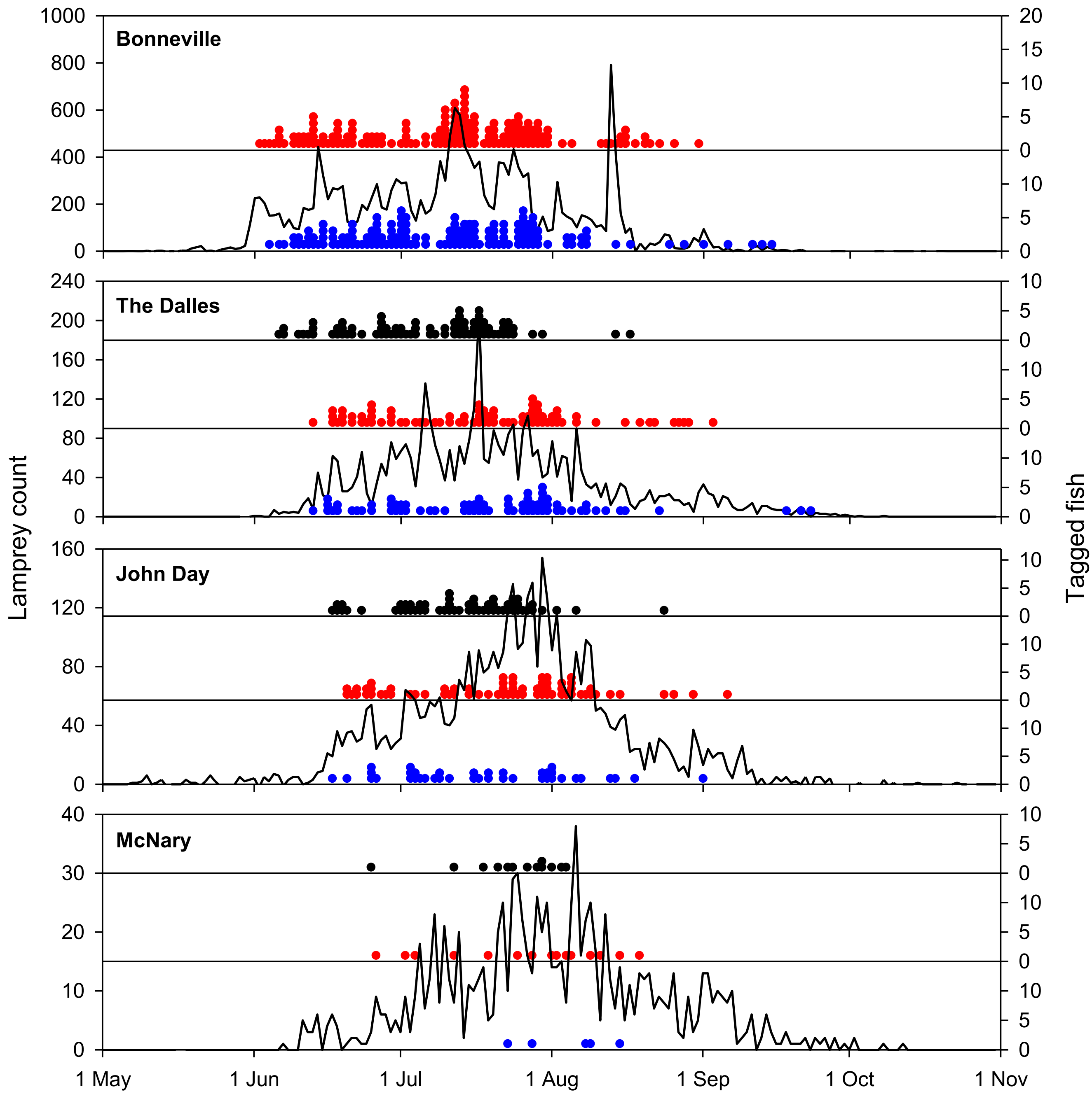

Figure 4. Daily numbers of adult Pacific Lampreys counted passing lower Columbia River dams in the daytime via fish ladders (black lines) and the numbers of tagged fish that were detected at top-of-fishway antennas (blue circles = double-tagged fish; red circles = HD PIT-tagged fish released downstream from Bonneville; black circles = HD PIT-tagged fish released upstream from Bonneville, in 2019. Notes: many tagged lampreys passed dams undetected, particularly at The Dalles and McNary dams; counts are daytime window counts only; y-axis scales differ.

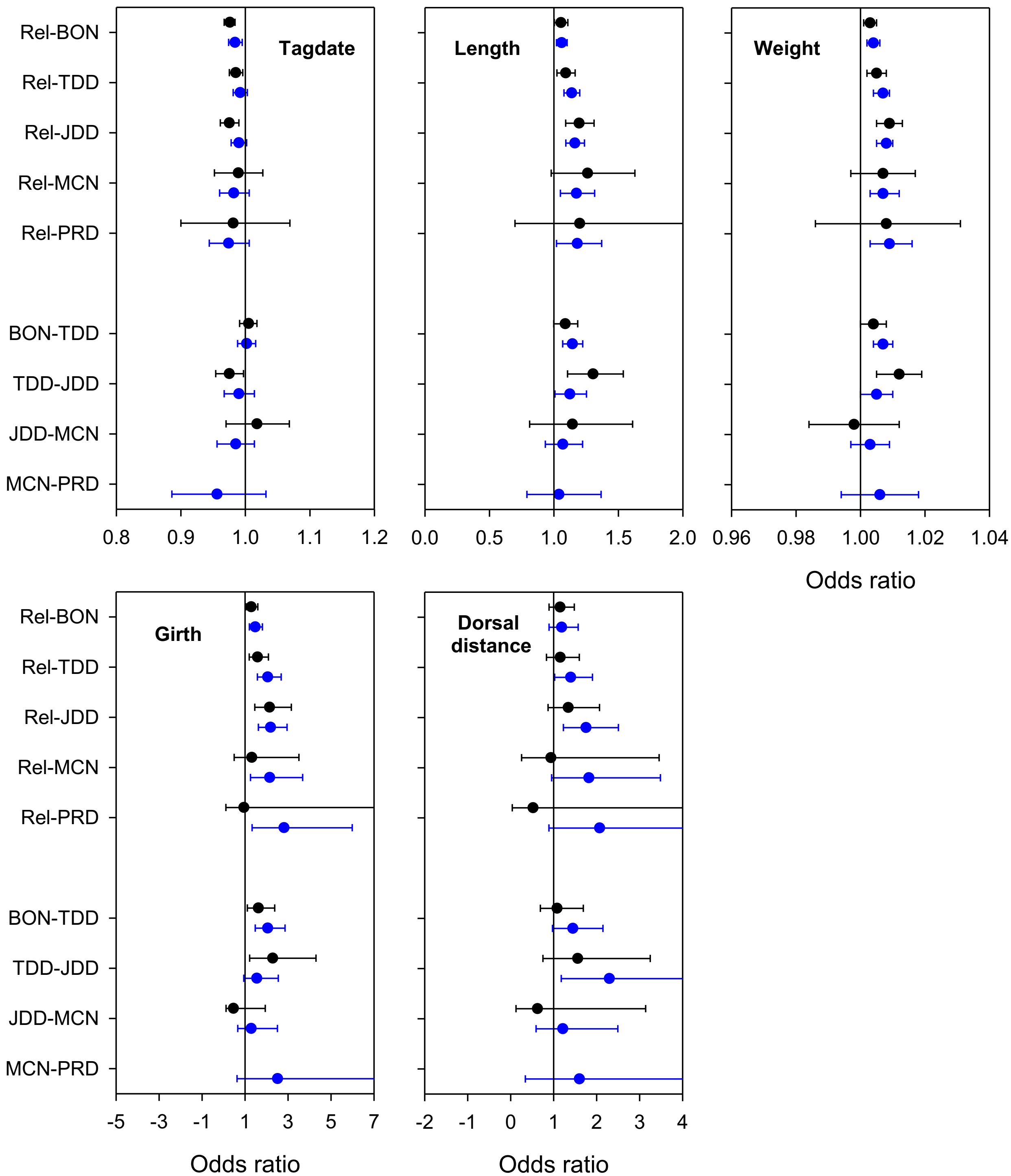

Figure 5. Odds ratios (+/- 95% CI) estimated from logistic regression models of upstream escapement through October 2019 by HD PIT-tagged lampreys (blue circles) and double-tagged lampreys (black circles) released downstream from Bonneville Dam in 2019. Odds ratios were scaled to the independent variables: 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. Odds ratios with CI not overlapping 1.0 were considered statistically significant.

