Technical Report 2013-3

ADULT PACIFIC LAMPREY MIGRATION IN THE LOWER COLUMBIA RIVER: 2012 HALF-DUPLEX PIT TAG STUDIES

A Report for Study Code ADS-P-00-8

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For

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

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Executive Summary

We tagged adult Pacific lamprey (*Entosphenus tridentatus*) collected at Bonneville Dam with half duplex (HD) passive integrated transponder (PIT) tags and monitored their passage and migration behaviors at Bonneville, The Dalles, John Day, McNary, Ice Harbor, Lower Monumental, Lower Granite, and Priest Rapids dams. Additional detection data from upper Columbia River dams and lower Columbia tributaries were provided by cooperating agencies. Our objectives were to calculate lamprey passage times through various river reaches, to estimate escapement past the monitored sites, and to evaluate potential correlation between lamprey migration and physiological and environmental factors. An additional objective in 2012 was to use the multi-year HD PIT-tag database to evaluate whether escapement rates past dams have changed through time.

In total, we HD PIT-tagged 899 lampreys in 2012: 823 were released downstream from Bonneville Dam near Hamilton Island, 25 were released upstream from Bonneville Dam near Stevenson, WA, and 50 were released directly into the Cascades Island lamprey passage structure (LPS). An additional 300 lampreys were double-tagged with HD-PIT tags and acoustic transmitters (JSATS); results from the JSATS sample are presented in a separate report.

The 2012 HD PIT sample was less proportional to the run than in previous years due to unexpectedly large run size and prioritization of JSATs tagging early in the migration. This sampling made it difficult to directly compare escapement results to previous estimates. With that caveat, the 2012 escapement from release below Bonneville Dam past the dam was 50% (recaptures treated as not passing) to 54% (recaptures treated as passing). These estimates were in the range of estimates from the 2005-2011 HD-PIT studies (41-58%). Escapement from the top of Bonneville Dam to the top The Dalles Dam (47%) was also similar to previous years, whereas escapement from the top of The Dalles Dam to the top of John Day Dam (86%) was higher than previous estimates. Large lampreys in the downstream release group were substantially more likely than small lampreys to pass through most dam-to-dam reaches. As in previous years, lampreys last detected at upriver sites were statistically larger than those last recorded closer to the release site, indicating that size-dependent effects on migration distance and final distribution were likely.

Increased cross-agency monitoring efforts improved our final accounting for tagged lamprey. A total of 52 (6%) of the downstream-released sample was last detected at dams in the upper Columbia River (Priest Rapids, Wanapum, Rock Island, Rocky Reach). Eleven (1%) were last detected at Snake River dams, and 22 (3%) were detected in tributaries to the Bonneville or The Dalles reservoirs (Hood River, Fifteenmile Creek, Deschutes River). We expect additional detections at many of these sites in spring 2013 as overwintering lampreys move to spawning areas.

Our multi-year (2006-2012) analyses indicated that there have been incremental increases in HD PIT-tagged lamprey escapement past dams. After statistically controlling for covariates including lamprey size, tag date, and river environment, lamprey escapement past two benchmark dams (Bonneville and John Day dams) has increased through time. This pattern may be associated with structural and operational improvements at the USACE dams, though we caution that the available time series is short and that it is difficult to prove causation in a non-experimental monitoring project.

Lamprey migration times were highly variable in 2012, as in all study years. The median passage time for the downstream-released fish was 11.3 days (< 1 $km \bullet d^{-1}$) from release to the top of Bonneville Dam. Some fish took more than two months to pass Bonneville Dam. Median times between top-of-ladder antennas were 4.7 days (16 $km \bullet d^{-1}$) between Bonneville and The Dalles dams, 3.3 days (12 $km \bullet d^{-1}$) between The Dalles and John Day dams, and 7.5 days (16 $km \bullet d^{-1}$) between John Day and McNary dams. Each of the reaches upstream from Bonneville Dam included one

reservoir and one dam. Lampreys generally migrated faster later in the summer through most reaches, coincident with increasing river temperatures and decreasing river discharge. Notably, slow lamprey passage times from release past Bonneville Dam were associated with reduced upriver escapement distance in our multi-year summary, a pattern that may be related to passage delay and/or the effects of initial fish condition.

Introduction

Pacific lamprey (*Entosphenus tridentatus*) is the largest lamprey species in the Columbia and Snake rivers. Pacific lampreys are anadromous, with parasitic adults spending 1-4 years in the ocean before returning to spawn in freshwater rivers (Beamish 1980; Close et al. 2002; Moser and Close 2003). Recent studies suggest that Pacific lamprey abundance has steadily declined in the Columbia River basin and in other regional rivers since the early 1960's (Kostow 2002; Clemens et al. 2010; USFWS 2010; Murauskas et al. 2013). Habitat loss, river impoundment, ocean conditions, ocean prey base, and water pollution have all likely contributed to the decline. Lampreys also have difficulty passing through Columbia and Snake River dam fishways designed for adult salmonids (Moser et al. 2002b; Johnson et al. 2009a, 2012a; Keefer et al. 2010a, 2011a, 2013).

Monitoring Columbia River basin lamprey populations has been a challenge. Lamprey counts at dam fish ladders have only been used as indicators of relative abundance and general run timing (e.g., Keefer et al. 2009b) because counts historically were collected during the day (most lamprey pass at night), and counting facilities were not designed to accurately enumerate lampreys (Moser et al. 2002a; Robinson and Bayer 2005; Clabough et al. 2012). Radiotelemetry was used in an intermittent series of studies from 1997-2010 to identify lamprey problem passage areas, evaluate structural and operational modifications to fishways (e.g., Clabough et al. 2011a; Johnson et al. 2012a), and estimate survival of adult Pacific lamprey in the basin (e.g., Moser et al. 2002b, 2005; Johnson et al. 2009a; Keefer et al. 2012, 2013a). Starting in 2005, half duplex (HD) passive integrated transponder (PIT) tag monitoring sites have been deployed at dams to monitor PIT-tagged adult lamprey. Like radio transmitters, PIT tags are uniquely identifiable, allowing individual fish monitoring. PIT tags are also relatively small and inexpensive and are not limited by battery life, a useful feature given that some adult lamprey overwinter in the Columbia River main stem (Daigle et al. 2008) and some lampreys are too small for radio transmitters. HD-PIT tags were selected for Pacific lamprey passage evaluations to avoid potential tag collisions with the full-duplex (FDX) PIT tags used to monitor salmonids in the basin and because HD-PIT tags have longer read ranges.

The objectives of the 2012 studies described in this report were to use HD-PIT systems to: (1) calculate adult lamprey passage rates past multiple dams and reservoirs; (2) estimate lamprey escapement past multiple dams, through individual dam-to-dam reaches, and into tributaries; (3) examine potential physiological and environmental correlates with upstream passage; and (4) examine year-to-year patterns in lamprey escapement. A more detailed evaluation of HD-PIT tagged lamprey use of lamprey passage systems (LPS) at Bonneville Dam is presented in a separate report (Corbett et al. *in prep*). Additionally, a parallel study of lamprey tagged with acoustic transmitters and monitored using the Juvenile Salmon Acoustic Telemetry System (i.e., JSATS) is described in Noyes et al. (*in review*).

Methods

Lamprey Collection and Tagging

Lampreys used in this study were collected at night in traps at Bonneville Dam (Columbia River kilometer [rkm] 235). Traps were located near the Adult Fish Facility (AFF). Additional fish were captured in a trap at the top of the Cascades Island LPS and using portable traps in auxiliary water supply (AWS) channels. In 2012, 899 lampreys were tagged with only half-duplex passive integrated transponder (HD-PIT) tags. Lampreys were unselectively PIT tagged (i.e., those that were tagged on any given day were a random sample of the fish that were collected the previous night). However, it was unknown whether lampreys collected inside Bonneville fishways were representative of the run at large. We have hypothesized that Pacific lamprey in the smallest adult size classes may be less likely to enter fishways; there is currently no way to test the degree to which the sampling inside the fishways was biased. Tagged lampreys were released downstream from Bonneville Dam near Hamilton Island at Columbia River rkm 232.5 (n = 823), into the Cascades Island LPS (n = 50), or near the Stevenson boat ramp (n = 25). An additional 300 fish were double-tagged with an HD-PIT tag and a JSATS acoustic transmitter (includes 1 mortality; see Noyes et al. *in review*).

Before tagging, all fish were anaesthetized using 60 ppm (3 mL×50 L^{-1}) eugenol, measured (length and girth to the nearest mm), and weighed (nearest g). HD-PIT fish were then outfitted with a uniquely-coded, glass-encapsulated HD-PIT tag (Texas Instruments, 4×32 mm, 0.8 g). HD-PIT tags were surgically implanted in the body cavity of anaesthetized fish through a small incision (< 1 cm) along the ventral midline and in line with the anterior insertion of the first dorsal fin as described in Moser et al. (2006). An additional physiological measure, muscle lipid content (% lipid), was collected for most lampreys using a Distell fat meter (e.g., Crossin and Hinch 2005). Fat meter readings from 2012 were converted to estimated % lipid (wet weight basis) using the regression equation 'percent lipid' = (3.618 × reading) – 2.436 ($P < 0.01$; $r^2 = 0.48$; $n = 33$). The regression equation was developed by comparing Fatmeter readings taken in 2008 on live lamprey captured at Bonneville (n = 20) and McNary (n = 13) dams to lipid levels determined by biochemical proximate analysis on the same individuals following euthanasia (B. Ho, unpublished data). The 2008 proximate analysis was performed by the Wildlife Habitat Nutrition Laboratory, Washington State University, Pullman, Washington. Collection and tagging protocols were reviewed and approved by the University of Idaho Institutional Animal Care and Use Committee.

Monitoring Sites

Lamprey movements were monitored using an array of HD-PIT interrogation sites (Table 1). Underwater HD-PIT antennas were located inside dam fishways at the four lower Columbia River dams, at Priest Rapids Dam on the upper Columbia River, and at Ice Harbor, Lower Monumental and Lower Granite dams on the lower Snake River. Antennas were located near top-of-ladder exits at all dams. At Bonneville Dam, additional sites were located at lamprey passage structures (LPS), inside the Washington-shore and Cascades Island fishway entrances, and in the flow-control section of the Cascades Island fishway. Antennas were also located near transition pools and/or the overflow weir portions of ladders at McNary and Ice Harbor dams and below the south (east) top-of-ladder site at The Dalles Dam (Table 1). Additional antennas were maintained at upper Columbia River dams by the Chelan and Grant County PUDs and by the Confederated Tribes of Warm Spring of Oregon (CTWSRO) in several lower Columbia River tributaries.

Data Analyses

Reach escapement rates were calculated by dividing the number of lamprey known to pass an upstream HD site by those known to pass a site downstream or by the number released. Fish were treated as having passed a site if they were detected at the site or at a location further upstream. Escapement rates were calculated across all release dates. Lamprey sizes (length, weight, and girth) were compared for groups that passed through a reach and those that did not using generalized linear models (PROC GLM, SAS) and analysis of variance. As a result of additional trapping effort, including at the Cascades Island LPS which did not have a volitional exit to the Bonneville forebay, the Cascades Island AWS, and the AFF, 75 lampreys were recaptured and these fish were transported to Stevenson, WA and released. Recaptured fish were excluded from escapement and passage time analyses where appropriate.

Table 1. Half-duplex PIT tag interrogation sites (antennas) used by UI/NMFS to monitor lamprey passage at lower Columbia and Snake river dams in 2012. Note: additional HD monitoring sites were operated at Priest Rapids, Wanapum, Rock Island, and Rocky Reach dams (Public Utility Districts) and in Hood River, Fifteenmile Creek, Warm Springs River, and Shitike Creek (CTWSRO). See Appendix B for maps showing antenna sites.

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

[1] did not operate in 2012

Lamprey migration times (d) and passage rates (km•d^{-1}) were calculated from release to top-of-ladder HD-PIT antennas at dams and between monitored sites. Linear regression was used to evaluate relationships between log_{10}-transformed lamprey passage times and the following: length, girth, weight, release date or date fish entered upstream reaches, river discharge, and water temperature either on the release date or the date each fish passed top-of-ladder sites at dams. Analyses using environmental data should be considered conservative as environmental conditions were constantly changing during the passage periods and the temporal variance may have obscured associations between behavior and environmental factors (Caudill et al. 2007).

Detection efficiencies for HD-PIT sites were estimated by dividing the number of fish detected at a site by the number that was detected upstream from that site. (Note: this method differs from some previous years, when double-tagged [radio and HD-PIT] fish were used to estimate efficiencies.) These estimates were conservative because fish could pass via unmonitored routes at many locations (e.g., navigation locks or alternate routes in and adjacent to fishways) and thus represent minimum estimates of detection efficiency in most cases.

To assess year-to-year patterns in lamprey escapement we used a series of multiple logistic regression models. These models included terms for lamprey size or release date to better account for year-to-year changes in sampling effort and known lamprey size effects on migration distance and dam passage success (e.g., Keefer et al. 2009c, 2012, 2013a). The multi-year dataset included all lampreys with only HD PIT tags that were released downstream from Bonneville Dam in 2006-2010 and 2011-2012 (n = 5,355). Dependent variables were escapement past Bonneville Dam and past John Day Dam, the two projects with the most consistent monitoring and relatively high detection efficiency. Covariates included lamprey size metrics (length, weight), release date, and Columbia River water temperature and river discharge on the release date. The basic hypothesis we addressed with this analysis was that escapement past dams has increased over time, potentially in response to operational and structural improvements at the USACE projects. This was a non-experimental, correlative analysis rather than an evaluation of causation. We also used logistic regression to evaluate the relationship between lamprey passage time at Bonneville Dam and escapement past upstream dams to address the hypothesis that longer dam passage time results in reduced upriver escapement.

Results

Lamprey Collection and Tagging

The approximate total adult lamprey count at Bonneville Dam in 2012 was 93,462 (daytime count station = 29,230; night video count = 49,647; LPS count = 10,372; collected and released upstream = 4,213). This total was higher than in 2008-2011, but still well below historic counts. A total of 899 lampreys were HD-PIT-tagged, or approximately 1.0% of the total estimated count of adult lampreys at Bonneville Dam (Figure 1). The tagged sample included 823 lampreys released downstream from Bonneville Dam, 25 released upstream from the dam near Stevenson, WA, and 50 released directly into the Cascades Island LPS (Figure 1). These three groups were analyzed separately for most of the summaries provided below. Sampling was generally less proportional to daily counts than in previous years. Reasons included prioritizing JSATS-tagging in the month of June, handling restrictions during a warm-water period in mid-August, and higher than average lamprey passage in September after tagging ended.

Lamprey size metrics and lipid content were positively correlated in the combined 2012 HD-PIT sample (Figure 2). Percent lipid was more variable than the other metrics, perhaps in part because of the relatively weak relationship (r^2 = 0.48) between Fatmeter estimates and true lipid content (as measured by proximate analysis in 2008; see Methods). For example, the coefficient of variation (CV) for mean %lipid was 35% versus 20% for weight, 7% for girth, and 6% for length for the total sample (Table 2). In general, release date was weakly, and negatively correlated with lamprey length, girth, weight, and %lipid ($-0.29 < r < -0.20$, $P \leq 0.05$).

Detection Efficiency

Downstream Release Group – Efficiencies described in this section were based on HD-PIT data only (i.e., no records from double-tagged fish; see Noyes et al. (*in review*) for additional details derived from lampreys double-tagged with HD-PIT tags and acoustic transmitters).

A total of 308 lampreys were detected at antennas upstream from Bonneville Dam. Of these, 238 (77.3%) were detected at one or more Bonneville HD antennas and 188 (61.0%) were detected at top-of-ladder or top-of-LPS antennas. Another 17 fish (5.6%) were recaptured at Bonneville Dam and released upstream, leaving 103 that passed the dam without a top-of-ladder or top-of-LPS detection record. Of the 103 fish that passed Bonneville Dam without detection at an exit site, 25 (25%) were last recorded at Bonneville Dam on an antenna inside the Washington-shore fishway, 12 (12%) were in the flow-control section of the Cascades Island fishway, 2 (2%) were at the opening to the Cascades Island fishway, and 64 (62%) were not detected at any site.

A total of 192 lampreys were detected at antennas upstream from The Dalles Dam. Of these, 148 (77.1%) were detected at one or more antennas at The Dalles Dam. We did not estimate efficiency for the top-of-ladder antennas separately because the antenna at the top of the east ladder was not operated in 2012. Eighty lampreys were detected upstream from John Day Dam, all of which (100.0%) were detected at the top-of-ladder antennas at John Day Dam.

Sixty-three lampreys were detected at sites upstream from McNary Dam, of which 54 (85.7%) were detected at one or more McNary antennas and 30 (47.6%) were detected at McNary top-of-ladder antennas. Of the 33 that passed top-of-ladder sites undetected, 18 (55%) were last detected at antennas inside the south fishway, 6 (18%) were last detected on antennas inside the north fishway, and 9 (27%) were not detected at any McNary site.

Sample sizes at the Snake River dams were small (≤ 11) and there were limited upstream detection sites. Five lampreys were detected upstream from Ice Harbor Dam, of which 5 (100%) were detected at an Ice Harbor antenna; 2 of the 5 (40.0%) were detected at top-of-ladder antennas. Two lampreys were detected at Lower Granite Dam, both of which were detected at Lower Monumental Dam (100%). No estimate was calculated for the Lower Granite antenna site.

A total of 26 lampreys were detected at either University of Idaho or PUD antennas at Wanapum Dam, all of which (100%) were detected at Priest Rapids antennas. We did not estimate efficiency for the Wanapum, Rock Island, or Rocky Reach antenna arrays.

Upstream Release Group – Antenna detection efficiency at combined HD antennas at The Dalles Dam was 100% (7 lampreys were detected at The Dalles of 7 detected at upriver locations). The single fish detected upstream from John Day Dam was detected at John Day Dam top-of-ladder antennas (efficiency = 100%).

Cascades Island Release Group – Antenna detection efficiency at combined HD antennas at The Dalles Dam was 62.5% (10 lampreys were detected at The Dalles of 16 detected at upriver locations). All 7 fish detected upstream from John Day Dam were detected at John Day Dam top-of-ladder antennas (efficiency = 100%). Five lampreys were detected upstream from McNary Dam and 3 (60%) were detected at McNary top-of-ladder antennas (efficiency = 60%).

Downstream Release Group

Upstream Progression – Of the 823 lampreys released downstream from Bonneville Dam, 535 (65.0%) were subsequently recorded at one or more Bonneville Dam HD antennas inside fishways, at LPS systems, or at dams further upstream (Table 3). A total of 414 fish passed Bonneville Dam (50.3% of the 823 released, and 77.4% of the 535 detected at one or more sites after release). Importantly, another 33 (4.0%) were recaptured in traps at Bonneville Dam and were released upstream; this recapture rate was higher than in previous years due to additional trapping effort.

The median tag date for HD-PIT tagged lampreys released downstream was 18 July (*mean* = 13 July). Median recorded passage dates at top-of-ladder sites were 29 July at Bonneville Dam (n = 309), 11 August at The Dalles Dam (n = 40), 11 August at John Day Dam (n = 177), 16 August at McNary Dam (n = 36), 7 September at Priest Rapids Dam (n = 33), 8 September at Wanapum Dam (n = 14), 9 September at Rock Island Dam (n = 11), and 5 September at Rocky Reach Dam (n = 3). In the Snake River, median passage dates were 9 September at Ice Harbor Dam (n =6), 31 July at Lower Monumental Dam (n = 5), and 8 August at Lower Granite Dam (n = 2). Additional fish passed each dam without detection at top-of-ladder (or LPS) antennas (i.e., passage date was uncertain). Top-of-ladder dates of detection for the HD-PIT tagged fish indicated underrepresentation early in the run at Bonneville Dam (Figure 3) and this carried over into the distributions at dams further upstream (Figures 3 and 4). We note that tagged-fish sample sizes at all dams upstream from John Day Dam were small.

Dam-to-Dam Escapement – Of 823 fish released, 54.3% (n = 447) were known to have passed Bonneville Dam (including the 33 that were recaptured and released upstream), 25.8% (n = 212) passed The Dalles Dam, 21.5% (n = 177) passed John Day Dam, 8.4% (n = 69) passed McNary Dam, 4.1% (n = 34) passed Priest Rapids Dam, 2.4% (n = 20) passed Wanapum Dam, 1.2% passed Rock Island Dam, and 0.5% (n = 4) passed Rocky Reach Dam (Tables 3 and 4). A total of 1.1% (n = 9) passed Ice Harbor Dam, 0.6% (n = 5) passed Lower Monumental Dam, and 0.2% (n = 2) passed Lower Granite Dam. Escapement from the top of Bonneville Dam was 47.4% to the top of The Dalles Dam, 39.8% to the top of John Day Dam, and 15.5% to the top of McNary Dam. Escapements were 83.4% between ladder tops at The Dalles and John Day dams and 39.0% between ladder tops at John Day and McNary dams. Of 69 lampreys that passed McNary Dam, 11 (13.0%) passed Ice Harbor Dam and 34 (49.3%) passed Priest Rapids Dam (Tables 3 and 4).

Lamprey that passed upstream sites were larger ($P < 0.05$) than those that did not pass, with the exception of the The Dalles-John Day reach (Table 5). This relationship between size metrics and reach escapement was the same whether recaptured fish were included or excluded. Escapement through a reach was not associated with the date that lampreys were released downstream from Bonneville Dam. Lampreys that passed The Dalles Dam encountered slightly higher water temperature, on average, than those that did not (Table 6). On average, those that passed McNary Dam had passed John Day Dam about a week earlier and encountered higher discharge than those that did not pass McNary Dam. Note that many lampreys passed The Dalles Dam without being detected on the most upstream antenna, reducing the statistical power of these tests.

