Technical Report 2015-3

ADULT PACIFIC LAMPREY MIGRATION BEHAVIOR AND SURVIVAL IN THE BONNEVILLE RESERVOIR AND LOWER COLUMBIA RIVER MONITORED USING THE JUVENILE SALMONID ACOUSTIC TELEMETRY SYSTEM (JSATS), 2011-2014

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for

U.S. Army Corps of Engineers
Portland District

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Executive Summary

A large percentage (~50%) of adult Pacific lamprey (*Entosphenus tridentatus*) that pass Bonneville Dam are not observed passing the The Dalles Dam. Between 2011 and 2014, we tagged adult Pacific lamprey with Juvenile Salmon Acoustic Telemetry System (JSATS) transmitters and half-duplex (HD) PIT tags and monitored their upstream migation behavior and final distribution in the Bonneville tailrace and reservoir and upstream of The Dalles Dam to the Deschutes River. Monitoring focused on the Bonneville Dam tailrace and reservoir, two areas with high unaccounted lamprey loss in past telemetry studies. Our objectives were to calculate lamprey travel rates, to estimate survival past the monitored sites, and to estimate final fates and distributions of tagged lamprey.

We double-tagged a total of 784 adult Pacific lamprey collected at Bonneville Dam with both JSATS transmitters and HD-PIT tags over three study years (2011-2013). All fish were trapped and tagged at the Adult Fish Facility at Bonneville Dam and were released at one of two tailrace locations: Tanner Creek (rkm 232.0) and Hamilton Island boat ramp (rkm 232.6) or one of two Bonneville Reservoir loctions: Stevenson boat ramp (rkm 242.7) and Cascades Locks (rkm 239.1). We deployed 15 to 33 JSATS autonomous receivers each year between the Bonneville Dam tailrace and the John Day River. Receivers were deployed singly or as detection gates of up to five receivers allowing us to calculate lamprey travel times, estimate survival, and estimate distribution and final lamprey fates for multiple reaches within the Bonneville Reservoir. Acoustic receivers were deployed starting in mid-March of each year and monitoring continued through October, with the exception of 2011-2012, when receivers were in place continuously from March of 2011 to October of 2012. In 2013 and 2014 receivers were redeployed in the early spring in the Bonneville and The Dalles Dam tailraces and at tributary sites. Full arrays, including reservoir sites, were in place each spring before fish were tagged and released. Estimated detection efficiencies for nearly all of the acoustic receiver gates were 90% or higher, and reached 98% at Miller Island near the Deschutes River.

Travel rates for tagged lamprey were variable among individuals, and were higher in reservoir reaches than in dam reaches. Reservoir-released lamprey had a median travel time across all years of 8.7 days (8.8 km/d; range = 1.8 – 29.0 km/d) from release to The Dalles Dam ladder top. The median travel time across all years for tailrace-released fish from release to the top of Bonneville Dam was 7.2 days (0.4 km/d; range = 0.03 – 10.1 km/d). Movement through Bonneville Reservoir was rapid and similar to rates observed in salmonids for both release groups in all 3 study years (Stevenson to The Dalles Dam tailrace: median = 47.4 km/d, n = 229).

The annual survival estimates varied widely for lampreys released into the Bonneville Dam tailrace past the dam. Survival estimates (i.e., minimum survival based on coded detections) were very similar to mark-recapture estimates that accounted for detection efficiency in nearly all reaches. Survival from release past Bonneville was low in 2011 (35%), while the 2012 (61%) and 2013 (64%) estimates were higher than those from previous HD-PIT studies (41-53%). Adjustment of survival accounting for detection efficiencies produced slightly higher estimates: using the Bonneville tailrace as the starting gate, adjusted survival estimates past Bonneville Dam were 77 % in 2011, 68% in 2012, and 73% in 2013. The annual adjusted survival estimate from release in Bonneville Reservoir past The Dalles Dam was 39-60%. A large majority of

adults (82-92%) that entered or were released into Bonneville Reservoir moved rapidly upstream and were detected in the upper reservoir or tailrace of The Dalles Dam, indicating low mortality rates in the lower and middle reservoir reaches.

Final distributions of JSATS-tagged fish were consistent with results from past studies at coarse scales, indicated tribtuary entry during both fall and spring periods, and revealed substantial proportions last detected in tailraces. Many (34-57%) of tailrace-released fish were last detected in the Bonneville Dam tailrace or at Bonneville Dam fishway HD-PIT antennas each year and had unknown fate. Similarly, 31-48% of reservoir-released lamprey had final records in the Bonneville Reservoir with unknown fates, and 26-40% were last recorded in The Dalles Dam tailrace or upper Bonneville Reservoir. Some JSATS-tagged lamprey were last detected entering or were inferred to have entered one of the ~3- to 4 monitored Bonneville Reservoir tributaries or the Deschutes or John Day rivers every year. Twelve percent of tailrace-released lamprey entered tributaries in 2012 and 2013, while no tailrace-released fish were recorded entering any tributary in 2011. Reservoir-released lamprey entered monitored tributaries at relatively higher rates each year (12-28%), in part because they did not have to pass Bonneville Dam. Winter (2011-2012 only) and early spring monitoring detected lamprey movements after overwintering and allowed us to refine final distribution estimates. Up to 6% of all tailrace-released lamprey and 8% of all reservoir-released fish were detected entering or were inferred to enter monitored tributaries after overwintering each year, representing 9% and 17% of fish, respectively, that had previously been assigned unknown final fates. We used tributary entry data to model the potential number of lamprey that entered unmonitored tributaries (*minimum* n = 10) to the Bonneville Reservoir during spring after overwintering under several scenarios. The most plausible scenarios suggest that a total of ~12-27% of lamprey entering the reservoir eventually enter tributaries. The simulations also illustrate the current uncertainty about true tributary entry rate.

Overall, the multi-year study demonstrated: 1) the utility of acoustic technology for tracking adult lamprey in mainstem habitats; 2) rapid migration with high survival through lower and mid-reservoir habitats; 3) substantial numbers of lamprey apparently overwintering in tailrace habitats; and 4) previously undocumented downstream and tributary entry movements by lamprey in spring. The primary remaining uncertainties include the fate of substantial numbers of adult lamprey last detected in dam tailraces, specifically, the proportions of undetected adults that move into downstream tributaries and spawn, spawn in dam tailraces, or died in the main stem Columbia River before spawning.

Introduction

The populations of anadromous Pacific lamprey (*Entosphenus tridentatus*) in the Pacific Northwest, particularly in the Columbia River Basin, have been in a decades-long decline (Close et al. 2002; Columbia River Inter-Tribal Fish Commission 2011; DART 2012). Pacific lamprey are an important prey species for other fish (Poe et al. 1991) and may act as a buffer against predation by fish, birds and marine mammals on endangered salmon (Moser and Close 2003). As with many other anadromous fish species, it is likely that Pacific lamprey are important in nutrient cycling pathways (Gresh et al. 2000; Wilcove and Wikelski 2008). Pacific lamprey have also played a major role in the culture of many Native American tribes, particularly those of the Columbia Basin (Vladykov 1973; Close et al. 1995, 2002; Palacios 2007).

Results from both radiotelemetry (RT) and HD-PIT studies have indicated that Pacific lampreys do not readily pass dams compared to anadromous salmonids and their poor passage efficiency may represent a critical limitation to their migration success and distribution (e.g., Moser et al. 2002b; Keefer et al. 2009c; Luzier et al. 2011). Specifically, Moser et al. (2002a, 2002b, 2003, 2005), Johnson et al. (2012), Clabough et al. (2011), and Keefer et al. (2013) found that fishway entrances, collection channel/transition areas, diffuser gratings, and serpentine weirs impede adult Pacific lamprey passage at lower Columbia River dams. These data have been used to design, implement, and test a number of passage improvements including Lamprey Passage Structures (LPS, Moser et al. 2011), and modified nighttime operations (Johnson et al. 2012).

In addition to identifying specific fishway passage bottlenecks, these studies found many tagged adults failed to re-initiate upstream migration after tagging and that substantial proportions of tagged samples were not accounted for between dams. For instance, dam counts, RT, and HD-PIT telemetry results all suggest that many adult lampreys that enter Bonneville Reservoir do not pass The Dalles Dam (TDA). Survival estimates, defined here as the minimum percentage of tagged adults known to have passed The Dalles Dam of those that entered or were released into Bonneville Reservoir were 47-67% for HD-PIT studies during 2006-2014, and 30-57% for RT studies during 1997-2002, 2007-2010, and 2014 (Keefer et al. 2012a, 2015). These estimates were comparable to or higher than the conversion rates estimated from daytime counts of adult lampreys at the dams between 1999-2014 (18-42%) and were generally higher in the HD-PIT than in the RT samples (Keefer et al. 2012a). The HD-PIT method probably provides the best estimate of inter-dam conversion, because of smaller tag effects than observed when using RT. Nonetheless, all estimates indicate considerable (33-70%) apparent loss in the Bonneville Reservoir in most years. In 2008, a year with the highest level of RT coverage (including at many tributary mouths), 42% of RT adults that passed Bonneville Dam (BON) subsequently passed TDA, 22% were recorded at TDA but were not recorded passing, 5% were recorded in tributaries, and 35% had records indicating a final fate in Bonneville Reservoir (Keefer et al. 2009b). Values for 2009-2013 were similar based on evaluations using PIT-tagged (Keefer et al. 2010, 2011, 2012a, 2012b) or JSATS-tagged adult lamprey (Noyes et al. 2012, 2013, 2014; summarized in this report).

The unknown fate of many Pacific lamprey during their migration through tailraces and/or reservoirs may be attributed to: (1) overwintering in the reservoir and resuming upstream migration the following spring; (2) pre-spawn or predation mortality; (3) undetected spawning in reservoir tributaries; and/or (4) spawning in the tailrace of The Dalles Dam or elsewhere in the Reservoir. Lampreys are an attractive prey item, and it is plausible that these unaccounted for fish represent predation mortalities. White sturgeon (*Acipenser transmontanus*) are abundant in Bonneville and The Dalles Dam tailraces, and sea lions (*Zalophus californicus*, *Eumetopias jubatus*) are seasonally abundant in Bonneville Dam tailrace (DeVore et al. 1995; Pitcher et al. 2007; Stansell et al. 2010). However, unsuccessful dam passage by lamprey does not necessarily represent mortality or failure to spawn. Lampreys may encounter suitable spawning tributaries emptying into reservoirs during their migration up the Columbia River and it is possible that a substantial proportion of the fish unaccounted for in reservoirs may have successfully spawned. Recent observations from a sample of lamprey PIT-tagged at John Day Dam in 2014 indicated 12% moved downstream after release above the dam and entered the Deschutes River (Keefer et al. 2015). Similarly, spawning in the tailraces of Columbia River dams has been observed by fall Chinook salmon (e.g., Hatten et al. 2009) and it is possible some lamprey also spawn in tailraces. Exploring these hypotheses requires information on the movement and the distribution of lamprey in reservoir and tailrace habitats after the overwintering period.

Unfortunately, the deep bathymetry of lower Columbia River reservoirs (33-80 m) and the river below Bonneville Dam limits the ability to detect radio transmitters and thereby limits the ability to determine the final fates of many RT-tagged lamprey. Acoustic telemetry has several advantages over RT and PIT technologies, including the ability to detect signals in deep water (>10 m). Acoustic transmitters also do not require a trailing antenna which may affect behavior and ultimately survival (Keefer et al. 2009d, 2015; Mesa et al. 2011). Until recently, transmitter design and battery size have precluded use of longer-lived acoustic transmitters on smaller species. Development of the juvenile salmonids acoustic telemetry system (JSATS; see McMichael et al. 2010 for review) has produced transmitters for Pacific lamprey with transmitter life allowing monitoring through the spring spawning period with slightly lower tag burden than radio-tags used in previous studies that expired during early winter. In 2010, we performed a pilot study with thirty JSATS-tagged adult Pacific lamprey to evaluate the technology for monitoring with fixed-site and mobile tracking hydrophone receivers (Naughton et al. 2011). In 2011, we continued the evaluation with a larger sample of tagged lamprey (n = 85) using JSATS tags modified for adult lamprey and increased monitoring effort (Noyes et al. 2012). In 2012, we increased the sample (n = 299), deployed additional receiver sites, and added three release locations (in the Bonneville Dam tailrace at Hamilton Island and the mouth of Tanner Creek, and in Bonneville Reservoir at the Cascade Locks Marina). Finally, in 2013, we continued the evaluation with a larger sample of tagged lamprey (n = 400) and a further refined receiver array. The results demonstrated that the technology could be adapted readily to adult lamprey studies in deep water habitats using fixed acoustic detectors. We also evaluated an acoustic mobile tracking device for monitoring the migration and fate of JSATS-tagged adult Pacific lampreys in Bonneville Reservoir and the Bonneville Dam tailrace. Unfortunately, the prototype tracking systems were ineffective in the reservoir and tailrace environments (Noyes et al. 2013). Here we focus on biological results across the three years (2011-2013) of tagging and four years of monitoring at fixed sites (2011-2014) and the estimation of detection efficiency at those sites; additional details of technology assessment and development are given in previous annual reports (Naughton et al. 2011, Noyes et al. 2012, 2013, 2014).

Our primary biological objectives over the 2011-2013 study years were to: 1) characterize adult Pacific lamprey migration behavior, including migration rates, tributary entry and distributions; 2) estimate the fate of lamprey in Bonneville Reservoir and tailrace using an array of stationary acoustic JSATS receivers; and 3) to evaluate the potential for spring movements and movement into unmonitored tributaries to account for previously unknown fate in the Bonneville Reservoir. Behavior and distribution was remarkably consistent in each year and thus we focus on multi-year summaries while noting important differences in the JSATS monitoring array among years.

Methods

Fish capture and tagging

Pacific lampreys were captured at night using two traps installed in the Washington-shore fishway at Bonneville Dam that collected fish as they passed weirs. We also deployed two portable pot traps between the two fixed traps in the fishway. A complete description of the collection and tagging methods is presented in Moser et al. (2002b) and Keefer et al. (2009c, 2012b). Lamprey were collected under the authority of Washington State Scientific Collection Permits. Collection, handling, and tagging protocols were reviewed and approved by the University of Idaho Institutional Animal Care and Use Committee. Collected fish were anesthetized with 60 ppm (3 mL/50 L) clove oil or AQUIS-20E®, measured (length and girth to the nearest mm) and weighed (nearest g).