Passage Times and Rates – Median HD PIT-tagged lamprey passage times were 7.2 d from the release site to the top of Bonneville Dam, 5.2 d between Bonneville and The Dalles dams, 3.9 d between The Dalles and John Day dams, and 9.0 d between John Day and McNary dams (top-of-ladder or LPS sites at all dams, Table 12). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 14.0 km•d^{-1} (Bonneville-The Dalles), 9.9 km•d^{-1} (The Dalles-John Day), and 13.7 km•d^{-1} (John Day-McNary). The release-Bonneville top rate included only tailrace and dam passage whereas other rates included passage of reservoir, tailrace, and dam segments. 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 76 (24.2%) of the 314 lampreys released downstream from Bonneville Dam were not subsequently detected through October 2019 (Table 9). Another 58 (18.5%) were last recorded at HD antennas inside Bonneville Dam fishways, and 57 (18.2%) were last detected at Bonneville top-of-ladder or LPS exit antennas. Six fish (1.9%) were last recorded in Fifteenmile Creek or its tributaries and 3 (1.0%) were recorded in the Klickitat River. A total of 38 (12.1%) was last detected at The Dalles Dam, and 4 (1.3%) were recorded in the Deschutes River. Above the Deschutes River, 50 (15.9%) were last detected at John Day Dam, 5 (1.6%) were at McNary Dam, 4 (1.3%) were at Snake River dams, and 13 (4.1%) were at dams in the upper Columbia River (Priest Rapids through Rocky Reach dams) (Table 13).

When lampreys were grouped based on final recorded location, median release dates varied considerably among groups (Figure 6). 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 or McNary Dam had the latest median date among lampreys with post-release records. Lampreys without records after release were more common later in the tagged sample. There were clearer among-group differences in lamprey size and lampreys recorded passing McNary Dam and other sites upstream were >20% larger on median than the tagged sample (Figure 7). On median, lampreys were largest in the groups last detected at McNary (588 g) and the upper Columbia River (519 g) followed by the Snake River (504 g) and John Day (503 g) dams. Lampreys were smallest in the groups last recorded in Bonneville tributaries (*median* = 400 g) and at release (*median* = 404 g).

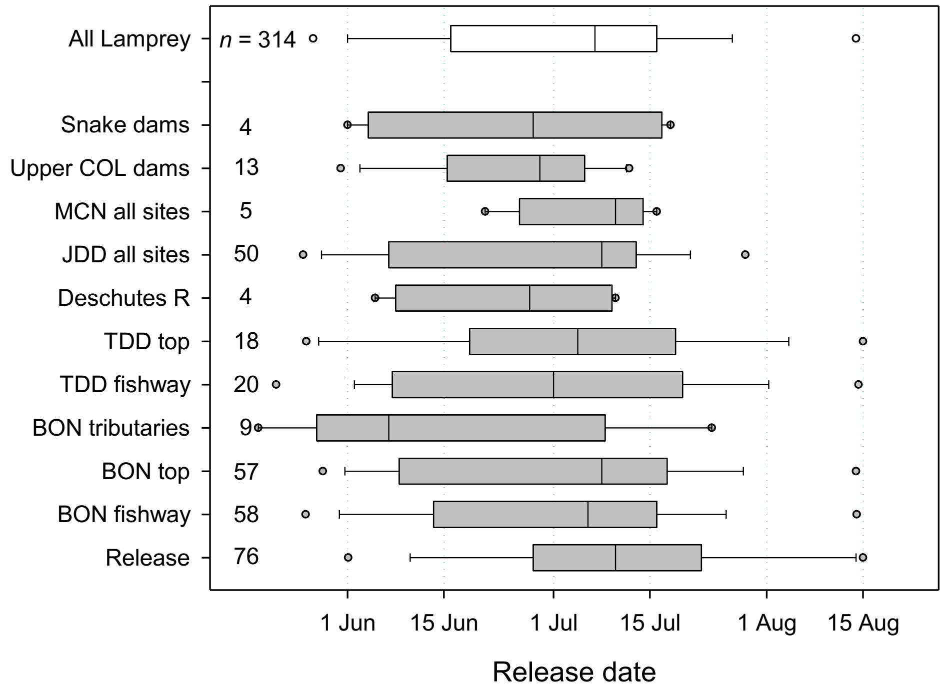

Figure 6. Distributions of HD PIT-tagged lamprey release dates by the final recorded locations for each fish through October 2019. Data shown are for lampreys released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

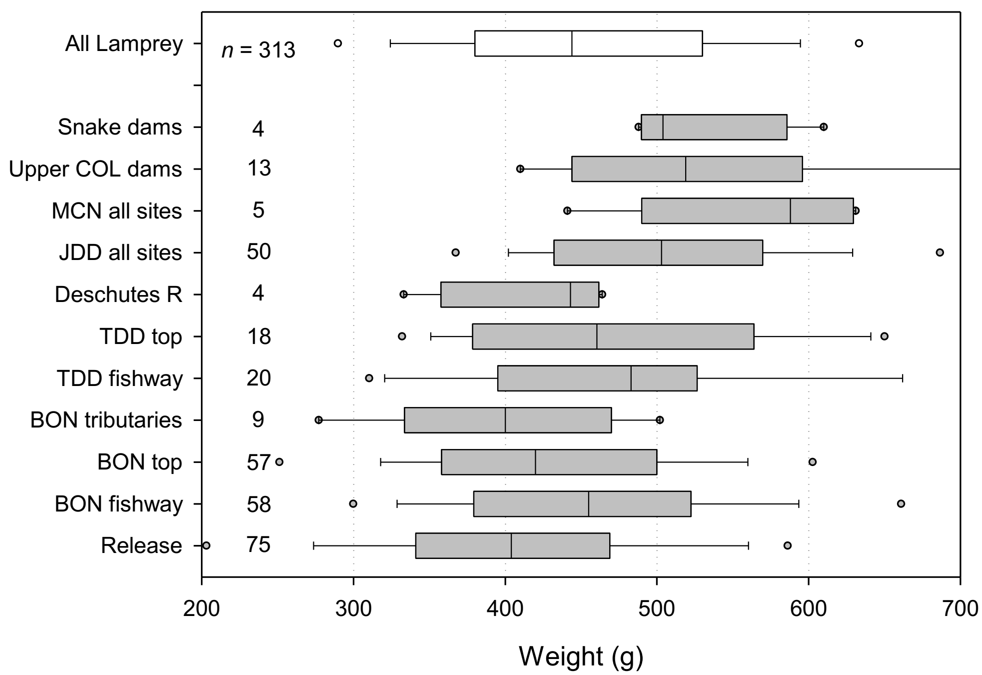

Figure 7. Distributions of HD PIT-tagged lamprey weights (g) by the final recorded locations for each fish (grey boxes) through October 2019. Data shown are for lampreys released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

Table 11. Lamprey escapement estimates for fish HD PIT-tagged and released downstream from Bonneville Dam or upstream from the dam near Stevenson, WA (STE) and for double-tagged fish released at two sites downstream from Bonneville Dam 2019, including all detections through October 2019. See Table 10 for sample sizes.

