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IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

ADULT PACIFIC LAMPREY MIGRATION IN THE LOWER COLUMBIA RIVER: 2008 RADIOTELEMETRY AND 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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Abstract

Monitoring adult Pacific lamprey (*Lampetra tridentata*) run size and migration behaviors in the Columbia River basin is difficult given their cryptic and photo-negative behaviors. In this study we tagged lamprey with half duplex (HDX) passive integrated transponder (PIT) tags and radio transmitters and monitored their passage at Bonneville, The Dalles, John Day, McNary, Ice Harbor, and Priest Rapids dams. Our objectives were to calculate lamprey passage times, to estimate escapement past the monitored sites, and to evaluate potential correlates with lamprey escapement and behaviors through the study reaches. We also examined system detection efficiencies and potential tagging effects using a subset of double-tagged lampreys.

In 2008, we radio-tagged 595 lampreys and HDX-PIT tagged 908 lampreys. Of these, 299 were double-tagged with both a radio transmitter and a PIT tag. Escapement estimates from release below Bonneville Dam to top-of-ladder antennas were 26% for radio-tagged fish and 52% for HDX-PIT tagged fish. Escapements from the top of Bonneville Dam to top-of-ladder antennas at The Dalles Dam were 40% for radio-tagged fish and 52% for HDX-PIT tagged fish. Escapements from the top of The Dalles Dam to top-of-ladder antennas at John Day Dam were 43% for radio-tagged fish and 66% for HDX-PIT tagged fish. Large lampreys in both the radiotelemetry and HDX-PIT studies were significantly more likely than small lampreys to pass through most of the monitored dam-to-dam reaches.

Lamprey migration times were highly variable, but tended to be slow at dams and relatively rapid through reservoirs. Median passage times for radio-tagged fish were 5.6 days from release past Bonneville Dam, 5.8 days between top-of-ladder antennas at Bonneville and The Dalles dams, and 5.0 days between top-of-ladder antennas at The Dalles and John Day dams. Median times for HDX-PIT tagged lamprey over these same reaches were 7.7 days, 4.9 days, and 3.7 days, respectively. Lampreys with both tag types migrated more rapidly later in the season, coincident with increasing river temperatures and decreasing river discharge.

The use of 299 double-tagged fish helped refine detection efficiency estimates for both monitoring systems. At top-of-ladder sites where both systems were deployed, the radiotelemetry arrays were generally more efficient at detecting double-tagged fish, although some fish were detected only on the HDX-PIT system. Higher escapement estimates by HDX-PIT tagged fish, compared to radio-tagged fish, was consistent with results from a similar study in 2007 and suggest that radio tagging and associated handling may negatively affect adult performance. This suggests a tradeoff between tagging effects and the collection of high resolution, fine-scale data provided by the active radio tag telemetry system. We conclude that the combined radiotelemetry and PIT-tag results provide complimentary data that can be used to inform adult lamprey management actions at a variety of scales.

Introduction

Pacific lamprey (*Lampetra tridentata*) 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 (Close et al. 2002; Kostow 2002). Habitat loss, river impoundment, ocean conditions, and water pollution have all likely contributed to the decline. Lampreys are also relatively poor swimmers and have difficulty passing through Columbia and Snake River dam fishways designed for adult salmonids (Moser et al. 2002b; Johnson et al. 2009).

Monitoring Columbia River basin lamprey populations has been a challenge. Lamprey counts at dam fish ladders can only be used as indicators of relative abundance and general run timing (e.g., Keefer et al. *in press a*) because counts generally take place only during the day and most lamprey passage occurs at night (Moser et al. 2002a; Robinson and Bayer 2005; Clabough et al. 2008). Radiotelemetry has been used in a series of studies over the last decade in an effort to improve monitoring, identify problem passage areas, and estimate survival of adult Pacific lamprey in the basin (e.g., Moser et al. 2002b; 2005). Starting in 2005, half duplex (HDX) passive integrated transponder (PIT) tag monitoring sites have been deployed at dams to monitor larger samples of PIT-tagged adult lamprey. Like radio transmitters, PIT tags are uniquely identifiable, allowing monitoring of individual fish. 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 Hydrosystem (Daigle et al. 2008) and some lamprey are too small for radio transmitters. HDX-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 they HDX-PIT tags have longer read ranges.