Lamprey were surgically implanted with a 4-mm × 32-mm glass-encapsulated HD-PIT transmitter (134.2 kHz; Texas Instruments, Dallas, TX) and a modified JSATS transmitter (Advanced Telemetry Systems, Isanti, MN). The JSATS transmitter was 4.0 mm × 8.0 mm × 23.0, weighed 1.7 g in air, and had an estimated battery life of 400 d with a 10 s burst rate. A portion (n = 20, 24%) of the fish tagged in 2011 were implanted with a smaller, shorter-lived JSATS transmitter: 3.0 mm × 5.0 mm × 17 mm, 0.550 g in the air, with an estimated battery life of 60 d with a 5s burst rate.

Both the JSAT transmitter and HD-PIT tag were inserted through a small (<1 cm) incision in the body cavity along the ventral midline, in line with the anterior insertion of the first dorsal fin. Incisions were closed with a single suture (3-0 surgical monocryl), and fish were placed in a post-surgery holding tank. Tagged adults were allowed to recover for at least 2 h post-surgery and were released between 1100 and 2300 h.

Lamprey were released in either the Bonneville Dam tailrace or Bonneville Reservoir and selection of the daily release site was randomized within year. In 2011, lamprey were released from sites on the Washington shore, while in 2012-2013, fish were released from both the Oregon and Washington shore. Tailrace release sites included two located at rkm 232.3: Hamilton Island on the Washington shore and near the mouth of Tanner Creek on the Oregon shore. Lamprey were released at two sites in Bonneville Reservoir: the Stevenson boat ramp on the Washington shore (rkm 242.7) and the Cascade Locks Marina on the Oregon shore (rkm 239.1). The reservoir sites were selected as the nearest sites to the dam that also minimized the potential for tagged fish to fallback over Bonneville Dam. The Hamilton Island and Tanner Creek tailrace sites were used to facilitate direct comparisons in dam passage behavior between JSATS-tagged and previous studies of radio-tagged and HD-PIT tagged lamprey.

Telemetry monitoring

JSATS-tagged fish were monitored with autonomous receivers (Advanced Telemetry Systems, Trident SR5000) which contained an internal rechargeable lithium battery pack (rated for 34 d), an externally-mounted hydrophone, water temperature and pressure sensor, and analog and digital circuit boards (see McMichael et al. 2010). The receivers were deployed to position the hydrophone about 3 to 4 m above the river or reservoir bottom. The standard deployment configuration consisted of the receiver affixed at a single point to a short section of wire cable (3/16 in. stainless steel) with two small floats for additional buoyancy. The receiver was then attached to an acoustic release mechanism (Inter-Ocean Model 111 or Teledyne Model 875-TD). JSATS receivers were deployed in Bonneville and The Dalles Dam tailraces, within or at the mouths of major tributaries, within Bonneville Reservoir, and upstream of The Dalles Dam. Receiver deployment dates varied slightly by year as documented in previous reports. Monitoring in tailraces and at tributary locations typically began in early spring. These locations were selected to detect post-overwintering movement and tributary entry by tagged lamprey. Receivers were deployed at reservoir and release sites starting in mid-April or May of each year. Monitoring at most locations continued through October of each year, with the exception of 2011-2012 when receivers were deployed throughout the winter. Data obtained from the autonomous receivers were used to record final locations, to partition final locations within the reservoir, and to estimate reach travel times and survival of tagged lamprey.

JSATS telemetry monitoring at most sites started in early spring and remained in place through October of each tagging year, with few exceptions. During the winter of 2011-2012 JSATS receivers were left at major tributary mouths and in Bonneville and The Dalles Dam tailraces to monitor for overwintering movements of tagged lamprey. In 2012 the receiver in the Klickitat River 300 meters upstream from the mouth was replaced with a receiver at the mouth of the river and an additional receiver slightly downstream of the mouth. The Klickitat River receiver was returned to its original site 300 meters upstream from the mouth in spring of 2013. In late September 2012 the Rooster Rock gate was removed due to interference with purse seining operations conducted by Washington Department of Fish and Wildlife. The Deschutes River mouth site was removed in late September 2013 by the Wasco County Sheriff's Department due to frequent calls from concerned anglers and was not redeployed. Most sites had nearly continuous coverage, with short (<1 h) periods of no coverage for receiver maintenance, while other sites had some significant gaps in coverage (up to 21 days), usually due to battery or electronics failure (See deployment tables in Noyes et al. 2012, 2013, 2014).

The study area encompassed the lower Columbia and Snake rivers monitored by HD-PIT antennas. The specific locations of JSATS receivers varied by year, but the overall configuration remained consistent. Receivers were deployed either as gates to partition the river into reaches or in or near the mouths of tributaries to monitor tributary entry. JSATS monitoring included the reach from the Bonneville Dam tailrace to the tailrace of The Dalles Dam (rkm 304.9), near Miller Island and the mouth of the Deschutes River, and within the John Day River (Figures 1-3). JSATS receivers were deployed as gates of one to five nodes mid-channel or on either the

Washington or Oregon shores of the Columbia River, within or at the mouths of tributaries, and in the tailraces of Bonneville and The Dalles Dams (Table 1). Data were also collected on JSATS arrays operated by Pacific Northwest National Laboratory at 26 locations in 2012 (Table 1) and detections from the PNNL array were used in the estimation of survival.

Figure 1. Receiver locations (numbered circles) used to monitor JSATS-tagged adult Pacific lamprey in 2011: 1) Bonneville Dam tailrace; 2) Bonneville Dam forebay; 3) Stevenson; 4) Wind Mt.; 5) L. White Salmon R.; 6) Bingen; 7) inside Klickitat R., 300m from the mouth; 8) Lyle; 9) The Dalles Dam tailrace.

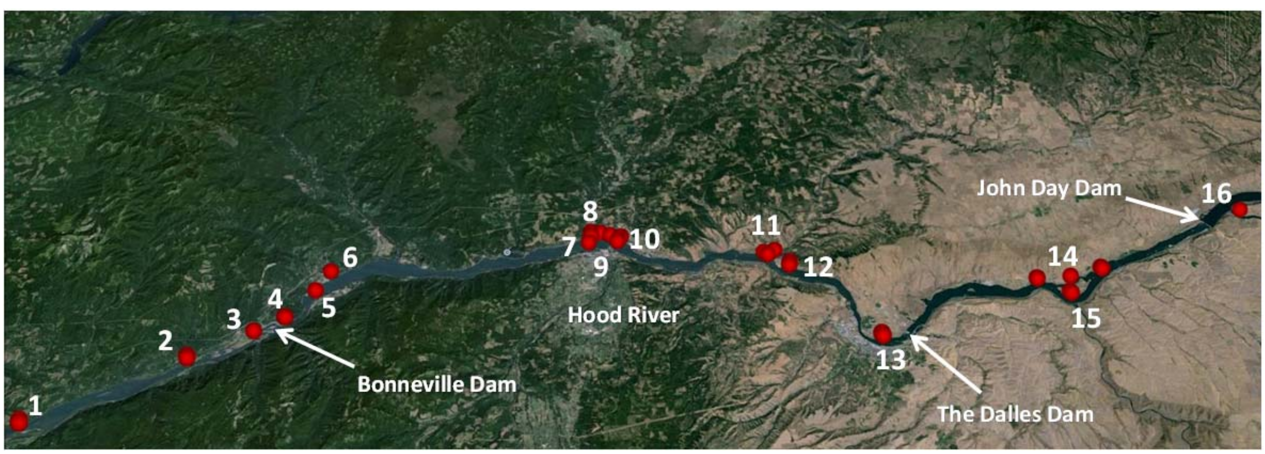

Figure 2. Receiver locations (numbered circles) used to monitor JSATS-tagged adult Pacific lamprey in 2012: 1) Rooster Rock; 2) Dodson/Skamania; 3) Bonneville Dam tailrace; 4) Bonneville Dam forebay; 5) Cascade Locks; 6) Stevenson; 7) White Salmon R.; 8) White Salmon R. mouth; 9) Hood R. mouth; 10) Hood R.; 11) Klickitat R.; 12) Lyle; 13) The Dalles Dam tailrace; 14) Miller Island; 15) Deschutes R. mouth; 16) John Day River.

Figure 3. Receiver locations (numbered circles) used to monitor JSATS-tagged adult Pacific lamprey in 2013 and 2014: 1) Dodson/Skamania; 2) Bonneville Dam tailrace; 3) Cascade Locks; 4) Stevenson; 5) White Salmon R.; 6) White Salmon R. mouth; 7) Hood R. mouth; 8) Hood R.; 9) inside Klickitat R., 300 m from the mouth; 10) Lyle; 11) The Dalles Dam tailrace; 12) Miller Island; 13) Deschutes R. mouth; 14) John Day River.

Lamprey detections on HD-PIT antennas were also used to monitor passage at Columbia and Snake River dams, and to determine detection efficiencies at downstream sites and refine final locations of Pacific lamprey. HD-PIT antennas were located at or near the tops of fish ladders at Bonneville, The Dalles, John Day, McNary, Priest Rapids, Wanapum, Rock Island, and Rocky Reach dams on the Columbia River, and at Ice Harbor, Lower Monumental, and Lower Granite dams on the Snake River. These sites were maintained by UI (lower Columbia and Snake River dams), and the Chelan and Grant County PUD's (upper Columbia River dams). Additional HD-PIT antennas were located in Fifteenmile Creek, a small tributary that empties into the Columbia River in The Dalles Dam tailrace, Hood River, and in some Deschutes River tributaries (maintained by the Confederated Tribes of Warms Springs Reservation of Oregon [CTWSRO]). A combination FD / HD-PIT antenna in the Deschutes River, just upstream from the mouth, became operational in March 2013.

Table 1. Locations JSATS receivers were deployed by University of Idaho (UI) and Pacific Northwest Laboratories (PNNL), 2011-2014. River mile kilometer (RKM) zero = mouth of Columbia River. Number of receivers at each site given parenthetically.

Agency	River	Location (# of receivers)	RKM	Year(s) deployed
UI	Columbia	Rooster State Park (2)	209.7	2012
UI	Columbia	Dodson/Skamania (2)	225.6	2012-14
UI	Columbia	Bonneville Dam tailrace (1-2)	232.0	2011-14
PNNL	Columbia	Bonneville Dam tailrace (3)	233.0	2012
PNNL	Columbia	Bonneville Dam (cabled array)	235.1	2012
PNNL	Columbia	Bonneville Dam forebay (4)	236.0	2012
UI	Columbia	Bonneville Dam forebay (2)	236.5	2011-12
UI	Columbia	Cascade Locks, OR (1)	239.1	2012-14
UI	Columbia	Stevenson, WA (1-2)	243.0	2011-14
UI	Columbia	Wind Mt. (1-3)	253.3	2011
UI	Columbia	L. White Salmon River (2)	262.4	2011
UI	Columbia	White Salmon River (4-5)	269.7	2012-14
UI	Columbia	White Salmon River, mouth (1)	271.4	2012-14
UI	Columbia	Hood River, mouth (1)	272.4	2012-14
UI	Columbia	Hood River (3-5)	273.0	2011-14
PNNL	Columbia	Hood River, OR (6)	275.0	2012
UI	Columbia	Within Klickitat River, 300m upstream from mouth	290.3	2011, 2013-14
UI	Columbia	Klickitat River, downstream of mouth (1)	289.8	2012
UI	Columbia	Klickitat River, mouth (1)	290.3	2012
UI	Columbia	Lyle, upstream of Klickitat R. (2-3)	291.8	2011-14
UI	Columbia	The Dalles Dam tailrace (2-3)	304.9	2011-14
PNNL	Columbia	The Dalles Dam tailrace (3)	307.0	2012
PNNL	Columbia	The Dalles Dam (cabled array)	308.1	2012
PNNL	Columbia	The Dalles Dam forebay (5)	311.0	2012
PNNL	Columbia	Celilo, OR (6)	325.0	2012
UI	Columbia	Miller Island downstream (2-3)	325.9	2012-14
UI	Columbia	Deschutes River, mouth (1)	328.2	2012-13
UI	Columbia	Miller Island, north channel (1)	329.3	2012
UI	Columbia	Miller Island upstream (2-3)	333.6	2012-14
PNNL	Columbia	John Day Dam tailrace (4)	346.0	2012
PNNL	Columbia	John Day Dam (cabled array)	346.9	2012
PNNL	Columbia	John Day Dam forebay (8)	351.0	2012
UI	Columbia	John Day River, ~1200 m upstream from mouth (1)	352.0	2011-14
PNNL	Columbia	Crowe Butte State Park (7)	422.0	2012
PNNL	Columbia	McNary Dam tailrace (3)	468.0	2012
PNNL	Columbia	McNary Dam (cabled array)	469.8	2012
PNNL	Columbia	McNary Dam forebay (8)	472.0	2012
PNNL	Snake	Snake River, mouth (4)	524.6	2012
PNNL	Snake	Ice Harbor Dam forebay (4)	538.6	2012
PNNL	Snake	Sheffler, WA (4)	561.6	2012
PNNL	Snake	Lower Monumental tailrace (3)	586.6	2012
PNNL	Snake	Lower Monumental forebay (4)	589.6	2012
PNNL	Snake	Ayers Landing (4)	603.6	2012
PNNL	Snake	Little Goose tailrace (3)	633.6	2012
PNNL	Snake	Little Goose forebay (3)	635.6	2012
PNNL	Snake	Lower Granite tailrace (3)	692.6	2012
PNNL	Snake	Lower Granite forebay (3)	695.6	2012
PNNL	Snake	Red Wolf Crossing Bridge (3)	742.6	2012

Data downloading and processing

Data were loaded into a database maintained at the University of Idaho. Autonomous nodes were downloaded monthly by transferring data to a portable computer. Clocks on all receivers and readers were synchronized to assure seamless integration of data collected at different sites. Records were screened to remove obvious error (noise) records and detections that occurred before fish were released. Valid detections were defined as those with three detections at any receiver within a 15-min time block within a plausible spatial range. Records were inspected for accuracy, and assigned codes summarizing the movements of tagged fish. Additional details are provided in Noyes et al. (2014).

We estimated detection efficiency for each JSATS receiver site as the proportion of adults that were detected at the location of those known to have passed the location based on detections at all upstream JSATS and HD-PIT detection sites.

Data analyses

Travel times and rates – Lamprey travel times (d) and migration rates (km/d) were calculated from the last record at a downstream receiver site to the first record at an upstream receiver site. Coded data were used to estimate several passage metrics, including travel times, migration rates, and residence times. Migration rates were estimated using detections recorded in the year a fish was tagged (i.e., post-overwintering records were not included). We tested for associations between lamprey migration rate and tag date, water temperature, and body length using univariate linear regression.