Passage Times and Rates – Median HD-PIT tagged lamprey passage times were 11.3 d from the release site to the top of Bonneville Dam, 4.7 d between Bonneville and The Dalles dams, 3.3 d between The Dalles and John Day dams, and 7.5 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 7). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 15.6 km•d^{-1} (Bonneville-The Dalles), 11.9 km•d^{-1} (The Dalles-John Day), and 16.4 km•d^{-1} (John Day-McNary). Above McNary Dam, median passage times were 10.5 d (16.2 km•d^{-1}) between McNary and Priest Rapids dams, 14.7 d (4.6 km•d^{-1}) between McNary and Ice Harbor dams, 6.8 d (4.4 km•d^{-1}) between Priest Rapids and Wanapum dams, 16.4 d (4.4 km•d^{-1}) between Wanapum and Rock Island dams, and 3.2 d (10.3 km•d^{-1}) between Rock Island and Rocky Reach dams. Median times between Ice Harbor and Lower Monumental and between Lower Monumental and Lower Granite dams were 7-8 d (6.4-15.2 km•d^{-1}) between Ice Harbor and Lower Monumental dams; note very small sample sizes at some upstream locations (Table 7).

Lamprey migration times were generally not correlated with fish size metrics ($P > 0.05$ in most tests, Table 8). Seasonal associations with lamprey migration times were evident in more reaches, with faster passage as water temperature and date increased and discharge decreased (Table 8). Overall, associations were moderate to weak, and individual predictor variables generally explained less than half of the variability in lamprey passage times through individual reaches.

Diel Passage – Lamprey passage distributions at top-of-ladder sites clearly showed that most dam passage occurred at night (Figure 5). This pattern was consistent across the four lower Columbia River dams, and at dams in the lower Snake River and upper Columbia River. The majority of passage events were between sunset and sunrise, though some fish passed during almost all hours at the lower river dams. There was also a tendency for more passage during early daylight hours, perhaps as fish that entered fishways at night continued to move upstream.

Last Detection Summary – A total of 288 (35.0%) of the 823 lampreys released near Hamilton Island were not subsequently detected (Table 9). Another 42 (5.1%) were last recorded at HD antennas inside Bonneville Dam fishways and 184 (22.4%) were at top-of-ladder exit sites or LPS sites. Fourteen fish (1.7%) were last recorded in Fifteenmile Creek or its tributaries and a single fish was recorded in the Hood River, though the Hood River antenna monitored only a portion of the season. A total of 102 (12.4%) were last detected at The Dalles Dam, and 7 (0.9%) were recorded in the Deschutes River. Above the Deschutes River, 106 (12.9%) were at John Day Dam, 17 (2.1%) were at McNary Dam, 11 (1.3%) were at Snake River dams, and 52 (6.3%) were at dams in the upper Columbia River (Priest Rapids through Rocky Reach dams) (Table 9).

When lampreys were grouped based on final recorded location, median release dates varied only slightly among groups with adequate sample size (Figure 6). Exceptions included fish last recorded in Bonneville tributaries (Hood River and Fifteenmile Creek) and in the Deschutes River, which were tagged earlier, on average, than the other groups. In contrast, there were clear among-group differences in lamprey size (Figure 7). On median, lampreys were largest in the Snake River (504 g) and upper Columbia River (496 g) groups. Lampreys were smallest in the groups last recorded in Bonneville tributaries (*median* = 408 g) and at the release site (*median* = 426 g).

Upstream Release Group

The 25 HD-PIT tagged lampreys released near Stevenson, WA were not tagged in proportion to the run (Figure 1). This subsample was collected from 24 August to 6 September (*mean* = 30 August). Mean size metrics for the upstream release group were lower than those for the downstream release group at the time of release (Table 2), reflecting the later collection dates. Top-of-ladder detections at The Dalles and John Day dams were also concentrated in the later portion of the run at these sites, reflecting the relatively late collection dates (Figure 3).

Dam-to-Dam Escapement – Of 25 fish released, 28.0% (*n* = 7) were known to have passed The Dalles Dam and 28.0% (*n* = 7) passed John Day Dam (Tables 3 and 4). None were detected passing McNary Dam. Escapement from the top of The Dalles Dam to the top of John Day Dam was 100.0%. As with the downstream release group, there was a tendency among upstream-released lampreys for higher reach escapement for larger fish. For example, the mean length of lampreys that passed The Dalles and John Day dams was 65.2 cm (*n* = 7) versus 63.2 cm (*n* = 18) for those that did not pass The Dalles Dam. We did not make statistical comparisons given the small sample size.

Passage Times and Rates – Six of the seven lampreys that passed The Dalles Dam were not detected at top-of-ladder antennas due to outages. The median passage time for the seven fish from the Stevenson release site to the top of John Day Dam was 16.4 d (*range* = 6.0-30.0 d). The median passage rate for this group was 6.4 $km \bullet d^{-1}$. Migration times for this small sample were positively correlated with release date (i.e., early-released fish migrated faster).

Last Detection Summary – Eleven (44.0%) of the 25 lampreys released near Stevenson were not detected after release (Table 9). Final detections at upstream sites included 7 (28%) at The Dalles Dam, 6 (24%) at John Day Dam, and 1 (4%) at McNary Dam.

Cascades Island Release Group

Fifty HD PIT-tagged lampreys were experimentally released into the lower Cascades Island LPS in 2012. Releases occurred on 14 dates from 31 July to 8 August and from 24 August to 6 September (Figure 1). On average, these lampreys, collected from the Cascades Island LPS rather than AFF traps, were slightly smaller than those in the downstream release group and slightly larger than those in the Stevenson release group (Table 2).

Forty-one of these fish were eventually recaptured in the LPS collection trap and were released upstream. Four were recorded passing Bonneville Dam via other routes (fishways or a different LPS). Another two were detected at sites upstream from Bonneville Dam, without definitive passage route records at Bonneville. Three fish did not pass Bonneville Dam, were not recaptured in the LPS, and were not detected elsewhere.

Final detections for the 50 fish were: 3 (6%) in the Cascades Island LPS, 18 (36%) at the release site upstream from Bonneville Dam after recapture in the LPS (i.e., never detected after transport), 1 (2%) at the top of the WA-shore ladder, 1 each (2%) in Fifteenmile Creek and Hood River, 9 (18%) inside The Dalles fishways, 1 (2%) in the Deschutes River basin, 9 (18%) at John Day Dam, 2 each (4%) at Priest Rapids and Wanapum dams, and 1 each (2%) at McNary, Lower Monumental, and Rocky Reach dams (Table 9). As with the Stevenson release group, relatively late collection dates, small sample size, and the high recapture and transport rates precluded direct comparisons with the downstream release group.

Detection of Lampreys Tagged in 2011

A total of 37 (3.6%) of the 1,014 lampreys tagged in 2011 were detected on HD antennas in 2012. These included 31 (3.9%) of the 800 HD-only fish released downstream from Bonneville Dam, 3 (2.8%) of the 109 HD-only fish released near Stevenson, WA, 2 (10.0%) of 20 released into the Cascades Island LPS, and 1 (1.2%) of 85 double-tagged (JSATS + HD PIT) fish released. The median 2011 release date for the 37 overwintering fish was 27 July (*range* = 1 July to 3 September). Final recorded locations included: 19 (51%) in Fifteenmile Creek, 11 (30%) at Bonneville Dam, 2 (5%) each at The Dalles and Priest Rapids dams, and 1 (3%) each in the Hood River, the Warm Springs River, and Wanapum Dam. Those last recorded in Fifteenmile Creek were first detected on the instream array there from 15 to 25 May. Those last recorded at Bonneville Dam were detected throughout the late spring and summer (*range* 26 April to 12 August). The 2012 detection dates for the remaining groups ranged from 26 May to 31 July.

Year-to-Year Patterns in Lamprey Escapement

Escapement Past Bonneville Dam – A total of 5,355 HD PIT-tagged lampreys were released downstream from Bonneville Dam in 2006-2009 and 2011-2012 (Figure 8). Mean lamprey size varied relatively little among years (*mean* length = 64.7 to 66.9 cm; *mean* weight = 434 to 482 g). Mean release dates varied among years by more than 20 days, primarily because lamprey run timing differed among years, but also due to temperature-related handling restrictions. River environment on lamprey release dates also differed considerably among years, with the lowest and highest mean discharge recorded in 2007 (200 kcfs) and 2012 (314 kcfs), respectively. Mean release date temperatures ranged from 17.4 °C in 2009 to 19.0 °C in 2007 (Figure 8).

Annual estimates of escapement past Bonneville Dam ranged from 0.41 in 2006 to 0.58 in 2011 (Table 11). Lamprey size was a strong predictor of escapement past Bonneville Dam. With all years combined, a 1 cm increase in lamprey length was associated with approximately a 6.3% (95% ci = 5.0-7.6%) increased probability of escapement (logistic model, $\chi^2 = 98.9$, $P < 0.001$). Results were similar for lamprey weight and girth. Release date alone and water temperature alone were not significant ($P > 0.10$) predictors of escapement past Bonneville, whereas escapement increased as river discharge increased ($\chi^2 = 13.0$, $P < 0.001$) in the univariate model. In a model that included lamprey length, release date, river discharge and water temperature, all but temperature were influential: length $\chi^2 = 105.2$, $P < 0.001$; date $\chi^2 = 18.0$, $P < 0.001$; discharge $\chi^2 = 8.7$, $P = 0.003$; temperature $\chi^2 = 1.7$, $P = 0.199$. Note that release date and water temperature were correlated within year.

The logistic regression analysis indicated that lamprey escapement past Bonneville Dam increased over the course of the study (Figure 9). Predicted escapement estimates generated from annual models where lamprey length was held constant at the 10th, 50th, and 90th percentiles of the multi-year size distribution showed increasing escapement through time of approximately 2% per year (linear regression slope ranged from 0.020 to 0.022; $0.29 \leq r^2 \leq 0.75$). Similarly, when the annual models included both lamprey length and release date, predicted escapement estimates increased over the course of the study when lamprey length was held constant at the median value (66 cm) and release date was held constant at the 10th, 50th, and 90th percentiles of the multi-year size distribution. Linear regression slope in this analysis ranged from 0.019-0.029 ($0.23 \leq r^2 \leq 0.52$). Patterns were similar when river discharge ($0.36 \leq r^2 \leq 0.63$) or water temperature ($0.25 \leq r^2 \leq 0.56$) were substituted for release date.

Escapement Past John Day Dam – Annual estimates of escapement from release below Bonneville Dam past John Day Dam ranged from 0.14 in 2009 to 0.24 in 2011 (Table 12). Lamprey size had a stronger effect on escapement probability over the release-John Day reach than for release past Bonneville. With all years combined, a 1 cm increase in lamprey length was associated with approximately a 14.9% (95% ci = 13.0-16.8%) increased probability of escapement past John Day Dam (logistic model, $\chi^2 = 271.7$, $P < 0.001$). Results were similar for lamprey weight and girth. Release date alone and water temperature alone were not significant ($P > 0.10$) predictors, whereas escapement increased as river discharge increased ($\chi^2 = 7.6$, $P = 0.006$). In the model with all covariates, all but temperature were influential: length $\chi^2 = 281.8$, $P < 0.001$; date $\chi^2 = 9.0$, $P = 0.003$; discharge $\chi^2 = 8.2$, $P = 0.004$; temperature $\chi^2 = 0.0$, $P = 0.943$.

The multiple logistic regression analysis consistently indicated that escapement past John Day Dam has increased over the study (Figure 10). Escapement estimates generated from annual models where lamprey length was held constant showed increasing escapement through time of approximately 1% per year (slope ranged from 0.009 to 0.016; $0.34 \leq r^2 \leq 0.42$). Slopes were all positive when the models included lamprey length and release date, lamprey length and river discharge, and lamprey length and river temperature (Figure 10).

Relationship between Bonneville Passage Time and Upriver Escapement – The most extensive HD PIT monitoring effort – including lower Columbia tributary sites, the Snake River dams, and the upper Columbia River dams – occurred in 2011-2012. We used data from these two years to evaluate the relationship between lamprey passage time at Bonneville Dam and escapement past John Day and McNary dams for lamprey recorded passing Bonneville Dam (Figure 11). The models included lamprey length and passage time from release to exit into the Bonneville forebay.

Escapement probability past John Day Dam increased with lamprey size ($\chi^2 = 41.6$, $P < 0.001$) and decreased with passage time at Bonneville Dam ($\chi^2 = 13.0$, $P < 0.001$). Each additional day of passage time was associated with a 1.8% (95% ci = 0.8-2.7%) decrease in escapement, whereas each 1 cm increase in lamprey length was associated with a 17.0% (95% ci = 11.6-22.8%) increase in escapement probability. The probability of John Day passage for a 66 cm lamprey ranged from 42% for a fish that passed Bonneville Dam in ~1 d versus 17% for a fish that passed in 70 d (Figure 11).

The relationships were similar in the model of escapement probability past McNary Dam. Escapement increased with lamprey size ($\chi^2 = 11.8$, $P < 0.001$) and decreased with Bonneville passage time ($\chi^2 = 4.2$, $P = 0.040$). Each additional day of passage time was associated with a 1.5% (95% ci = 0.1-2.9%) decrease in escapement, whereas each 1 cm increase in lamprey length was associated with an 11.6% (95% ci = 4.8-18.9%) increase in escapement probability. The probability of McNary passage for a 66 cm lamprey was approximately 2.4 times higher for those with the fastest Bonneville passage times versus the slowest migrants (Figure 11).

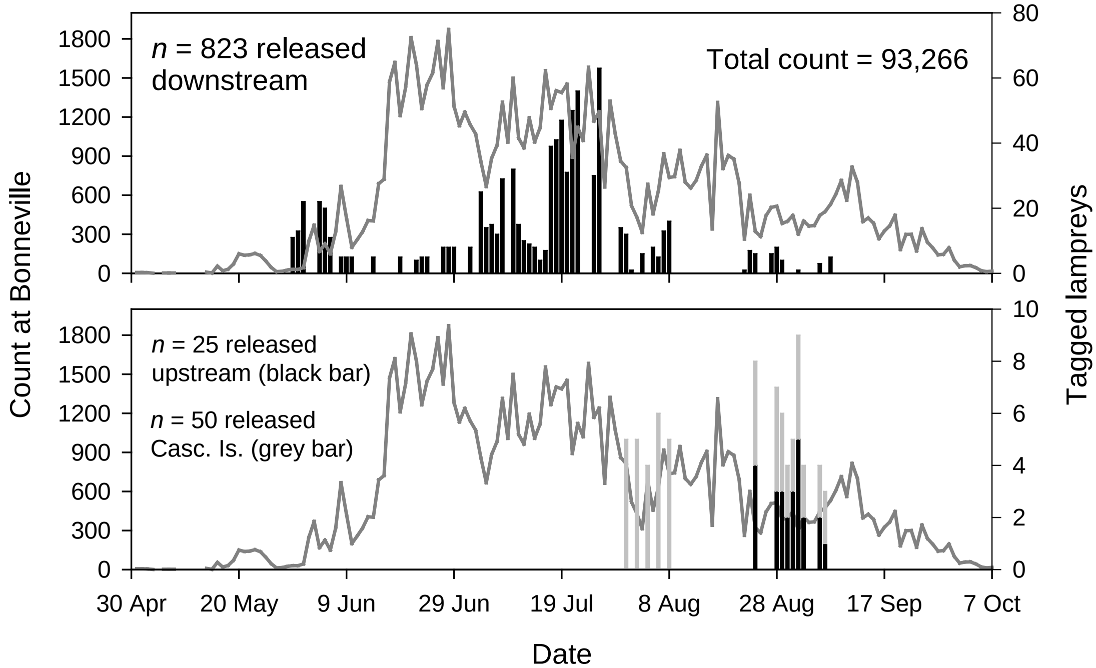

Figure 1. Number of adult Pacific lamprey counted passing Bonneville Dam during the day and night (solid line) and the numbers that were collected and HD-PIT tagged (bars) in 2012. Top panel shows fish released downstream from Bonneville Dam near Hamilton Island and bottom panel shows fish released upstream from the dam near Stevenson, WA or directly into the Cascades Island LPS.

Table 2. Length, girth, weight, and percent lipid of adult Pacific lampreys collected and tagged with HD-PIT tags and released downstream from Bonneville Dam near Hamilton Island (HAM), upstream from the dam near Stevenson, WA (STE), or in the Cascades Island LPS (CI) in 2012. Lipid estimates were based on four readings per fish.

	Length (cm)			Girth (cm)			Weight (g)			Percent lipid (%)		
Type	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*
PIT-HAM	819	65.3	4.1	817	10.9	0.8	755	447.9	89.8	816	25.6%	9.0%
PIT-STE	25	63.8	3.3	25	10.3	0.9	13	420.6	75.7	25	26.5%	9.9%
PIT-CI	50	64.1	4.8	50	10.6	0.8	37	395.2	77.9	50	25.0%	8.8%
All fish	894	65.2	4.2	892	10.8	0.8	805	445.0	89.8	891	25.6%	9.0%

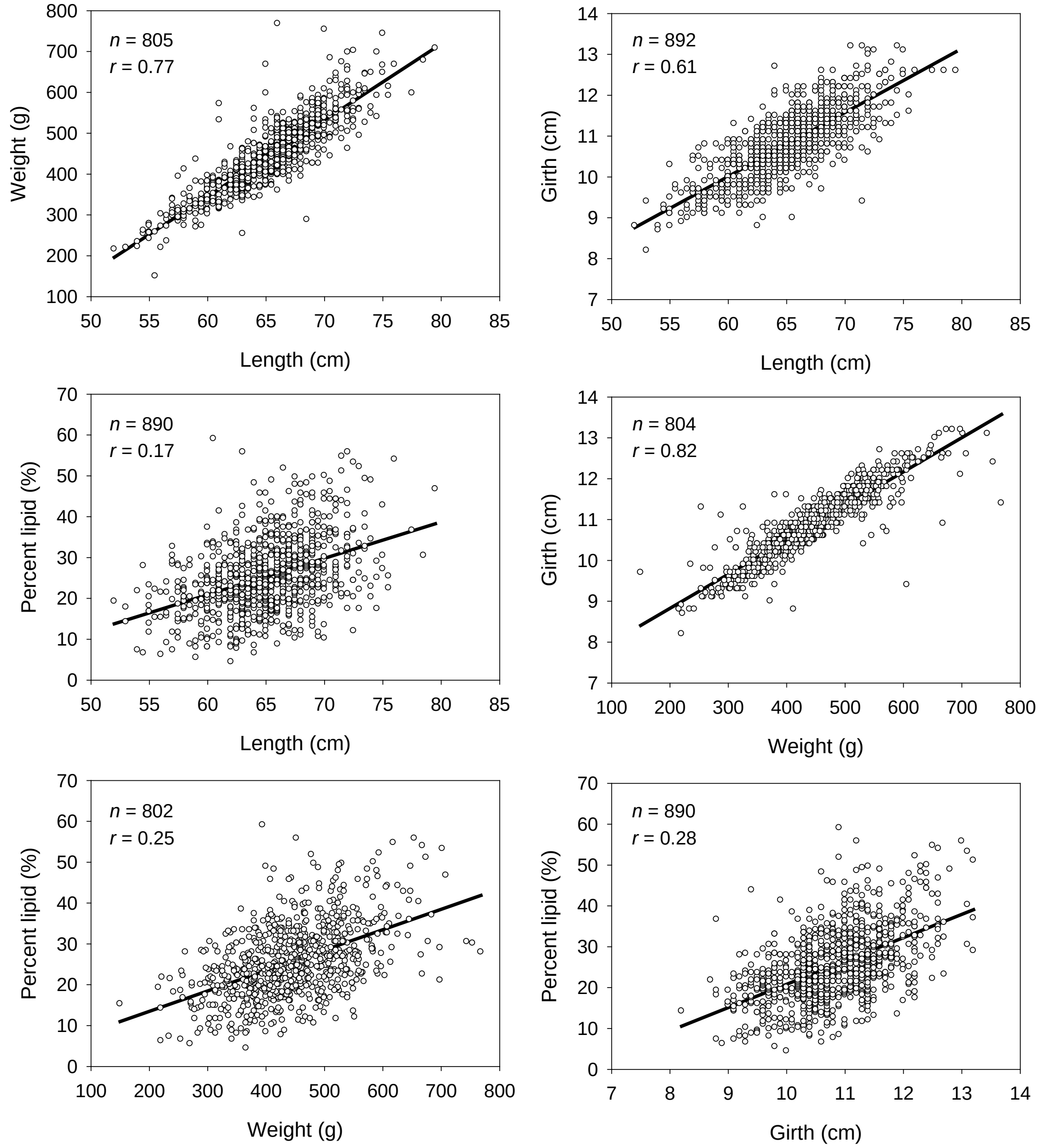

Figure 2. Linear relationships between length, weight, girth, and %lipid metrics for adult lampreys HD-PIT tagged in 2012. Note: all release groups combined.