The objectives of the 2008 studies described in this report were to use both radiotelemetry and HDX-PIT systems to: (1) calculate adult lamprey passage rates past multiple dams and reservoirs; (2) estimate lamprey escapement past multiple dams and through individual dam-to-dam reaches; (3) examine potential physiological and environmental correlates with upstream passage; (4) compare results by tag type; and (5) to evaluate radiotelemetry and HDX-PIT system detection efficiencies and radio tag effects using a sub-sample of double-tagged fish. Results from a separate set of study objectives, which included describing fine-scale lamprey passage behaviors at individual dams, will be presented in a separate report.

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 and at the Washington-shore fishway entrance. In 2008, 908 lampreys were tagged with half-duplex passive integrated transponder (HDX-PIT) tags, and 595 were tagged with radio transmitters. Of these samples, 299 were tagged with both a radio transmitter and an HDX-PIT tag. No fish with girth < 9 cm at the dorsal fin were radio-tagged. All fish with only a HDX-PIT tag were released approximately three kilometers downstream near Hamilton Island. Radio-tagged and double-tagged fish were released near Hamilton Island (n = 312) or near Tanner Creek (n = 283) at Columbia River rkm 232.5.

Before tagging, all fish were anaesthetized using 60 ppm (3 mL•50 L^{-1}) clove oil, and measured (length and girth to the nearest mm), and weighed (nearest g). HDX-PIT fish were then outfitted with

a uniquely-coded glass encapsulated HDX-PIT tag (Texas Instruments, 4×32 mm, 0.8 g). HDX-PIT tags were surgically implanted in the body cavity of anaesthetized fish through a small incision (< 1 cm) along the ventral midline and in line with the anterior insertion of the first dorsal fin as described in Moser et al. (2006). Uniquely-coded radio tags (18.3 mm length, 8.3 mm diameter, 2.1 g in water; model NTC-4-2L, Lotek Wireless Inc.) were surgically implanted using the methods described in Moser et al. (2002a). Double-tagged fish had both a transmitter and a PIT tag inserted through the same incision. An additional physiological measure, muscle lipid content (% lipid), was collected for all radio-tagged and most HDX-PIT tagged lampreys using a Distell fat meter (e.g., Crossin and Hinch 2005). Fat meter readings were converted to estimated % lipid (wet weight basis) using the regression equation % lipid = 3.618 * reading – 2.436 ($P < 0.01$; $R^2 = 0.4808$; N = 33). The regression equation was developed by comparing Fatmeter readings taken on live lamprey captured at Bonneville (N=20) and McNary (N = 13) to lipid levels determined by biochemical proximate analysis on the same individuals following euthanasia. Proximate analysis was performed by the Wildlife Habitat Nutrition Laboratory, Washington State University, Pullman, Washington.

Monitoring Sites

Lamprey movements were monitored using an array of fixed-site radiotelemetry antennas and receivers (Table 1) and HDX-PIT interrogation sites (Table 2). Radio receivers at the lower Columbia River dams and in reservoirs and tributaries were equipped with digital spectrum processors (DSP's) to receive transmissions on several frequencies simultaneously. Aerial antennas were used to monitor dam tailraces and several tributary confluence areas. Underwater antennas and a few directed aerial antennas detected radio-tagged fish as they approached, entered, and exited fishway openings, movements inside fishways and transition pools, and exits from ladders into dam forebays. (Note: dam maps showing relative positions of monitoring sites are included in Appendix A.)

Underwater HDX-PIT antennas were located inside dam fishways at the four lower Columbia River dams, and at Priest Rapids and Ice Harbor dams. Antennas were located near top-of-ladder exits at all dams. At Bonneville Dam, additional sites were located at lamprey bypass structures, inside the Washington-shore entrance, and in 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 2).

Data Analyses

Reach escapement rates were calculated by dividing the number of lamprey known to pass an upstream HDX or radiotelemetry site by those known to pass a downstream site or by the number released. Fish were treated as passing a site if they were detected at the site or were detected at a location further upstream. Escapement rates were calculated across all release dates as well as for individual release days and blocks of days to evaluate seasonal effects. Lamprey sizes — including length, weight, and girth — were compared for groups that migrated through a reach and those that did not pass using general linear models (PROC GLM, SAS) and analysis of variance.