Final distribution – We described the final locations of individual fish using both JSATS and HD-PIT detection records. Final locations were described using last detections from the year of tagging or the spring following tagging, when available. We used pairwise Kolmogorov-Smirnov tests to test for differences in final distribution between reservoir-released lamprey and tailrace-released lamprey that passed Bonneville Dam each year. The null hypothesis was that the distribution of these two groups would be similar after excluding the downstream-released fish that did not pass Bonneville Dam.

Tag effects – For each study year, we compared the proportions of JSATS and HD-PIT only tagged adults passing Bonneville, The Dalles, John Day, and McNary dams to test whether there was evidence of a greater tag burden in the JSATS-tagged adults (i.e., adults were double tagged with JSATS + HD-PIT or HD-PIT only) using Pearson's χ^2 tests. In 2011, JSATS tagging started late and HD-PIT tagging ended early (see Results). In addition, the 2011 tailrace release group sample sizes were small. Therefore, comparisons in 2011 were made using only lamprey that were released at Stevenson during the overlapping tagging period.

Reach survival – We estimated reach-specific survival rates using Cormack-Jolly-Seber (CJS) survival models (Lebreton et al. 1992; Perry et al. 2012). This method has frequently been used to estimate reach survival for juvenile salmonids in the Columbia River system (e.g., Muir et al. 2001; Sandford and Smith 2002; McMichael et al. 2010) and to estimate adult salmon reach survival and escapement to tributaries (e.g., Keefer et al. 2005, 2014). CJS models allow simultaneous estimation of detection probabilities (ρ, accounting for undetected fish) and survival probabilities (φ). Detection data from both the JSATS array and HD PIT antennas were used in the modeling.

We used program RMark (White and Burnham 1999; Laake 2013) to estimate conversion rates through seven (downstream release groups) or five (upstream release groups) study reaches that had monitoring infrastructure in all three years: (1) Bonneville tailrace to the top of Bonneville Dam; (2) top of Bonneville Dam to the Stevenson / Cascades Locks gate; (3) Stevenson / Cascades Locks gate to the Hood River gate; (4) Hood River gate to the Klickitat River gate; (5) Klickitat River gate to The Dalles tailrace gate; (6) The Dalles tailrace gate into Fifteenmile Creek or the top of The Dalles Dam; and (7) top of The Dalles Dam to the Miller Island gate. In all cases, lampreys that were classified as having entered tributaries were treated as 'successful' in the reach where the tributary entered the Columbia River. Within RMARK, we used the live recaptures CJS model with a logit link function. This type of mark-recapture model uses maximum likelihood estimation to generate the parameter estimates (Perry et al. 2012).

Because lamprey size and migration timing have been associated with upstream migration distance (Keefer et al. 2009b; Hess et al. 2014), we tested several covariate models that included these terms during data exploration. These models included a model where survival probability (φ) was presumed constant across reaches, a model where survival varied across reaches, and models with reach-varying survival plus various combinations of the covariates lamprey length and migration date. In all models, detection probabilities (ρ) were allowed to vary across reaches given known differences in the detection efficiency of various JSATS and HD-PIT sites. Results from an AIC-based model comparison (Burnham and Anderson 2002) indicated that the model with lamprey length, migration date, and reach-varying survival was often the most parsimonious and hence we present survival estimates from this model.

In addition to the CJS modeling, we calculated minimum point estimates of reach survival by analyzing JSATS and PIT detections from upstream sites. Reaches were bracketed by JSATS gates throughout Bonneville Reservoir and The Dalles Dam pool in addition to HD-PIT sites at Columbia and Snake River dams. A lamprey was determined to have 'survived' if it was detected on JSATS or PIT receivers at or above the upstream end of a given reach. Annual reach survival estimates were made for Reservoir release and tailrace release groups. Reach survival was also estimated separately for the subsample of tailrace released lamprey that were known to have passed Bonneville Dam.

Estimated Bonneville Reservoir tributary entry

Detections on JSATS receivers deployed in the Klickitat and John Day Rivers, and HD-PIT antennas in Hood River, Fifteenmile Creek, and Deschutes River provided definitive evidence of lamprey entry into these tributaries. Final detections from JSATS receivers deployed at the mouths of the White Salmon, Hood, and Deschutes Rivers were used to infer entry into these tributaries. However, not all potential spawning tributaries emptying to the Bonneville Reservoir could be monitored in this study due to logistics of node deployment (minimum depth of 4-6 m). Two major tributaries in the Bonneville Reservoir, the Wind River and Little White Salmon River were not monitored during this study, nor were multiple small creeks. Thus, we used detections on HD-PIT antennas and at JSATS receivers in and at the mouths of Bonneville Reservoir tributaries to extrapolate entry into several unmonitored tributaries to estimate potential total tributary entry. The first approach provides point estimates by applying estimated entry rates to both monitored tributaries and unmonitored tributaries under four entry-rate scenarios. Observed annual average tributary entry rates of JSATS-tagged lamprey were used to define 'low' (minimum), 'middle' (average), or 'high' (maximum) entry rates and these were applied to five unmonitored known or suspected Pacific lamprey spawning tributaries to Bonneville Reservoir. The fourth scenario applied observed rates of entry of radio-tagged lamprey into these five tributaries from previous studies (e.g., Keefer et al. 2009d, 2010). We then compared the total tributary entry estimate with the annual observed entry rate and made inferences about potential changes to final fates and distributions of unaccounted-for lamprey in Bonneville Reservoir.

In a second approach, we developed a simulation model that incorporated uncertainty in tributary entry rates to represent annual variation in rates as well as the sensitivity of the outcome to uncertainty in the true rates. In the model, we estimated distributions of the annual proportion of the population entering tributaries (trib) or passing The Dalles Dam (TDA) by randomly drawing an annual proportion in each iteration *i* (with replacement) from a distribution with a mean rate and error (S.D.):

$$P_{(\mathrm{trib})i} = P_{\mathrm{mean(trib)}i} + \mathrm{error}_i$$

$$P_{\mathrm{TDA}i} = P_{\mathrm{mean(TDA)}i} + \mathrm{error}_i$$

$$P_{(\mathrm{unk})i} = 1 - P_{\mathrm{mean(trib)}i} - P_{\mathrm{mean(TDA)}i}$$

The mean proportions were estimated using JSATS, HD-PIT and radiotelemetry data for the groups that passed The Dalles Dam or entered Fifteenmile, Herman, or Mill creeks, or the Hood, White Salmon, Little White Salmon, or Klickitat rivers. We also included an 'other tributary' category (*mean* entry = 0.02) to estimate the potential effects of tributary entry into the many small creeks that were not monitored in any adult lamprey studies (e.g., Herman, Eagle, Catherine, Phelps, Penham, Dry, Chenoweth, etc.). For all tributary groups, we chose $0.5 \times P_{\mathrm{mean}}$ as the standard deviation, which is slightly lower than the observed value (SD = 0.67) from the tributary time series with the most annual estimates (Fifteenmile Creek, N=15 HD-PIT and RT annual release groups). Estimates for passage of The Dalles Dam were based on reported values from HD-PIT tag studies (*mean* = 0.55, SD = 0.11). Each scenario used 500 iterations. Larger error values produced qualitatively similar results, but with broader distributions within each class and greater overlap among classes. We developed two scenarios with this model using the observed mean tributary entry rate across all years for $P_{\mathrm{mean(trib)}}$. The first used observed mean rates of tributary entry (*means* = 0.004-0.038 per tributary). These values are known to underestimate the true rate because of movement into unmonitored tributaries and missed detections. Thus, we also ran a model that doubled the observed mean tributary entry rate as an upper-limit scenario similar to the High scenario in the point estimate model.

Results

Lamprey tagging and release

The total number of adult lamprey recorded at Bonneville Dam between 2011 and 2013 varied (Table 2), but sampling in each year was in approximate proportion to the run (Figure 4). Due to contractual issues, tagging was delayed or interrupted in two study years. In July 2011 tagging was interrupted for three weeks due to delayed transmitter delivery, and in 2013 we did not receive transmitters until late June and the first portion of the lamprey run was not sampled. Tagging was temporarily suspended due to high water temperatures (>20° C) in mid-August each year. Lamprey were larger, on average, in 2012 than in 2011 or 2013 (F = 26.54, ndf = 2, ddf = 772, P < 0.001), though there was broad overlap in the size of JSATS-tagged fish in all years (Table 3).

Table 2. Total numbers and release locations of adult Pacific lamprey double tagged with HD-PIT and JSAT transmitters at Bonneville Dam, 2011-2013. Total count at Bonneville Dam includes day, night, and LPS counts.

		Tailrace release			**Reservoir release**			
Year	Total # tagged	Dodson, WA	Hamilton Is., WA	Tanner Cr., OR	Stevenson, WA	Cascade Locks, OR	Total count at Bonneville Dam	% of run tagged
2011	85	n/a	23	n/a	62	n/a	51,606	0.2
2012	299	5	74	74	73	73	93,462	0.3
2013	400	n/a	102	95	98	105	90,933	0.4

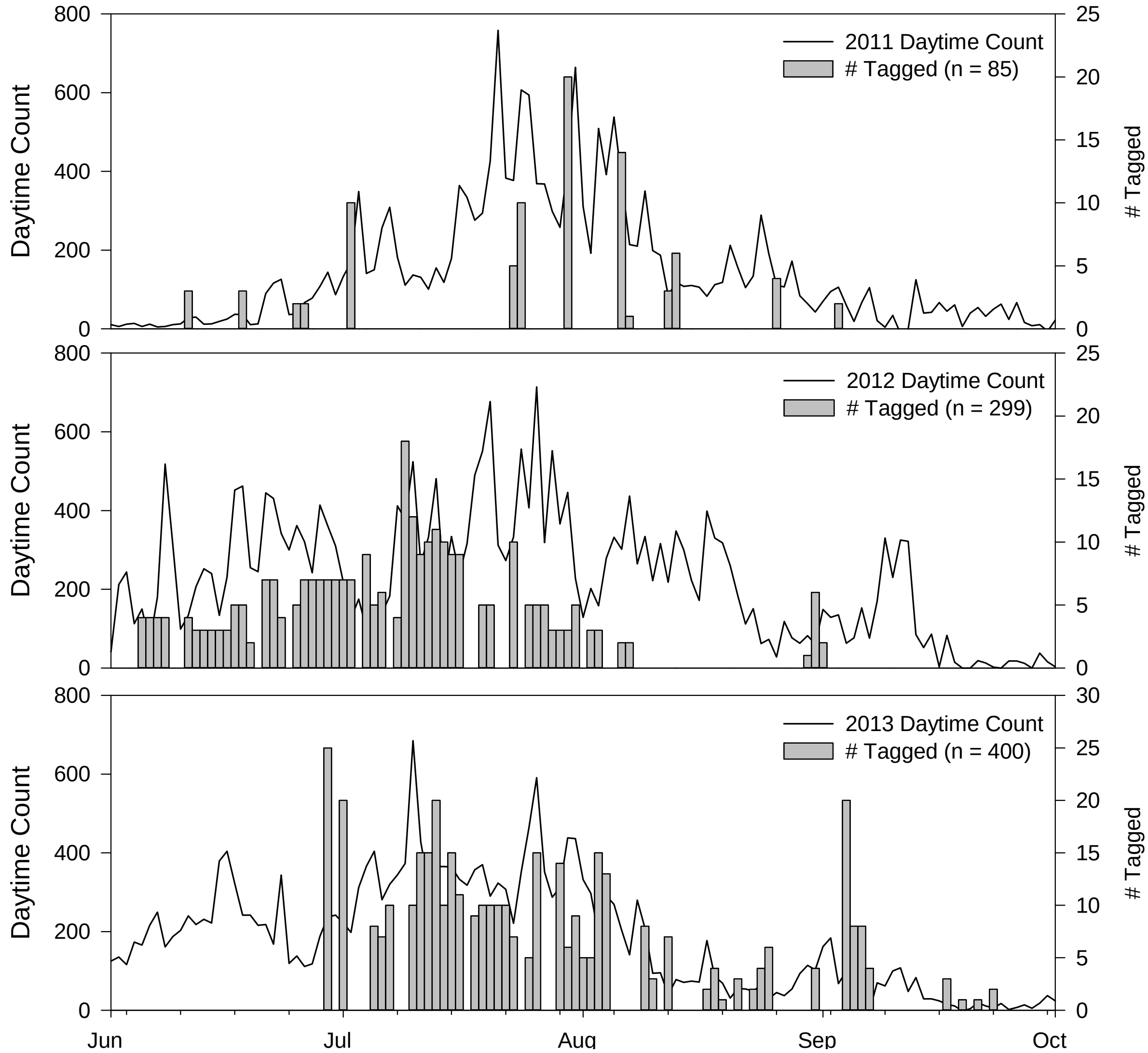

Figure 4. Daytime counts of adult Pacific lamprey (lines) and the number that was JSATS-tagged (bars) at Bonneville Dam, 2011-2013.

Table 3. Length, weight, and girth of adult Pacific lamprey double tagged with HD-PIT and JSAT transmitters at Bonneville Dam, 2011-2013.

	Length (cm)			Girth (cm)			Weight (g)		
Year	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*
2011	85	65.0	4.4	85	10.7	0.8	85	438.2	83.3
2012	299	67.0	3.9	299	11.2	0.8	298	479.5	83.4
2013	400	64.8	4.3	400	10.7	0.9	392	432.8	86.9

Telemetry monitoring

JSATS receiver detection efficiencies differed by location and year (Figure 5). Most receiver gates had detection efficiencies ranging between 90-99%. Lower detection efficiencies were usually attributable to acoustically challenging environments (e.g., Bonneville and The Dalles tailraces), or outages caused by interference with commercial and Tribal fishing operations (e.g., Lyle in 2012).

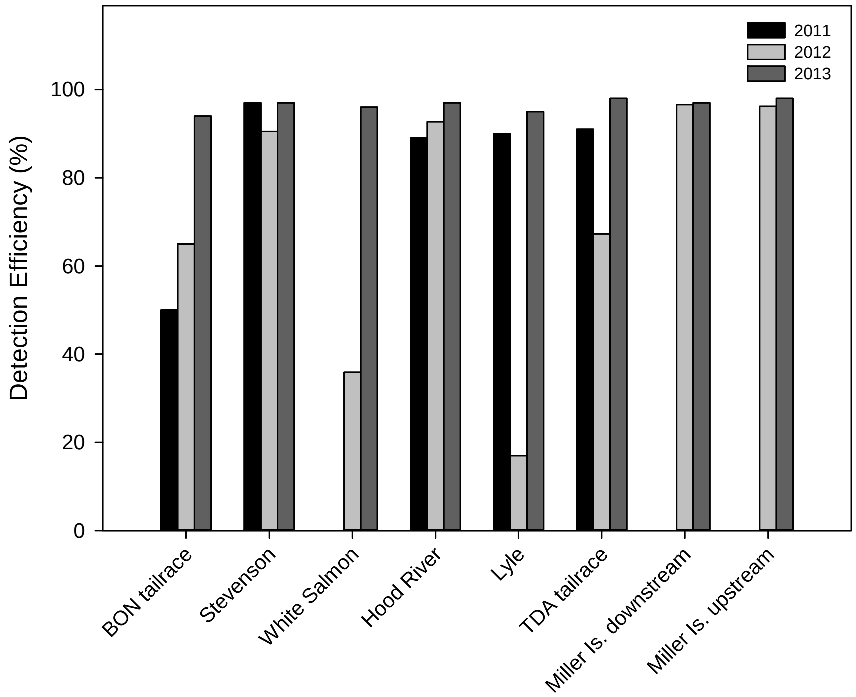

Figure 5. Detection efficiencies of JSATS receivers by gate for all tagged Pacific lamprey, 2011-2013.