Reach	PIT Escapement	PIT-STE Escapement	Double-tagged Escapement
Release-Bonneville	75.8%	n/a	84.4%
Release-Bonneville top	52.2-57.9%	n/a	33.2-38.5%
Release-The Dalles	36.3%	53.0%	25.8%
Release-The Dalles top	29.9-30.3%	39.6-41.0%	16.5-17.1%
Release-John Day	23.2%	39.5%	11.6%
Release-John Day top	21.7-22.0%	25.8-26.3%	8.9%
Release-McNary	7.0%	12.0%	2.4%
Release-McNary top	5.4%	8.8%	1.1%
Release-Ice Harbor top	1.3%	1.8%	0.4%
Release-Lower Monumental top	1.0%	1.4%	0.0%
Release-Lower Granite top	0.6%	-	0.0%
Release-Priest Rapids top	3.2%	5.5	0.2%
Release-Wanapum top	2.5%	5.5	0.2%
Release-Rock Island top	1.3%	0.9%	0.2%
Release-Rocky Reach top	n/a	n/a	n/a
Bonneville-Bonneville top[1]	68.9-76.5%	n/a	42.0-45.6%
Bonneville top-The Dalles top	52.2%	n/a	44.5%
Bonneville top-John Day top	37.9%	n/a	23.1%
Bonneville top-McNary top	12.1%	n/a	2.9%
Bonneville top-Ice Harbor top	2.2%	n/a	1.2%
Bonneville top-L. Monum. top	1.6%	n/a	-
Bonneville top-L. Granite top	1.1%	n/a	-
Bonneville top-Pr. Rapids top	5.5%	n/a	0.6%
Bonneville top-Wanapum top	4.4%	n/a	0.6%
Bonneville top-Rock Island top	2.2%	n/a	0.6%
Bonneville top-Rocky Reach top	n/a	n/a	n/a
The Dalles top-John Day top	72.6%	64.0%	51.9%
The Dalles top-McNary top	17.9%	21.3%	6.5%
The Dalles top-Ice Harbor top	4.2%	4.5%	2.6%
The Dalles top-L. Monum. top	3.2%	3.4%	-
The Dalles top-L. Granite top	1.1%	-	-
The Dalles top-Pr. Rapids top	10.5%	13.5%	1.3%
The Dalles top-Wanapum top	8.4%	13.5%	1.3%
The Dalles top-Rock Island top	4.2%	1.7%	1.3%
The Dalles top-Rocky Reach top	n/a	n/a	n/a

Note: lower estimate treats recaptured at Bonneville, The Dalles or John Day as not passing; higher estimate treats them as passed; all other estimates included recaptured fish as passing dams where applicable.

Table 11 (cont).

Reach	PIT Escapement	PIT-STE Escapement	Double-tagged Escapement
John Day top-McNary top	24.6%	33.3%	12.5%
John Day top-Ice Harbor top	5.8%	7.0%	5.0%
John Day top-L. Monum. top	4.3%	5.3%	-
John Day top-L. Granite top	2.9%	-	-
John Day top-Priest Rapids top	14.5%	21.1%	2.5%
John Day top-Wanapum top	11.6%	21.1%	2.5%
John Day top-Rock Island top	5.8%	3.5%	2.5%
John Day top-Rocky Reach top	n/a	n/a	n/a
McNary top-Ice Harbor top	23.5%	21.1%	40.0%
McNary top-L. Monum. top	17.6%	15.8%	-
McNary top-L. Granite top	5.9%	-	-
McNary top-Priest Rapids top	58.8%	63.2%	20.0%
McNary top-Wanapum top	47.1%	63.2%	20.0%
McNary top-Rock Island top	23.5%	10.5%	20.0%
McNary top-Rocky Reach top	n/a	n/a	n/a
Priest Rapids top-Wanapum top	80.0%	83.3%	100.0%
Priest Rapids top-Rock Island top	40.0%	16.7%	100.0%
Priest Rapids top-Rocky Reach top	n/a	n/a	n/a
Wanapum top-Rock Island top	50.0%	16.7%	100.0%
Wanapum top-Rocky Reach top	n/a	n/a	n/a
Rock Island top-Rocky Reach top	n/a	n/a	n/a
Ice Harbor top-L. Monum. Top	75.0%	75.0%	-
Ice Harbor top-L. Granite top	25.0%	-	-
L. Monum. top-L. Granite top	33.3%	-	-

Table 12. Summary of HD PIT-tagged adult lamprey passage times (d) through monitored reaches of the lower Columbia and Snake rivers, for fish released downstream from Bonneville Dam in 2019.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to pass Bonneville Dam	161	7.20	10.44	2.34	14.29
Release to pass The Dalles Dam	83	16.48	18.42	9.41	23.39
Release to pass John Day Dam	69	20.15	22.23	13.30	27.03
Release to pass McNary Dam[1]	15	30.38	30.74	23.80	37.37
Release to pass Priest Rapids Dam	4	44.77	46.73	32.91	58.59
Release to pass Wanapum Dam	7	55.39	52.10	44.38	58.36
Release to pass L. Granite Dam[2]	1	49.50	49.50	-	-
Bonneville top to pass The Dalles Dam	76	5.17	6.88	3.87	9.07
Bonneville top to pass John Day Dam	63	9.93	12.35	7.86	14.25
Bonneville top to pass McNary Dam[1]	13	21.23	20.41	12.29	23.92
Bonneville top to pass Priest Rapids Dam	3	40.84	40.59	31.46	49.85
Bonneville top to pass Wanapum Dam	6	44.57	43.48	38.74	49.06
The Dalles top to pass John Day Dam	59	3.87	5.36	2.85	5.90
The Dalles top to pass McNary Dam[1]	11	18.10	15.83	7.14	20.45
The Dalles top to pass Priest Rapids Dam	4	25.65	28.78	19.28	35.16
The Dalles top to pass Wanapum Dam	7	32.40	33.15	31.60	34.67
John Day top to pass McNary Dam[1]	15	8.98	11.46	5.78	16.29
John Day top to pass Priest Rapids Dam	4	25.65	28.78	19.28	35.16
John Day top to pass Wanapum Dam	7	32.40	33.15	31.60	34.67
McNary top[1] to pass Priest Rapids Dam	4	12.72	17.16	11.22	18.66
McNary top[1] to pass Wanapum Dam	7	24.09	24.61	22.70	26.09

[1]No UI HD antennas installed at McNary Dam in 2019. 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 2019. 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 13. Last recorded locations for lampreys HD PIT-tagged and released downstream from Bonneville Dam or upstream from the dam near Stevenson (STE), WA and for double-tagged fish released downstream from Bonneville Dam in 2019; includes all detections through October 2019. WA = Washington-shore fishway; LPS = lamprey passage structure. Notes: Fifteenmile Creek sites were maintained by the CTWRSO; Wanapum, Priest Rapids (also PTAGIS), and Rocky Reach sites were maintained by Chelan and Grant county PUDs. Klickitat River, McNary (PIT) and lower Snake River dams PIT detections were from PTAGIS.

	PIT (n = 314)		PIT-STE (n = 217)		Double-tagged (n = 449)	
Last recorded location	*n*	%	*n*	%	*n*	%
Release site	76	24.2%	94	43.3%	4	0.9%
Bonneville tailrace	-	-	-	-	97	21.6%
Bonneville – Brad. Is. fishway	-	-	-	-	91	20.3%
Bonneville – WA-shore fishway	4	1.3%	-	-	53	11.8%
Bonneville – Casc. Is.fishway	19	6.1%	-	-	36	8.0%
Bonneville – WA ladder	26	8.3%	-	-	-	-
Bonneville – Brad. Is. ladder	9	2.9%	-	-	-	-
Bonneville – recapture[1]	7	2.2%	-	-	7	1.6%
Bonneville – WA ladder exit / LPS[2]	32	10.2%	-	-	13	2.9%
Bonneville – Casc. Is. LPS	1	0.3%	-	-	-	-
Bonneville – Bradford exit / LPS[2]	17	5.4%	-	-	27	6.0%
Klickitat River	3	1.0%	2	0.9%	-	-
Fifteenmile Creek + tributaries	6	1.9%	6	2.8%	-	-
The Dalles tailrace	-	-	-	-	10	2.2%
The Dalles Dam fishways	20	6.4%	22	10.1%	37	8.2%
The Dalles Dam recapture[3]	-	-	3	1.4%	2	0.4%
The Dalles Dam ladder exits	18	5.7%	10	4.6%	14	3.1%
Deschutes River + tributaries	4	1.3%	17	7.8%	3	0.7%
John Day tailrace	-	-	-	-	12	2.7%
John Day Dam fishways	9	2.9%	5	2.3%	6	1.3%
John Day Dam recapture[4]	1	0.3%	1	0.5%	-	-
John Day Dam ladder exits	40	12.7%	31	14.3%	26	5.8%
McNary Dam fishways	5	1.6%	6	2.8%	7	1.6%
McNary Dam ladder exits	-	-	-	-	-	-
Ice Harbor Dam	-	-	1	0.5%	-	-
Lower Monumental Dam	1	0.3%	1	0.5%	2	0.4%
Little Goose Dam	1	0.3%	1	0.5%	-	-
Lower Granite Dam	2	0.6%	2	0.9%	-	-
Priest Rapids Dam	6	1.9%	2	0.9%	1	0.2%
Wanapum Dam	3	1.0%	11	5.1%	-	-
Rocky Reach Dam	4	1.3%	2	0.9%	1	0.2%