Lamprey migration times (d) and passage rates ($km \bullet d^{-1}$) were calculated from release to top-of-ladder HDX-PIT and radiotelemetry antennas at dams and between monitored sites. Linear regression was used to evaluate relationships between log-transformed lamprey passage times and fish size (length, girth, weight), release date or date fish entered upstream reaches, and 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 qualitative as it was difficult to assign fully representative metrics to radiotelemetry records given the variable and often long passage times.

Table 1. Radiotelemetry receiver and antenna sites used to monitor lamprey passage at lower Columbia River dams, in reservoirs, and in tributaries in 2008. (Note: additional radiotelemetry sites were used at Snake River dams upstream from Ice Harbor Dam.) See Appendix B for maps of dam antenna sites.

Site	Location	Antenna(s) Type	Antenna(s) Number
Bonneville Dam	Tailrace	Aerial	2
	PH 1, South-shore entrance	Underwater	3
	PH 1, North-shore entrance	Underwater	5
	PH 1, A-Branch transition pool	Underwater	3
	PH 1, A- and B-Branch junction pool	Underwater	4
	PH 1, Bradford Island makeup water channel	Underwater	3
	PH 1, Bradford Island exit	Underwater	1
	B-Branch entrance	Underwater	5
	B-Branch transition pool	Underwater	3
	Cascades Island entrance	Underwater	4
	Cascades Island transition pool	Underwater	4
	Cascades Island makeup water channel	Underwater	10
	PH 2, South-shore entrances	Underwater	7
	PH 2, North-shore entrances	Underwater	7
	PH 2, WA-shore transition pool	Underwater	6
	PH 2, WA-shore ladder and turnpool	Underwater	4
	PH 2, WA-shore entrance lamprey trap	Underwater	3
	PH 2, WA-shore ladder / UMT channel pool	Underwater	3
	PH 2, WA-shore ladder makeup water channel	Underwater	3
	PH 2, WA-shore counting window	Underwater	5
	PH 2, WA-shore ladder exit	Underwater	1
The Dalles Dam	Tailrace	Aerial	2
	South spillway entrance	Underwater	2
	Powerhouse entrances	Underwater	4
	East ladder entrance	Underwater	5
	East ladder entrance	Aerial	1
	East ladder transition pool	Underwater	5
	East ladder exit	Underwater	1
	North ladder entrance	Underwater	1
	North ladder entrance	Aerial	1
	North ladder entrance / transition pool	Underwater	5
	North ladder exit	Underwater	1
John Day Dam	Tailrace	Aerial	2
	South ladder exit	Underwater	1
	North ladder exit	Underwater	1
McNary Dam	Tailrace	Aerial	2
	South-shore entrance	Underwater	2
	South-shore entrance	Aerial	2
	South-shore transition pool / ladder	Underwater	7
	South ladder exit	Underwater	3
	North powerhouse entrance	Underwater	3
	North powerhouse entrance	Aerial	2
	North-shore entrance	Underwater	1
	North-shore entrance	Aerial	2
	North-shore transition pool / ladder	Underwater	5
	North ladder exit	Underwater	3

Table 1. Continued.

Site	Location	Antenna(s) Type	Antenna(s) Number
Priest Rapids Dam	East ladder exit	Underwater	1
	West ladder exit	Underwater	1
Reservoir sites	Bridge of the Gods	Aerial	1
	Fort Raines	Aerial	1
Tributaries	Rock Creek	Aerial	1
	Wind River	Aerial	1
	Little White Salmon River	Aerial	1
	White Salmon River	Aerial	1
	Hood River	Aerial	5
	Klickitat River	Aerial	1
	Fifteenmile Creek	Aerial	1
	Deschutes River	Aerial	4
	John Day River	Aerial	1
	Umatilla River	Aerial	1
	Walla Walla River	Aerial	1
	Yakima River	Aerial	1