Travel times and migration rates

Lamprey migration rates were consistent between years within release location. Tagged lamprey released downstream from Bonneville Dam passed the dam slowly, but then migrated rapidly through all reservoir reaches (Figure 6). Similarly, reservoir-released lamprey moved quickly through the reservoir reaches. Analyses using univariate linear regression found weak, but significant correlations between migration rate through the Bonneville Reservoir and water temperature in the reaches with the largest sample size (L. White Salmon to Lyle in 2011 and White Salmon to Hood River in 2012 and 2013) (n = 63, r^2 = 0.152, P = 0.002), as well as release date (n = 63, r^2 = 0.173, P < 0.001) in 2012, and fork length (n = 233, r^2 = 0.023, P = 0.022) in 2013 (Figure 7). The fork length relationship was similar in 2012 (n = 63, r^2 = 0.053, P = 0.068).

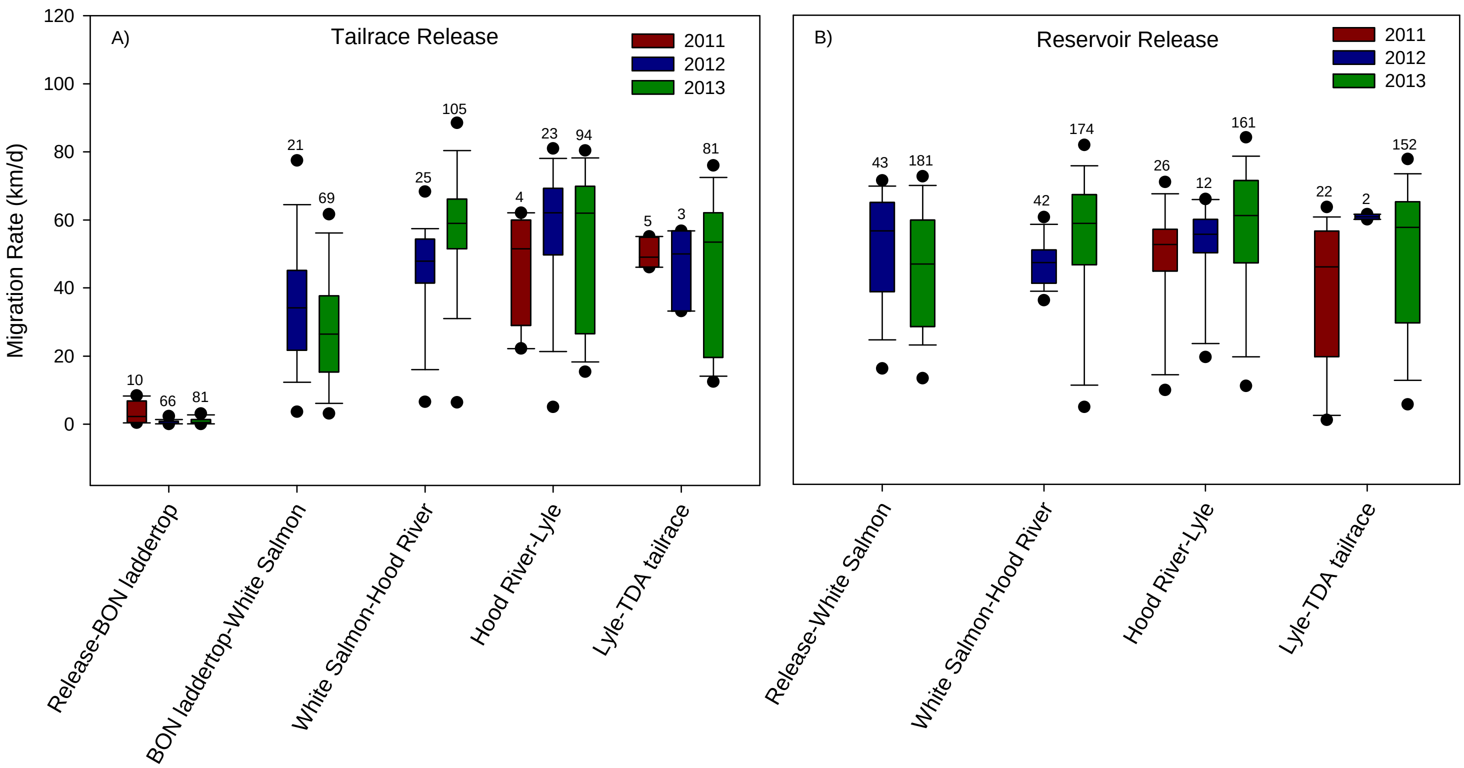

Figure 6. Migration rates (km/d) by reach for JSATS-tagged Pacific lamprey released into the Bonneville Dam tailrace (A) or Bonneville Reservoir (B), 2011-2013. Sample sizes are shown above each bar. Box plots show 5th, 25th, 50th, 75th and 95th percentiles.

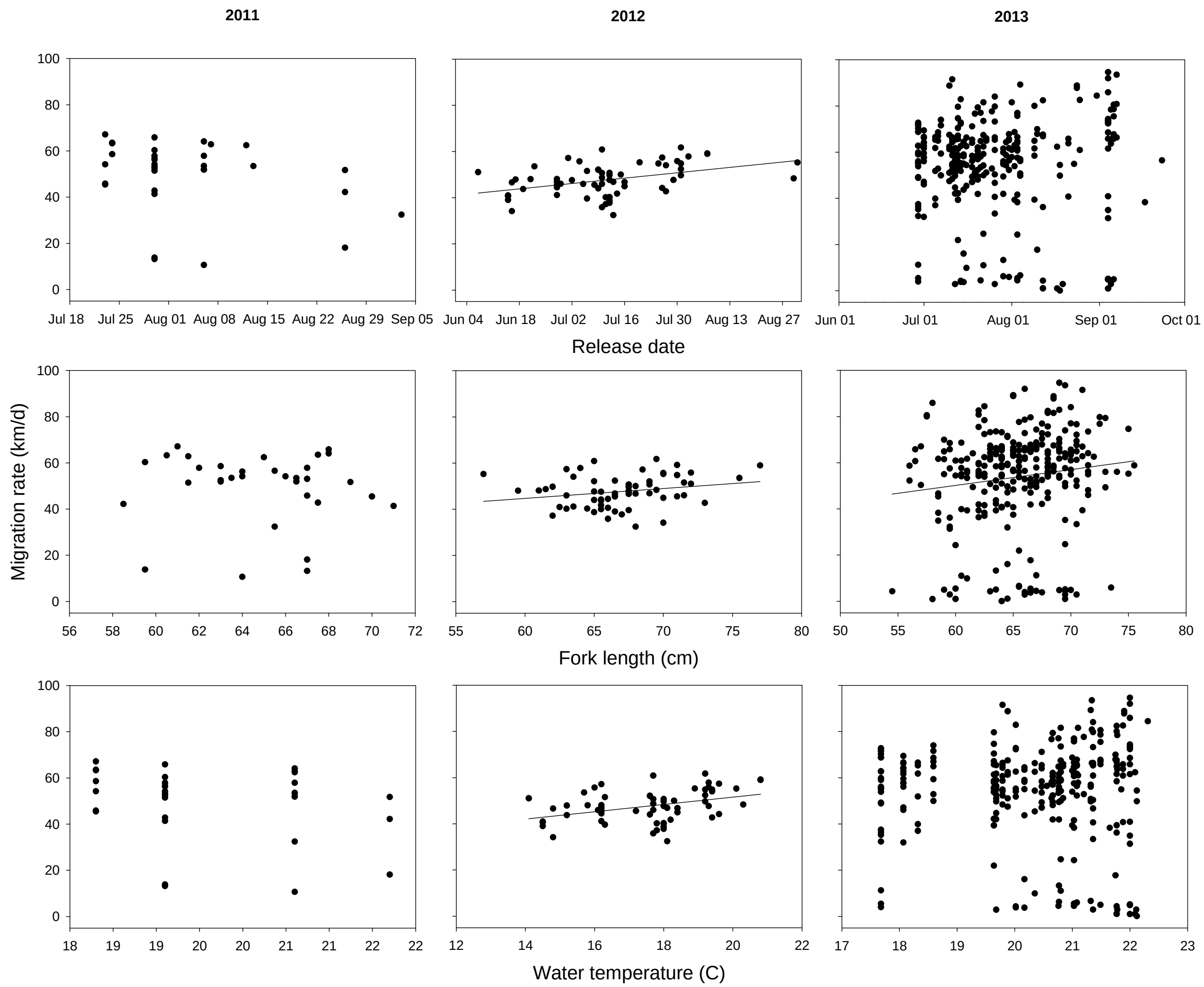

Figure 7. Linear regression relationships between migration rate (L. White Salmon-Lyle reach in 2011, White Salmon River-Hood River reach in 2012 and 2013) and release date (top row), fork length (middle row), and water temperature at release (bottom row) for adult Pacific lamprey tagged in 2011 (left column), 2012 (middle column), and 2013 (right column) (both release groups combined). Note x-axes are different.

Reach survival

Most (82-92%) of the adults from both release groups that were detected in the Bonneville Reservoir were later detected at upper reservoir sites (Figures 8-10, Tables 4-5). Estimates of survival by reach and per kilometer for both release groups were high in reservoir reaches, but substantially lower when passing Bonneville and The Dalles Dams (Figures 11-12, Tables 6-7).

Bonneville tailrace past Bonneville Dam – Point estimates of survival past Bonneville Dam ranged from half to nearly three-quarters (0.500-0.738) of tailrace-released lampreys annually (Figures 8-9, Tables 4-5). In the CJS models, annual estimated survival past Bonneville Dam ranged from 0.683 to 0.767; survival through this reach was 0.706 with data from all years combined (Figure 11).

Bonneville Reservoir – Annual point estimates of survival in the Stevenson-White Salmon reach ranged from 88% to 92.6% for tailrace release groups and 0.921 to 0.986 for reservoir-released fish. Survival estimates in the White Salmon to Hood River reach ranged from 0.931 and 0.973 for tailrace release groups and 0.979 to 0.993 for reservoir release groups. The Hood River to Lyle reach survival ranged from 0.963 to 1.000 for tailrace release groups and 0.934 to 0.963 for reservoir-released fish. Estimates for the Lyle to The Dalles tailrace reach were between 0.875 and 0.975 for tailrace release groups and between 0.808 and 0.993 for reservoir release groups annually (Figures 8-10, Tables 4-5). CJS-modeled survival through the first Bonneville Reservoir reach (top of Bonneville-Stevenson) was estimated for the downstream release groups only. Annual estimates ranged from 0.707 to 0.868 and the combined estimate was 0.848. Modeled survival estimates through the Stevenson-Hood River reach with all years combined were 0.959 (tailrace releases) and 0.968 (reservoir releases). Combined estimates for the Hood River-Lyle reach were 0.949 (tailrace releases) and 0.966 (reservoir-releases) and were 1.000 (tailrace releases) and 0.954 (reservoir releases) through the Lyle-The Dalles tailrace reach (Figures 11).

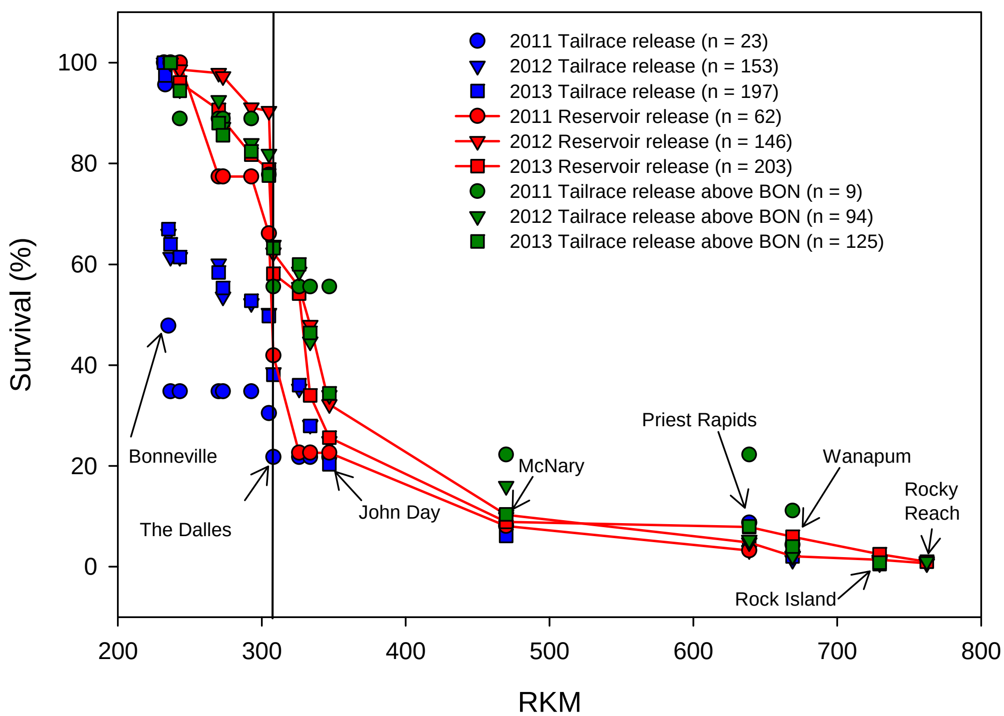

Figure 8. Percentage of JSATS tagged Pacific lamprey detected at Bonneville Reservoir and upriver receiver gates and HD-PIT antennas by release group, 2011-2014. The 'Tailrace release above BON' group refers to those fish that were released to the Bonneville Dam tailrace and passed the dam. Lines omitted for tailrace release groups for clarity. Vertical black line shows The Dalles Dam (rkm 308.1).