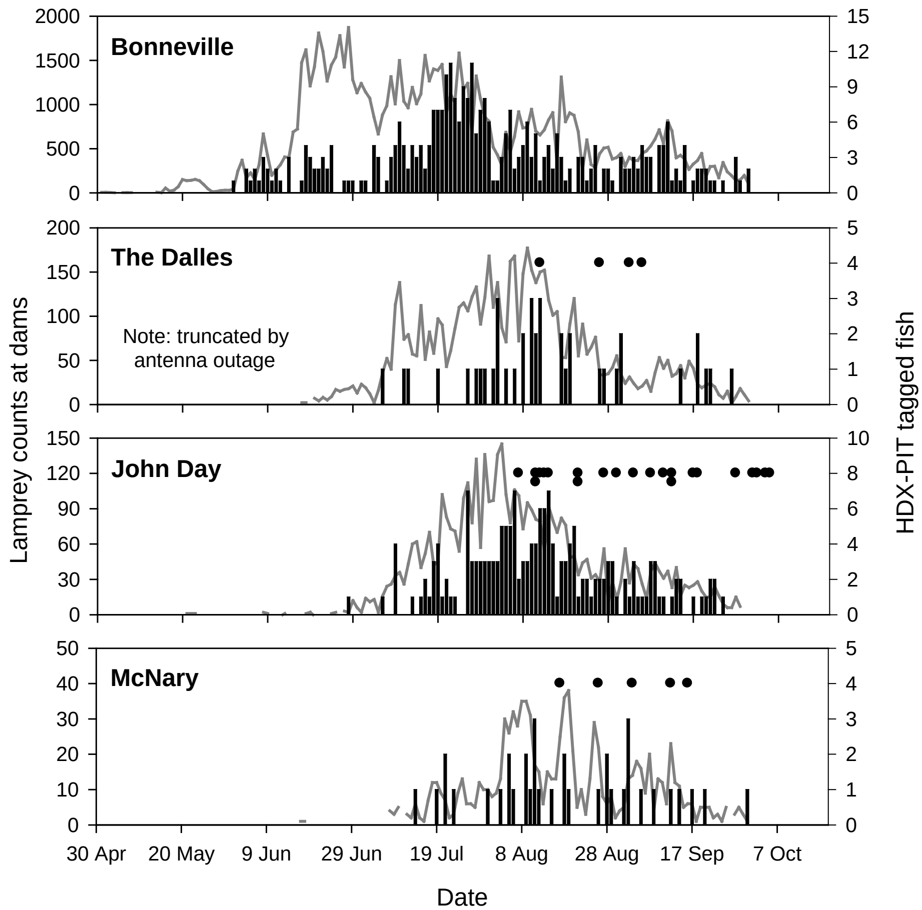

Figure 3a. Daily numbers of adult Pacific lamprey counted passing lower Columbia River dams via fish ladders (gray lines) and the numbers of HD-PIT tagged fish that were detected at top-of-ladder antennas (black bars = detections from fish released downstream from Bonneville; ● = detections from fish released upstream from Bonneville Dam or into the Cascades Island LPS) in 2012. Notes: many lampreys passed dams undetected, particularly at The Dalles and McNary dams; BON count includes all counts (day, night, LPS, capture) whereas counts at other dams are daytime count station only.

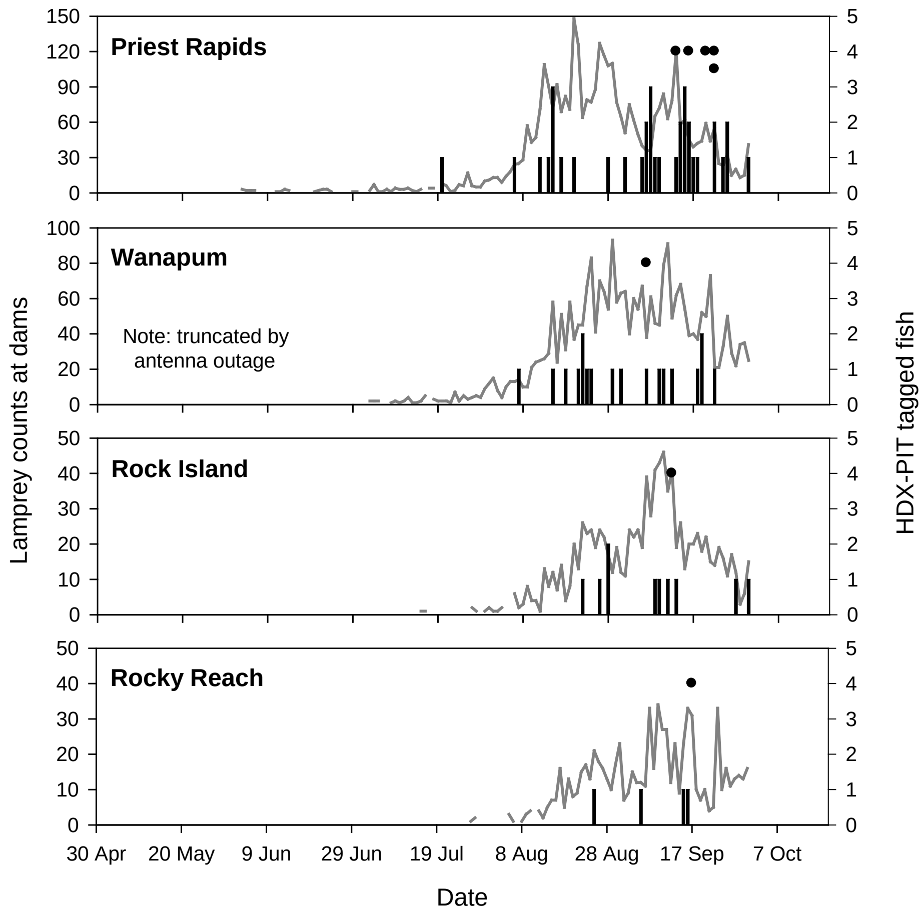

Figure 3b. Daily numbers of adult Pacific lamprey counted passing upper Columbia River dams via fish ladders (gray lines) and the numbers of HD-PIT tagged fish that were detected at top-of-ladder antennas (black bars = detections from fish released downstream from Bonneville; ● = detections from fish released upstream from Bonneville Dam or into the Cascades Island LPS) in 2012. Notes: some or all detection data at Wanapum, Rock Island, and Rocky Reach dams provided by Chelan and Grant County PUDs; count data are daytime count station only.

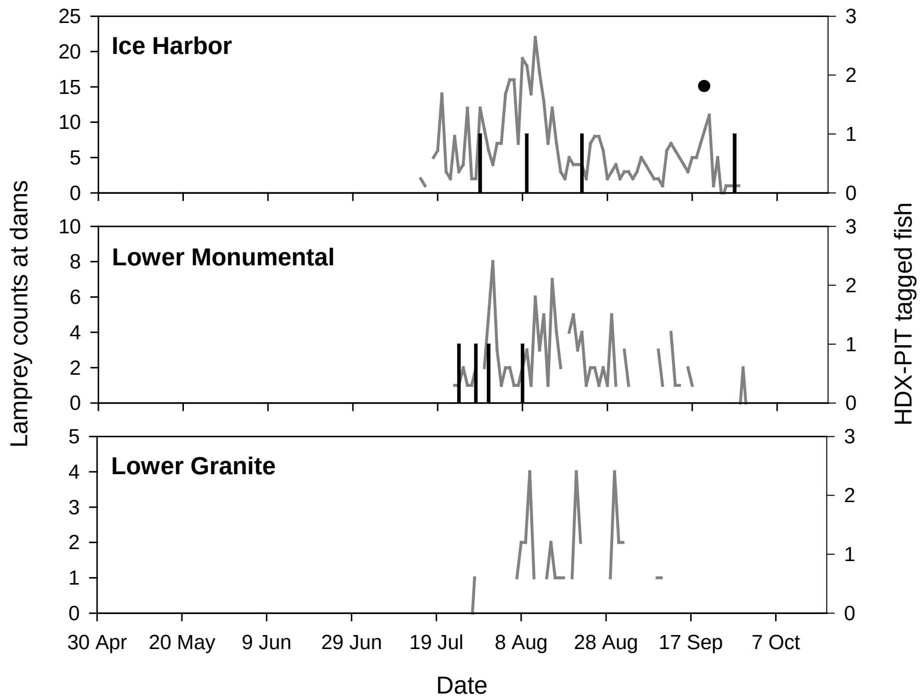

Figure 4. Daily numbers of adult Pacific lamprey counted passing Snake River dams via fish ladders (gray lines) and the numbers of HD-PIT tagged fish that were detected at top-of-ladder antennas (black bars = detections from fish released downstream from Bonneville**;** ● = detections from fish **re**leased upstream from Bonneville Dam or into the Cascades Island LPS) in 2012. Notes: small numbers of fish passed undetected; count data are daytime count station only.

Table 3. Minimum numbers of adult lampreys that passed each site estimated as the number of adult HD-PIT tagged lamprey detected at dam antennas or inferred to pass sites based on upstream detections in 2012. Lampreys were released **d**ownstream from Bonneville Dam near Hamilton Island, upstream from the dam near Stevenson, WA, or into the Cascades Island LPS. See Table 2 for antenna locations.

	Release group		
	Hamilton Island	Stevenson	Cascades Island
Site	Minimum past (n)	Minimum past (n)	Minimum past (n)
Release	823	25	50
Bonneville[1]	535	-	-
Bonneville top[2]	414-447[4]	-	6-47[4]
The Dalles[1]	294	14	26
The Dalles top[2]	212	7	17
John Day[1]	186	7	16
John Day top[2]	177	7	15
McNary[1]	80	1	7
McNary top[2]	69	-	7
Ice Harbor[1]	11	-	1
Ice Harbor top[2]	9	-	1
L. Monument top[2,3]	5	-	1
L. Granite top[2,3]	2	-	-
Priest Rapids[5]	52	-	5
Priest Rapids top[5]	34	-	4
Wanapum[5]	26	-	3
Wanapum top[5]	20	-	1
Rock Island[5]	10	-	1
Rock Island top[5]	10	-	1
Rocky Reach[5]	6	-	1
Rocky Reach top[5]	4	-	1

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

Table 4. Adult HD-PIT tagged lamprey escapement estimates for fish released downstream from Bonneville Dam near Hamilton Island, upstream from the dam near Stevenson, WA, or into the Cascades Island LPS in 2012. Estimates exclude double-tagged fish. See Table 3 for sample sizes.

Reach	Hamilton Island Escapement	Stevenson Escapement	Cascades Island Escapement
Release-Bonneville	65.0%	-	-
Release-Bonneville top[1]	50.3-54.3%	-	Most recaptured
Release-The Dalles	35.7%	56.0%	52.0%
Release-The Dalles top	25.8%	28.0%	34.0%
Release-John Day	22.6%	28.0%	32.0%
Release-John Day top	21.5%	28.0%	30.0%
Release-McNary	9.7%	4.0%	14.0%
Release-McNary top	8.4%	-	14.0%
Release-Ice Harbor top	1.1%	-	2.0%
Release-Lower Monumental top	0.6%	-	2.0%
Release-Lower Granite top	0.2%	-	-
Release-Priest Rapids top	4.1%	-	8.0%
Release-Wanapum top	2.4%	-	2.0%
Release-Rock Island top	1.2%	-	2.0%
Release-Rocky Reach top	0.5%	-	2.0%
Bonneville-Bonneville top[1]	77.4-83.6%	-	-
Bonneville top-The Dalles top	47.4%	-	36.1%
Bonneville top-John Day top	39.8%	-	31.9%
Bonneville top-McNary top	15.5%	-	14.9%
Bonneville top-Ice Harbor top	2.0%	-	2.1%
Bonneville top-L. Monum. top	1.1%	-	2.1%
Bonneville top-L. Granite top	0.4%	-	-
Bonneville top-Pr. Rapids top	7.6%	-	8.5%
Bonneville top-Wanapum top	4.5%	-	2.1%
The Dalles top-John Day top	84.5%	100.0%	88.2%
The Dalles top-McNary top	32.5%	14.3%	41.2%
The Dalles top-Ice Harbor top	4.2%	-	5.9%
The Dalles top-L. Monum. top	2.4%	-	5.9%
The Dalles top-L. Granite top	0.9%	-	-
The Dalles top-Pr. Rapids top	16.0%	-	23.5%
The Dalles top-Wanapum top	9.4%	-	5.9%
John Day top-McNary top	39.0%	14.3%	46.7%
John Day top-Ice Harbor top	5.1%	-	6.7%
John Day top-L. Monum. top	2.8%	-	6.7%
John Day top-L. Granite top	1.1%	-	-
John Day top-Priest Rapids top	19.2%	-	26.7%
John Day top-Wanapum top	11.3%	-	6.7%
McNary top-Ice Harbor top	13.0%	-	14.3%
McNary top-L. Monum. top	7.2%	-	14.3%
McNary top-L. Granite top	2.9%	-	-
McNary top-Priest Rapids top	49.3%	-	57.1%
McNary top-Wanapum top	29.0%	-	14.3%

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

Table 5. Mean HD-PIT tagged lamprey size metrics and tag dates in relation to their escapement through the monitored reaches, for fish released downstream from Bonneville Dam in 2012. Top-of-ladder sites were used for the upper end of each reach[1]. *F* and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Length (*n*)	Weight (*n*)	Girth (*n*)	%Lipid (*n*)	Tag date (*n*)
Release - Bonneville top	No	64.7 (374)	436.8 (349)	10.8 (373)	24.9 (374)	14 Jul (376)
	Yes	65.9 (445)	457.4 (406)	10.9 (444)	26.1 (442)	13 Jul (447)
	F	18.56	9.92	10.77	3.66	0.20
	P	**<0.001**	**0.002**	**0.001**	0.056	0.655
Release - The Dalles top	No	64.8 (608)	438.3 (562)	10.8 (607)	24.9 (607)	13 Jul (611)
	Yes	66.8 (211)	475.8 (193)	11.2 (210)	27.4 (209)	14 Jul (212)
	F	37.52	25.91	37.49	11.77	0.60
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.439
Release - John Day top	No	64.9 (643)	44.3 (594)	10.8 (642)	25.1 (642)	13 Jul (646)
	Yes	66.8 (176)	475.7 (161)	11.2 (175)	27.4 (174)	14 Jul (177)
	F	29.75	20.15	31.78	9.09	0.74
	P	**<0.001**	**<0.001**	**<0.001**	**0.003**	0.390
Release - McNary top	No	65.1 (751)	443.2 (692)	10.8 (750)	25.2 (750)	13 Jul (754)
	Yes	67.6 (68)	498.9 (63)	11.4 (67)	29.4 (66)	13 Jul (69)
	F	23.57	22.82	29.29	12.92	0.04
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.835
Bonneville top - The Dalles top	No	65.1 (234)	440.7 (213)	10.8 (234)	25.0 (233)	13 Jul (235)
	Yes	66.8 (211)	475.8 (193)	11.2 (210)	27.4 (209)	15 Jul (212)
	F	21.76	16.98	27.77	8.24	1.40
	P	**<0.001**	**<0.001**	**<0.001**	**0.004**	0.238
Bonneville top - John Day top	No	65.3 (268)	445.5 (244)	10.8 (268)	25.3 (267)	12 Jul (269)
	Yes	66.8 (176)	475.7 (161)	11.2 (175)	27.4 (174)	14 Jul (177)
	F	15.67	11.83	21.82	5.79	1.27
	P	**<0.001**	**<0.001**	**<0.001**	**0.017**	0.260
Bonneville top - McNary top	No	65.6 (376)	449.9 (342)	10.9 (376)	25.6 (375)	14 Jul (377)
	Yes	67.6 (68)	498.9 (63)	11.4 (67)	29.4 (66)	14 Jul (69)
	F	15.62	17.32	22.85	10.39	0.02
	P	**<0.001**	**<0.001**	**<0.001**	**0.001**	0.900
The Dalles top - John Day top	No	66.8 (33)	478.3 (30)	11.1 (33)	27.6 (33)	14 Jul (33)
	Yes	66.8 (176)	475.7 (161)	11.2 (175)	27.4 (174)	14 Jul (177)
	F	0.00	0.03	0.09	0.02	0.29
	P	0.967	0.870	0.761	0.893	0.589
The Dalles top - McNary top	No	66.4 (141)	464.9 (128)	11.1 (141)	26.5 (141)	15 Jul (141)
	Yes	67.6 (68)	498.9 (63)	11.4 (67)	29.4 (66)	14 Jul (69)
	F	5.53	8.44	9.06	5.07	0.67
	P	**0.020**	**0.004**	**0.003**	**0.025**	0.413
John Day top - McNary top	No	66.3 (108)	460.8 (98)	11.0 (108)	26.2 (108)	16 Jul (108)
	Yes	67.6 (68)	498.9 (63)	11.4 (67)	29.4 (66)	13 Jul (69)
	F	6.70	10.60	9.75	6.05	0.83
	P	**0.010**	**0.001**	**0.002**	**0.015**	0.364

[1] lamprey recaptured at Bonneville and released upstream were treated as passing

Table 6. Mean HD-PIT tagged lamprey migration dates (release date or top-of-ladder date), water temperature (°C) and discharge (kcfs) in relation to their passage through the monitored reaches, **f**or fish released downstream from Bonneville Dam in 2012. Environmental data were assigned on the date each fish was recorded passing the lower end of each reach (fish that passed downstream dams undetected were excluded because environmental data could not be assigned). *F* and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Date (*n*)	Temperature (*n*)	Discharge (*n*)
Release - Bonneville top[1]	No	14 Jul (376)	17.86 (376)	309.5 (376)
	Yes	13 Jul (447)	17.84 (447)	306.3 (447)
	F	0.20	0.03	0.83
	P	0.655	0.864	0.364
Bonneville top - The Dalles top	No	2 Aug (181)	18.71 (168)	250.5 (181)
	Yes	1 Aug (128)	19.09 (126)	251.3 (128)
	F	0.10	2.95	0.01
	P	0.750	0.087	0.927
The Dalles top - John Day top	No	19 Aug (22)	19.98 (19)	185.7 (22)
	Yes	9 Aug (18)	20.25 (18)	209.2 (18)
	F	2.62	0.47	1.61
	P	0.114	0.498	0.213
John Day top - McNary top	No	15 Aug (108)	20.22 (102)	203.1 (108)
	Yes	8 Aug (69)	19.90 (68)	228.5 (69)
	F	7.93	3.34	6.14
	P	**0.005**	0.069	**0.014**

[1] lamprey recaptured at Bonneville and released upstream were treated as passing Bonneville

Table 7. Summary of HD-PIT tagged adult lamprey passage times (d) through monitored reaches of the lower Columbia River, for fish released downstream from Bonneville Dam in 2012.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to pass Bonneville Dam	308	11.31	19.29	4.28	26.34
Release to pass The Dalles Dam	40	19.73	24.75	8.20	34.84
Release to pass John Day Dam	176	25.19	28.48	15.00	37.72
Release to pass McNary Dam	35	27.98	34.01	21.03	43.08
Release to pass Priest Rapids Dam	32	50.33	54.08	42.21	66.20
Release to pass Wanapum Dam	18	50.39	51.20	39.39	61.51
Release to pass Rock Island Dam	9	56.58	55.57	44.28	65.04
Release to pass Rocky Reach Dam	3	50.32	53.03	49.52	59.24
Release to pass Ice Harbor Dam	6	54.50	52.99	24.34	78.51
Release to pass L. Monumental Dam	5	26.54	43.05	20.37	56.63
Release to pass L. Granite Dam	2	24.76	24.76	22.16	27.36
Bonneville top to pass The Dalles Dam	28	4.67	6.73	3.12	7.81
Bonneville top to pass John Day Dam	105	9.79	12.65	6.75	15.08
Bonneville top to pass McNary Dam	19	15.88	21.60	12.75	28.00
Bonneville top to pass Priest Rapids Dam	19	38.45	42.15	37.58	50.45
Bonneville top to pass Wanapum Dam	14	38.63	41.04	28.14	53.49
Bonneville top to pass Ice Harbor Dam	4	24.99	24.85	15.04	34.66
Bonneville top to pass L. Monumental Dam	2	19.77	19.77	19.34	20.19
Bonneville top to pass L. Granite Dam	1	26.33	26.33	-	-
The Dalles top to pass John Day Dam	18	3.25	3.28	2.56	5.79
The Dalles top to pass McNary Dam	2	9.79	9.79	5.90	13.67
The Dalles top to pass Priest Rapids Dam	3	31.77	26.85	13.89	34.88
The Dalles top to pass Wanapum Dam	4	31.99	34.86	24.53	45.20
John Day top to pass McNary Dam	36	7.50	9.75	5.93	13.41
John Day top to pass Priest Rapids Dam	33	27.44	27.29	18.19	32.13
John Day top to pass Wanapum Dam	19	29.62	32.35	20.05	38.97
John Day top to pass Ice Harbor Dam	6	16.04	16.53	8.27	22.26
John Day top to pass L. Monumental Dam	5	14.84	16.43	10.47	16.23
John Day top to pass L. Granite Dam	2	19.71	19.71	16.19	23.22
McNary top to pass Priest Rapids Dam	14	10.46	17.42	8.71	25.97
McNary top to pass Wanapum Dam	8	20.04	20.68	14.26	27.11
McNary top to pass Ice Harbor Dam	3	14.72	12.94	5.02	19.07
McNary top to pass L. Monumental Dam	3	7.33	13.33	4.19	28.46
McNary top to pass L. Granite Dam	1	13.09	13.09	-	-
Priest Rapids top to pass Wanapum Dam	14	6.81	9.27	4.37	12.11
Wanapum top to pass Rock Island Dam	6	13.65	16.57	12.41	22.13
Rock Island top to pass Rocky Reach Dam	3	3.18	4.65	2.92	5.65
Ice Harbor top to pass L. Monumental Dam	2	7.98	7.98	5.09	10.86
L. Monumental top to pass L. Granite Dam	1	6.99	6.99	-	-

Note: overwintering fish not included

Table 8. Correlation coefficients (*r*) for log-transformed HD-PIT tagged lamprey passage times (d), for fish released downstream from Bonneville Dam in 2012. Predictor variables included size metrics (length, weight, girth) recorded at the time of tagging and date, river discharge, and water temperature at the start of each reach. Gray shading indicates $P < 0.05$.