Table 2. Half-duplex PIT tag interrogation sites (antennas) used to monitor lamprey passage at lower Columbia and Snake river dams in 2008. NOAA-Fisheries maintained sites in the Bonneville lamprey bypass systems and at the Cascades Island fishway site. See Appendix B for maps of dam 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
	Cascades Island	1
The Dalles Dam	Below East ladder count window	4
	East ladder exit (above count window)	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
Priest Rapids Dam	East ladder exit	3
	West ladder exit	3

Detection efficiencies for both HDX-PIT and radiotelemetry sites were estimated by dividing the number of fish known to pass a site by the number detected. These estimates were imprecise because fish could pass via alternate routes at many locations (e.g., navigation locks). It was unknown how many fish passed undetected at any dam, and estimated efficiencies were qualitative. However, use of double-tagged fish in 2008 allowed more precise estimates of detection efficiencies at fishway antennas compared to previous years. Efficiencies for both tag types were evaluated at sites where radiotelemetry and HDX-PIT antennas were in close proximity, primarily at top-of-ladder locations.

Double-tagged fish were treated differently in analyses depending upon the objective. For example, in some cases it was appropriate to compare three tagging groups (radio-tag only, HDX-PIT tag only, and double-tag). In other analyses, all radio-tagged fish were lumped together (i.e., including double-tagged fish). In the results below we specified which groups were used for each analysis.

Results

Lamprey Collection and Tagging

Tagging effort differed for the three primary tag groups (Figure 1). Radio-tagging occurred from 31 May through 18 August, with the effort concentrated during traditional peak lamprey passage months of June and July. A total of 595 lampreys were radio-tagged, and about half of these (n = 299) were also tagged with HDX-PIT tags. The tagging schedules for radio-only and double-tagged fish were nearly identical. In contrast, HDX-PIT tagging (n = 908) occurred from 31 May through 5 September, with relatively larger numbers of fish tagged in June and in late August–early September compared to the radio-tagged group (Figure 1). Mean tag dates differed (F = 12.9, $P < 0.001$, ANOVA) among the radio-tagged-only, HDX-PIT-only and double-tagged groups; mean tag dates were 5-6 d earlier for the HDX-PIT-only group.

Regardless of how the sample was separated, lamprey size metrics in 2008 were all positively correlated: length×girth $0.61 < r < 0.77$; length×weight $0.86 < r < 0.89$; length×%lipid $0.18 < r < 0.35$; girth×weight $0.83 < r < 0.95$; girth×%lipid $0.24 < r < 0.41$; weight×%lipid $0.29 < r < 0.37$ (Figure 2, Table 3). Percent lipid was more variable than the other metrics. For example, for the full sample the coefficient of variation (CV) for mean %lipid was 28% versus 19% for weight, 8% for girth, and 7% for length (Table 4). We note that %lipid was not collected for all lampreys. None of the size metrics was correlated with fish release date ($P > 0.05$) for the radio-tagged or double-tagged groups. However, release date was negatively correlated with lamprey length, girth, and weight metrics for the larger sample of HDX-PIT-only lampreys and for the full sample ($P \leq 0.01$), but correlations were low ($-0.27 < r < -0.11$).

On average, HDX-PIT tagged lampreys were smaller than radio-tagged and double-tagged fish (Table 4) at least in part because of the 9 cm girth restriction for radio tagging. Length, weight, and girth were all lower ($18.3 < F < 22.1$, $P < 0.001$) for lamprey tagged with only an HDX-PIT tag. In some cases, double-tagged fish were also larger ($P < 0.05$) than those with only radio tags. The %lipid metric had a different pattern, with HDX-PIT-only fish showing higher mean %lipid measures than fish with radio tags, though %lipid was not collected for all fish.