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

Migration Summaries for Downstream Release Group: Double-Tagged

Upstream Progression – Of the 449 double-tagged lampreys released downstream from Bonneville Dam, 379 (84.4%) were subsequently recorded at one or more Bonneville Dam antennas or at dams further upstream through October 2019 (Table 10). A total of 149 fish volitionally passed Bonneville Dam based on top-of-fishway or LPS detections or upstream detections (33.2% of the 449 released, and 39.3% of the 379 detected at one or more sites after release). Twenty-four lampreys (5.3% of the 449 released) were recaptured in traps at Bonneville Dam and were released upstream.

The median tag date for double-tagged lampreys released downstream was 9 July (*mean* = 8 July). Median recorded passage dates at top-of-ladder sites were 12 July at Bonneville Dam (n = 147), 21 July at The Dalles Dam (n = 74), 17 July at John Day Dam (n = 39), and 8 August at McNary Dam (n = 5). 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).

Point Estimates of Dam-to-Dam Escapement – Of 449 lampreys released downstream from Bonneville Dam, 38.5% (n = 173) were known to have passed the dam through October 2019 (including 24 that were recaptured and released upstream), 17.1% (n = 77 with 3 recaptures) passed The Dalles Dam, 8.9% (n = 40 with 0 recaptures) passed John Day Dam, 1.1% (n = 5) passed McNary Dam, 0.1% (n = 1) passed Priest Rapids Dam, and 0.1% (n = 1) passed Wanapum Dam (Tables 10 and 11). Two double-tagged lampreys (0.4% of the 449 released) were detected in the adult fishway at Lower Monumental Dam after having passed Ice Harbor Dam. No double-tagged lampreys were detected upstream from Lower Monumental Dam. Escapement from the top of Bonneville Dam was 44.5% to the top of The Dalles Dam, 23.1% to the top of John Day Dam, and 2.9% to the top of McNary Dam. Inter-dam escapements were 51.9% between ladder tops at The Dalles and John Day dams and 12.5% between ladder tops at John Day and McNary dams. Of five lampreys that passed McNary Dam, 2 (40.0%) passed Ice Harbor Dam and 1 (20.0%) passed Priest Rapids Dam (Tables 10 and 11).

Consistent with past observations, lampreys in the double-tagged sample that passed upstream sites were longer, heavier, and had larger girth and dorsal distance than those that did not pass in most reaches in single variable logistic regression models (Figure 5). 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 5).

Passage Times and Rates – Median double-tagged lamprey passage times were 9.3 d from the release site to the top of Bonneville Dam, 5.2 d between Bonneville and The Dalles dams, 3.4 d between The Dalles and John Day dams, and 12.5 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 14). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 14.0 km•d^{-1} (Bonneville-The Dalles), 11.2 km•d^{-1} (The Dalles-John Day), and 9.8 km•d^{-1} (John Day-McNary). Sample sizes were limited upstream from John Day Dam. Passage rates through reservoirs were much faster than through reaches that included dams (Table 14).

Table 14. Summary of double-tagged adult lamprey passage times through dam-to-dam and multi-dam reaches of the lower Columbia River in 2019. 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	354	0.28	2.40	0.17	2.47
Release to enter Bonneville fishway	267	1.20	3.14	0.22	4.19
Release to pass Bonneville Dam	147	9.32	10.41	3.31	14.27
Release to The Dalles tailrace	20	14.19	16.36	9.13	16.83
Release to pass The Dalles Dam	74	15.24	16.97	9.39	22.11
Release to John Day tailrace	22	15.22	17.18	11.65	22.44
Release to pass John Day Dam	39	20.33	21.67	14.84	27.69
Release to McNary tailrace	-	-	-	-	-
Release to pass McNary Dam	5	29.33	32.42	24.30	35.09
Bonneville top to The Dalles tailrace	18	2.04	5.93	1.91	5.06
Bonneville top to pass The Dalles Dam	65	5.22	7.06	3.23	7.94
Bonneville top to John Day tailrace	19	8.39	10.40	6.33	12.33
Bonneville top to pass John Day Dam	34	10.16	12.69	7.00	15.91
Bonneville top to McNary tailrace	-	-	-	-	-
Bonneville top to pass McNary Dam	5	20.04	21.39	12.88	30.80
The Dalles tailrace to pass The Dalles Dam	10	3.14	4.15	2.20	4.50
The Dalles top to John Day tailrace	22	1.81	1.95	1.22	2.10
The Dalles top to pass John Day Dam	38	3.45	5.78	2.77	7.64
The Dalles top to McNary tailrace	-	-	-	-	-
The Dalles top to pass McNary Dam	5	12.87	16.00	9.99	23.01
John Day tailrace to pass John Day Dam	15	4.96	5.07	1.97	7.37
John Day top to McNary tailrace	-	-	-	-	-
John Day top to pass McNary Dam	4	12.49	13.46	8.86	17.08
McNary tailrace to pass McNary Dam	-	-	-	-	-

Last Detection Summary – A total of 4 (0.9%) of the 449 lampreys released below Bonneville Dam were never detected through October 2019 (Table 13). Another 97 (21.6%) were last recorded at Bonneville tailrace radiotelemetry antennas, 180 (40.1%) were last detected at Bonneville Dam fishways, and 40 (8.9%) were at Bonneville top-of-ladder exit sites or LPS sites. No fish were last detected in tributaries to the Bonneville reservoir where no radiotelemetry monitoring sites were operated in 2019. A total of 10 (2.2%) were last detected at The Dalles tailrace, 37 (8.2%) were at The Dalles fishways, and 14 (3.1%) were last recorded at The Dalles exit antennas. Three (0.7%) were recorded on PIT antennas in the Deschutes River. Upstream from the Deschutes River, 44 (9.8%) were at John Day Dam, 7 (1.6%) were at McNary Dam, 1 (0.2%) was at Priest Rapids Dam, and 1 (0.2%) was at Rocky Reach Dam. No lampreys were last detected upstream from Lower Monumental Dam (Table 13).

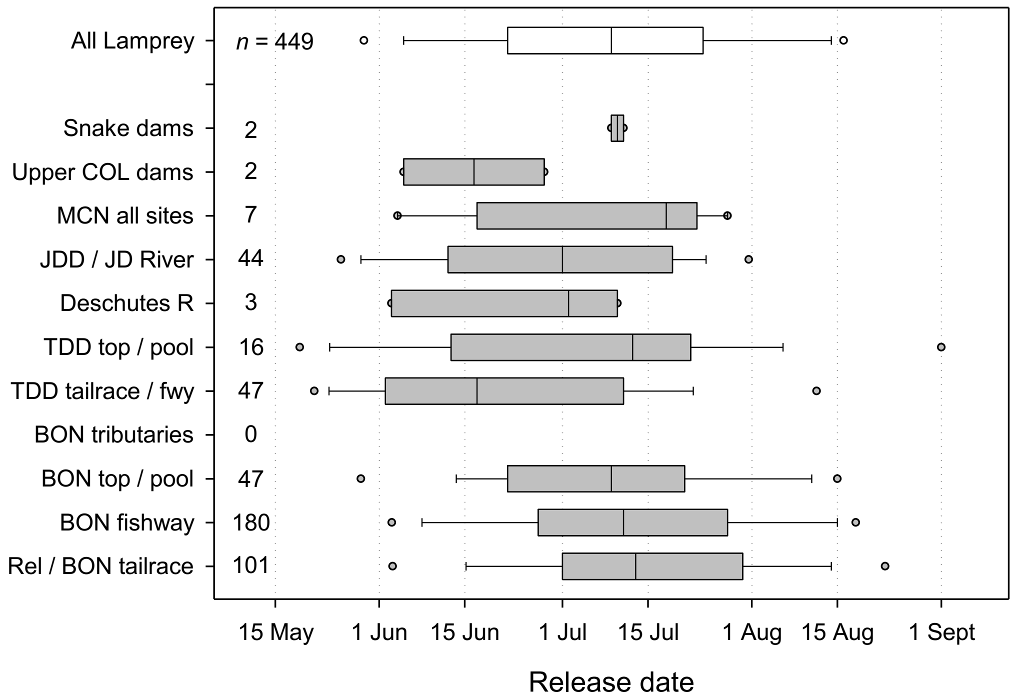

Figure 8. Distributions of double-tagged lamprey release dates by the final recorded locations for each fish through October 2019. Data shown are for lampreys released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles.