			Correlation coefficient (*r*)					
Reach start	Reach end	*n*[1]	Length	Weight	Girth	Date	Flow	Temp.
Release	Bonneville top	307	0.11	0.14	0.10	-0.16	0.06	-0.16
Release	The Dalles top	40	0.00	0.29	0.20	-0.46	0.38	-0.53
Release	John Day top	175	0.16	0.26	0.22	-0.49	0.25	-0.50
Release	McNary top	35	0.35	0.43	0.43	-0.39	0.18	-0.34
Release	Priest Rapids top	31	0.36	0.43	0.31	-0.57	0.38	-0.51
Release	Wanapum top	17	0.36	0.29	0.15	-0.21	0.06	-0.19
Release	Rock Island top	8	0.46	0.28	0.01	-0.47	-0.04	-0.36
Release	Rocky Reach top	3	-	-	-	-	-	-
Release	Ice Harbor top	6	-0.16	0.45	0.65	-0.18	0.15	0.09
Release	L. Monumental top	5	-0.14	0.58	0.42	-0.52	-0.07	-0.66
Release	L. Granite top	2	-	-	-	-	-	-
Bonneville top	The Dalles top	28	-0.40	-0.34	-0.36	0.09	-0.08	0.21
Bonneville top	John Day top	104	-0.06	0.06	-0.01	-0.45	0.35	-0.52
Bonneville top	McNary top	19	0.01	-0.03	-0.08	-0.65	0.54	-0.74
Bonneville top	Priest Rapids top	18	0.29	0.26	0.21	-0.68	0.58	-0.71
Bonneville top	Wanapum top	13	0.31	0.07	-0.01	-0.42	0.21	-0.43
The Dalles top	John Day top	18	0.05	0.22	0.14	-0.48	0.47	-0.51
The Dalles top	McNary top	2	-	-	-	-	-	-
The Dalles top	Priest Rapids top	3	-	-	-	-	-	-
The Dalles top	Wanapum top	4	-	-	-	-	-	-
John Day top	McNary top	36	0.04	0.07	0.09	-0.01	-0.01	0.23
John Day top	Priest Rapids top	32	0.43	0.40	0.40	-0.06	-0.04	0.15
John Day top	Wanapum top	18	0.38	0.35	0.31	-0.00	-0.06	0.05
John Day top	Ice Harbor top	6	-0.40	0.16	0.47	0.22	-0.21	-0.44
John Day top	L. Monumental top	5	0.03	0.33	0.48	0.84	-0.84	0.71
John Day top	L. Granite top	2	-	-	-	-	-	-
McNary top	Priest Rapids top	14	0.56	0.43	0.28	0.15	-0.17	0.67
McNary top	Wanapum top	8	-0.19	-0.07	-0.22	-0.07	0.20	-0.28
McNary top	Ice Harbor top	3	-	-	-	-	-	-
McNary top	L. Monumental top	3	-	-	-	-	-	-

[1] sample size varied slightly among covariates

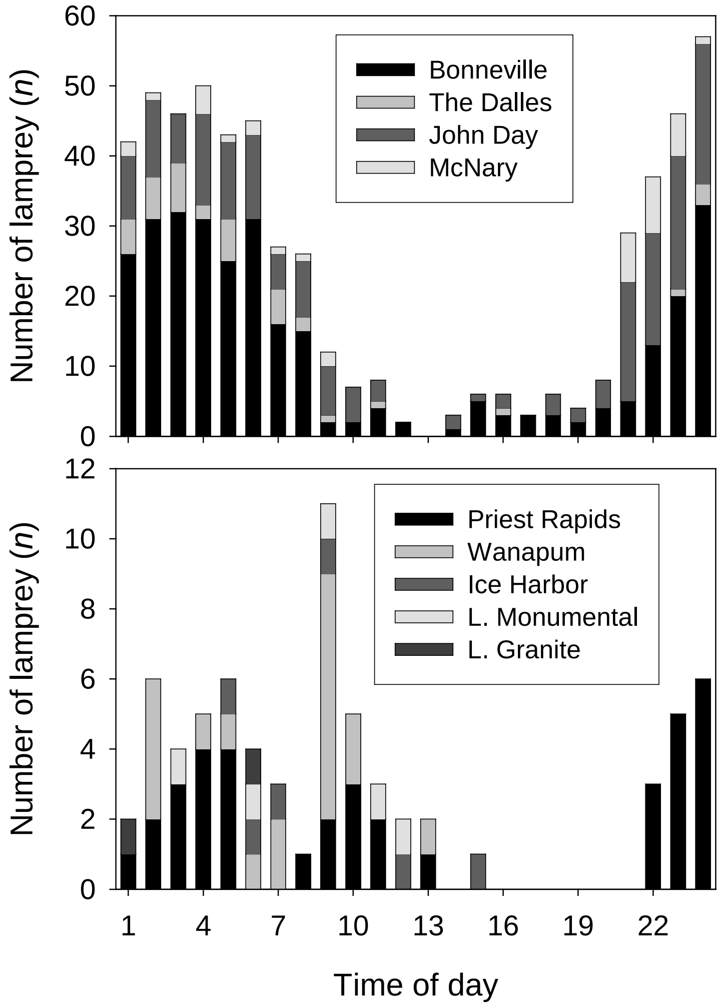

Figure 5. Distributions of the times (binned by hour) that HD PIT-tagged lampreys were detected passing top-of-ladder or LPS sites at Bonneville, The Dalles, John Day, McNary, Priest Rapids, Wanapum, Ice Harbor, Lower Monumental, and Lower Granite dams in 2012 for fish released downstream from Bonneville Dam.

Table 9. Last recorded locations for HD-PIT-only tagged adult Pacific lampreys in 2012 released downstream from Bonneville Dam near Hamilton Island, into the Cascades Island LPS, and upstream from the dam near Stevenson, WA. WA = Washington shore fishway; LPS = lamprey passage structure. Note: Hood River, Fifteenmile Creek, and Warm Springs River sites were maintained by the CTWRSO; some Wanapum sites and all Rock Island, Rocky Reach sites were maintained by Chelan and Grant county PUDs.

	Hamilton Island (*n* =823)		**Cascades Island (*n* = 50)**		**Stevenson (*n* = 25)**	
Last recorded location	*n*	%	*n*	%	*n*	%
Release site	288	35.0%			11	44.0%
Bonneville Dam – Casc. Is. entrance	1	0.1%				
Bonneville Dam – Casc. Is. flow cont.	26	3.2%				
Bonneville Dam – portable trap	2	0.2%				
Bonneville Dam – lamprey rest boxes	8	1.0%				
Bonneville Dam – Casc. Is. LPS[1]	3	0.4%	21	42.0%		
Bonneville Dam – WA ladder[2]	62	7.5%	1	2.0%		
Bonneville Dam – WA LPS	7	0.9%				
Bonneville Dam – WA ladder exit	72	8.7%				
Bonneville Dam – Bradford LPS[3]	15	1.8%				
Bonneville Dam – Bradford ladder exit	29	3.5%				
Hood River	1	0.1%	1	2.0%		
Fifteenmile Creek	14	1.7%	1	2.0%		
At The Dalles Dam	83	10.1%	9	18.0%	7	28.0%
The Dalles ladder exits	19	2.3%				
Warm Springs R. (Deschutes)	5	0.6%	1	2.0%		
Shitike Creek (Deschutes)	-	-	-	-		
Sherars Falls (Deschutes)	2	0.2%				
At John Day Dam	9	1.1%	1	2.0%		
John Day ladder exits	97	11.8%	8	16.0%	6	24.0%
At McNary Dam	11	1.3%				
McNary Dam ladder exits	6	0.7%	1	2.0%	1	4.0%
Ice Harbor Dam	6	0.7%				
Lower Monumental Dam	3	0.4%	1	2.0%		
Lower Granite Dam	2	0.2%				
Priest Rapids Dam	26	3.2%	2	4.0%		
Wanapum Dam	17	2.1%	2	4.0%		
Rock Island Dam	3	0.4%				
Rocky Reach Dam	6	0.7%	1	2.0%		

[1] recaptured fish; [2] includes 11 recaptured fish
[3] includes 2 not recorded at uppermost LPS site

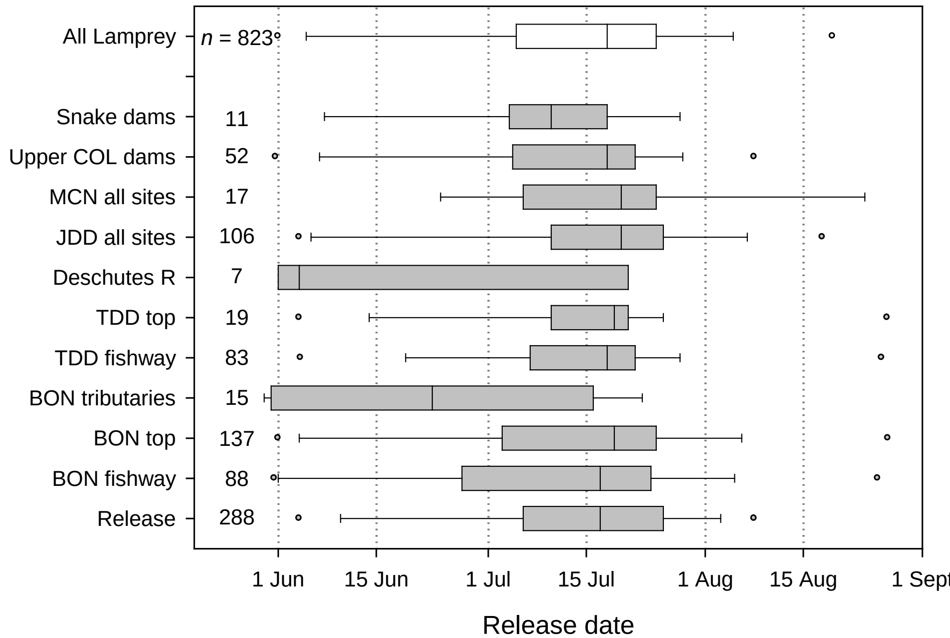

Figure 6. Distributions of lamprey release dates downstream from Bonneville Dam by the final recorded locations for each fish. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 25th, 50th, 75th and 95th percentiles.

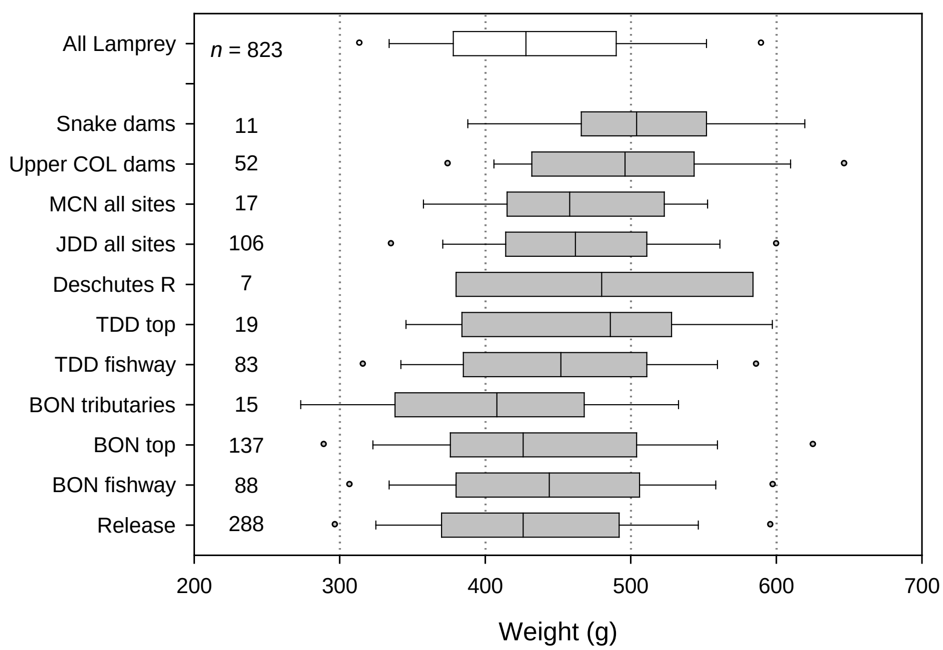

Figure 7. Distributions of lamprey weights (g) by the final recorded locations for each fish (grey boxes). Data shown are for lamprey released downstream from Bonneville Dam. Fishway locations include fish last recorded inside fishways without known passage. Box plots show 5th, 25th, 50th, 75th and 95th percentiles. Note: weight was not collected for 68 fish (8% of the sample.

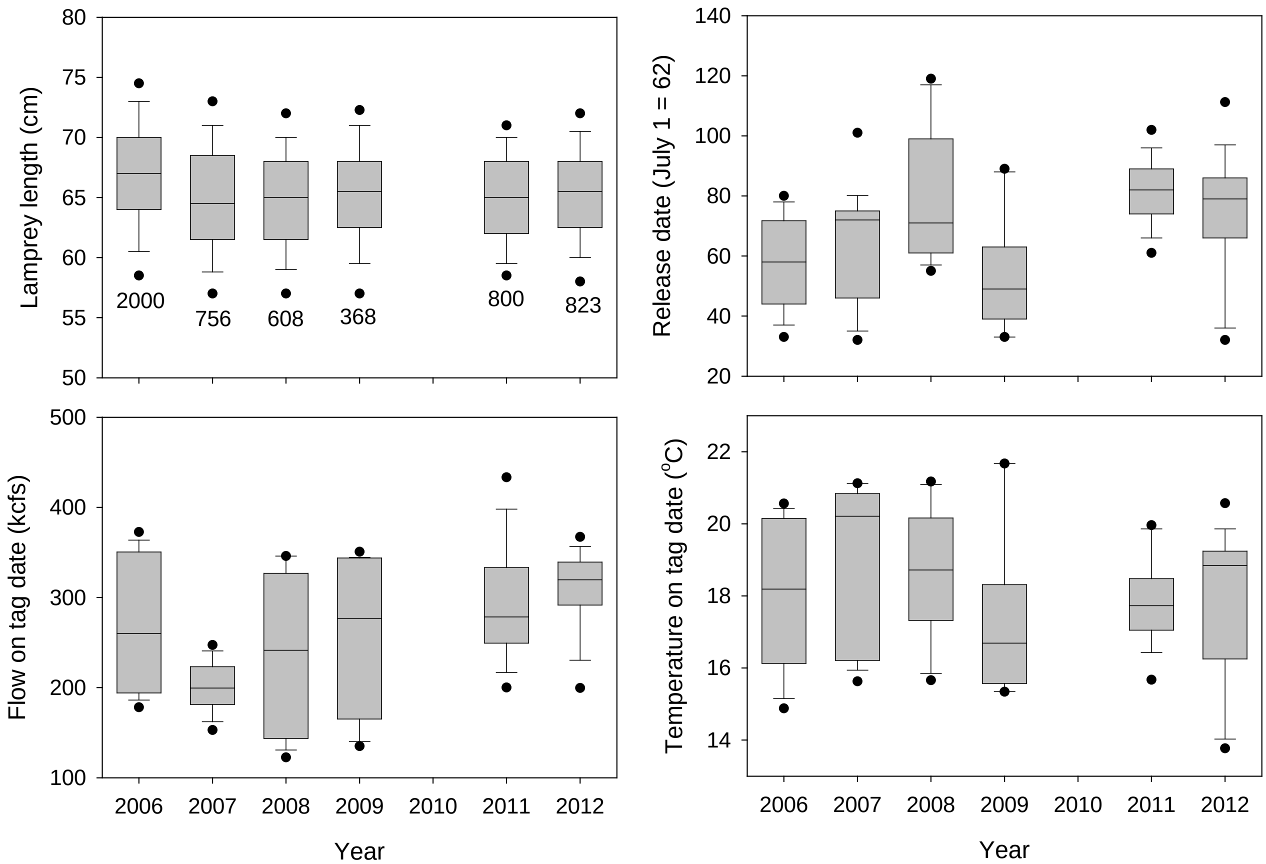

Figure 8. Annual distributions of HD PIT-tagged Pacific lamprey lengths (cm), release dates downstream from Bonneville Dam, and Columbia River discharge (‘flow’, kcfs) and water temperature (°C) on the release dates. Box plots show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. The 2010 study was not included due to small sample size (*n* = 13).

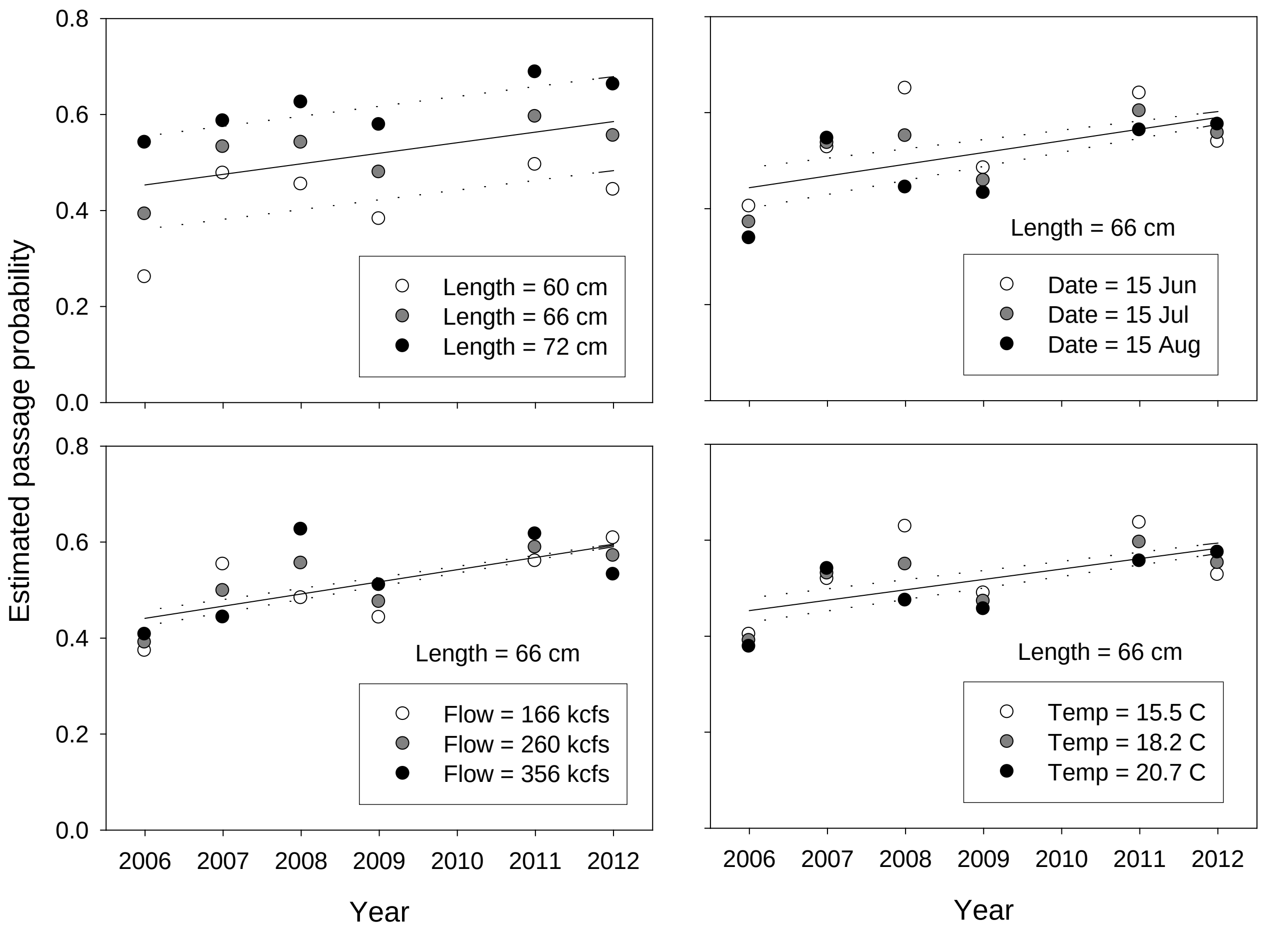

Figure 9. Probability that HD PIT-tagged lamprey would pass Bonneville Dam, as estimated using a series of logistic regression models. Top left: escapement = lamprey length; data shown are point estimates from each annual model with lamprey length held constant at 60, 66, and 72 cm (10^{th}, 50^{th}, and 90^{th} percentiles). Top right: escapement = lamprey length + release date; lamprey length held constant at 66 cm and release date at 15 June, 15 July, or 15 August. Bottom left: escapement = lamprey length + river discharge ('flow'); lamprey length held constant at 66 cm and discharge at 166.1, 260.0, or 355.7 kcfs (10^{th}, 50^{th}, and 90^{th} percentiles). Bottom right: escapement = lamprey length + water temperature; lamprey length held constant at 66 cm and temperature at 15.5, 18.2, or 20.7 °C (10^{th}, 50^{th}, and 90^{th} percentiles). Lines are from linear regressions and show increasing escapement across years.