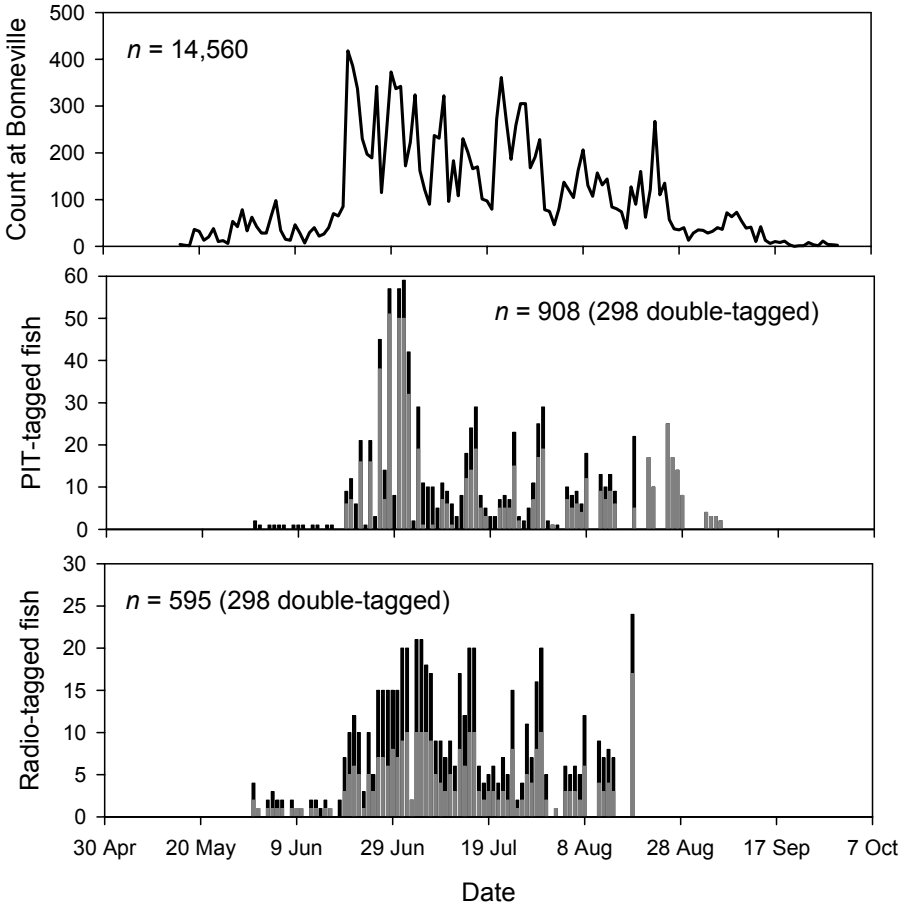

Figure 1. Number of adult Pacific lamprey counted passing Bonneville Dam via fish ladders during the day (top panel) and the numbers that were collected and HDX-PIT tagged (middle panel) or radio-tagged (bottom panel) in 2008. Double-tagged fish are indicated by the black portion of the bars on each figure. Note different y-axis scales.

Table 3. Sample sizes (*n*) and correlation coefficients (*r*) for adult Pacific lamprey size metrics in 2008 for radio-tagged, HDX-PIT-only, double-tagged, and all fish combined. All correlations had $P < 0.05$. Note: one outlying HDX-PIT tagged lamprey was excluded (length = 31 cm, girth = 6.4 cm, weight = 74 g, %lipid = 47.1%).

	Radio only		HDX-PIT only		Double-tagged		All fish	
	n	*r*	*n*	*r*	*n*	*r*	*n*	*r*
Length×Girth	295	0.705	607	0.769	299	0.611	1201	0.730
Length×Weight	296	0.889	607	0.882	299	0.862	1202	0.884
Length×%Lipid	289	0.350	500	0.247	282	0.180	1071	0.223
Girth×Weight	295	0.884	607	0.950	299	0.834	1201	0.914
Girth×%Lipid	288	0.359	500	0.405	282	0.243	1070	0.319
Weigth×%Lipid	289	0.373	500	0.354	282	0.297	1071	0.306

Table 4. Length, girth, weight, and percent lipid of adult Pacific lampreys collected and tagged with radio transmitters, with HDX-PIT tags, and that were double-tagged at Bonneville Dam in 2008. (Total *n* = 595 radio, 908 HDX-PIT, and 299 double-tagged.) 1 HDX-PIT-only outlier excluded