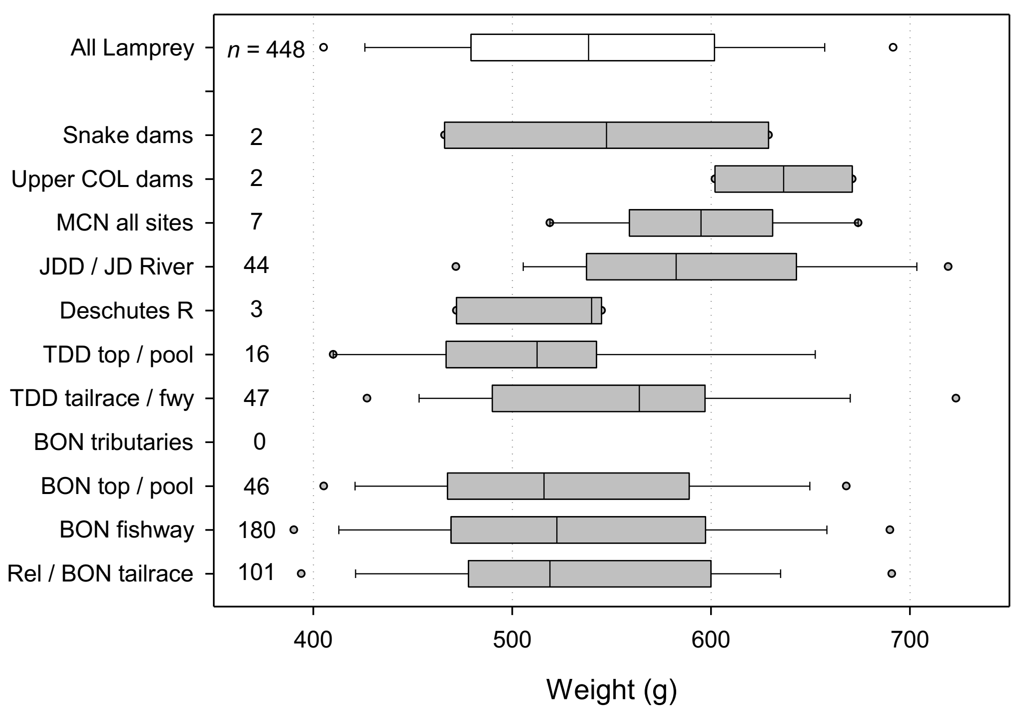

Figure 9. Distributions of double-tagged lamprey weights (g) by the final recorded locations for each fish through October 2019. Data shown are for lampreys released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 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 8). The earliest-timed group was last detected at one of the Upper Columbia River dams and the latest median dates were for fish last detected at McNary Dam. There were also clear among-group differences in double-tagged lamprey size (Figure 9). On median, lampreys were largest in the groups last detected in the upper Columbia River (636 g), at McNary Dam (595 g) and at John Day Dam (582 g). Lampreys were smallest in the groups last recorded at The Dalles Dam ladder top and recaptured and released into The Dalles forebay (*median* = 512 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 2019. 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 15). In six of seven reaches, double-tagged fish had a lower probability of upstream detection than those with HD PIT tags only (tagtype effect: $11.9 \leq \chi^2 \leq 45.04$, $P \leq 0.001$). Lamprey size effects were also evident in six of the reaches, with larger fish escaping at higher rates than smaller fish ($P \leq 0.003$). Tagdate was a statistically significant effect in two of seven reaches, with lower likelihood of reach passage later in the migration (Table 15).

Double-tagged lampreys had reach escapement probabilities that averaged ~10.5% (*range* 3-16%) lower than those for HD PIT-tagged lamprey, based on point estimates for fish with median tagdate and median weight (Figure 10). The largest absolute difference was for the TDD-JDD reach, where double-tagged fish had 16.2% lower probability to pass than HD only fish.

Table 15. Results of logistic regression models of reach escapement by HD PIT-tagged and double-tagged lampreys released downstream from Bonneville Dam in 2019. The models were: reach escapement = tagtype (HD only, double) + tagdate + lamprey weight. Includes all detections through October 2019.

	HD PIT	Double	Tagtype		Tagdate		Weight	
Reach	*n*	*n*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Release-BON	314	449	30.76	<0.001	28.12	<0.001	9.97	0.002
Release-TDD	314	449	35.38	<0.001	2.77	0.096	32.25	<0.001
Release-JDD	314	449	45.04	<0.001	4.58	0.032	38.32	<0.001
Release-MCN	314	449	13.99	<0.001	0.81	0.368	9.06	0.003
BON-TDD	182	173	11.19	0.001	1.93	0.165	22.47	<0.001
TDD-JDD	95	77	13.54	<0.001	1.76	0.185	9.59	0.002
JDD-MCN	69	40	2.26	0.133	0.06	0.814	0.37	0.543

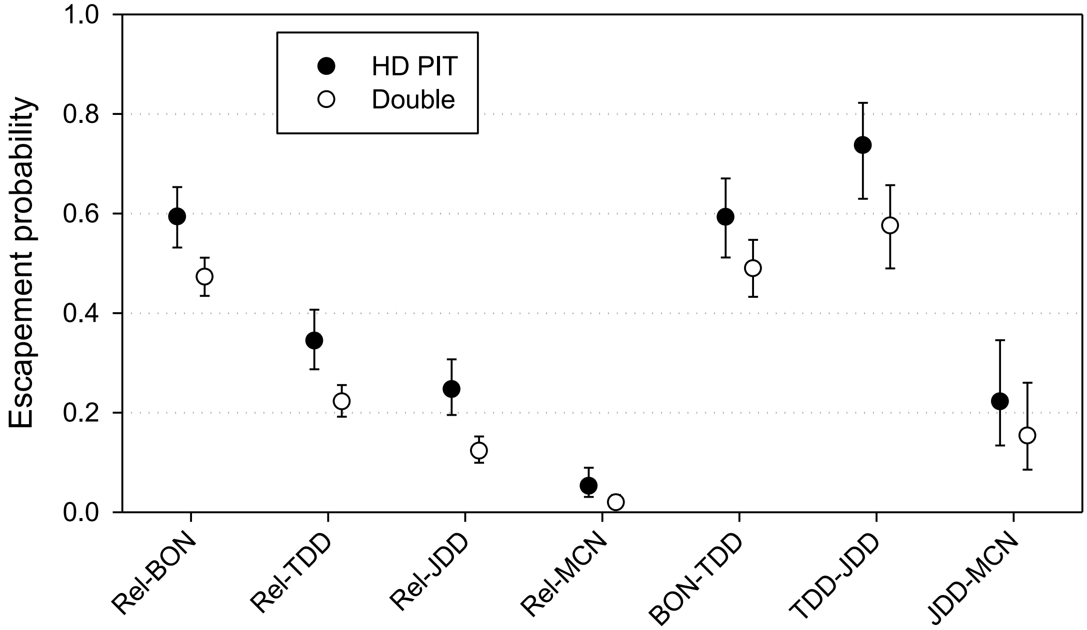

Figure 10. Estimated reach escapement probabilities (+/- 95% ci) of HD PIT-tagged (●) and double-tagged (○) lampreys released downstream from Bonneville Dam in 2019. Point estimates are from logistic regression models where: escapement = tagtype + tagdate + lamprey weight. Estimates were for the median lamprey weight (506 g) and the median release date (8 July) for the combined HD PIT- and double-tagged samples. Includes all detections through October 2019.