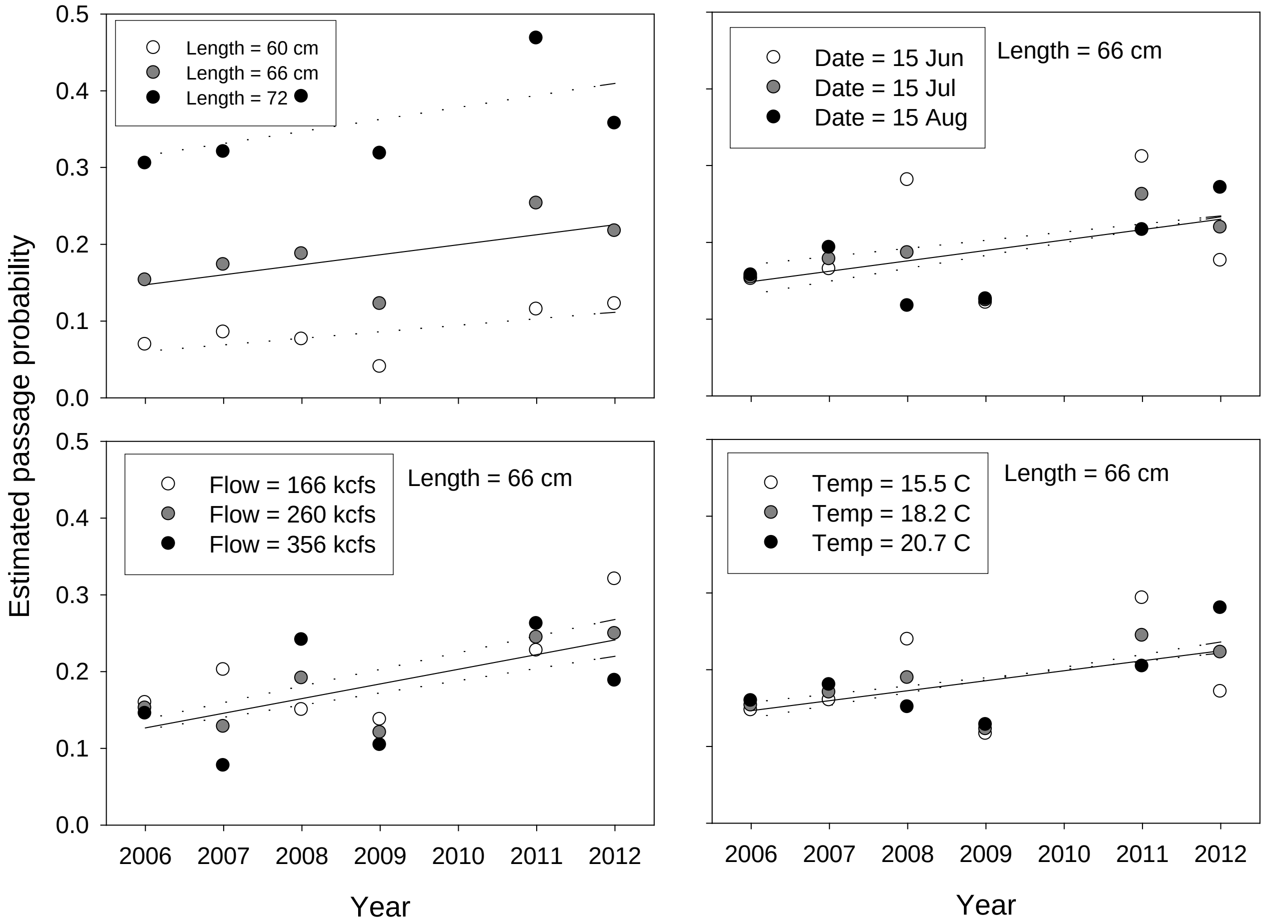

Figure 10. Probability that HD PIT-tagged lamprey would pass John Day Dam, as estimated using a series of logistic regression models. Top left: escapement = lamprey length; data shown are point estimates from each annual model with lamprey length held constant at 60, 66, and 72 cm (10^{th}, 50^{th}, and 90^{th} percentiles). Top right: escapement = lamprey length + release date; lamprey length held constant at 66 cm and release date at 15 June, 15 July, or 15 August. Bottom left: escapement = lamprey length + river discharge ('flow'); lamprey length held constant at 66 cm and discharge at 166.1, 260.0, or 355.7 kcfs (10^{th}, 50^{th}, and 90^{th} percentiles). Bottom right: escapement = lamprey length + water temperature; lamprey length held constant at 66 cm and temperature at 15.5, 18.2, or 20.7 °C (10^{th}, 50^{th}, and 90^{th} percentiles). Lines are from linear regressions and show increasing escapement across years.

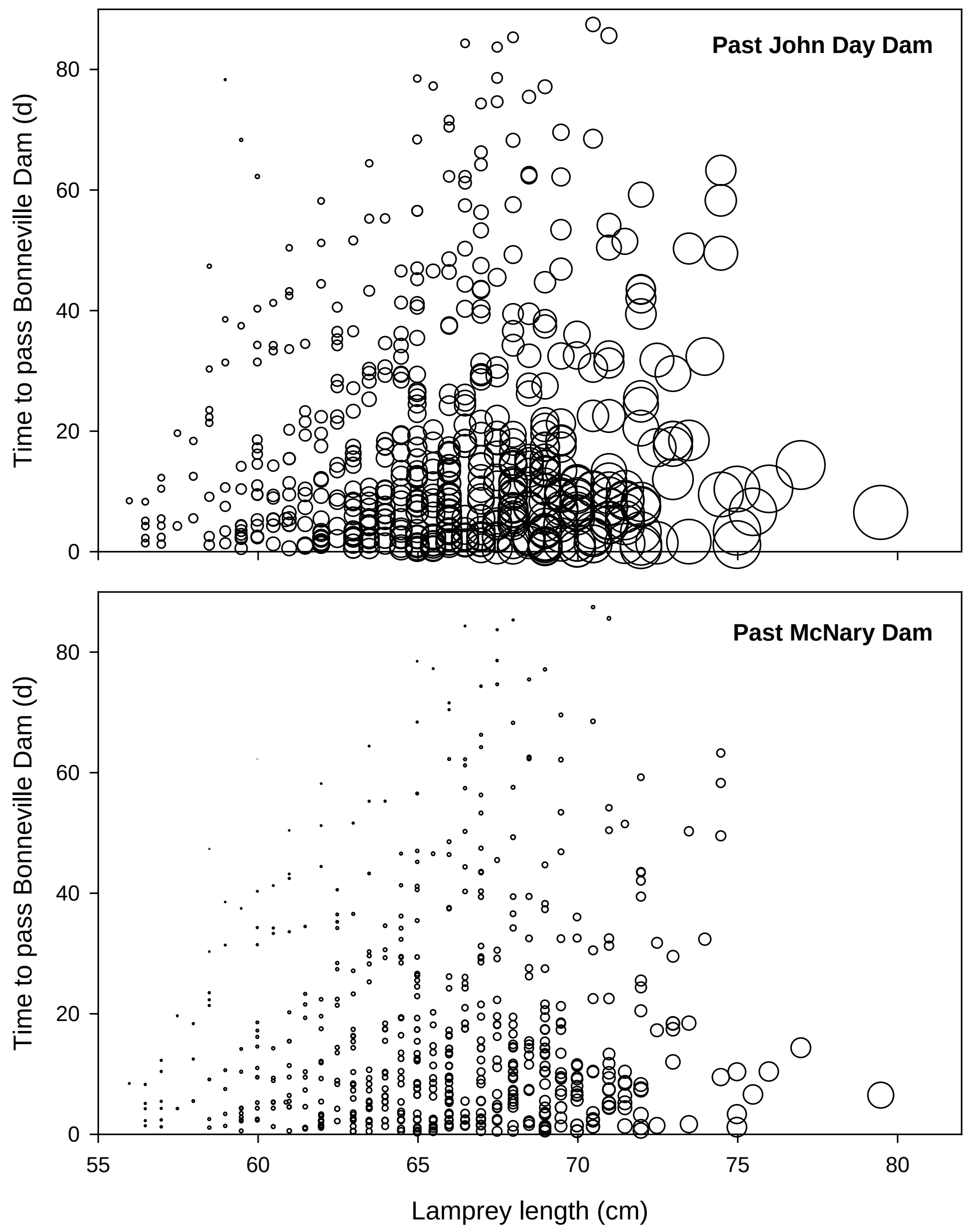

Figure 11. Bubble plots showing the relationship between Pacific lamprey length (cm), passage time from release past Bonneville Dam, and the probability of escaping past John Day (top) and McNary (bottom) dams in 2011-2012 (*n* = 581 lampreys). Bubbles are scaled to the probability of escapement, with the largest bubble in the top panel = 0.84 and the largest bubble in the bottom panel = 0.42. A small number of outliers are not shown and overwintering fish were excluded.

Discussion

The 2012 adult lamprey studies used an integrated set of technologies to address multiple questions about lamprey migration in the Columbia River Hydrosystem at a variety of scales. The results summarized in this report primarily address reach-scale and system-wide migration using HD-PIT detection data. Companion 2012 study reports provide results from lampreys tagged with acoustic transmitters (JSATS) and released both upstream and downstream from Bonneville Dam (Noyes et al. *in review*), behaviors of the HD-PIT tagged fish in and near Bonneville lamprey passage structures (Corbett et al. *in prep*), and results from using dual frequency identification sonar (DIDSON) to monitor adult lampreys inside and near fishways at Bonneville and John Day dams (Johnson et al.2013).

2012 HD-PIT Sample. – The unexpectedly large adult lamprey run in 2012, in combination with study objectives that prioritized tagging fish with JSATS transmitters in June and early July, resulted in a non-proportional HD-PIT sample relative to the run at large. This partially constrained our ability to make direct comparisons between the 2012 results and results from previous years. The multi-year escapement and distribution analyses largely accounted for the less proportional 2012 sampling by statistically controlling for the effects of lamprey size, release date, and encountered environmental conditions.

Escapement. – The migration-scale escapement summaries generated by the 2005-2012 HD-PIT studies provide the most consistently collected baseline monitoring data for tagged lampreys in the Columbia Basin. In 2012, lamprey escapement for the downstream release group from release past Bonneville Dam (50%) was in the middle of the distribution of estimates in HD-PIT samples from 2005-2011 (41-56%, Table 11). The past-Bonneville estimate of 50% was likely an underestimate because additional fish were recaptured inside the fishways and were transported upstream in 2012; this recapture rate was higher than in any prior year. The percentage of lampreys that passed John Day Dam (22%) and McNary Dam (8%) in 2012 compared favorably with previous estimates of 14-24% past John Day Dam and 2-8% past McNary Dam. Dam-to-dam estimates in 2012 were higher than in previous years for the The Dalles-John Day (83%) and John Day-McNary (39%) reaches (Table 11).

As mentioned above, full-migration comparisons of the 2012 escapement estimates to estimates from other years were problematic. We would expect that the bias in the 2012 sample for later migrants would result in lower escapement past upriver dams because we have seen a reduction in upstream passage in late summer when water temperatures reach annual highs (e.g., Keefer et al. 2012, 2013a). The relatively high-discharge, low-temperature conditions in 2012 (Appendix A) may have partially countervailed the sample bias. The above average discharge in 2012 resulted in increased discharge through Powerhouse 1 at Bonneville Dam. This operation provides additional attraction flow to the Bradford Island fishway, which has historically had relatively higher lamprey passage efficiency than the Washington-shore and Cascades Island fishways (Moser et al. 2002a; Clabough et al. 2011b; Keefer et al. 2013b). Attracting more lampreys to Powerhouse 1 likely contributed to more passing Bonneville Dam. It is also likely that the cool 2012 conditions extended the period of suitable conditions for upstream migration. The relatively high 8% escapement from release past McNary Dam and relatively high escapement to the upper Columbia in 2012 was likely due, at least in part, to the favorable migration temperatures and to additional monitoring effort.

Our multi-year analysis of lamprey escapement past Bonneville and John Day dams indicate that there have been incremental improvements in adult passage at the lower river dams. Importantly, this conclusion was supported after statistically controlling for lamprey size, release date, and environmental factors. Positive operations-related effects on lamprey passage include increased fishway entrance efficiency at Bonneville Dam as a result of night-time fishway velocity reductions at Powerhouse 2 (Johnson et al. 2012a). A variety of other improvements inside Bonneville fishways, along with the installation of LPSs have increased overall dam passage efficiency at Bonneville Dam (Clabough et al. 2010a; Moser et al. 2011; Corbett et al. *in prep*). Upstream from Bonneville Dam, the USACE has implemented operational and structural changes to fishways to

Table 11. Summary of release to top-of ladder and dam-to-dam reach escapement estimates for HD-PIT tagged (only) lampreys released downstream from Bonneville Dam from 2005-2012 and recorded at or known to pass top-of-ladder sites at monitored dams. Data are from Keefer et al. (2009c, 2009d, 2010b, 2011b, 2012). 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.

	Escapement estimates							
	2005	2006	2007	2008	2009	2010	2011	2012
Released	841	2000	757	608	368	13	800	823
Release – Top BO	0.53 (446)	0.41 (822)	0.52 (393)	0.52 (318)	0.47 (172)	[1]0.58 (7)	[2]0.56 (451)	[3]0.50 (414)
Release – Top TD	-	0.28 (558)	0.33 (246)	0.27 (166)	0.25 (90)	0.23 (3)	0.30 (238)	0.26 (212)
Release – Top JD	-	0.19 (382)	0.17 (129)	0.18 (109)	0.14 (50)	0.15 (2)	0.24 (190)	0.22 (177)
Release – Top MN	0.05 (40)	0.04 (80)	0.05 (35)	0.05 (28)	0.02 (8)	-	0.08 (65)	0.08 (69)
Top BO – Top TD	n/a	0.67 ([3]840)	0.63 (393)	0.52 (318)	0.52 (172)	0.38 (8)	0.52 (462)	0.47 (447)
Top TD – Top JD	n/a	0.69 (565)	0.52 (247)	0.66 (166)	0.56 (90)	0.67 (3)	0.80 (238)	0.83 (212)
Top JD – Top MN	n/a	0.21 (387)	0.27 (129)	0.26 (109)	0.16 (50)	-	0.34 (190)	0.39 (177)
Top MN – Top IH	0.05 (40)	0.06 (82)	0.14 (35)	0.18 (28)	0.0 (8)	-	0.23 (65)	0.16 (69)
Top MN – Top PR	n/a	n/a	n/a	0.11 (28)	0.50 (8)	-	0.54 (65)	0.49 (69)

[1] 0.62 (n = 8); [2] 0.58 (n = 460); [3] 0.54 (n = 447) when recaptures were treated as passing the dam
[4] includes recaptured fish

Table 12. Numbers of HD-PIT tagged lampreys (only) released downstream from Bonneville Dam from 2005-2012, mean lamprey length, weight, and girth and the median passage time (days) to pass selected reaches in the lower Columbia River. Pre-2011 data are from Daigle et al. (2008) and Keefer et al. (2009a, 2009d, 2010b, 2011b, 2012). The navigation lock was unmonitored in 2007-2010. Note: weight was not collected for all fish in all years.

	Year							
	2005[1]	2006	2007	2008	2009	2010	2011	2012
Number Released	841	2000	757	607	368	13	800	823
Mean Length (cm)	67.9	67.0	64.8	64.7	65.3	63.0	64.8	65.3
Mean Weight (g)	500	482	445	434	443	-	437	449
Mean Girth (cm)	11.5	11.2	10.9	10.6	10.8	-	10.8	10.9
Release – Top BO	n/a	9.6 d	6.5 d	7.7 d	11.5 d	-	10.2 d	11.3 d
Top BO – Top TD	n/a	5.1 d	4.0 d	4.9 d	6.7 d	-	4.3 d	4.7 d
Top TD – Top JD	n/a	4.1 d	4.3 d	3.7 d	4.1 d	-	3.4 d	3.3 d
Top JD – Top MN	n/a	12.8 d	8.8 d	5.4 d	9.8 d	-	9.1 d	7.5 d

[1] released into the Bradford Island fishway

benefit lampreys (e.g., orifice rounding, addition of diffuser plating, weir modifications, addition of ramps to raised orifices, raising picket leads, blocking access to routes without exits, etc.) at lower Columbia and lower Snake River dams. The cumulative effects of these changes presumably contributed to the increasing year-to-year escapement estimates. We do note that the conclusion of increasing passage rates through time is dependent on inclusion or exclusion of values from a few years in a short time series (e.g., 2006, 2011; Figure 6). We caution that the trend could represent the effects of unmeasured covariates in addition to (or instead of) the effects of passage modifications. Continued monitoring is recommended to determine whether the trend will hold, particularly in years with warmer conditions and lower flows than experienced in the recent two years.

The 2012 escapement data for the downstream release group consistently indicated higher passage efficiency for larger fish at a variety of spatial scales. The size effect is consistent with results from HD-PIT tagged lampreys described in Keefer et al. (2009c), and also reported in the 1997-2010 radiotelemetry studies (e.g., Keefer et al. 2013a, 2013b). Several hypotheses may explain the higher escapement of larger fish. First, larger fish may be stronger swimmers and more able to ascend through the difficult passage environments at dams (e.g., Beamish 1974; Mesa et al. 2003). Second, larger fish may have greater energetic reserves, allowing for longer upstream passage distances before they seek spawning areas or initiate overwintering behavior. Third, larger fish may be disproportionately from upriver populations, though this would be at odds with a general consensus that anadromous lampreys (Pacific and other species) lack strong geographic stock structure (Bryan et al. 2005; Almada et al. 2008; Goodman et al. 2008; Spice et al. 2012). Fourth, negative handling and tagging effects may have been greater for smaller lampreys (e.g., Moser et al. 2007). However, handling effects almost certainly cannot fully account for the size effects reported across all our recent studies because the size effect has been evident regardless of tag type and size (i.e., HD vs. radiotelemetry) and handling time (i.e., longer for radiotelemetry) and there has been no evidence of an interaction between size and tag effects.

Evidence for broad-scale environmental effects on lamprey escapement have been mixed across years. In some years, escapement has been higher for fish released earlier in the season, when river discharge was relatively high and water temperature was relatively low (e.g., Keefer et al. 2011b). In other years, escapement was higher for fish released later in the summer (e.g., Keefer et al. 2010b). In 2012, we found almost no statistically notable relationships between river environment variables and escapement. The exceptions were that escapement from John Day Dam past McNary Dam was higher for earlier migrants that encountered higher discharge. To date, we do not have a clear explanation for the varying results within and among years over reach-scale distances. However, we are confident that proximate conditions such as water velocity and volume near fishway entrances or near spillways impact lamprey behaviors like passage delay and fishway fallout (e.g., Keefer et al. 2011a; 2013b; Johnson et al. 2012), with consequent effects on escapement. Broad metrics like total river discharge may poorly represent the specific conditions encountered by individual fish, particularly near and inside fishways. We also emphasize that the strong correlations among discharge, water temperature and date of migration make it difficult to isolate cause and effect with our observational data.

We did confirm in 2012 that longer passage time from release below Bonneville Dam past the dam was associated with reduced upriver migration escapement. Each additional day lamprey used to pass Bonneville Dam was associated with a predicted decrease in escapement past John Day Dam of about 2%. This ‘delay’ effect likely accounts for some of the variability in upriver escapement among years and among tagged samples, though the effect was not as large as the one for lamprey size. The relationship between passage time and upstream escapement may reflect the negative effects of poor passage conditions and delay, covariation between passage time and unmeasured variables, or both slow passage at Bonneville Dam and reduced passage probability at upstream locations that resulted from relatively poor phenotypic condition or traits beyond those related to body size (Caudill et al. 2007). On-going analyses are attempting to evaluate the potential for the latter mechanism.

Passage Times. – Lamprey migration times through dam-to-dam study reaches generally fell within the ranges reported in previous HD-PIT study years (Table 12). An exception was that lamprey passed through the reach between The Dalles and John Day dams slightly faster than in any other year, perhaps as a result of the relatively late sampling in 2012. Because HD-PIT monitoring was limited to dam fishways, it was not possible to separate the time lampreys spent passing dams versus migrating through reservoirs. Median migration rates from ladder top to ladder top (i.e., past one reservoir + one dam) were mostly 11-17 km•d^{-1}. These rates were similar to the median (11 km•d^{-1}) and maximum (21 km•d^{-1}) passage rates recorded for radio-tagged lampreys in the unimpounded John Day River (Robinson and Bayer 2005) and were faster than rates recorded for radio-tagged lampreys in the Willamette River (Clemens et al. 2012). Radio and acoustic telemetry results from the lower Columbia studies have shown that lamprey pass quickly through reservoirs (*median* rates often > 20 km•d^{-1}), but can take several days or weeks to pass single dams (Moser et al. 2002b, *in press*; Boggs et al. 2008; Keefer et al. 2009a; Johnson et al. 2009a, 2009b; Naughton et al. 2011; Noyes et al. 2012).

Overall, environmental conditions and lamprey size explained relatively small proportions of the variability in lamprey passage times in 2012. This was consistent with previous lamprey summaries and suggests that other factors were important. The foremost effect on migration speed over long distances in the lower river appears to slowed movement at dams. Slow passage associated with high entrance velocity barriers, poor conditions in transition pools and other features seem to be the primary drivers behind the considerable among- and within-year variability in passage time we have recorded (Keefer et al. 2013b). Additional contributing factors may include diel cycles in activity level, confusing orientation and navigation cues at the dams, distribution and density of predators (esp. white sturgeon), individual physiology, sex, or maturation status, and the lampreys' relatively flexible migration timetable.

Final Distribution. – More locations were monitored with HD-PIT antennas in 2012 than in any previous year. Increased coverage was provided by Chelan and Grant County PUDs at the upper Columbia River dams, CTWSRO added sites in the Hood River and Fifteenmile Creek drainage, and there was detection capability at Three Mile Dam in the Umatilla River. These sites helped with a final accounting for fish that would not have been possible previously. Similarly, some of the lampreys recorded by CTWSRO biologists in the Hood River, Fifteenmile Creek, and the Deschutes River basin would have been assigned to the Bonneville or The Dalles reservoirs in previous years. We note that the addition of new monitoring sites complicates direct inter-annual comparisons of reach escapement and final distribution estimates.