	Length (cm)			Girth (cm)			Weight (g)			Percent lipid (%)		
Type	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*
Radio-all	595	66.2	4.2	594	10.9	0.8	595	464.5	78.8	571	25.8%	7.5%
Radio-only	296	65.7	4.4	295	10.8	0.8	296	457.2	81.3	289	24.6%	6.8%
PIT-all	906	65.3	4.4	906	10.8	0.9	906	446.6	85.7	782	28.0%	8.0%
PIT-only	607	64.7	4.5	607	10.6	0.9	607	434.2	87.6	500	8.58%	7.7%
Double	299	66.6	4.1	299	11.0	0.7	299	471.7	75.7	282	27.0%	8.0%
All fish	1202	65.4	4.4	1201	10.8	0.9	1202	449.2	84.7	1071	27.1%	7.6%

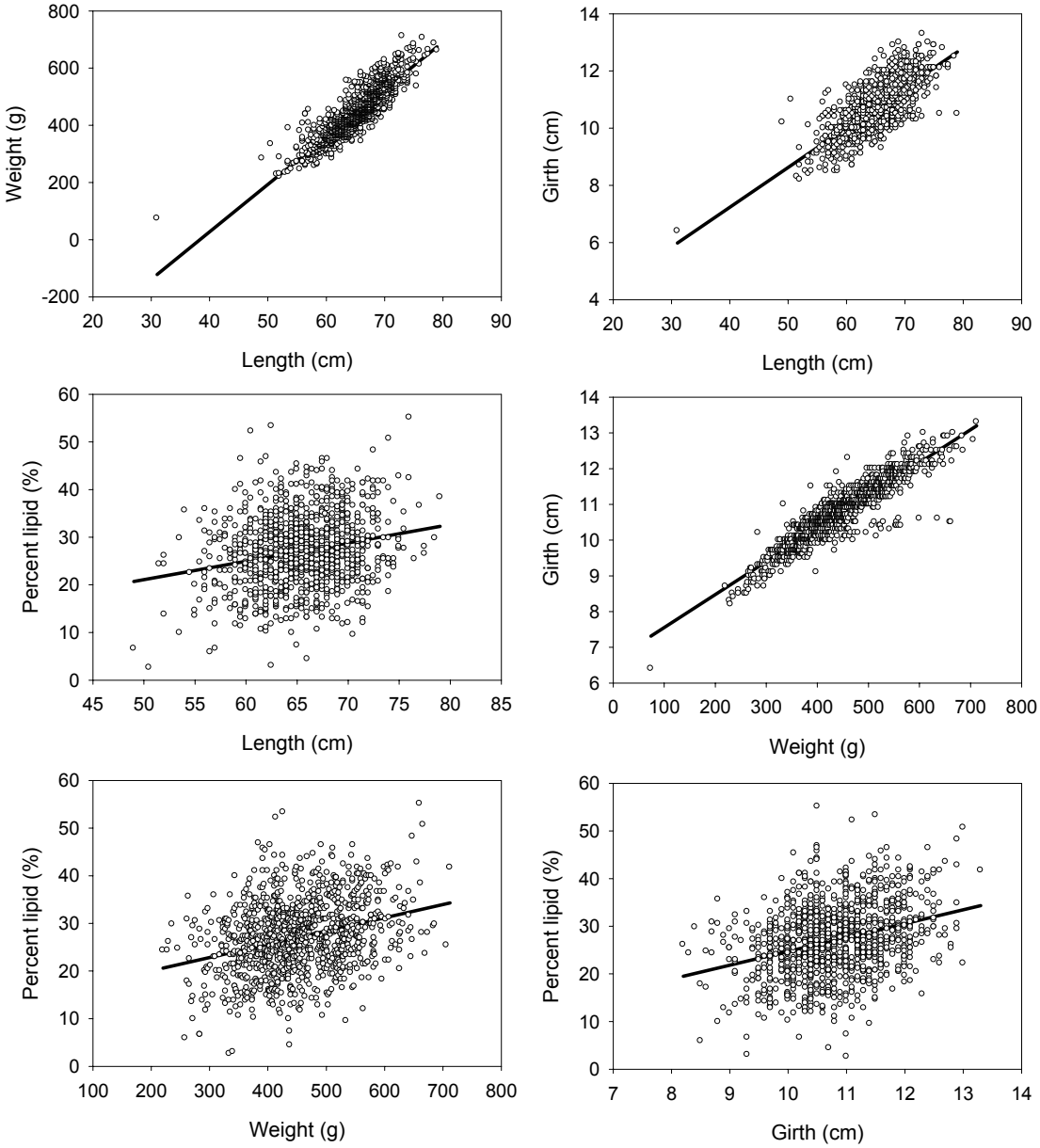

Figure 2. Linear relationships between length, weight, girth, and % lipid metrics for all adult lamprey tagged in 2008 (includes radio-only, HD-PIT-only and double-tagged fish). See Table 3 for correlation coefficients.