Migration Summaries for Stevenson Release Group: HD PIT

The 217 HD PIT-tagged lampreys released near Stevenson, WA, were not tagged in proportion to the lamprey run because of limits on tagging during the 2019 migration (Figure 2). The Stevenson release 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. This subsample was collected between 20 May and 17 July (*mean* = 20 June). 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).

Point Estimates of Dam-to-Dam Escapement – Escapement for the 217 lampreys from release was 41% (n = 89) past The Dalles Dam, 26.3% (n = 57) past John Day Dam, 8.8% (n = 19) past McNary Dam, 5.5% (n = 12) past Priest Rapids Dam, and 1.8% (n = 4) past Ice Harbor Dam (Tables 10 and 11). Escapement estimates were 64.0% between ladder tops at The Dalles and John Day dams and 33.3% between John Day and McNary dams. Of the 19 lampreys that passed McNary Dam, 16 went on to pass upstream dams: 12 (75.0%) passed Priest Rapids Dam and 4 (25.0%) passed Ice Harbor Dam (Tables 10 and 11).

Last Detection Summary – A total of 94 (43.3%) of the 217 lampreys released near Stevenson were not subsequently detected through October 2019 (Table 13). Eight fish were last detected in Bonneville tributaries: 2 (0.9%) in the Klickitat River and 6 (2.8%) in Fifteenmile Creek. A total of 35 (16.1%) were last detected at The Dalles Dam, and 17 (7.8%) were recorded in the Deschutes River. Upstream from the Deschutes River, 37 (17.1%) were at John Day Dam, 6 (2.8%) were at McNary Dam, 5 (2.3%) at lower Snake River dams, and 15 (6.9%) were at dams in the upper Columbia River (Priest Rapids through Rocky Reach dams) (Table 13).

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 2019 migration was unique to prior study years except 2018 in three important ways. First, we identified furunculosis symptoms in about 13% of the fish collected and released below Bonneville Dam during the collection period (late May to early September). 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 asymptomatic fish. Symptoms of furunculosis have been present in other run-years (Ralph Lampman, *personal communication*) and symptoms were present in 2018 during the period we monitored for the disease (22% symptomatic July-September).

The second unusual factor was the collection of small-bodied 'dwarf' Pacific Lampreys at the AFF trap at Bonneville Dam. Dwarfs comprised <1% of the adults collected in 2019, 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 and 2019, 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 was the incorporation of PIT antennas that were capable of reading both HD and FD PIT tags at some dam locations. The dual-reader antennas at the Columbia and Snake River dams were fully operational in 2019, 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 some uncertainty.

Below, we compare observed rates from 2019 to previous study years and identify potential mechanisms that may have influenced the migration and final distribution of adult Pacific lampreys during 2019. Overall, rates were generally within the range observed in prior years

Effects of Furunculosis, Tag Date and Size on Passage

Overall, the percentage of lampreys symptomatic for furunculosis was lower in 2019 (13%) than in 2018 (22%). Fish without symptoms of furunculosis passed all four dams at higher rates than fish with symptoms in 2019, a pattern that also occurred in 2018. Logistic regression models for double-tagged fish revealed a significant relationship between furunculosis symptoms and reduced passage at Bonneville, The Dalles and John Day dams in 2019. This pattern was also evident for double-tagged fish at Bonneville and John Day dams in 2018. Symptomatic fish with only HD PIT tags were significantly associated with reduced passage only at Bonneville Dam in 2019 compared to at Bonneville and John Day dams in 2018.

In addition to examining the influence of furunculosis on lamprey passage, we also included two previously identified predictors (tag date and lamprey weight) of passage success in the logistic regression models. Tag date was also significantly and negatively associated with dam passage of double-tagged fish at all dams in 2019, but only at Bonneville Dam for HD PIT fish. Interestingly, lamprey condition (K) declined through the season and may have played a role in lower passage success in late summer and early fall, though this remains speculative given observed intercorrelations among date, K and size metrics. In comparison, lampreys tagged later in the migration in 2018 had significantly reduced dam passage for both double- and HD PIT fish at all dams in that year. Sampling in 2018 was truncated however, so direct comparisons may be less meaningful. The increased dam passage success earlier in the run is consistent with previous research where earlier-migrating fish were more likely to be detected upstream (e.g., Keefer et al. 2013a, 2020).

In 2019, lamprey weight was also significantly and positively associated with dam passage of double-tagged fish at Bonneville and The Dalles Dam and at all dams for HD-tagged fish. In contrast, weight was not a significant predictor of passage at any dam for double-tagged fish 2018 but was significant at all dams for HD PIT tagged fish in 2018. This pattern is also consistent with previous studies on Pacific lampreys where larger bodied fish were more likely to be detected upstream (Keefer et al. 2013a, 2020). Lamprey length, girth, and weight generally have had similar predictive relationships within annual tag groups.

The Monitoring Array and Lamprey Detection Efficiency

Consideration of 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 in some cases; 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 97% (radiotelemetry), 86% (HD PIT; excluding the non-functioning site at The Dalles east fishway), and 92% (PTAGIS dual readers) in 2019. 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 (e.g., slot orifices) 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 were 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), and ~13% (The Dalles), with fish recaptured in traps classified as detected. No fish passed undetected at John Day Dam. 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 slightly downstream at antennas near the east count station.

HD PIT-Tagged Samples

Downstream Release Group – In 2019, HD PIT-tagged lamprey escapement for the downstream release group from release past Bonneville Dam (52%) was near the mean and median of estimates for HD PIT samples from 2006-2014 and 2018 (*range* = 41-61%, Table 16). The percentages of lampreys that passed The Dalles Dam (30%), John Day Dam (22%), and McNary Dam (5%) in 2019 were slightly higher than the means and medians of previous estimates of ~29% past The Dalles Dam, ~19% past John Day Dam and slightly lower than previous estimates (6-7%) past McNary Dam. Dam-to-dam estimates in 2019 were similar to or slightly higher than mean and median estimates in previous years for the Bonneville-The Dalles (52%) and Dalles-John Day (73%) reaches; the estimate for the John Day-McNary (25%) was slightly lower than the previous mean and median values.

Table 16. 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 (2006-2019) 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. The 2019 estimate includes detections through October 2019.

		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	[9]0.53 (306)	[c]0.29 (165)	[d]0.18 (102)	0.06 (35)
2019	314	[e]0.52 (164)	[f]0.30 (94)	[g]0.22 (68)	0.05 (17)

	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)
2019	0.52 (182)	0.73 (95)	0.25 (69)	0.24 (17)	0.59 (17)

[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); [9] 0.57 (*n* = 329); [c] 0.29 (*n* = 167); [d] 0.19 (*n* = 108) ; [e] 0.58 (*n* = 182); [f] 0..30 (*n* = 95) ; [g] 0..22 (*n* = 69) when recaptures were treated as passing the dam; [a] Detections through March 2019; [b] Detections through 1 August 2019

The 2019 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, 2019,2020). 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.

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). Overall river flow and temperature conditions in 2019 were near the 10-year average values for both parameters and thus were not likely a major factor affecting escapement trends (Appendix A). Unfortunately, furunculosis was not systematically monitored prior to 2018 and it remains unknown to what degree passage metrics in previous years may have been affected by the disease. Nonetheless, we speculate the prevalence of furunculosis observed in 2018 and 2019 and the negative association between symptoms at the time of tagging and migration metrics suggests the disease may have offset cumulative reach-scale benefits of lamprey passage improvements at dams in 2019 when accounting for body sizes effects (see also Figure 11 below).