Despite improvements, monitoring tributary entry remains a critical challenge for adult lamprey tagging studies, and particularly for HD-PIT studies. In the Columbia River radiotelemetry studies, tributary detection was primarily at the Deschutes, Klickitat, and John Day rivers plus Fifteenmile Creek. However, transmitter battery life precluded spring-time monitoring and only a fraction of the lampreys that entered tributaries were likely detected. With the exception of Fifteenmile Creek, main stem sites in these tributaries would be difficult to monitor with HD-PIT antennas – although capability is potentially expanding. For example, the planned PIT antennas in the lower Deschutes River main stem will be able to detect HD-PIT tags starting 2013. The existing FD-PIT site on the John Day River would need to be retrofitted to include HD capability. Gaps persist at many other tributaries potentially used by adult lamprey (e.g., sites below Bonneville Dam, Wind, White Salmon, Willow Creek, Umatilla, Yakima, Walla Walla, etc.). In 2012, the JSATS acoustic telemetry study that was companion research to this HD-PIT monitoring has provided some additional reservoir use and tributary entry data (Noyes et al. *in review*).

As in previous HD-PIT studies, lampreys last recorded in the Snake River, upper Columbia River, and other upriver sites were considerably larger at time of tagging than those last recorded at more downstream locations. Unlike in some previous years, there was only limited evidence in 2012 that lampreys released early in the migration were more likely to migrate further. The underlying mechanisms producing these patterns remain unknown and may be primarily related to environmental factors (e.g., suitable tributary temperatures at the time adults were passing confluences) or to lamprey physiology (e.g., condition, age, maturation status).

About 45% of HD-PIT tagged adults did not pass Bonneville Dam in 2012 (or were not recaptured and transported upstream). While this is a lower percentage than in several previous years, it continues to be cause for concern. The underlying reasons for failed passage and the ultimate fate of these adults remain unknown. These fish may have been lost to the reproductive population (true migration and reproductive failure), moved upstream without detection, and/or they may have moved into downstream tributaries or used the tailrace for spawning. Identifying the fate of non-passing fish remains an important question and has begun to be addressed by the JSATS-tagged fish.

HD Antenna Detection Efficiency**.** – There was no radiotelemetry component to the 2012 adult lamprey studies, and therefore no opportunity to directly estimate HD-PIT antenna detection efficiency using double-tagged fish. Instead, efficiencies were estimated using a combination of fish detections at individual dams (or combined top-of-ladder sites) in combination with detections at upstream antenna sites. This is an imperfect method for several reasons. First, there is a risk of underestimating detection efficiency when fish pass a dam via unmonitored routes (e.g., navigation locks or off-fishway routes that do not pass through antennas) but are subsequently detected upstream. Second, sample sizes for individual sites are limited to the number of fish detected upstream from that site. For example, 80 lampreys were detected upstream from John Day Dam and were used to estimate detection efficiency, but at least 186 passed John Day Dam (i.e., 106 fish detected at John Day antennas were excluded from efficiency estimates at the dam).

As in past years, the highest detection efficiencies at HD-PIT antennas were at the top-of-ladder sites at John Day Dam. The fishways at these sites have relatively small cross-sections and there are no alternative routes past the antennas. Efficiencies were also high at the combined antenna sites at Ice Harbor, Lower Monumental, and Priest Rapids dams. However, the samples were small at the Snake River sites. More lampreys were detected at Priest Rapids Dam than in any other HD-PIT study year. This may have been related to increased monitoring effort there, including new antennas maintained by Grant County PUD.

Several combined sites had lower detection efficiency in 2011-2012 than in previous years (note: estimation techniques differed in previous years). In part, this reflects aging antenna infrastructure. Many individual antennas have been in place since 2005, and opportunities to repair or replace these sites are intermittent. The growing number of ‘new' detection sites, including at the PUD dams and in lower river tributaries also has an effect on efficiency estimates (i.e., many lamprey that passed a dam undetected in previous years would not have been identified by detection in tributaries). Relatively low detection efficiency at McNary Dam is partially a function of the availability of alternate passage routes (e.g., the juvenile salmon passage channels). The principal challenge at The Dalles Dam continues to be the large volume of the East ladder at the HD top-of-ladder antenna site, as well as power issues in the north ladder site. It is possible for lampreys to swim through the East ladder antenna and yet be out of detection range. Improving efficiency for the HD-PIT system can be achieved by building antenna redundancy into the most important monitoring sites, as has been done for the highly efficient full duplex (FD) arrays. In the meantime, detection efficiencies for HD-PIT antenna sites will remain lower than preferred; these issues continue to add uncertainty into escapement estimates.

Experimental Release Groups. – The 25 lampreys released near Stevenson and the 50 released directly into the Cascades Island LPS trap were treated as experimental groups. Corbett et al. (*in prep*) will provide more details on the LPS-released sample. We did not attempt to directly compare the Stevenson release group to the downstream release group, both because of the small sample size (*n* = 25) and because the two samples were distributed very differently in the run at large. Qualitatively, the Stevenson group was similar to the downstream group in that about 45% were not detected moving upstream after release; distributions among other sites were also broadly similar. We are hesitant to draw conclusions from the undetected group, but the similarity between upstream and downstream releases may indicate a common effect of handling and transport. A more rigorous experimental design approach, preferably with paired samples, would help resolve this important question.

Conclusions. **–** The multi-year HD-PIT studies have provided a wealth of information about lamprey behavior at reach and full migration scales and the resulting multi-year dataset is by far the best baseline data for evaluating changes in lamprey passage performance in the hydrosystem. The multi-year analyses described here suggest that many of the structural and operational changes made by the USACE (and others) at dams have incrementally improved adult lamprey passage, particularly at Bonneville Dam where much of the effort to date has occurred. Continued investments in fishway improvements that can benefit lampreys will likely further improve passage metrics at Bonneville and at upstream dams.

A pressing gap in our understanding of adult lamprey migration in the Columbia system is the lack of information about lamprey distribution and fate. Nearly half of the tagged fish in radiotelemetry and HD-PIT studies failed to pass Bonneville Dam in most years, and almost nothing is known about where these fish go or whether they spawn. There is little evidence to assess whether large numbers return to tributaries downstream from the dam because monitoring at these sites has been limited with the exception of the Willamette River. We have mobile-tracked radio-tagged lampreys in the main stem Columbia downstream from Bonneville into the late fall, and some fish may spawn in main stem, tailrace or off-channel habitats or hold in the main channel prior to tributary entry in the spring after expiration of radio-tags. Alternatively, previous final detections of radio-tags in the Bonneville Dam may represent predation mortalities caused by sturgeon or sea lions. Radio transmitter life has precluded monitoring in these locations during the spring spawning period. Signal attenuation for radio transmitters has also limited monitoring in deep water habitats below Bonneville Dam, as well as in reservoirs upstream. The addition of HD-PIT monitoring sites in Fifteenmile Creek, Hood River, some Deschutes River locations, and in the Snake and upper Columbia rivers have reduced this information gap. The JSATS acoustic telemetry research, begun as a pilot in 2010 (Naughton et al. 2011) and continued with a modest sample in 2011 (Noyes et al. 2012) and 300 fish in 2012 (Noyes et al. *in review*) is also helping resolve some questions related to lamprey movement and distribution to spawning areas. Fine scale mobile tracking or the use of 3-D acoustic receiver arrays in the Bonneville Dam tailrace could help resolve the fate of lampreys which do not pass and simultaneously provide useful information on distribution and passage behavior during the approach of the dam face and fishway entrances.

The current HD PIT monitoring array is not designed to monitor lamprey behavior at the spatial scales needed to diagnose passage problems inside fishways. Unless additional antennas are installed at known or suspected problems areas, continued active (e.g., radio or acoustic telemetry) or passive (e.g., video or DIDSON) monitoring will likely be needed to provide information about the selection and design of fishway modifications. Planned experiments in the lamprey test fishway flume at Bonneville Dam (scheduled for summer 2013) should also help clarify mechanisms of lamprey passage failure. Understanding the mechanism(s) generating the consistent higher passage probability for larger adults, for example, may aid in the identification of passage bottlenecks or velocity barriers at fishways and inform design of improvements. We think that this type of integrated, multi-scale approach will continue to advance our understanding of lamprey passage at dams and their subsequent distribution throughout the Columbia basin.

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Appendix A. 2012 Columbia River discharge and temperature profiles.

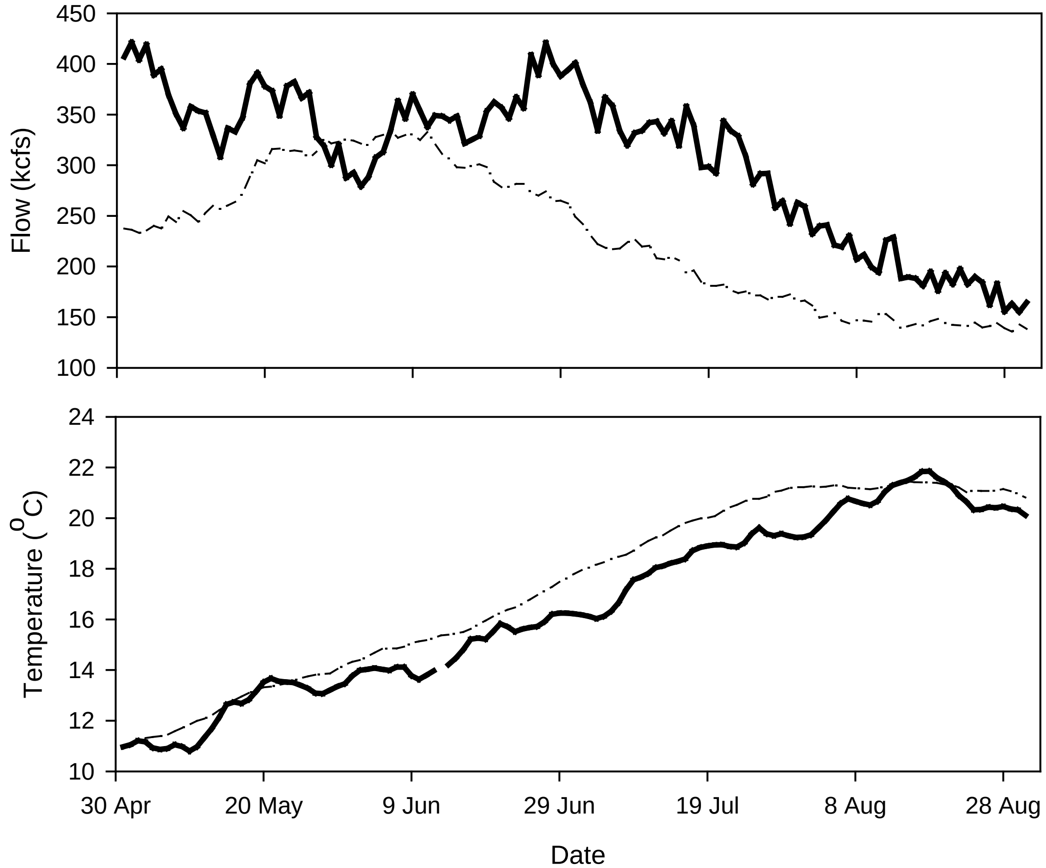

Figure A1. Mean daily Columbia River flow (kcfs) and temperature (°C) at Bonneville Dam in 2012 (solid line) and the 2002-2011 average (dashed line).

Appendix B. 2012 maps of HD PIT antennas at Columbia and Snake River dams

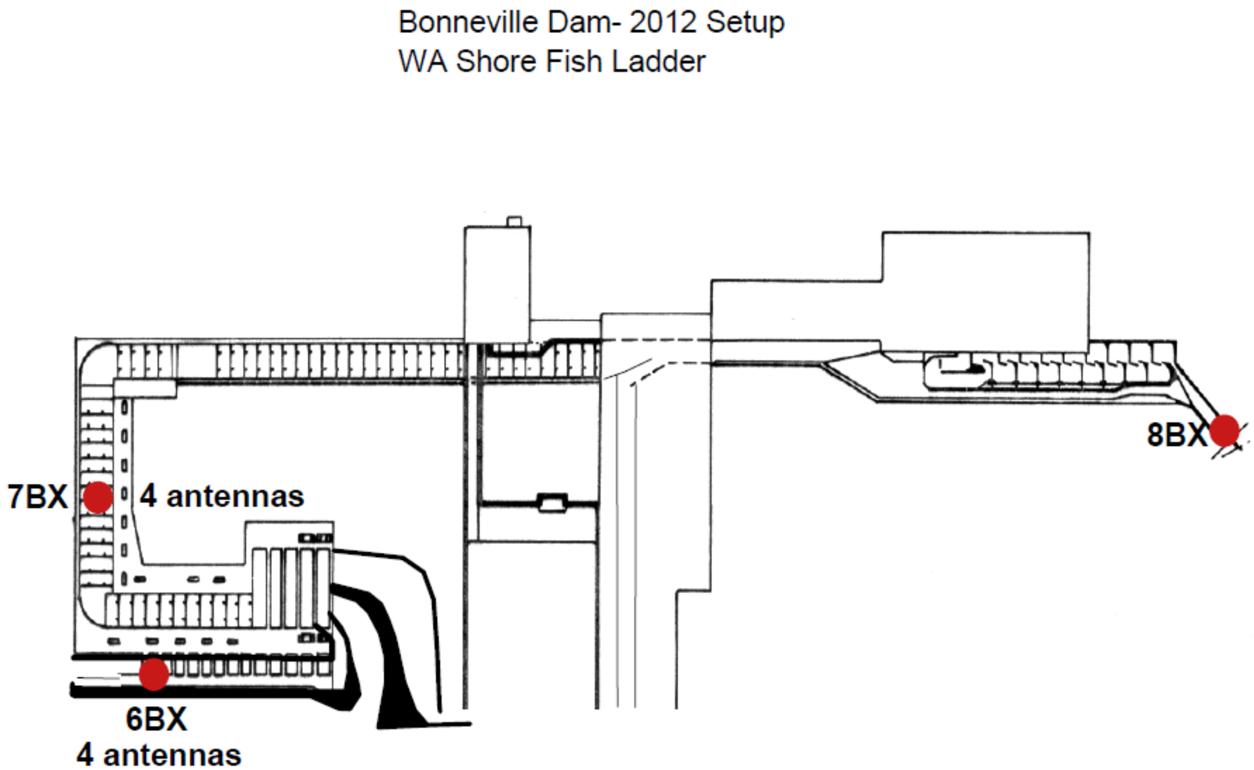

Figure B1. University of Idaho HD PIT antenna locations at Bonneville Dam in 2012 (Washington shore).

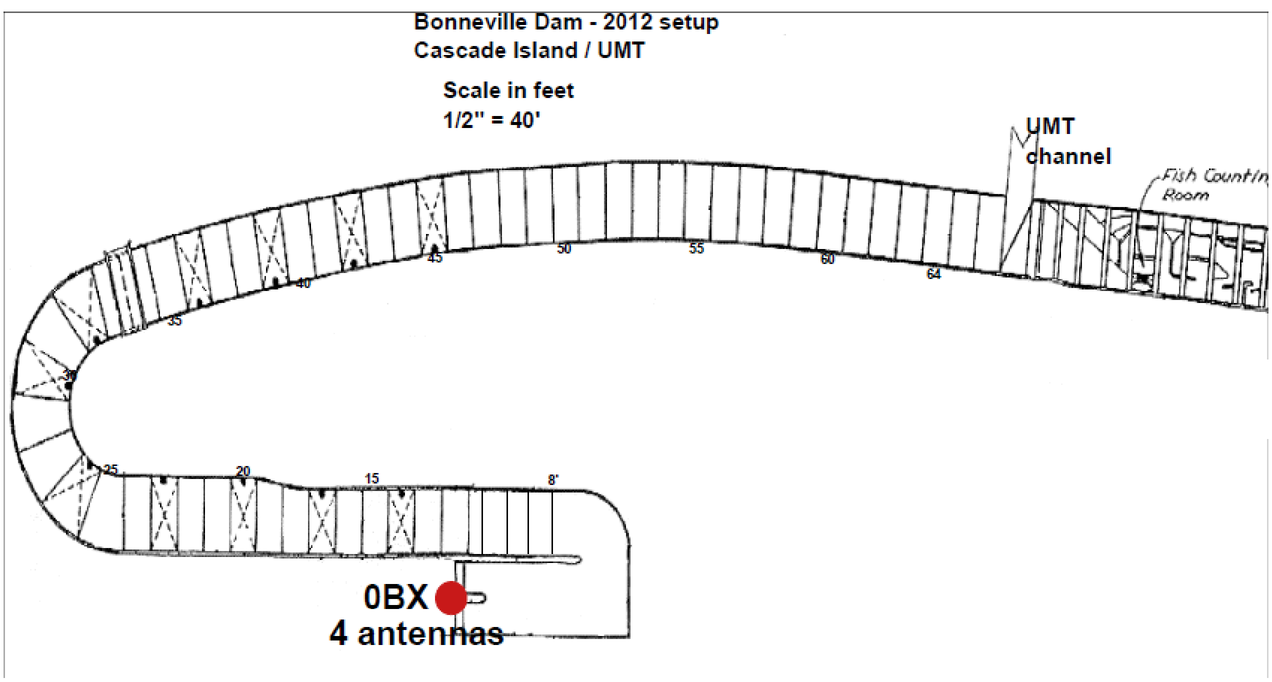

Figure B2. University of Idaho HD PIT antenna locations at Bonneville Dam in 2012 (Cascades Island entrance).

Bonneville Dam - 2012 setup
Bradford Island Fish Exit

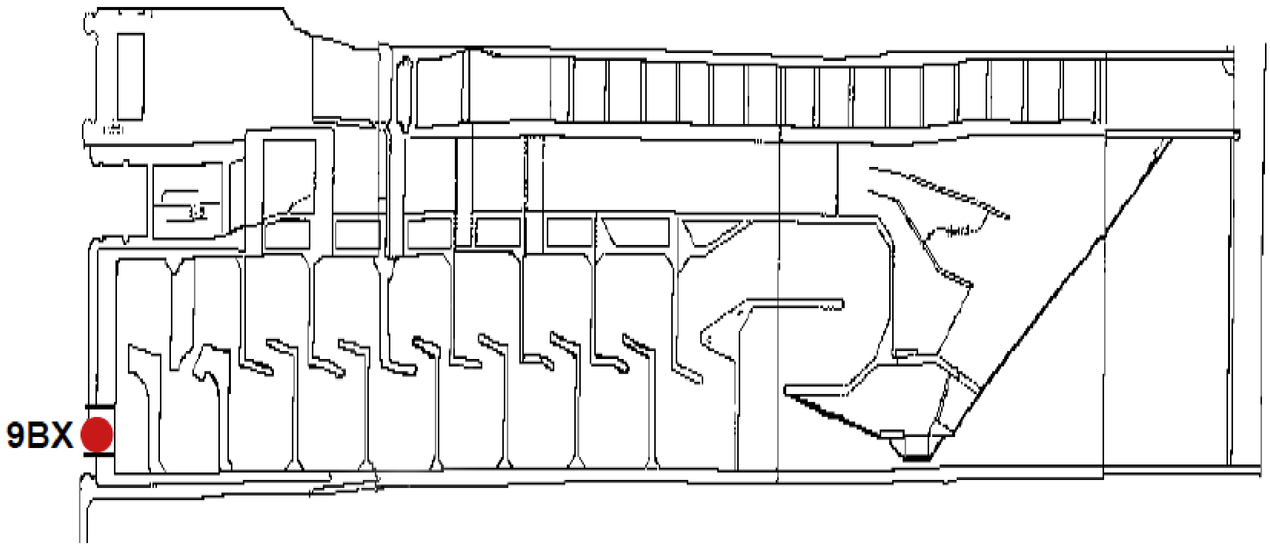

Figure B3. University of Idaho HD PIT antenna locations at Bonneville Dam in 2012 (Bradford Island exit).