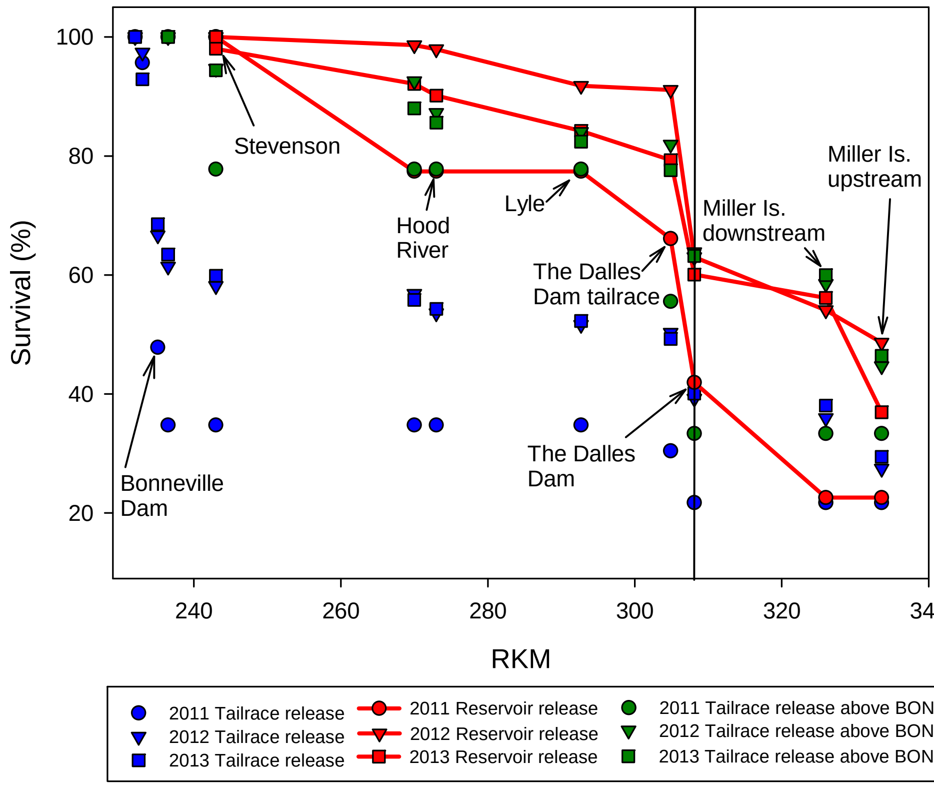

Figure 9. Percentage of JSATS tagged Pacific lamprey detected at receiver gates and HD-PIT antennas from release to Miller Island by release group, 2011-2014. The 'Tailrace release above BON' group refers to the subsample of the Bonneville Dam tailrace sample that were recorded passing the dam. Vertical black line shows The Dalles Dam (rkm 308.1).

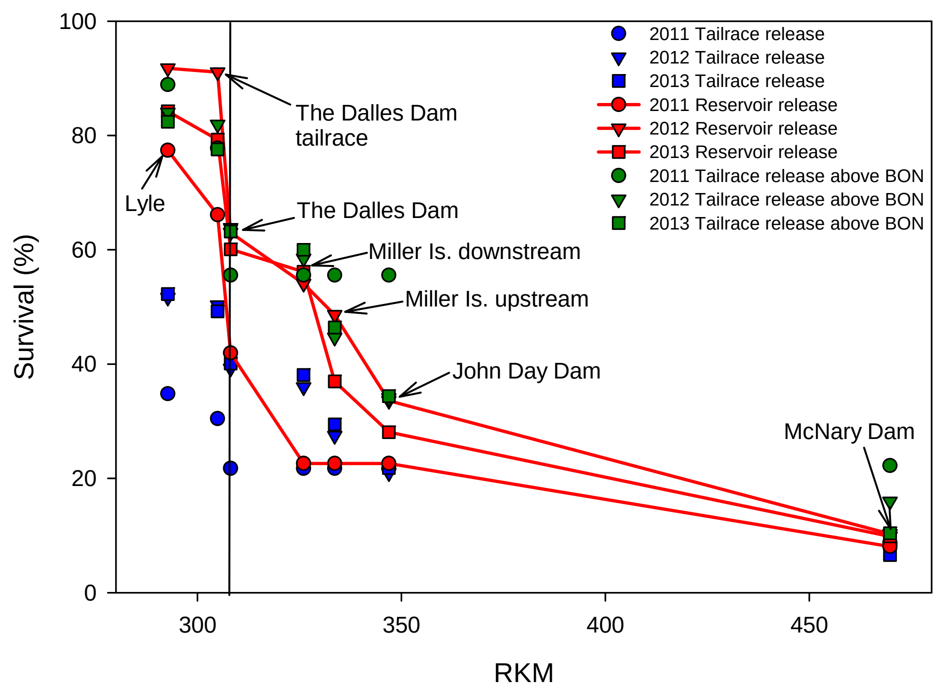

Figure 10. Percentage of JSATS tagged Pacific lamprey detected at receiver gates and HD-PIT antennas from Lyle to McNary Dam by release group, 2011-2014. Vertical black line shows The Dalles Dam (rkm 308.1).

Table 4. Point estimates of survival from release for JSATS-tagged Pacific lamprey in the tailrace release groups, 2011-2014. Estimates include detections from the spring following tagging.

Tailrace release	**2011 (*n* = 23)**		**2012 (*n* = 153)**		**2013 (*n* = 197)**	
Reach	***n***	**%**	***n***	**%**	***n***	**%**
Release to Bonneville Dam tailrace	22	95.7	149	97.4	183	92.9
Release to Bonneville Dam	11	47.8	102	66.7	135	68.5
Release to Bonneville forebay	8	34.8	94	61.4	125	63.5
Release to White Salmon River gate	--	--	87	56.9	110	55.8
Release to Hood River gate	8	34.8	81	52.9	107	54.3
Release to Lyle, WA	8	34.8	79	51.6	103	52.3
Release to The Dalles Dam tailrace	7	30.4	77	50.3	97	49.2
Release to The Dalles Dam	5	21.7	60	39.2	79	40.1
Release to The Dalles Dam top of the ladder HD-PIT antennas	5	21.7	55	35.9	76	38.6
Release to downstream of Miller Island	--	--	55	35.9	75	38.1
Release to upstream of Miller Island	--	--	42	27.5	58	29.4
Release to John Day Dam	5	21.7	32	20.9	43	21.8
Release to McNary Dam	2	8.7	15	9.8	13	6.6
Release to Ice Harbor Dam	--	--	5	3.3	--	--
Release to Lower Monumental Dam	--	--	5	3.3	--	--
Release to Little Goose Dam	--	--	3	2.0	--	--
Release to Priest Rapids Dam	2	8.7	5	3.3	10	5.1
Release to Wanapum Dam	1	4.3	2	1.3	5	2.5
Release to Lower Granite Dam	--	--	3	2.0	--	--
Release to Rock Island Dam	--	--	1	0.7	1	0.5
Release to Rocky Reach Dam	--	--	1	0.7	--	--

Table 5. Point estimates of survival from release for JSATS-tagged Pacific lamprey in the reservoir release groups, 2011-2014. Estimates include detections from the spring following tagging.

Reservoir release	**2011 (*n* = 62)**		**2012 (*n* = 146)**		**2013 (*n* = 203)**	
Reach	***n***	**%**	***n***	**%**	***n***	**%**
Release to White Salmon River gate	--	--	144	98.6	187	92.1
Release to Hood River gate	54	87.1	143	97.9	183	90.2
Release to Lyle, WA	52	83.9	134	91.8	171	84.2
Release to The Dalles Dam tailrace	42	67.7	133	91.1	161	79.3
Release to The Dalles Dam	26	41.9	92	63.0	122	60.1
Release to The Dalles Dam top of the ladder HD-PIT antennas	24	38.7	88	60.3	117	57.6
Release to downstream of Miller Island	--	--	79	54.1	114	56.2
Release to upstream of Miller Island	--	--	71	48.6	75	36.9
Release to John Day Dam	14	22.6	49	33.6	57	28.1
Release to McNary Dam	5	8.1	15	10.3	20	9.9
Release to Ice Harbor Dam	1	1.6	--	--	1	0.5
Release to Lower Monumental Dam	--	--	--	--	--	--
Release to Little Goose Dam	--	--	--	--	--	--
Release to Priest Rapids Dam	2	3.2	10	6.8	17	8.4
Release to Wanapum Dam	--	--	4	2.7	12	5.9
Release to Lower Granite Dam	--	--	--	--	--	--
Release to Rock Island Dam	--	--	2	1.4	5	2.5
Release to Rocky Reach Dam	--	--	1	0.7	2	1.0

The Dalles tailrace to The Dalles Dam – Annual point estimates of survival in The Dalles tailrace to The Dalles Dam reach were lower than those for the reservoir and ranged from 0.714 to 0.814 for tailrace release groups and 0.619 to 0.758 for reservoir release groups. In the CJS models, annual estimated survival from The Dalles tailrace to any detection at The Dalles Dam or entry into Fifteenmile Creek was 0.791 (tailrace releases) and 0.741 (reservoir releases) with data from all years combined (Figure 11).

The Dalles top to Miller Island – Annual point estimates of survival from the top of The Dalles Dam to Miller Island ranged from 0.987 to 1.000 for tailrace released fish and 0.898 to 0.974 for reservoir released fish. CJS estimates for this reach were 0.848 (tailrace releases) and 0.854 (reservoir releases) (Figure 11).

Downstream versus forebay release groups – When we compared the final detection rkms of lampreys that passed Bonneville Dam (tailrace release groups) with the final rkms of lampreys that were released in the reservoir, there were no statistical differences in the distributions in any study year (pairwise Kolmogorov-Smirnov tests: 2011: D = 0.2839, P = 0.424; 2012: D = 0.1140, P = 0.425; 2013: D = 0.0995, P = 0.409).

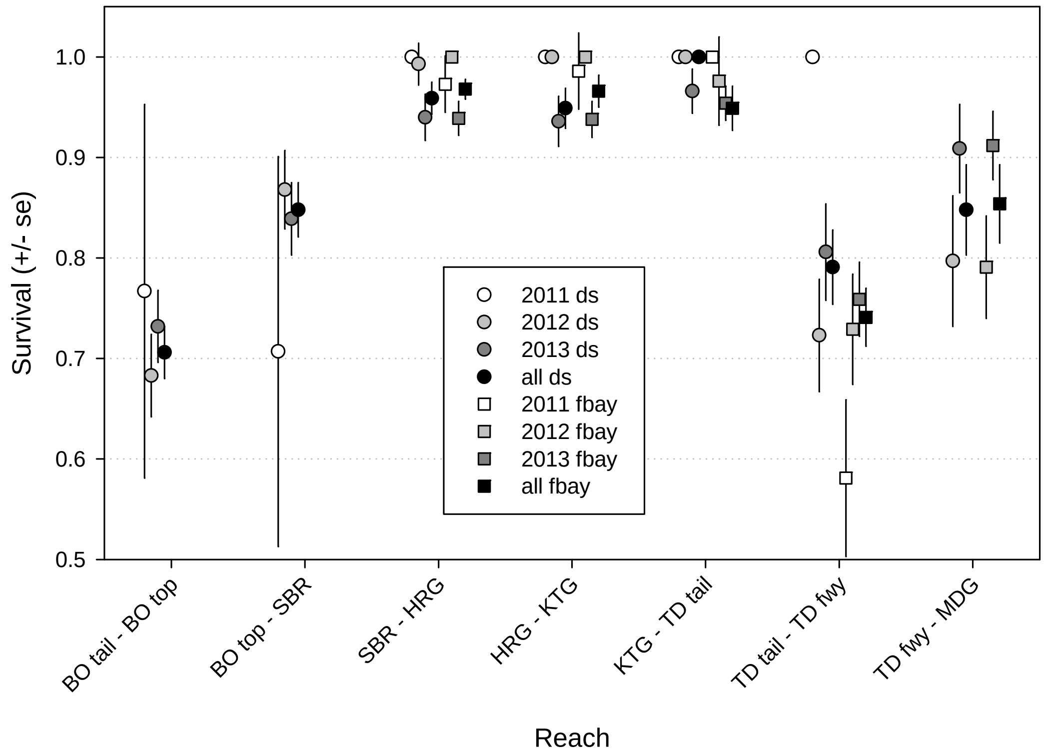

Figure 11. Annual survival estimates by reach for tailrace (shaded circles) and reservoir (shaded squares) release groups. Total survival estimates by reach for all years combined depicted as black circles and squares. BO = Bonneville Dam, SBR = Stevenson gate, HRG = Hood River gate, KTG = Lyle gate, TD = The Dalles Dam, MDG = Miller Island gate. RMark models included lamprey length and release date as covariates.

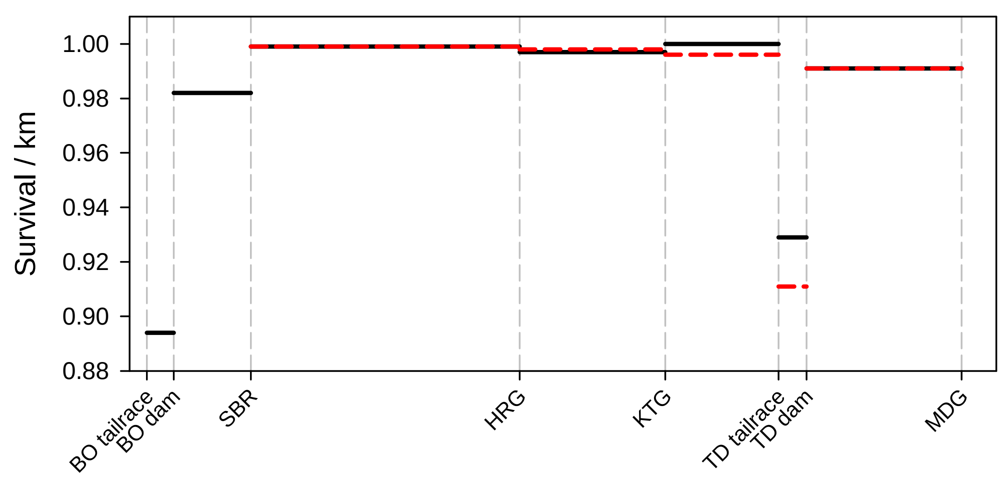

Figure 12. Survival per kilometer for tailrace (black lines) and reservoir (red lines) release groups, 2011-2013 combined. BO = Bonneville Dam, SBR = Stevenson gate, HRG = Hood River gate, KTG = Lyle gate, TD = The Dalles Dam, MDG = Miller Island gate. CJS models included lamprey length and release date as covariates.