Table 17. Numbers of HD PIT-tagged lampreys released in the Bradford Island fishway (2005) or downstream from Bonneville Dam (2006-2019), 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
2019	[4]314	65.2	452	11.1	7.2 d	[2]5.2 d	[2]3.8 d	9.0 d

[1] released into the Bradford Island fishway
[2] top of East fishway not monitored in 2013-2014 and 2018-2019
[3] includes dwarf lampreys (*n* = 18)
[4] includes dwarf lampreys (*n* = 6)

Lamprey migration times through dam-to-dam study reaches generally fell within the ranges reported in previous HD PIT study years (Table 17). 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. In 2019, times for the release-Bonneville Dam reach

(7.2 d) was a day faster than previous years (mean and median values). Above-average water temperatures in 2018 compared to near-average water temperatures in 2019 (Appendix A) may have contributed to relatively rapid passage in 2018. 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 10-14 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), were faster than rates recorded for radio-tagged lampreys in the Willamette River (Clemens et al. 2012), and were slower than rates recorded for JSATS-tagged lampreys through reservoir-only reaches in the lower ColumbiaRiver (Keefer et al. 2020).

About 24% of downstream-released HD PIT-tagged lampreys were not detected after release in 2019. This was the lowest non-detected percentage in the multi-year study (the second lowest percentage [27%] occurred in 2014 and 2018) but this 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 collection timing and release locations among samples. The flume group was selected primarily from the early portion of the 2019 migration and therefore encountered different environmental conditions than the downstream-released sample. Release upstream from Bonneville Dan also eliminated the significant barrier to dispersal presented by Bonneville Dam and passage rates and upstream migration distances after translocation above Bonneville Dam were similar to those for previous studies that released lampreys into the Bonneville reservoir near Stevenson, WA (Keefer et al. 2020).

About 43% of the flume fish were never detected after release, a rate that was higher than the 24% undetected from the downstream release group and slightly higher than the 39% for Stevenson-released flume fish in 2014 (an early-timed sample) but slightly lower than 46% in 2018 (a late-timed sample). The nearest upstream PIT antennas from the Bonneville forebay were in the Hood and Klickitat rivers, 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 41%, which was higher than for lampreys tagged with acoustic and PIT tags during 2011-2013 released at Stevenson (35.5%; Keefer et al. 2020), but somewhat lower than for lampreys released downstream that passed Bonneville Dam in 2019 (52% from the top of Bonneville Dam past the Dalles Dam). Differences in escapement estimates between The Dalles and John Day dams were slightly higher for the downstream release group (73%) than for the Stevenson release group (64%), but the Stevenson release group had higher escapement through the John Day-McNary reach (33% versus 25% for the downstream release group).

Despite the potentially confounding effects of size-bias in the downstream-released sample that passed Bonneville Dam, these results 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 2019 escapement estimate for double-tagged lampreys from release to top-of-ladder and LPS sites at Bonneville Dam was 33% (excluding recaptures counted as passing the dam), within the range of the estimates in the 1997-2002, 2007-2010, and 2014 radiotelemetry studies (21-46%, Table 18). The most directly comparable study years were 2007-2010 and 2014 and 2018, when smaller transmitters allowed more representative tagging. The 2019 escapement past Bonneville (through October 2019) was slightly higher than the 2007-2009 estimates (21-31%), was 4-8% lower than the 2010 and 2014 estimates, and was 6% lower than the 2018 estimate. This result was surprising in part because mean body size of double-tagged fish in 2019 was slightly higher than in recent years (Figure 11). We elected to tag slightly larger fish to maximize the number available for the nighttime fishway velocity experiments (see Clabough et al. 2020), which would tend to increase escapement. Furunculosis effects on escapement were more consequential for double-tagged fish than for PIT-tagged fish in both 2018 and 2019 (see Keefer et al. 2019 and compare tables 5 and 7 in this report) and it remains unclear if disease effects help explain the lower-than-average Bonneville Dam escapement by double-tagged fish in 2019 compared to 2018.

About 84% of the double-tagged lampreys were detected near fishway openings at Bonneville Dam, a rate of post-release upstream movement that was slightly lower than the mean and median values (85-88%) in all previous radiotelemetry study years (Table 19). Dam passage efficiency, calculated as the number that passed Bonneville Dam divided by the number that approached fishway openings, was 45% in 2019; this value was equal to the multi-year median (45%) and slightly higher than the multi-year mean (43%). A more detailed summary of lamprey behaviors and passage metrics at all four lower Columbia River dams is presented in a companion report (Clabough et al. 2020).

Multi-dam escapement estimates for double-tagged lampreys in 2019 were 16% (past The Dalles), 9% (past John Day), and 1% (past McNary, Table 18). 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 18. Summary of release to top-of ladder and dam-to-dam reach escapement estimates for radio and/or double-tagged lampreys released (Rel) downstream from Bonneville Dam from 1997-2002, 2007-2010, 2014, and 2018-2019 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. The 2019 estimate includes detections through October 2019.

		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)
2019[c]	449	[d]0.33 (149)	[e]0.16 (74)	0.09 (40)	0.01 (5)

[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); [d] 0.39 (n = 173); [e] (0.17 (n = 77) when recaptures were treated as passing the dam
[a] Detections through March 2019; [b] Detections through 1 August 2019; [c] Detections through October 2019

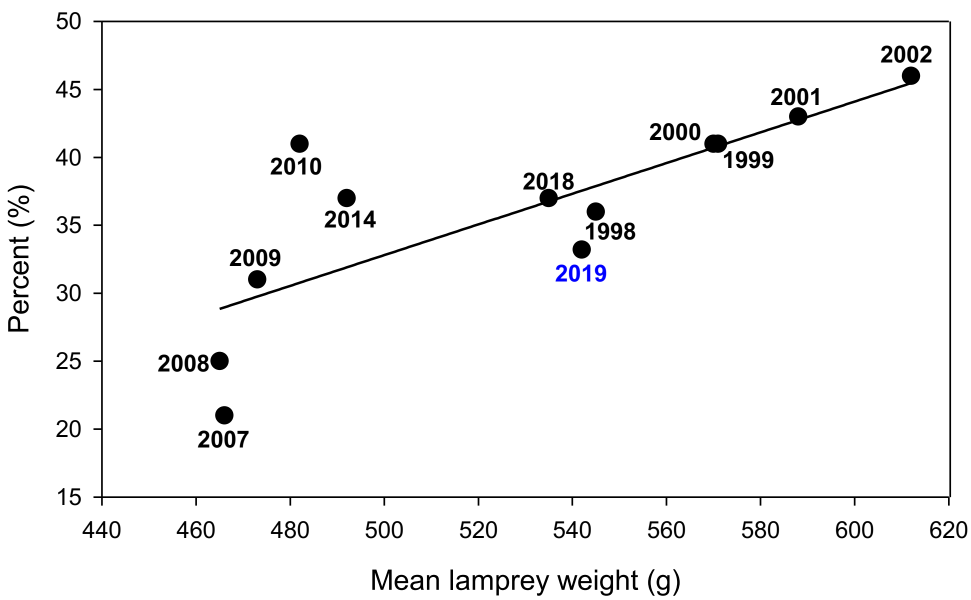

Figure 11. Linear regression relationship between annual mean radio and/or double-tagged Pacific Lamprey weights and the percentage that passed Bonneville Dam of those released (linear regression, r^2 = 0.61, $P < 0.05$).

Lampreys recaptured at the Bonneville AFF were treated as not passing. Note: weight data were not collected in 1997.

Table 19. Numbers of radio and/or double-tagged lampreys released below Bonneville Dam from 1997-2002, 2007-2010, 2014, and 2018-2019 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 2018-2019.

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%	[a]34%	5.6 d
2009	596	67	56-79	473	276-860	79%	[a]39%	7.5 d
2010	312	67	55-77	482	272-722	88%	[a]46%	12.6 d
2014	599	67	53-79	492	262-788	80%	[a]49%	5.4 d
2018	595	69	55-81	535	330-775	90%	[a]42%	6.3 d
2019	449	69	57-79	542	317-801	84%	[a]42%	8.2 d

[1] Differs from Table 17 because limited to fish that approached a fishway; [a] excludes 10 (2008), 21 (2009), 3 (2010), 19 (2014), 15 (2018), and 24 (2019) lampreys recaptured at a trap and released upstream or in LPS

A notable departure from earlier study years was that we did not use radiotelemetry in any tributaries in 2018 or 2019. We were able to identify some lamprey use of tributaries by detections at instream PIT detection arrays, but only about 4% of the fish that passed Bonneville Dam were detected in lower Columbia River tributaries, the Snake River, or passed Priest Rapids Dam through October 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). No double-tagged lampreys were detected in Fifteenmile Creek or in the Hood, Klickitat, or John Day rivers in 2019, although some fish entered these sites in almost all prior years.