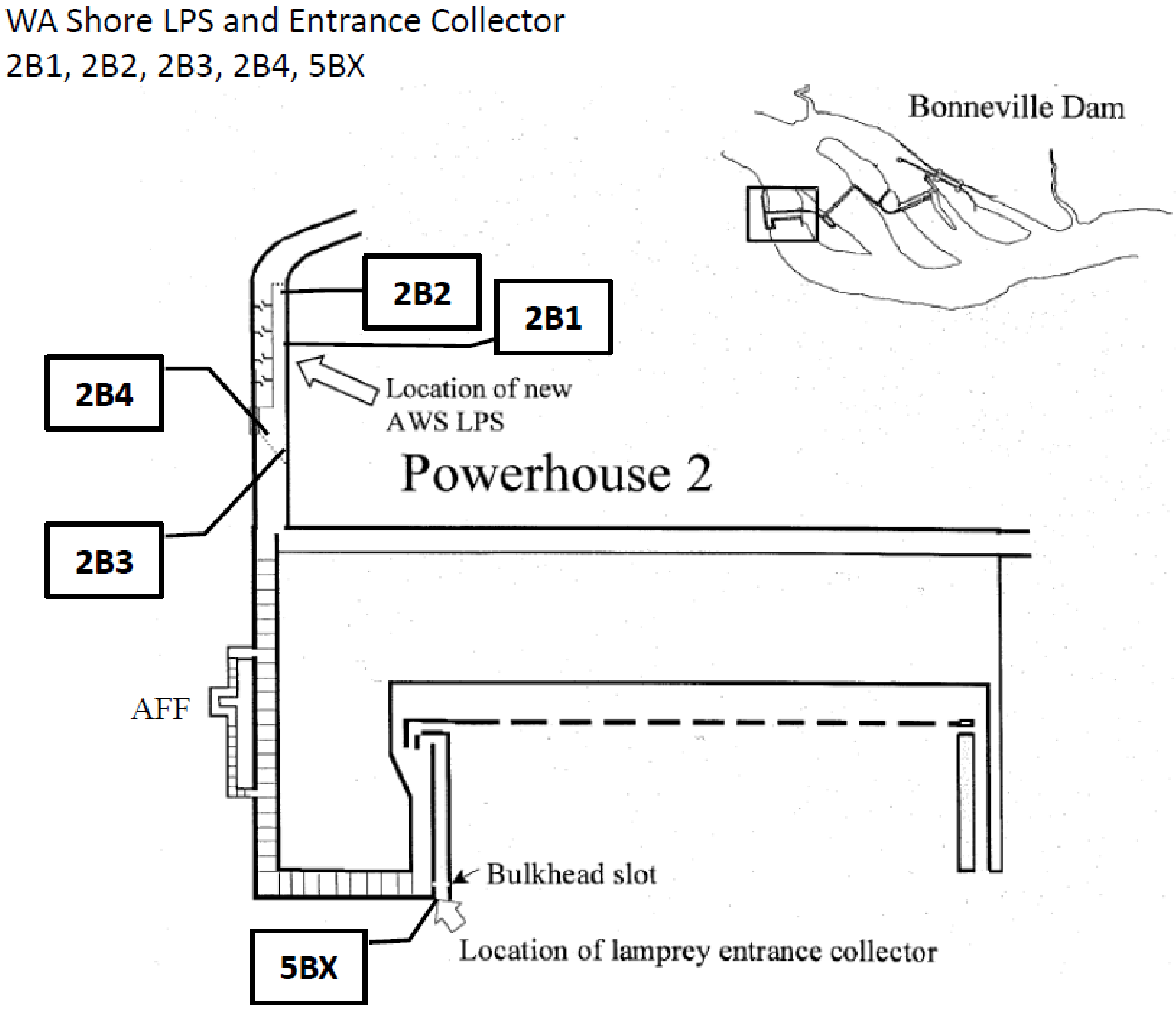

Figure B4. NOAA HD PIT antenna locations at Bonneville Dam in 2012 (Washington-shore).

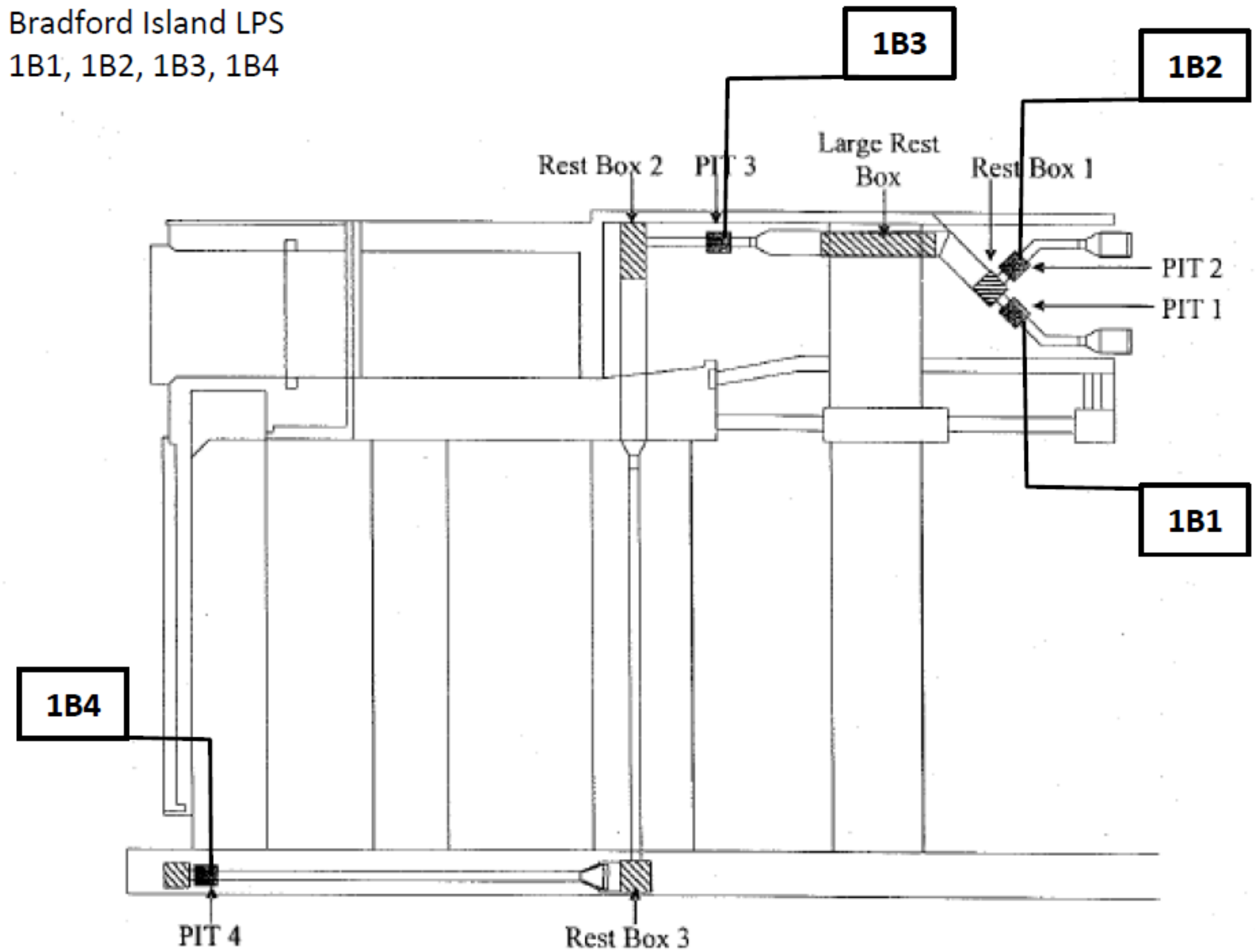

Figure B5. NOAA HD PIT antenna locations at Bonneville Dam in 2012 (Bradford Island).

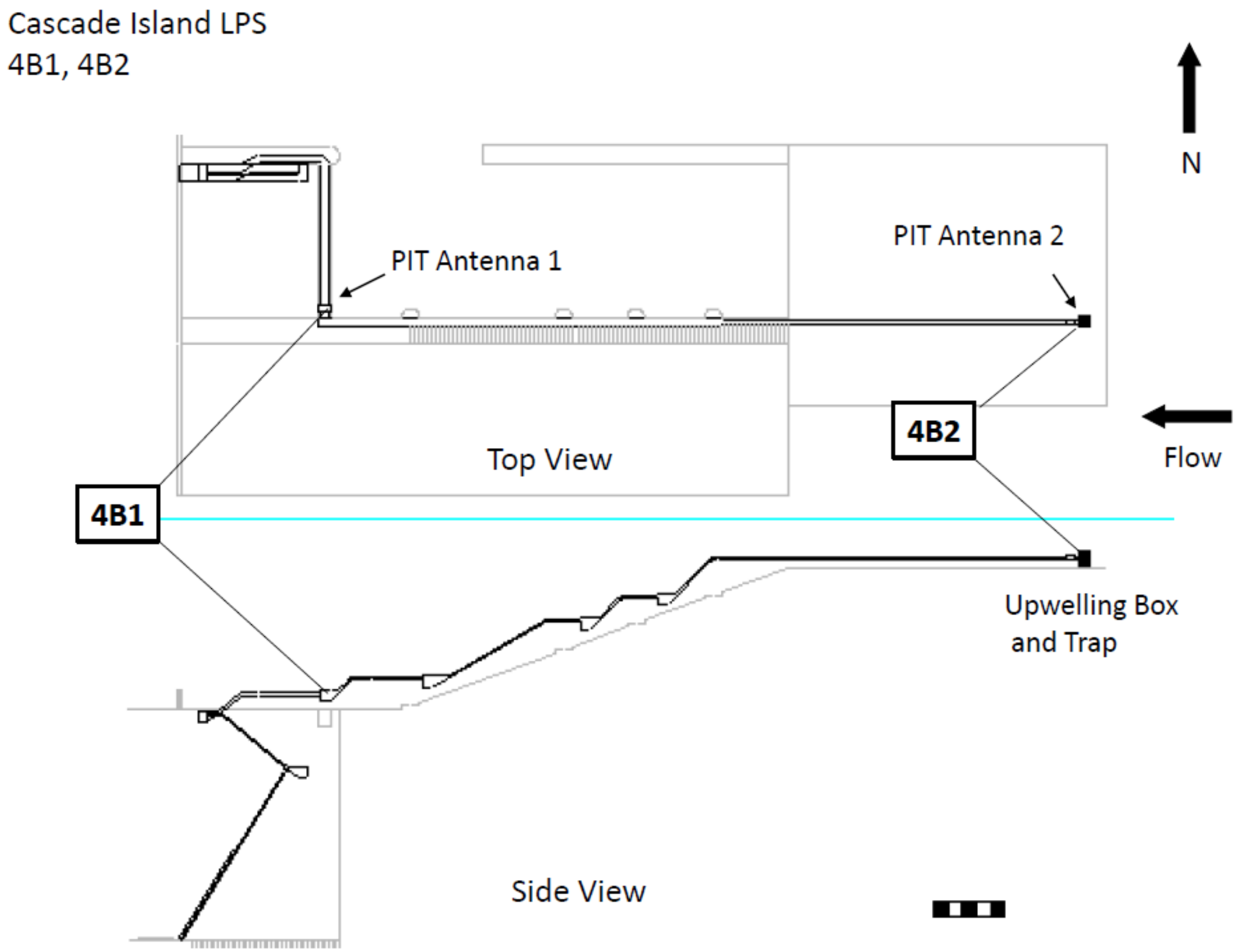

Figure B6. NOAA HD PIT antenna locations at Bonneville Dam in 2012 (Cascades Island LPS).

Cascade Island Flow Control
3BX

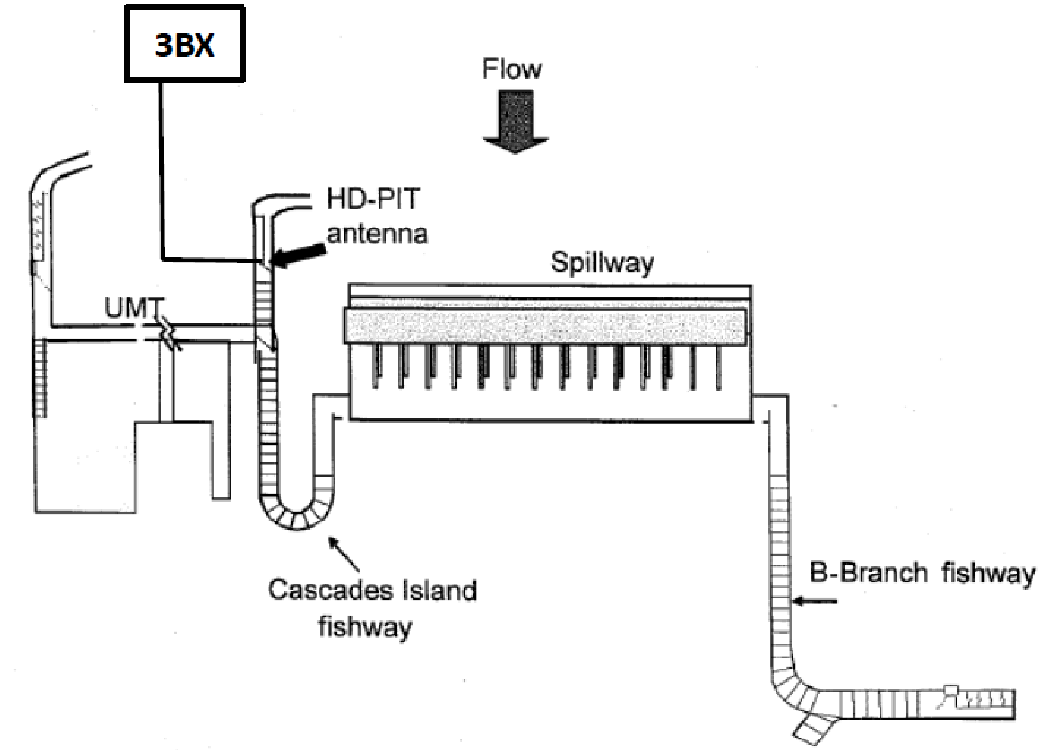

Figure B7. NOAA HD PIT antenna locations at Bonneville Dam in 2012 (Cascades Island flow control).

The Dalles Dam - 2012 setup

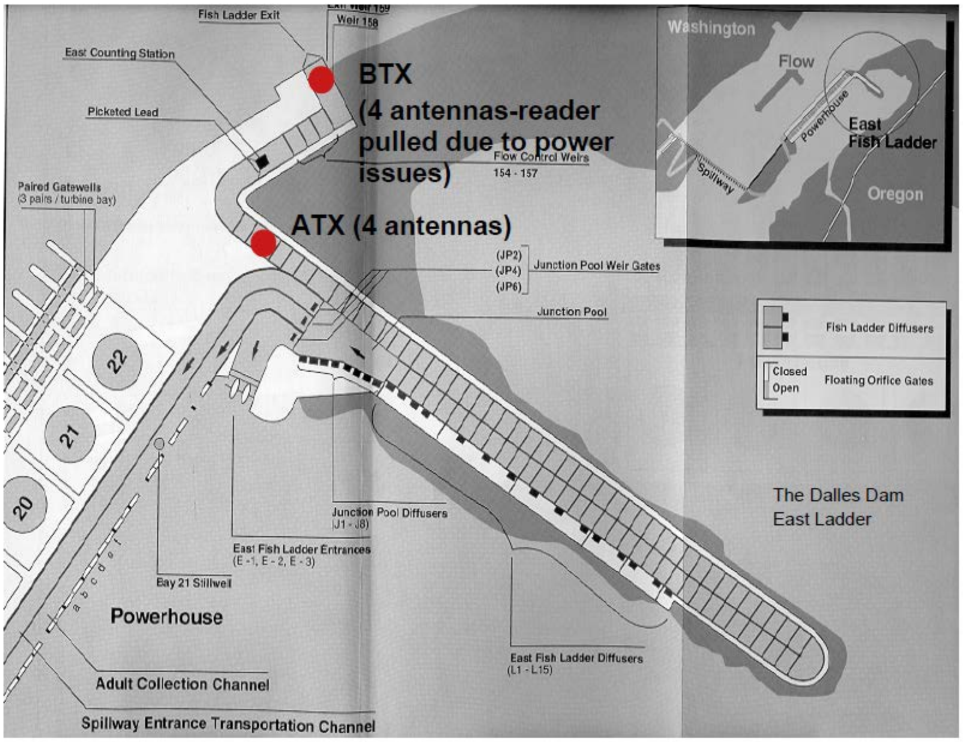

Figure B8. University of Idaho HD PIT antenna locations at The Dalles Dam in 2012 (East fishway).

The Dalles Dam - 2012 Setup

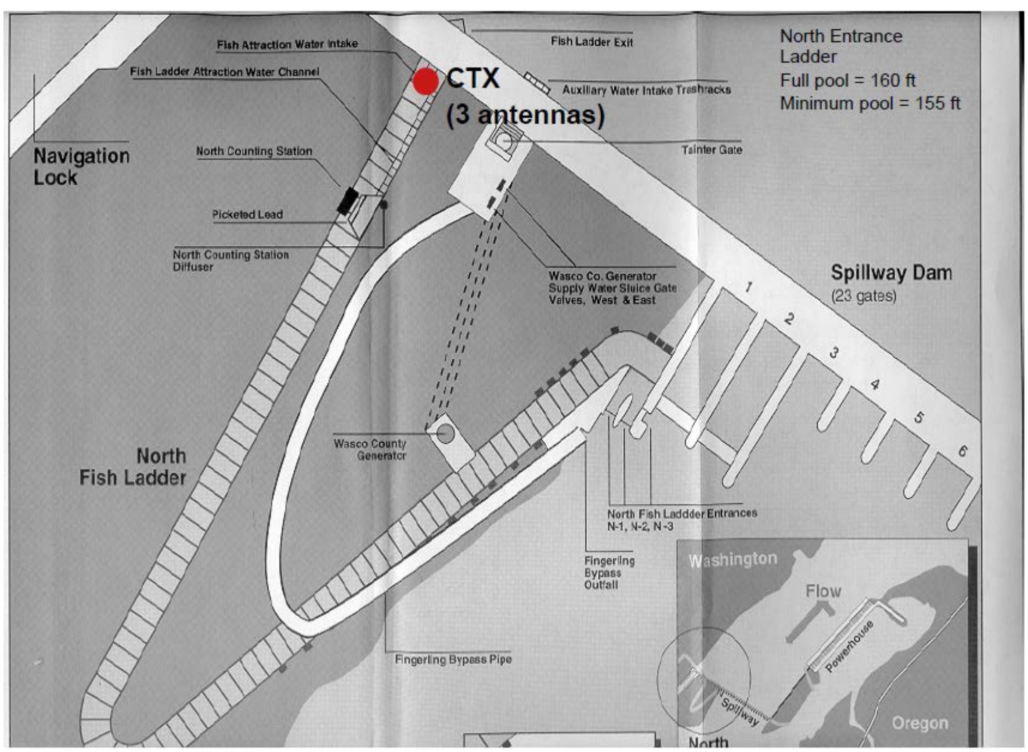

Figure B9. University of Idaho HD PIT antenna locations at The Dalles Dam in 2012 (North fishway).

John Day Dam - 2012 Setup

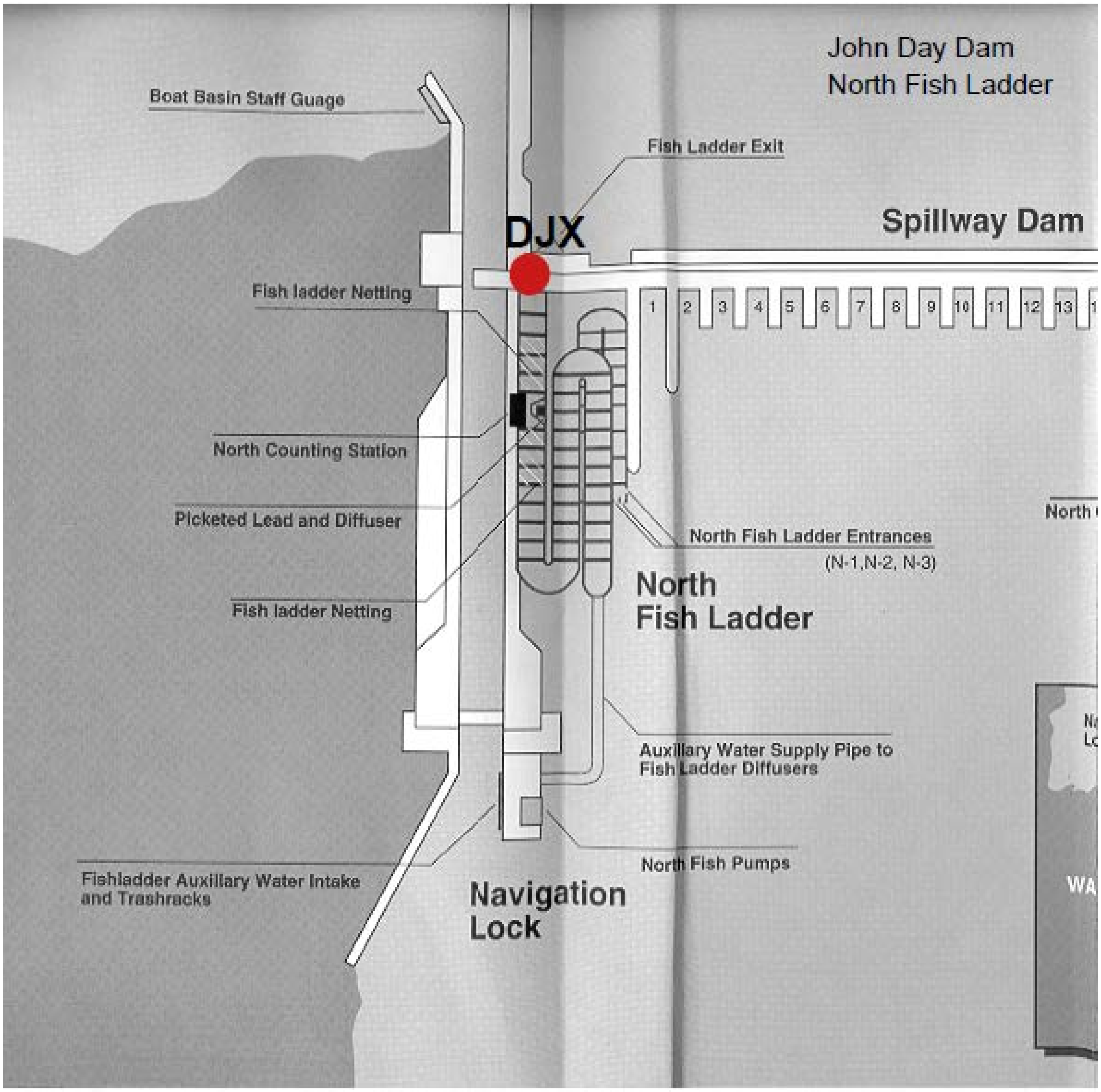

Figure B10. University of Idaho HD PIT antenna locations at John Day Dam in 2012 (North fishway).