Table 6. Point estimates of survival, by reach, for JSATS-tagged Pacific lamprey in the tailrace release groups, 2011-2014. Estimates include detections from the spring following tagging.

Tailrace release	**2011 (*n* = 23)**		**2012 (*n* = 153)**		**2013 (*n* = 197)**	
Reach	***n***	**%**	***n***	**%**	***n***	**%**
Release to Bonneville Dam tailrace	22	95.7	149	97.4	183	92.9
Bonneville Dam tailrace to Bonneville Dam Ladder	11	50.0	102	68.5	135	73.8
Bonneville Dam Ladder to Bonneville forebay	8	72.7	94	92.2	125	92.6
Bonneville forebay to White Salmon R. gate	--	--	87	92.6	110	88.0
White Salmon River gate to Hood River gate	--	--	81	93.1	107	97.3
Hood R. gate to Lyle gate	8	100.0	79	97.5	103	96.3
Lyle gate to The Dalles Dam tailrace gate	7	87.5	77	97.5	97	94.2
The Dalles Dam tailrace gate to The Dalles Dam Ladder	5	71.4	60	77.9	79	81.4
The Dalles Dam Ladder to The Dalles Dam Exit	5	100	55	91.7	76	96.2
The Dalles Dam Exit to downstream of Miller Is.	--	--	55	100.0	75	98.7
Downstream of Miller Is. to upstream of Miller Is.	--	--	42	76.4	58	77.3
Upstream of Miller Island to John Day Dam Exit	--	--	32	76.2	43	74.1
John Day Dam Exit to McNary Dam Exit	2	40.0	15	46.9	13	30.2
Upstream of McNary Dam	2	100.0	10	66.7	10	76.9

Table 7. Point estimates of survival, by reach, for JSATS-tagged Pacific lamprey in the reservoir release groups, 2011-2014. Estimates include detections from the spring following tagging.

Reservoir release	**2011 (*n* = 62)**		**2012 (*n* = 146)**		**2013 (*n* = 203)**	
Reach	***n***	**%**	***n***	**%**	***n***	**%**
Release to White Salmon R. gate	--	--	144	98.6	187	92.1
White Salmon River gate to Hood River gate	--	--	143	99.3	183	97.9
Hood R. gate to Lyle gate	52	96.3	134	93.7	171	93.4
Lyle gate to The Dalles Dam tailrace gate	42	80.8	133	99.3	161	94.2
The Dalles Dam tailrace gate to The Dalles Dam Ladder	26	61.9	92	69.2	122	75.8
The Dalles Dam Ladder to The Dalles Dam Exit	24	92.3	88	95.7	117	95.9
The Dalles Dam Exit to downstream of Miller Is.	--	--	79	89.8	114	97.4
Downstream of Miller Is. to upstream of Miller Is.	--	--	71	89.9	75	65.8
Upstream of Miller Island to John Day Dam Exit	--	--	49	69.0	57	76.0
John Day Dam Exit to McNary Dam Exit	5	35.7	15	30.6	20	35.1
Upstream of McNary Dam	3	60.0	10	66.7	18	90.0

Tagging effects

Analyses using Chi-square tests found little evidence of any additional tagging effects associated with JSATS transmitters compared to HD-PIT tagging alone. The probability of passing Bonneville, The Dalles, John Day, or McNary dams based on PIT tag detections did not differ ($P > 0.10$, χ^2 test) between adult lampreys double-tagged with JSATS + HD-PIT tags versus adults tagged with only an HD-PIT tag in all but two comparisons. Contrary to the expected effects of additional tag burden, JSATS tagged fish were more likely than HD-PIT tagged fish to pass The Dalles Dam ($P = 0.009$) in 2012 and to pass McNary Dam ($P = 0.038$) in 2011 (Table 8).

Table 8. Results of Pearson's χ^2 tests of upstream dam passage percentages between JSATS and HD-PIT tagged Pacific lamprey released at Stevenson (2011) or in the Bonneville Dam tailrace (2012 and 2013). Here *n is* defined as the minimum number of lamprey known to have passed a dam, based on upstream detections.

		HD-PIT		JSATS			
		n	%	*n*	%	*χ2*	*P*
2011	% past The Dalles	42	43	13	33	0.09	0.766
	% past John Day	27	28	6	15	2.35	0.126
	% past McNary	1	1	3	8	4.32	**0.038**
2012	% past Bonneville	447	54	94	61	2.65	0.104
	% past The Dalles	212	26	55	36	6.74	**0.009**
	% past John Day	177	22	32	21	0.03	0.869
	% past McNary	69	8	13	9	0.002	0.964
2013	% past Bonneville	364	62	125	64	0.15	0.699
	% past The Dalles	197	34	76	39	1.68	0.195
	% past John Day	122	21	36	18	0.56	0.454
	% past McNary	54	9	13	7	1.26	0.262

Final distribution

Tailrace release groups – Final distributions were estimated using last JSATS or HD-PIT detections of tagged lamprey at the end of fall in their year of tagging (Figures 13A and 16A), and updated when possible with any detections from the spring following the year of tagging (Figures 13B and 16B). At the broadest scale, tailrace-released lamprey were classified in one of four fates: undetected, last detected in the Bonneville Dam tailrace (including moving downstream out of the tailrace), in the Bonneville Dam fishway on HD-PIT antennas, or passing Bonneville Dam (Tables 9-10). Reservoir-released lamprey and those passing Bonneville Dam were further classified as passing The Dalles Dam, entering a tributary, falling back over Bonneville Dam, or last detected in the reservoir with unknown final fate.

Patterns in lamprey final distributions in the fall of their tagging year varied among release groups and across all study years. About 39% of all lamprey released into the tailrace in 2011 were last detected on a receiver site upstream from Bonneville Dam (not including tributary receiver sites), while in 2012 and 2013 this number increased to 49% and 52%, respectively (Figure 13A). Up to 12% of tailrace-released fish each year was last detected at tributary sites (Figure 13A). Between 34-57% of all tailrace-released lamprey was last detected in the Bonneville Dam tailrace or inside Bonneville Dam fishways in each year, and between 3-5% of tagged lamprey was undetected as of the fall of their tagging year (Figure 13A).

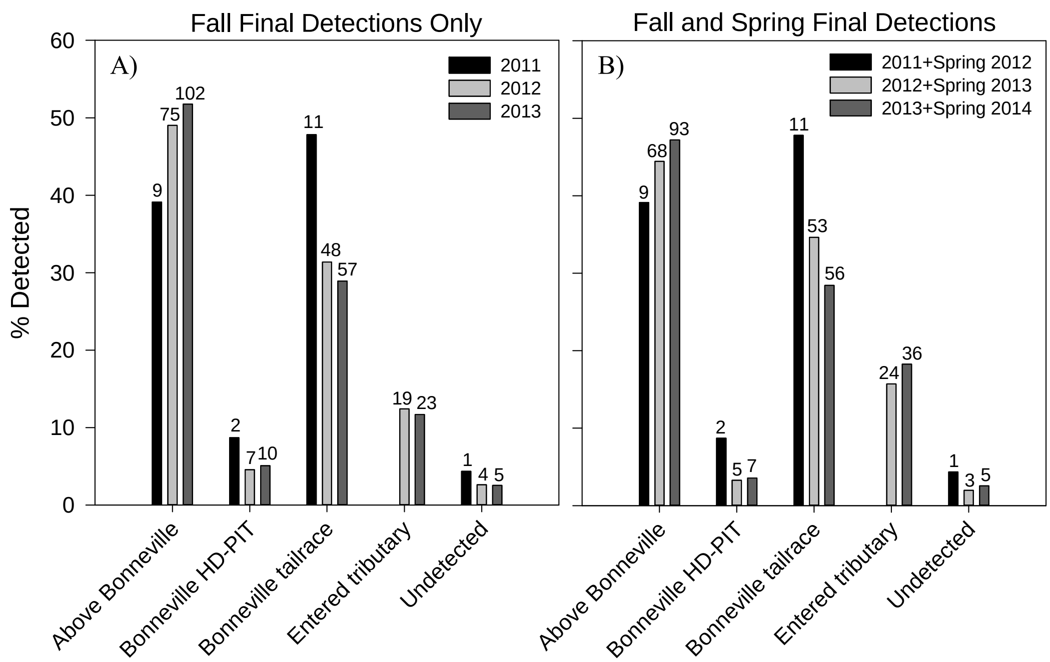

Figure 13. Final distribution of tailrace-released JSATS-tagged Pacific lamprey based on last detections in the fall of their tagging year only (A), and including detections from the spring following tagging (B), 2011-2014. Sample sizes are shown above each bar.

Monitoring in the early spring following the tag year resulted in little change to the overall pattern of distribution each year (Figure 13B). Up to 6% of all tailrace-released fish each year were reclassified as entering a tributary, representing up to 9% of lamprey that had previously been unaccounted for in the Bonneville Reservoir-The Dalles Dam tailrace (Figure 13B). Among the tailrace-released fish that passed Bonneville Dam each year, the majority (53-64%) were last detected as far upstream as The Dalles Dam tailrace, and over one-quarter of the fish tagged in 2012 (26%) and 2013 (28%) was last detected entering a monitored tributary (Figure 14) based on both fall and spring detections. The number of tailrace-released fish last detected entering monitored tributaries was evenly distributed across locations and years, with the exception of substantially higher numbers detected entering the Deschutes River in 2013 (Figure 15). The observed increased entry into the Deschutes River was likely a result of improved monitoring. The PIT antenna array located at the mouth of the Deschutes River came online in March of 2013 and many (39%, n = 24) of the lamprey tagged in 2013 last detected entering the river were recorded on it. Sixteen lamprey (25.8%, n = 16) of the lamprey last detected entering the Deschutes River were recorded on the JSATS receiver at the river mouth.

Table 9. Final distribution by reach of JSATS-tagged Pacific lamprey in the tailrace release groups, 2011-2014. Estimates include detections from the spring following tagging.

Tailrace release	**2011 (*n* = 23)**		**2012 (*n* = 153)**		**2013 (*n* = 197)**	
Reach	***n***	**%**	***n***	**%**	***n***	**%**
Undetected	1	4.3	3	2.0	5	2.5
Release to Bonneville Dam tailrace	1	4.3	3	2.0	17	8.6
Exited Bonneville Dam tailrace downstream	--	--	12	7.8	9	4.6
Bonneville Dam tailrace to Bonneville Dam	10	43.5	38	24.8	30	15.2
Bonneville Dam to Bonneville forebay	2	8.7	5	3.3	7	3.6
Bonneville forebay to White Salmon R. gate	1	4.3	5	3.3	13	6.6
White Salmon River gate to Hood River gate	0	0.0	0	0.0	1	0.5
Entered White Salmon R.	--	--	1	0.7	0	0.0
Entered Hood R.	--	--	4	2.6	2	1.0
Hood R. gate to Lyle gate	1	4.3	2	1.3	4	2.0
Entered Klickitat R.	0	0.0	3	2.0	3	1.5
Lyle gate to The Dalles Dam tailrace gate	2	8.7	2	1.3	6	3.0
The Dalles Dam tailrace gate to The Dalles Dam	3	13.0	17	11.1	26	13.2
Entered Fifteenmile Cr.	0	0.0	5	3.3	1	0.5
The Dalles Dam to The Dalles Dam forebay	0	0.0	5	3.3	0	0.0
The Dalles Dam forebay to downstream of Miller Is.	0	0.0	1	0.7	1	0.5
Downstream of Miller Is. to upstream of Miller Is.	0	0.0	8	5.2	2	1.0
Entered Deschutes R.	--	--	4	2.6	23	11.7
Upstream of Miller Island to John Day Dam	0	0.0	10	6.5	11	5.6
John Day Dam to McNary Dam	1	4.3	10	6.5	17	8.6
Entered John Day R.	0	0.0	2	1.3	7	3.6
Upstream of McNary Dam	1	4.3	13	8.5	12	6.1

Table 10. Final distribution by reach of JSATS-tagged Pacific lamprey in the reservoir release groups, 2011-2014. Estimates include detections from the spring following tagging.

Reservoir release	**2011 (*n* = 62)**		**2012 (*n* = 146)**		**2013 (*n* = 203)**	
Reach	***n***	**%**	***n***	**%**	***n***	**%**
Fallback over Bonneville	0	0	3	2.1	7	3.4
Release to White Salmon R. gate	--	--	2	1.4	9	4.4
White Salmon River gate to Hood River gate	8	12.9	0	0.0	3	1.5
Entered White Salmon R.	--	--	1	0.7	0	0.0
Entered Hood R.	1	1.6	3	2.1	3	1.5
Hood R. gate to Lyle gate	1	1.6	0	0.0	10	4.9
Entered Klickitat R.	8	12.9	7	4.8	4	2.0
Lyle gate to The Dalles Dam tailrace gate	4	6.5	1	0.7	10	4.9
The Dalles Dam tailrace gate to The Dalles Dam	12	19.4	38	26.0	42	20.7
Entered Fifteenmile Cr.	2	3.2	8	5.5	1	0.5
The Dalles Dam to The Dalles Dam forebay	2	3.2	3	2.1	5	2.5
The Dalles Dam forebay to downstream of Miller Is.	--	--	0	0.0	3	1.5
Downstream of Miller Is. to upstream of Miller Is.	--	--	0	0.0	9	4.4
Entered Deschutes R.	--	--	11	7.5	39	19.2
Upstream of Miller Island to John Day Dam	--	--	20	13.7	11	5.4
John Day Dam to McNary Dam	20	32.3	32	21.9	20	9.9
Entered John Day R.	0	0.0	2	1.4	10	4.9
Upstream of McNary Dam	3	4.8	15	10.3	17	8.4

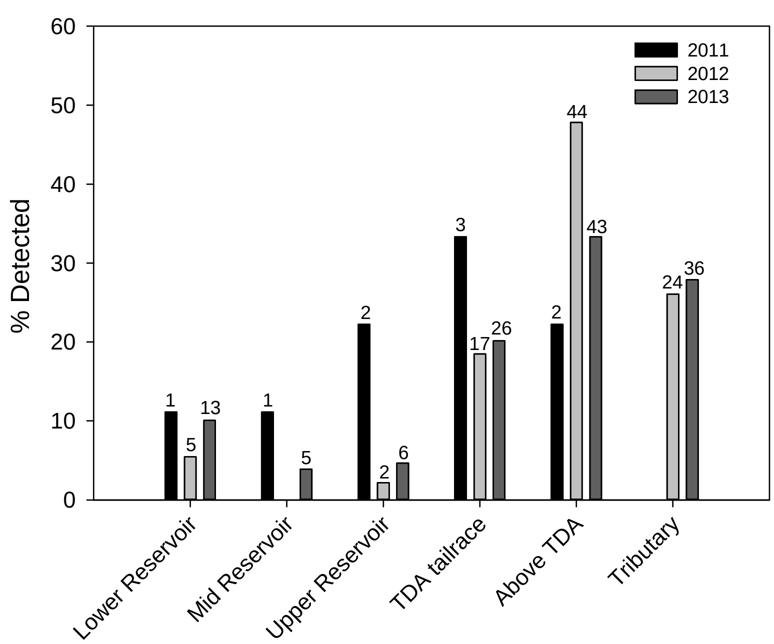

Figure 14. Final distribution of all tailrace-released JSATS-tagged Pacific lamprey that passed Bonneville Dam (i.e., excluding all fish last detected in the Bonneville Dam tailrace or on Bonneville Dam HD-PIT antennas but not passing), 2011-2014. Percentages are based on last detections, including detections from the spring following tagging. Sample sizes are shown above each bar.