Radio-Tagged Lampreys (All Fish)

Upstream Progression – Of the 595 radio-tagged lamprey released downstream from Bonneville Dam, 444 (74.6%) were subsequently recorded at antennas at Bonneville Dam (excluding the aerial tailrace sites that potentially covered the release location) or at sites further upstream. A total of 156 fish passed the dam (26.2% of the 595 released, and 35.1% of the 444 detected at Bonneville antenna sites). The 156 total past the dam included three fish detected on the HDX system that passed with non-functioning radio transmitters (or had lost transmitters) and ten fish that were recaptured in the adult trap and released upstream from the dam.

The most upstream recorded locations for the 439 fish that did not pass the dam were: 147 (33%) in the tailrace only; 122 (28%) approaching fishway entrances; 110 (25%) inside fishways, collection channels, or transition pools; and 56 (13%) in the ladders either upstream from transition pools or at sites near the tops of ladders. Four lampreys were never detected after release.

Fish that returned to the Bonneville fishways (i.e., were detected at fishway entrance antennas or further upstream) were slightly larger than fish that did not return. On average, returning fish were 1.3 cm longer, 19.8 g heavier, and had 0.1 cm wider girth (ANOVA $P \leq 0.008$, length and weight) (Table 5). Returning fish were also tagged 5 d earlier, on average, than non-returning fish ($P < 0.001$), suggesting possible timing-related survival effects after release or seasonal changes in migration behavior. Lampreys that passed Bonneville Dam were larger than fish that were recorded at fishway antennas but did not pass; however, these size differences were not statistically significant (length, $P = 0.064$; weight, $P = 0.150$; girth, $P = 0.243$).

The median tag date for all radio-tagged lampreys was 10 July. Median recorded passage dates at top-of-ladder sites were 15 July at Bonneville Dam ($n = 142$ recorded), 27 July at The Dalles Dam ($n = 60$), 8 August at John Day Dam ($n = 21$), and 27 August at McNary Dam ($n = 4$). Top-of-ladder migration timing distributions for the radio-tagged fish approximated those for daytime lamprey counts at the dams (Figure 3), except that the early portion of the run was under-represented and the sample size was very small at McNary Dam.

Dam-to-Dam Escapement – Of 595 fish released, 26.2% ($n = 156$) were known to have passed Bonneville Dam, 10.6% ($n = 63$) passed The Dalles Dam, 4.5% passed John Day Dam, and 1.2% passed McNary Dam (Table 6). Importantly, these estimates included both ten fish that were recaptured at the Bonneville adult trap and released upstream from Bonneville Dam and a handful of fish that were detected passing only on the HDX-PIT systems. Estimates based solely on radio radiotelemetry data only were 0.1-1.0% lower (Table 6). Escapement estimates from the top of Bonneville Dam (including the ten recaptured fish) were 40.4% to the top of The Dalles Dam, 17.3% to the top of John Day Dam, and 4.5% to the top of McNary Dam. From the top of The Dalles Dam, estimates were 42.9% and 11.1% to the top of John Day and top of McNary dams, respectively. Dam-to-dam estimates based on radiotelemetry data only were 0.5-8.5% lower, reflecting an increasing percentage of fish detected only on the HDX-PIT systems at upstream dams (Table 6).

Daily release group escapement estimates from release sites to the top of Bonneville Dam were quite variable, with few strong patterns (Figure 4). However, the lowest daily escapement estimates were concentrated in the early June portion of the run. Sample sizes during this time were small (≤ 4 fish/d).

In most cases, lampreys that passed dams upstream from Bonneville Dam and dam-to-dam reaches were larger than those that did not pass (Table 5). Length and weight differences were statistically significant ($P < 0.05$, ANOVA) for the reaches from the release site to the top of The Dalles, John Day, and McNary dams and between pairs of dams (except John Day to McNary).