Two additional, important escapement results from the double-tagged study element were consistent with those from previous studies. Specifically, a majority (~61%) of tagged adults did not pass Bonneville Dam in 2019 and over half (~55%) 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, Keefer et al. 2020). Most JSATS-tagged lampreys 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 in 2019 spawned in unmonitored tributaries or tailraces, were predated, or were prespawn mortalities remains unknown.

The 2019 double-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, 2020). Median times in 2019 were ~2.0 d through the Bonneville reservoir and ~1.8 d through The Dalles reservoir. These times were faster than or within the range of times calculated for double-tagged lampreys passing Bonneville Dam in 2007-2010 (Table 19), consistent with the near average river conditions lampreys encountered during 2019. Median lamprey passage rates through the Bonneville and The Dalles reservoirs were 34 and 20 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), were consistent with those for radio- and PIT-tagged lampreys in the Columbia River in previous years (e.g., Keefer et al. 2009b, 2015), and are slower than rates estimated within Bonneville Reservoir using JSATS (~50-62 km/day; Keefer et al. 2020) because radiotelemetry reaches included lower tailraces.

Negative Effects of Radio Tagging

An ongoing concern in the adult lamprey research program has been consistently lower escapement for radio-tagged fish than for 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 transmitters and associated handling negatively affects survival relative to HD PIT tagging. Total handling time (including anesthetized time) for double-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 Higher escapement of JSATS-tagged adults from release to top of Bonneville Dam (64.2-71.2%; Keefer et al. 2020) relative to radio-tagged adults (~42-49% 2010-2019; Table 19) is consistent with an effect of an external antenna, though we note that JSATS and radiotelemetry study years did not overlap, JSATS surgeries were less intensive and JSATS tag burdens were lower. 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 2019, double-tagged lamprey reach escapement was ~10.5% lower, on average, than estimates for HD PIT-tagged lampreys. This difference was similar in scale to results from 2009, 2014 and 2018 which are all recent years with adequate samples of both HD PIT and double-tagged fish (Keefer et al. 2010, 2015, 2019). The predicted escapement average difference in 2019 may be lower after accounting for overwintering fish that may potentially pass dams in the spring. As noted in previous reports, the informational value of radiotelemetry data for future studies must be weighed against reduced upstream escapement; radiotelemetry was required in 2018-2019 for the detailed fishway movement analyses presented in Clabough et al (2019, 2020). Monitoring adult lampreys in tailraces and at many fishway locations, including entrances, cannot currently be achieved using PIT telemetry.

Conclusions

- HD PIT and radio telemetry lamprey escapement estimates in 2019 fell within the range of prior study years.

    - In both HD and double-tagged samples, lampreys that successfully passed upstream sites were longer, heavier, and had larger girth and dorsal distance than those that did not pass in most reaches.

- The percentage of lampreys symptomatic for furunculosis was lower in 2019 (13% - evaluations were conducted throughout the tagging season) than in 2018 (22% - evaluations began in June 2018).

    - Compared to asymptomatic fish, double-tagged lampreys with symptoms had significantly reduced passage at Bonneville, The Dalles and John Day dams in 2019 whereas symptomatic HD PIT fish had reduced passage only at Bonneville Dam.

    - We recommend that any future escapement studies integrate evaluations and quantifications of disease prevalence at the time of tagging.

- The University of Idaho HD sites performed similarly to dual-reader sites except at the Bonneville Washington-shore (which may have been due to aging antenna infrastructure).

    - Future studies may need to invest in new or additional HD-PIT monitoring antennas, depending on study objectives and scope.

    - The escapement-scale objectives of the current study may be met in the future with dual PIT readers at dams, but tributary monitoring is currently limited.

- There has been consistently lower escapement in double-tagged fish than HD PIT-tagged fish in most study reaches.

    - Additional tag burden, handling time, and an external trailing antenna may likely account for this.

    - When evaluating future study designs, any gains associated with the greater spatial resolution that radiotelemetry data can provide should be weighed against the likely reduced upstream escapement of the double-tagged sample.

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Appendix A. 2019 Columbia River discharge and temperature profiles.

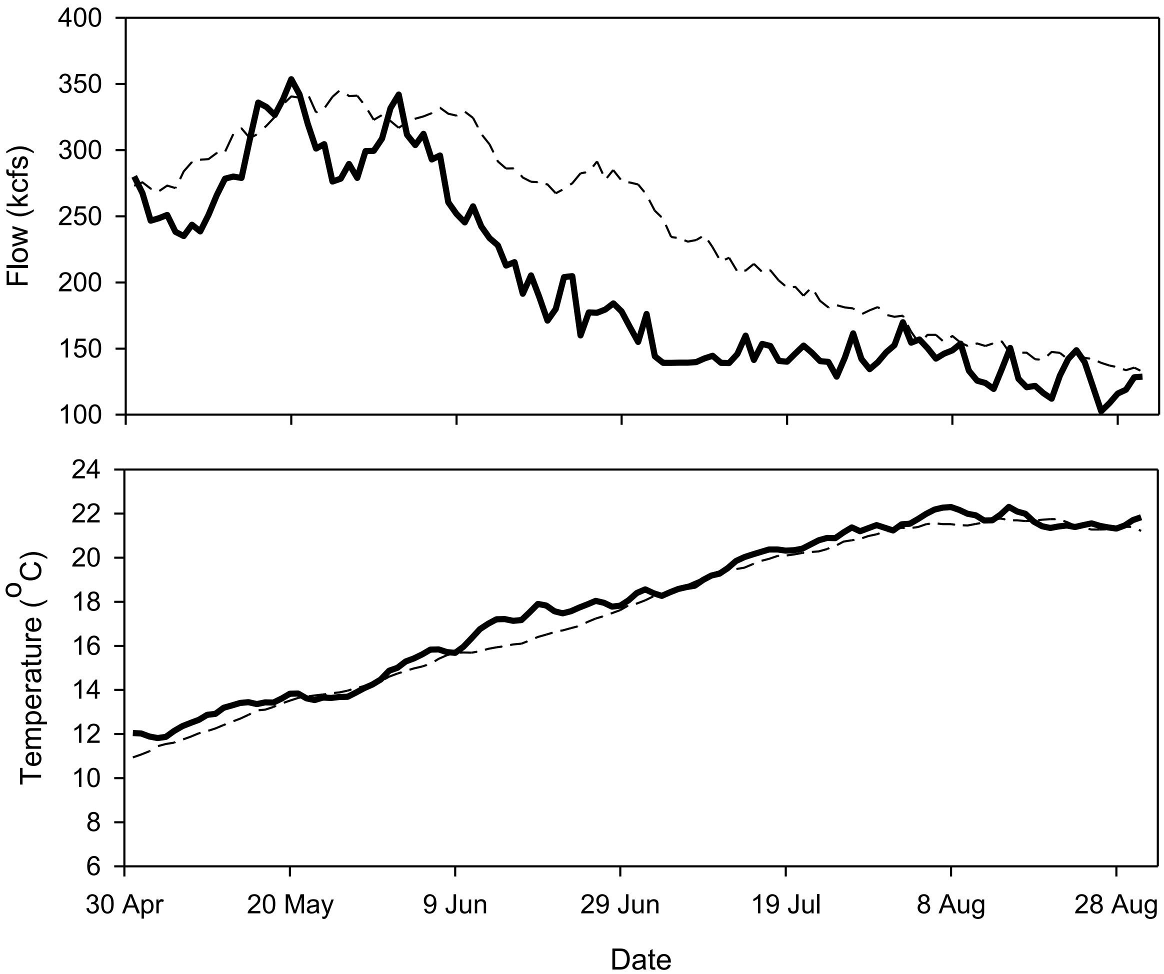

Figure A1. Mean daily Columbia River flow (kcfs) and WQM temperature (°C) at Bonneville Dam in 2019 (solid line) and the 2009-2018 average (dashed line).