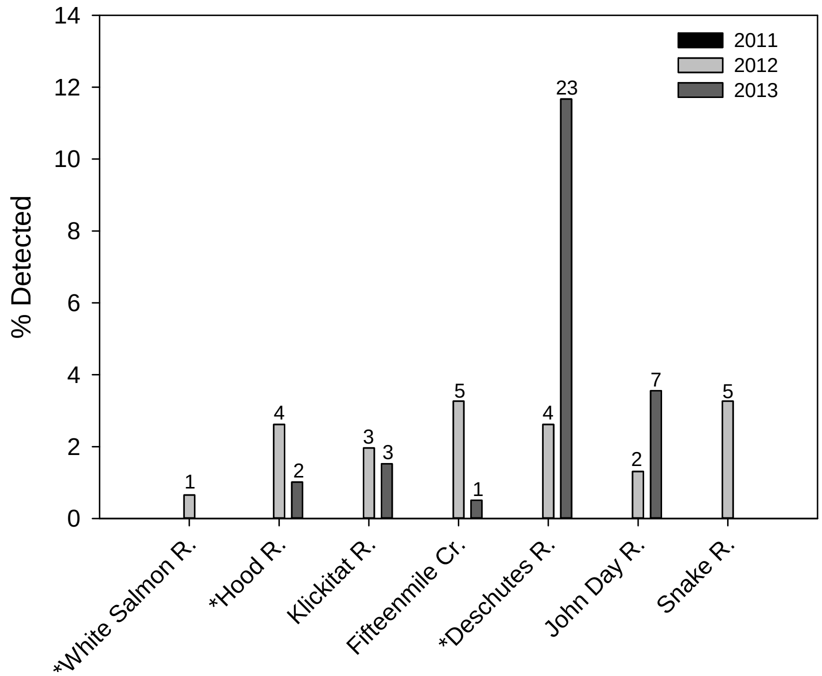

Figure 15. Tributary entry rates of all tailrace-released JSATS-tagged Pacific lamprey, 2011-2014. Percentages are based on last detections, including detections from the spring following tagging. Hood River and Fifteenmile Creek values from all study years include detections on HD-PIT antennas. Sample sizes are shown above each bar. *Deschutes River values include detections from HD-PIT antennas in 2013 only (the antenna installation year) and JSATS monitoring began in February of 2012.

Reservoir release groups – Final distributions of reservoir-released lamprey were also similar between years and paralleled results for tailrace-release lamprey that had passed Bonneville Dam. A majority (67.7-91.1%) was detected reaching The Dalles Dam tailrace and nearly half (39-49%) of reservoir-released lamprey passed The Dalles Dam by the fall of their tagging year (Figure 16A). When monitoring ended each year, 11-21% of lamprey was last detected entering a monitored tributary, and a small number (up to 2%) of fish was detected falling back over Bonneville (Figure 16A). A substantial portion of reservoir-released fish (31-48%) was last detected in the fall of their tagging year in Bonneville Reservoir with unknown final fates (Figure 16A) and many of these were recorded in The Dalles Dam tailrace. Monitoring in the year following tagging revealed that 3-8% of all reservoir-released fish entered monitored tributaries in the early spring and summer (Figure 16B), accounting for 4-17% of fish that were last detected the previous year in Bonneville Reservoir with unknown final fates (Figure 16B). In all years, about one quarter of reservoir-released lamprey was last detected in the upper reservoir or The Dalles Dam tailrace (Figure 17). Reservoir-released lamprey entered nearly every monitored tributary each year, with relatively larger numbers entering the Klickitat River in 2011 and the Deschutes River in 2013 (Figure 18).

JSATS monitoring in early spring found that some lamprey in both release groups were detected moving downstream and entering monitored tributaries after overwintering in dam tailraces. In particular, twenty JSATS-tagged lamprey that were last detected in the John Day Dam tailrace in the fall of 2013 (37% of all lamprey last recorded in John Day Dam tailrace in fall) were redetected in the spring of 2014 entering the Deschutes River in May and June (Figure 19).

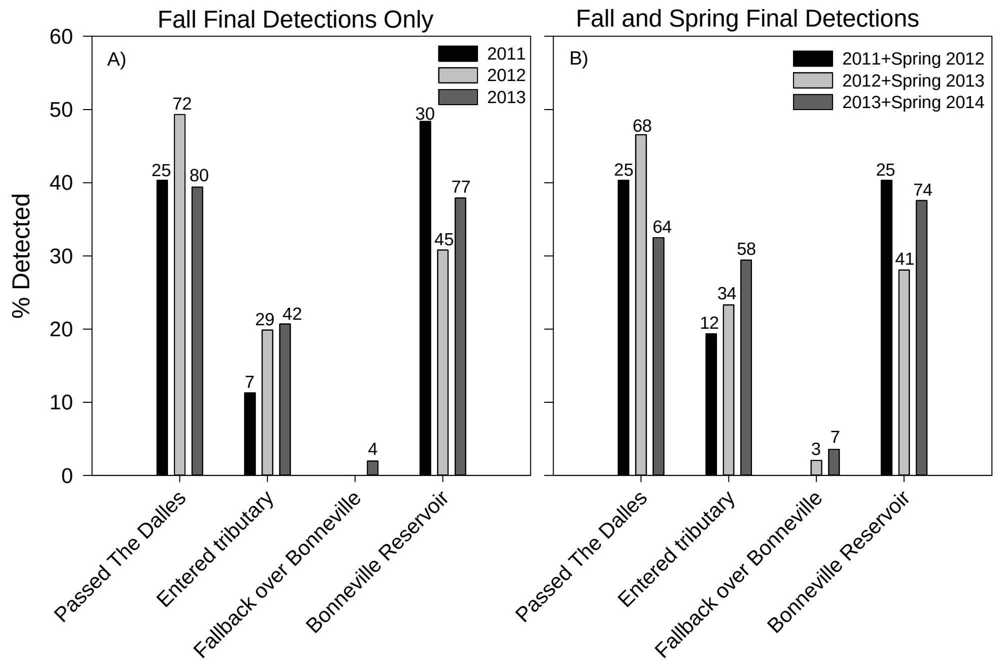

Figure 16. Final distribution of reservoir-released JSATS-tagged Pacific lamprey based on last detections in the fall of their tagging year only (A), and including detections from the spring following tagging (B), 2011-2014. Sample sizes are shown above each bar.

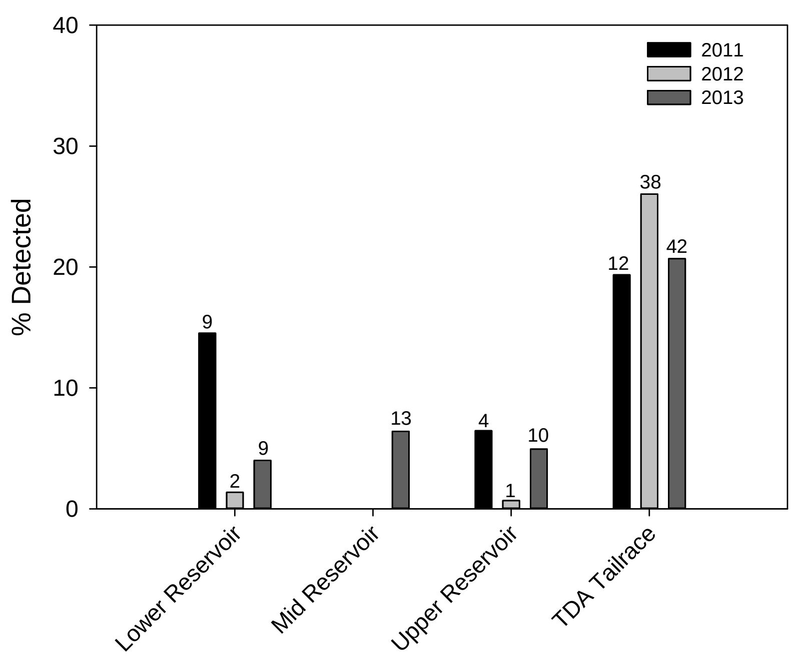

Figure 17. Final distribution of reservoir-released JSATS-tagged Pacific lamprey with unknown final fates in Bonneville Reservoir, 2011-2014. Percentages are based on last detections, including detections from the spring following tagging. Sample sizes are shown above each bar.

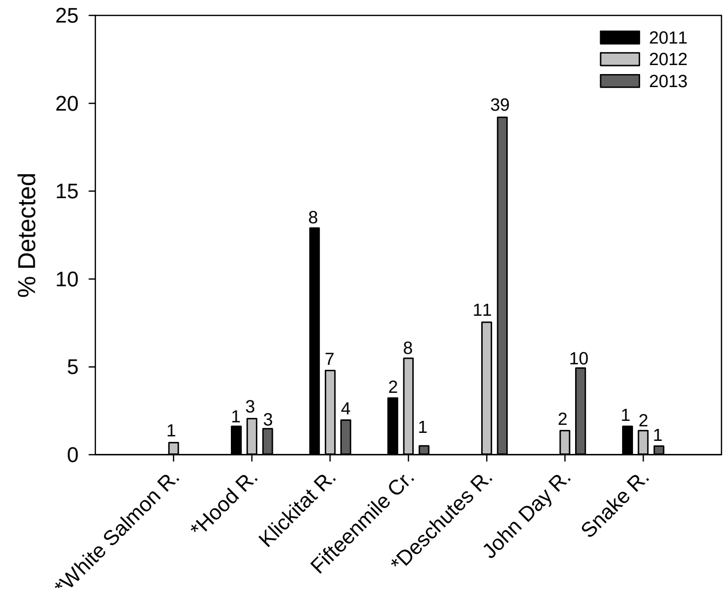

Figure 18. Tributary entry rates of all reservoir-released JSATS-tagged Pacific lamprey, 2011-2014. Percentages are based on last detections, including detections from the spring following tagging. Hood River and Fifteenmile Creek values from all study years include detections on HD-PIT antennas. Deschutes River values include detections from HD-PIT antennas in 2013 only. Sample sizes are shown above each bar. *JSATS monitoring began in February of 2012.

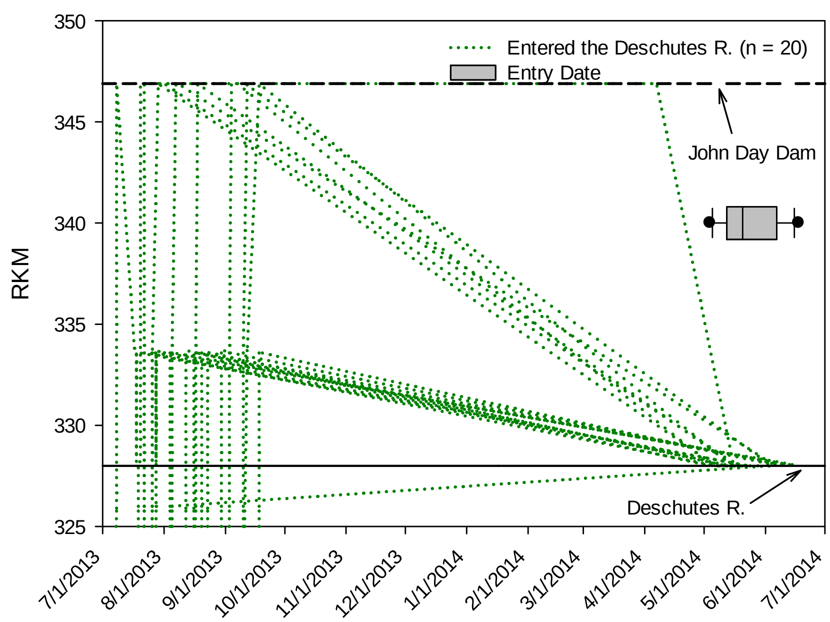

Figure 19. River kilometer as a function of time for 2013 JSATS-tagged lamprey that entered the Deschutes River after overwintering in the John Day Dam tailrace (green dotted lines). Box plot depicts date of entry into the Deschutes River. Box plot shows 5th, 25th, 50th, 75th and 95th percentiles.

Estimated Bonneville Reservoir tributary entry

The observed average tributary entry percentage over all study years was used to estimate potential entry of tagged lamprey into several unmonitored Bonneville Reservoir tributaries (Table 11). The four scenarios represent different assumptions about detection efficiency and possible tributary entry rates at unmonitored sites. The minimum scenario used observed rates during this study and observed rates from earlier radiotelemetry studies and estimated that ~12.6% of lamprey that entered Bonneville Reservoir eventually entered a Bonneville tributary. Three other scenarios based on percentages of JSATS-tagged fish that entered tributaries predicted 12.5%-40.5% of lamprey that entered the reservoir subsequently entered tributaries. Assuming ~55% of adults that entered the Bonneville Reservoir passed The Dalles Dam, the 'Low' scenario suggests ~13% entered tributaries and ~32% of lamprey that entered the reservoir remained unaccounted for. The 'Mid' scenario suggests that ~25% entered tributaries and ~20% remained unaccounted for in the Bonneville Reservoir. Applying the 'High' scenario to all unmonitored tributaries indicates all or nearly all lamprey that entered the reservoir subsequently entered Bonneville Reservoir tributaries, with no lamprey left unaccounted for. We note that this latter scenario is unlikely given observed spatial variation in relative tributary entry rates within each year.

Table 11. Observed and estimated average tributary entry rates into select Bonneville Reservoir tributaries of all JSATS-tagged lamprey released in or detected upstream from Bonneville Dam, 2011-2014, and observed entry rates of radio-tagged fish known to have passed Bonneville Dam in 2008 (Wind R.) and 2009 (Herman Cr.).