John Day Dam - 2012 Setup

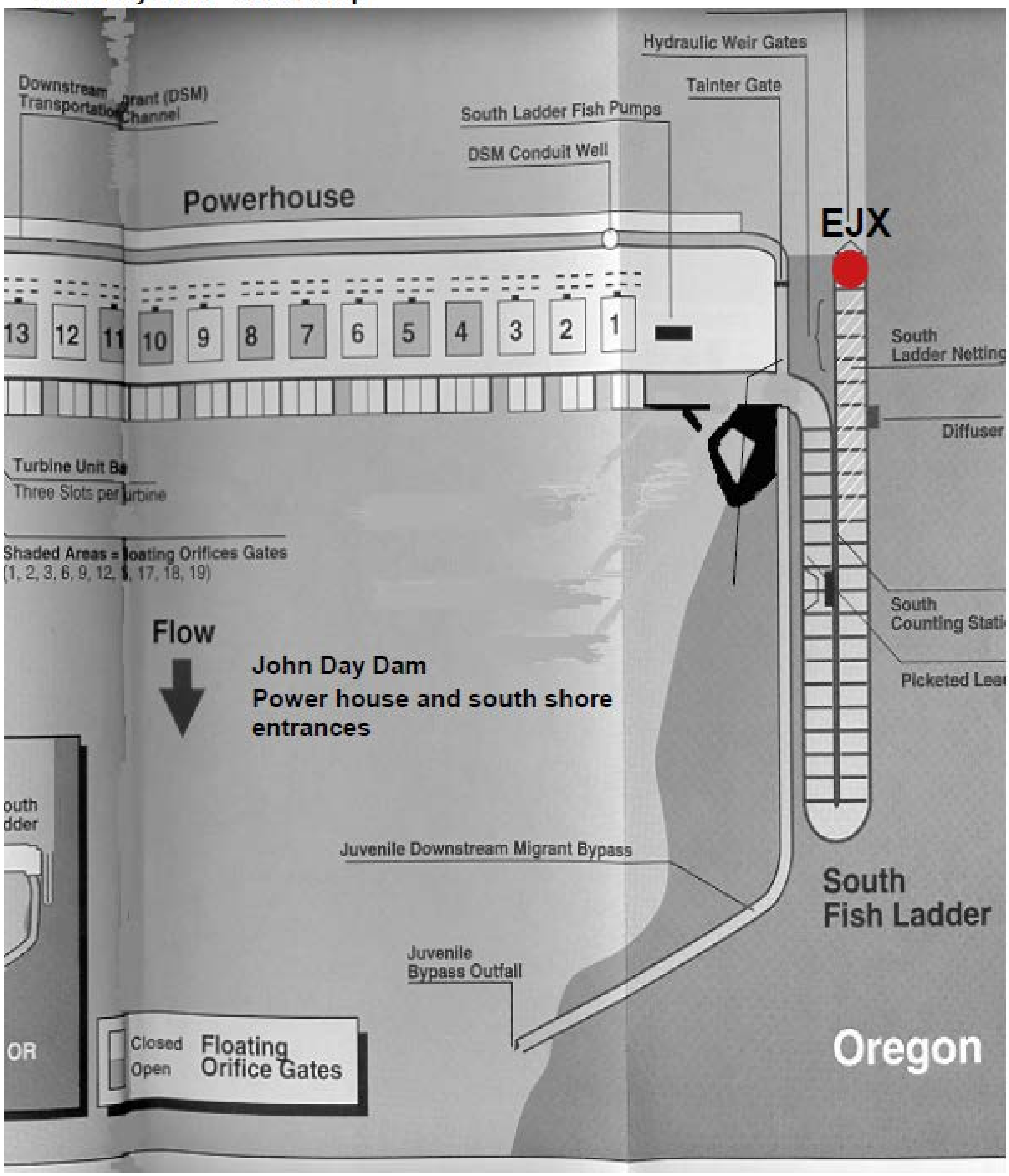

Figure B11. University of Idaho HD PIT antenna locations at John Day Dam in 2012 (East fishway).

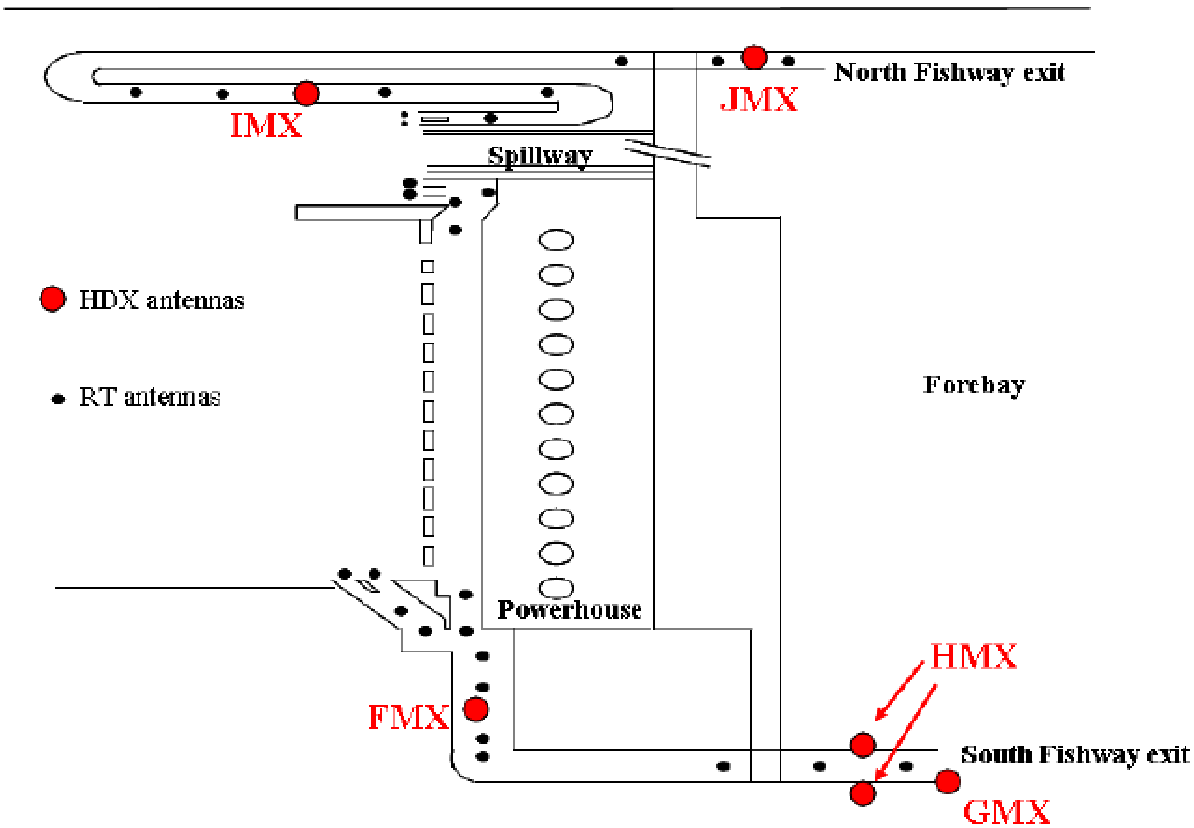

Figure B12. University of Idaho HD PIT antenna locations at McNary Dam in 2012.

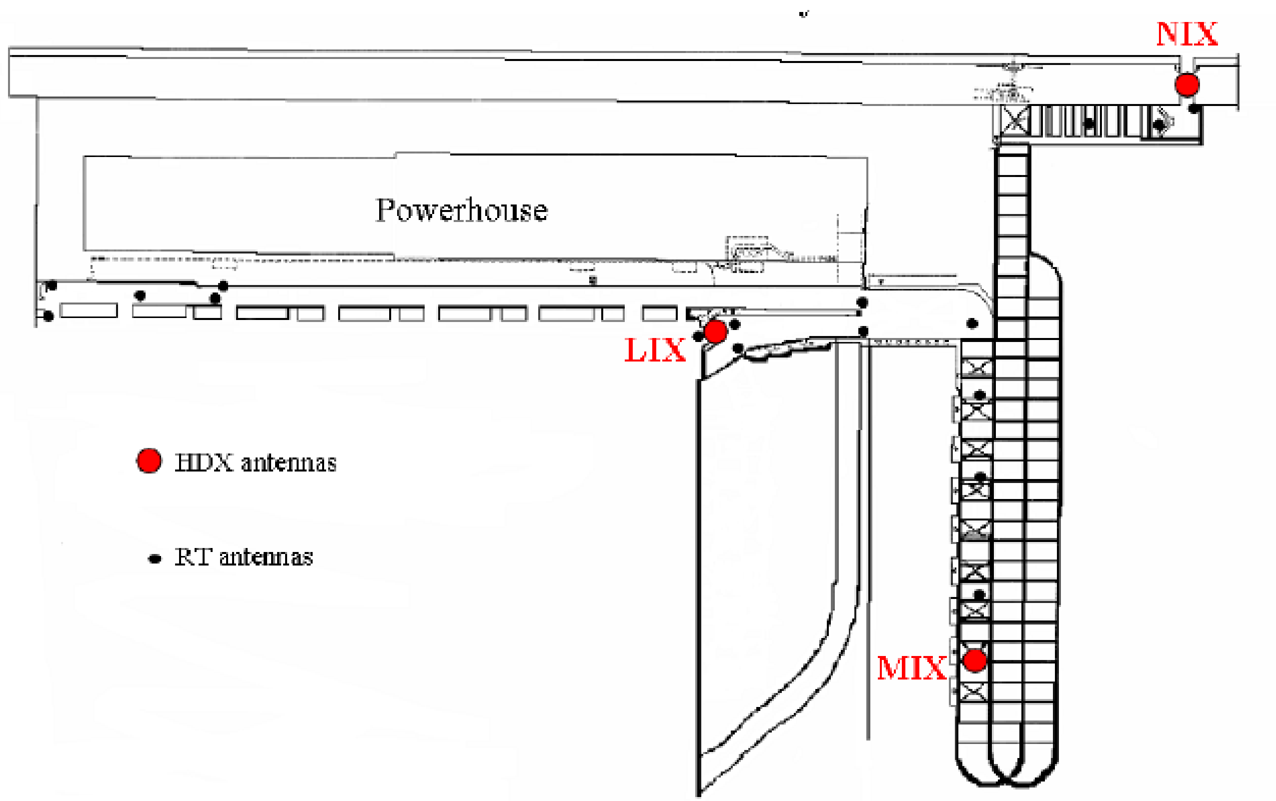

Figure B13 University of Idaho HD PIT antenna locations at Ice Harbor Dam in 2012 (South fishway).

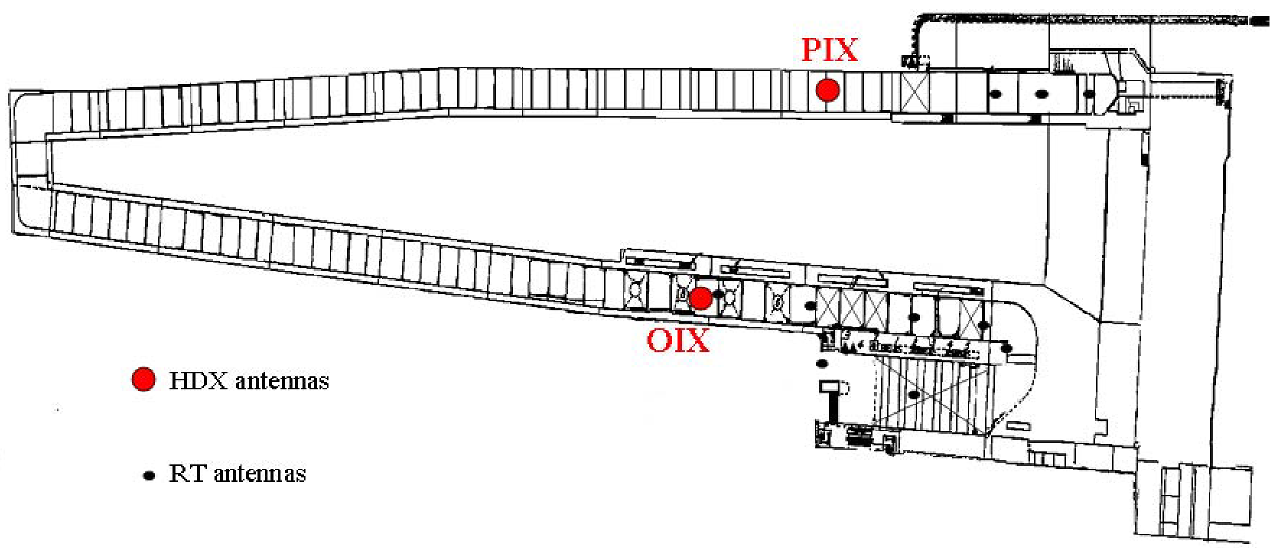

Figure B14. University of Idaho HD PIT antenna locations at Ice Harbor Dam in 2012 (North fishway).

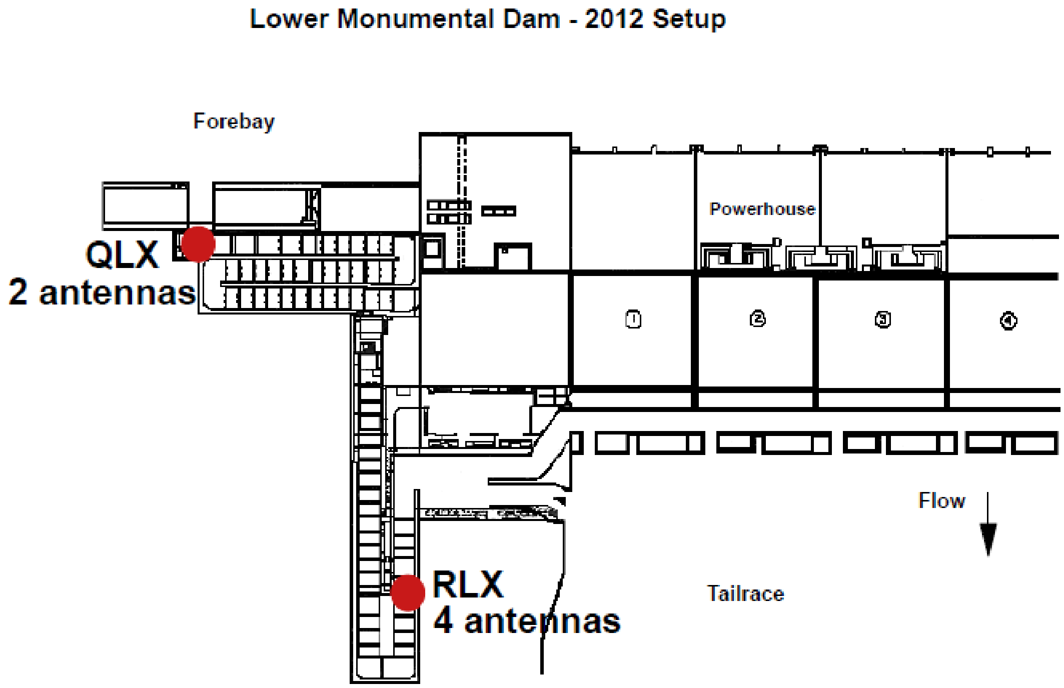

Figure B15. University of Idaho HD PIT antenna locations at Lower Monumental Dam in 2012 (North fishway).

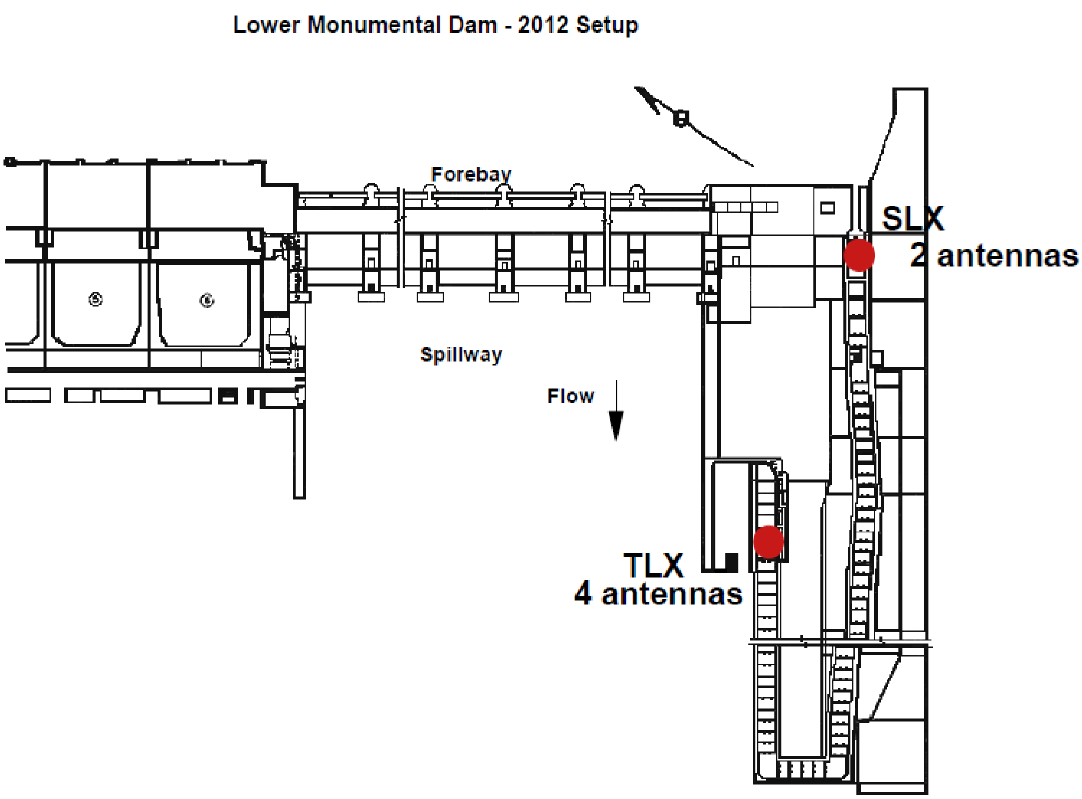

Figure B16. University of Idaho HD PIT antenna locations at Lower Monumental Dam in 2012 (South fishway).

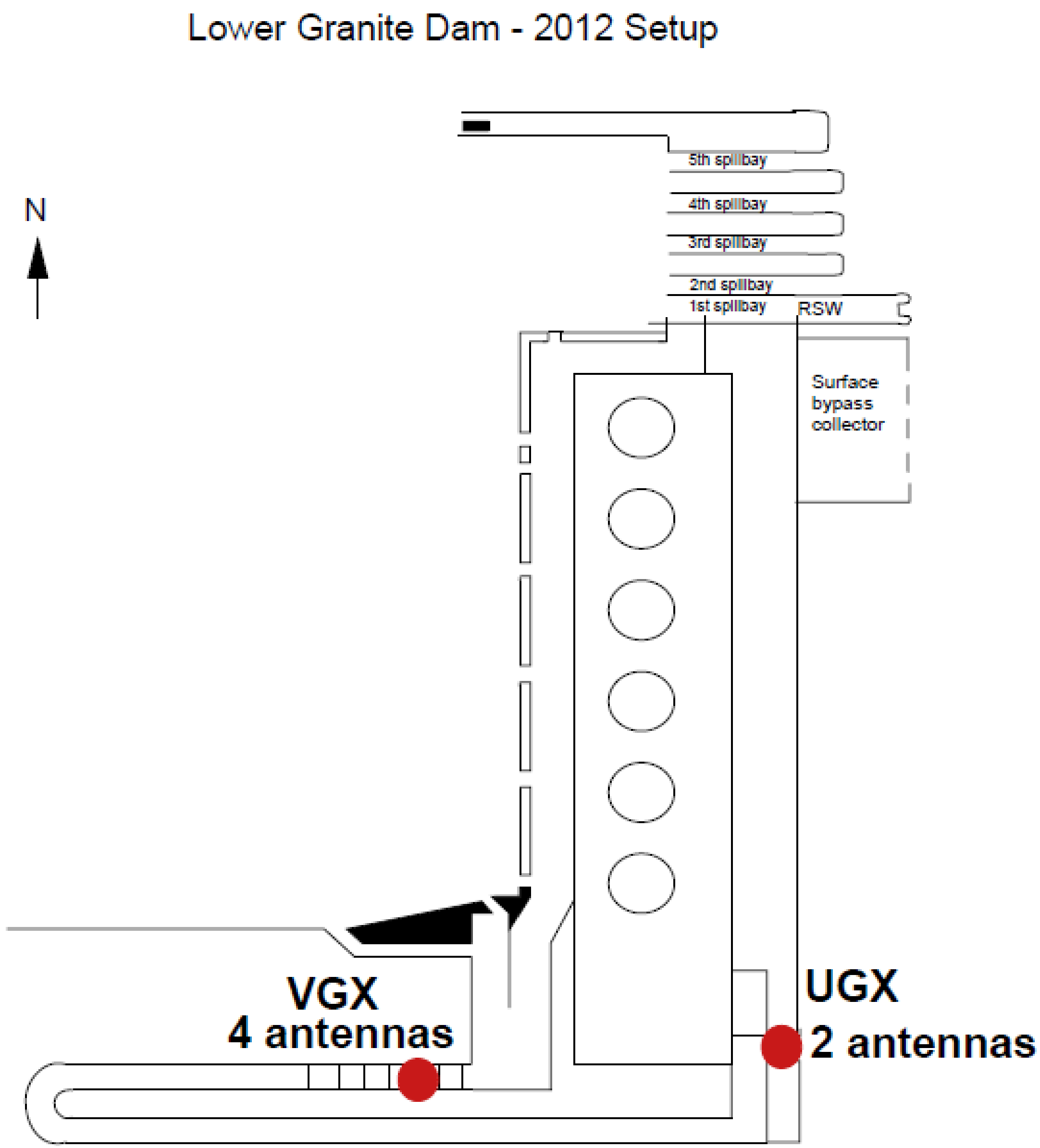

Figure B17. University of Idaho HD PIT antenna locations at Lower Granite Dam in 2012.