	Tributary	2011-2014 Average JSATS Rate	Low	Mid	High	JSATS Rate + 2008-09 Radiotelemetry Rate
Observed rate	Fifteenmile Cr.	2.9%	2.9%	2.9%	2.9%	2.9%
	Klickitat R.	5.9%	5.9%	5.9%	5.9%	5.9%
	Hood R.	1.9%	1.9%	1.9%	1.9%	1.9%
	White Salmon R.	0.3%	0.3%	0.3%	0.3%	0.3%
Hypothesized rate	Little White Salmon R.	--	0.3%	2.9%	5.9%	0%
	Wind R.	--	0.3%	2.9%	5.9%	0.6%
	Herman Cr.	--	0.3%	2.9%	5.9%	1.0%
	Rock Cr.	--	0.3%	2.9%	5.9%	0%
	Eagle Cr.	--	0.3%	2.9%	5.9%	0%
	Total	11.0%	12.5%	25.5%	40.5%	12.6%

The simulation model of tributary entry incorporating variation in tributary entry rate that used baseline radiotelemetry, HD-PIT and JSATS data indicated that ~13.3% of lamprey entered Bonneville tributaries, on average (Figure 20). The tributary estimates across iterations fell within in a fairly narrow range, with 9.9% for the 10th percentile and 17.1% for the 90th

percentile. On average, 53.9% of the fish passed The Dalles Dam in this model (10^{th} and 90^{th} percentiles = 40.9% and 70.4%, respectively). The unaccounted for lamprey were on average 31.6% of those entering Bonneville Reservoir (10^{th} = 16.7%, 90^{th} = 46.3%).

In the simulation that doubled the tributary entry rates (and standard deviations), mean model estimates were: 26.6% (10^{th} to 90^{th} percentile range = 20.2-33.8%) to Bonneville tributaries, 54.3% (40.2-68.0%) past The Dalles Dam, and 19.1% (3.7-35.5%) unaccounted for. The higher error (SD) values representing a combination of uncertainty and annual variation in true rates resulted in a broader distribution of possible tributary entry relative to the baseline estimates (Figure 20).

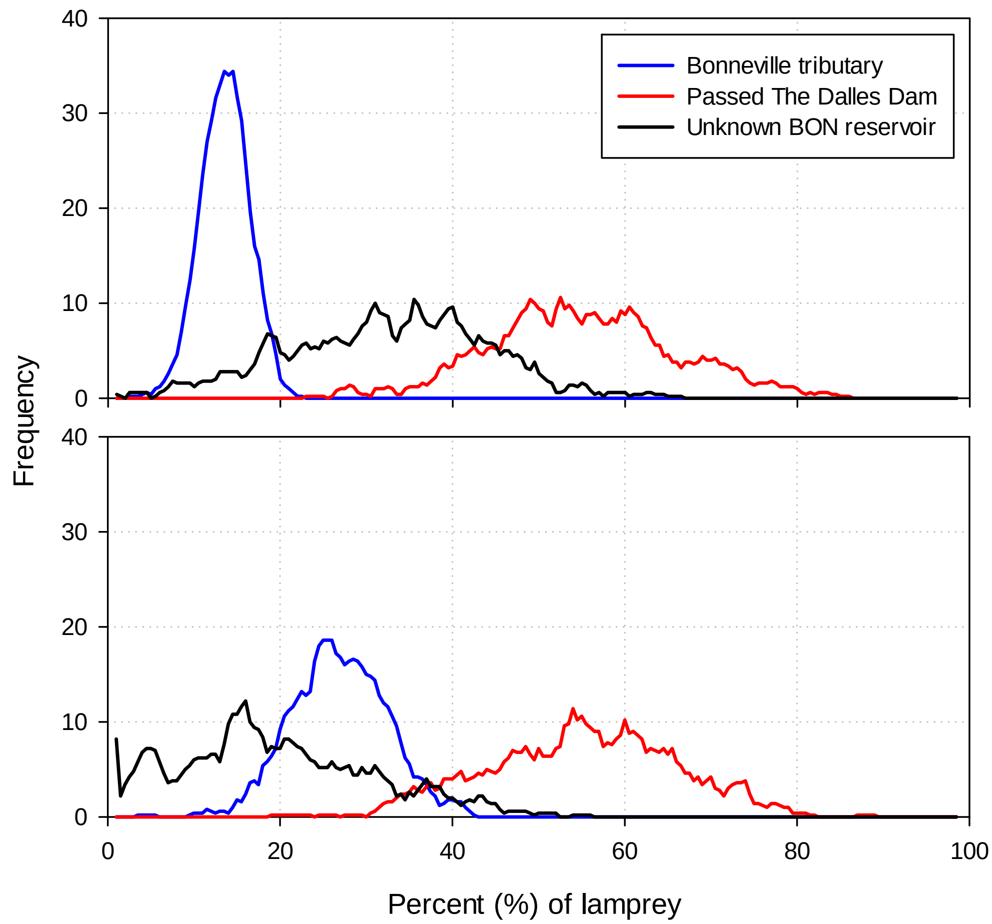

Figure 20. Results of simulation models estimating the annual percentage of adult Pacific lamprey that enter tributaries of Bonneville Reservoir (blue line), pass The Dalles Dam (red line), or have unknown fate (black line) using two scenarios. Top panel: results using the observed mean tributary rates and standard deviation = 0.5×mean. Bottom panel: results using mean = two times the observed tributary entry rate and standard deviation = 0.5×mean. The second simulation illustrates the potential of additional undetected movement into tributaries to affect fate composition. The models generated estimates in 500 simulation years each by drawing random annual rates from a distribution with a mean and standard deviation.

Discussion

Results of the JSATS telemetry studies differed little between years, with the exception of considerably lower dam passage rates by both release groups in 2011. Discharge at Bonneville and The Dalles Dams was substantially higher in 2011 and may have contributed to challenging passage conditions for lamprey. We found little evidence in any year of tagging effects associated with use of the JSATS transmitters over PIT tags alone. Escapement percentage of JSATS-tagged adults past the four Lower Columbia dams was not significantly different to those of PIT-tagged only fish. Most adults moved quickly through the Bonneville Reservoir, but migration rates were substantially lower while lamprey were passing dams. There was evidence of tributary entry by 4-16% of all adults tagged, and most lampreys with unaccounted for fates at the end of their tagging year were distributed in the upper Bonneville Reservoir and tailrace of The Dalles Dam, or in The Bonneville Dam tailrace. Detections of lamprey in the spring following their tagging year revealed that many unaccounted-for fish overwinter in dam tailraces or reservoirs before entering tributaries downstream of the overwintering site. In total, these data suggest that a substantial proportion of adults previously unaccounted for in the Bonneville Reservoir likely enter tributaries, though considerable uncertainty remains regarding the true proportion.

Travel times and migration rates

JSATS monitoring allowed us to calculate lamprey migration rates within the Bonneville Reservoir without the influence of dam passage time (a complicating factor for HD-PIT only samples) or tailrace times (past radiotelemetry studies). The majority of tagged lamprey migrated quickly through Bonneville Reservoir and entered The Dalles Dam tailrace. Within-reservoir travel times and migration rates varied greatly among individual lamprey, but were rapid compared to passage past dams. Median rates were similar (Stevenson - The Dalles Dam tailrace: *range* = 45.3 - 50.8 km/d) across all study years (Noyes et al. 2012, 2013, 2014). Linear regression results indicated little or no statistically significant correlation between lamprey migration rates and seasonal or environmental factors, or lamprey body size. This was in contrast to some previous studies, which found evidence of a relationship between migration rates and lamprey size – particularly when including the time that lamprey use to pass dams (e.g., Keefer et al. 2013) – as well as seasonal effects where lamprey migrate more rapidly as water temperature increases and river discharge decreases (e.g., Keefer et al. 2009b; Moser et al. 2013). The general lack of association between migration rate and body size or environmental factors may be related to lower sample size in the current study and /or the relatively low-velocity and low-turbulence conditions within the lower reservoir versus the more hydraulically complex environments in tailraces and fishways that may act as trait filters.

Final distribution and survival

Estimating the final distribution of lamprey with last records in FCRPS reservoirs was a primary biological objective of this study. The distribution patterns reported in previous telemetry studies were from detections on radio and HD-PIT antennas located at dams.

Tributary entry monitoring had been relatively limited, with some radiotelemetry sites (fall only) and just a few HD-PIT sites starting in ~2011-2013 (Keefer et al. 2012b, 2015) and indicated that relatively few moved into tributaries to Bonneville Reservoir in the fall or early winter (prior to the expiration of radio tag battery life; e.g., Moser et al. 2002; Keefer et al. 2010). Generally, of the tagged lamprey observed to successfully migrate past a given dam in past studies about half were not detected at upstream dams (e.g., Keefer et al. 2009a, 2009d).

A key finding of the JSATS studies is that the majority (82-92%) of adults that entered or were released to Bonneville Reservoir rapidly and successfully passed ~80% of the length of the reservoir and were detected at the Lyle gate, approximately 16 rkm downstream from The Dalles Dam. The high percentages of JSATS-tagged fish that reach the upper Bonneville Reservoir suggest that migration conditions and factors in the reservoir such as predation and prespawn mortality did not strongly contribute to the overall unaccounted-for fates in the Bonneville Reservoir during the summer and fall migration and decreases in dam counts between Bonneville and The Dalles dams. High detection rates near The Dalles Dam also suggest that few fish moved downstream after reaching the tailrace and then overwintered in the downstream two-thirds of Bonneville Reservoir.

Potential fates for the lamprey detected in the upper reservoir in fall include: 1) lamprey overwintered in The Dalles Dam tailrace and resumed upstream migration in the spring; 2) lamprey overwintered in The Dalles Dam tailrace and returned to downstream spawning tributaries in the spring; 3) lamprey spawned in The Dalles Dam tailrace in the spring; 4) adults with final records at Lyle and The Dalles Dam tailrace were prespawn or predation mortalities. This study and previous HD-PIT studies showed that a small percentage of the fish moved upstream past dams in the main stem in the spring following tagging (e.g., <3% of tagged sample; Keefer et al. 2012b). Early spring monitoring for lamprey that were JSATS-tagged the previous year also show that a small number of fish overwintered in dam tailraces before moving upstream or passing dams (e.g., n = 7, 2% of the 2012 tagged sample; Noyes et al. 2013). An emerging pattern revealed by JSATS and HD-PIT monitoring from the spring of 2014 was that more than three times as many fish (n = 25, 6.3% of 2013 tagged sample) were recorded overwintering in dam tailraces before moving *downstream* and entering tributaries. Specifically, these lampreys overwintered in the John Day and The Dalles tailraces before moving downstream and entering the Deschutes and Klickitat Rivers, respectively. The last two fate categories above, tailrace spawning and tailrace mortality, could not be distinguished with the current JSATS, radiotelemetry, and PIT capabilities. Advanced mobile-tracking technology, biotelemetry (e.g., accelerometers for detecting spawning activity), and/or underwater video may help to refine fates of lampreys last detected in dam tailraces.

A secondary goal of this study was to evaluate fate of lamprey not passing Bonneville Dam. Between 20-48% of tailrace-released lamprey remained unaccounted-for in the Bonneville Dam tailrace each year and a small number were last detected moving downstream out of the tailrace on our single downstream JSATS array. Detection efficiency could not be evaluated at this site and we suspect efficiency was relatively low. Dam operations and safety concerns made it difficult to monitor lamprey in the powerhouse channels and spillways of Bonneville and The Dalles Dams where many tagged lamprey were last detected. Modified JSATS receivers that could be deployed in shallow tributaries or from shore in noisy or hard to access areas (e.g., near fishways entrances or in Boat Restriction Zones in dam tailraces and forebays) could help refine the final fates and distributions of unaccounted for lamprey. Additionally, with the exception of the HD-PIT array at Willamette Falls on the Willamette River, there was no monitoring of the numerous tributaries downstream from Bonneville Dam. Sea lion predation on lamprey in the Bonneville Dam tailrace is well documented (Stansell et al. 2014), although not likely to account for a large portion of lampreys last detected in the Bonneville Dam tailrace because peak sea lion and lamprey passage periods do not overlap. Given the substantial number of lampreys that are observed entering downstream tributaries after overwintering in John Day and The Dalles Dam tailraces, it seems likely that similar behavior occurs downstream from Bonneville Dam, and warrants additional monitoring. JSATS monitoring would be effective for the mainstem Columbia and larger tributaries downstream of Bonneville Dam (e.g., Willamette River). Monitoring in smaller, known spawning tributaries such as Tanner Creek in the Bonneville Dam tailrace could be augmented with HD-PIT arrays. Expanded monitoring in the Willamette and lower Columbia River would also allow for comparison between lamprey behavior between more natural barriers (Willamette Falls) and constructed barriers (lower Columbia dams).

Estimated Bonneville Reservoir tributary entry

Tributary entry rates based on tag detections underestimate of the percentage of lamprey that enter tributaries after overwintering in the Columbia River main stem or in dam tailraces because some lamprey are not detected at monitored sites and because many potential spawning tributaries lack monitoring. The JSATS receiver configuration was not ideal for use in many of these tributaries due to insufficient water depth, high acoustic noise levels, and frequent encounters of monitoring gear with anglers and boaters. Consequently, many tributaries were unmonitored or only monitored at their mouths (e.g., the White Salmon River). As a result, tributary entry must be inferred based on final detections at tributary mouth receivers, or, for unmonitored tributaries, may be extrapolated based on detections at monitored tributaries. Thus, some portion of the unaccounted-for fish likely entered one of the many unmonitored tributaries to Bonneville Reservoir, which we evaluated using simple scenarios.

Direct telemetry records suggested that approximately 12-13% of adults that enter the Bonneville Reservoir eventually moved into Bonneville tributaries. Expansion to other unmonitored locations suggested that the total Bonneville tributary entry rate may be ~25% (Low scenario) to slightly over 50% ('Mid' scenario) of adults entering the reservoir. Applying the highest rates to all tributaries resulted in passage out of the reservoir into Bonneville Reservoir tributaries or over the The Dalles Dam by all adults – a scenario that was clearly unrealistic. Results from the simulation models indicated that ~13% of lamprey entered tributaries based on the baseline data. Doubling the tributary entry rates to better account for missed entries and unmonitored locations produced a mean tributary entry estimate of ~27%, or similar to the 'Mid' scenario. In combination, these estimation methods illustrate both the potential for tributary entry to account for some lamprey with unknown fate in the Bonneville Reservoir and highlight the need for additional monitoring in tributaries. Specifically, future efforts should attempt to resolve whether the group of lamprey with unaccounted-for fate, likely 20-40% of lamprey entering Bonneville Reservoir, represent primarily mortality or undetected spawning in tailraces and tributaries.

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