Differences in girth were somewhat less statistically significant, though fish that passed upstream consistently had larger girth. The %lipid metric did not differ significantly in any comparison, while tag date differed only from the release to Bonneville fishway approach segment (Table 5).

Table 5. Mean radio-tagged lamprey size metrics and tag dates in relation to their escapement through the monitored reaches in 2008. Top-of-ladder sites were used for the upper end of each reach. *F* and *P* values are from analysis of variance tests (ANOVA). Results include double-tagged fish recorded passing dams on the HDX system only.

Reach	Passed	Length (*n*)	Weight (*n*)	Girth (*n*)	%Lipid (*n*)	Tag date (*n*)
Release-Bonneville[1]	No	65.2 (151)	449.7 (151)	10.8 (151)	26.5 (145)	16 Jul (151)
	Yes	66.5 (444)	469.5 (444)	10.9 (443)	25.4 (426)	11 Jul (444)
	F	11.81	7.20	2.67	1.45	11.61
	P	**<0.001**	**0.008**	0.124	0.230	**<0.001**
Bonneville[1]- Bonneville top A	No	66.3 (288)	465.5 (288)	10.9 (287)	25.4 (274)	11 Jul (288)
	Yes	67.0 (156)	476.9 (156)	11.0 (156)	25.4 (152)	12 Jul (156)
	F	3.44	2.08	1.37	0.05	0.62
	P	0.064	0.150	0.243	0.816	0.432
Release-Bonneville top A	No	65.9 (439)	461.4 (439)	10.9 (438)	25.8 (419)	13 Jul (439)
	Yes	67.0 (156)	480.8 (156)	11.0 (156)	25.8 (152)	12 Jul (156)
	F	8.31	5.24	2.75	0.04	0.18
	P	**0.004**	**0.022**	0.098	0.841	0.672
Release-The Dalles top	No	66.0 (532)	460.6 (532)	10.9 (531)	25.8 (508)	13 Jul (532)
	Yes	68.1 (63)	497.7 (63)	11.1 (63)	26.1 (63)	12 Jul (63)
	F	14.57	12.72	5.64	0.37	0.01
	P	**<0.001**	**<0.001**	**0.018**	0.545	0.920
Release-John Day top	No	66.0 (568)	461.4 (568)	10.9 (567)	25.8 (544)	12 Jul (568)
	Yes	69.7 (27)	529.5 (27)	11.5 (27)	26.9 (27)	13 Jul (27)
	F	20.03	19.84	15.10	0.46	0.01
	P	**<0.001**	**<0.001**	**<0.001**	0.498	0.917
Release-McNary top	No	66.1 (588)	463.5 (588)	10.9 (587)	25.8 (564)	13 Jul (588)
	Yes	70.9 (7)	550.3 (7)	11.4 (7)	27.2 (7)	12 Jul (7)
	F	8.68	8.50	2.45	0.31	0.00
	P	**0.003**	**0.004**	0.118	0.579	0.975
Bonneville top A-The Dalles top	No	66.3 (93)	462.8 (93)	10.9 (93)	25.1(89)	12 Jul (93)
	Yes	68.1 (63)	497.7 (63)	11.1 (63)	26.1 (63)	12 Jul (63)
	F	7.13	6.30	2.47	0.67	0.04
	P	**0.008**	**0.013**	0.118	0.413	0.845
The Dalles top-John Day top	No	66.9 (36)	473.8 (36)	10.9 (36)	26.1 (36)	12 Jul (36)
	Yes	69.7 (27)	529.5 (27)	11.5 (27)	26.9 (27)	13 Jul (27)
	F	9.26	7.03	8.33	0.10	0.07
	P	**0.004**	**0.010**	**0.005**	0.752	0.789
John Day top-McNary top	No	69.3 (20)	522.2 (20)	11.5 (20)	26.5 (20)	13 Jul (20)
	Yes	70.9 (7)	550.3 (7)	11.4 (7)	27.2 (7)	12 Jul (7)
	F	1.44	0.75	0.18	0.06	0.02
	P	0.241	0.395	0.674	0.815	0.898

[1] not including tailrace antennas

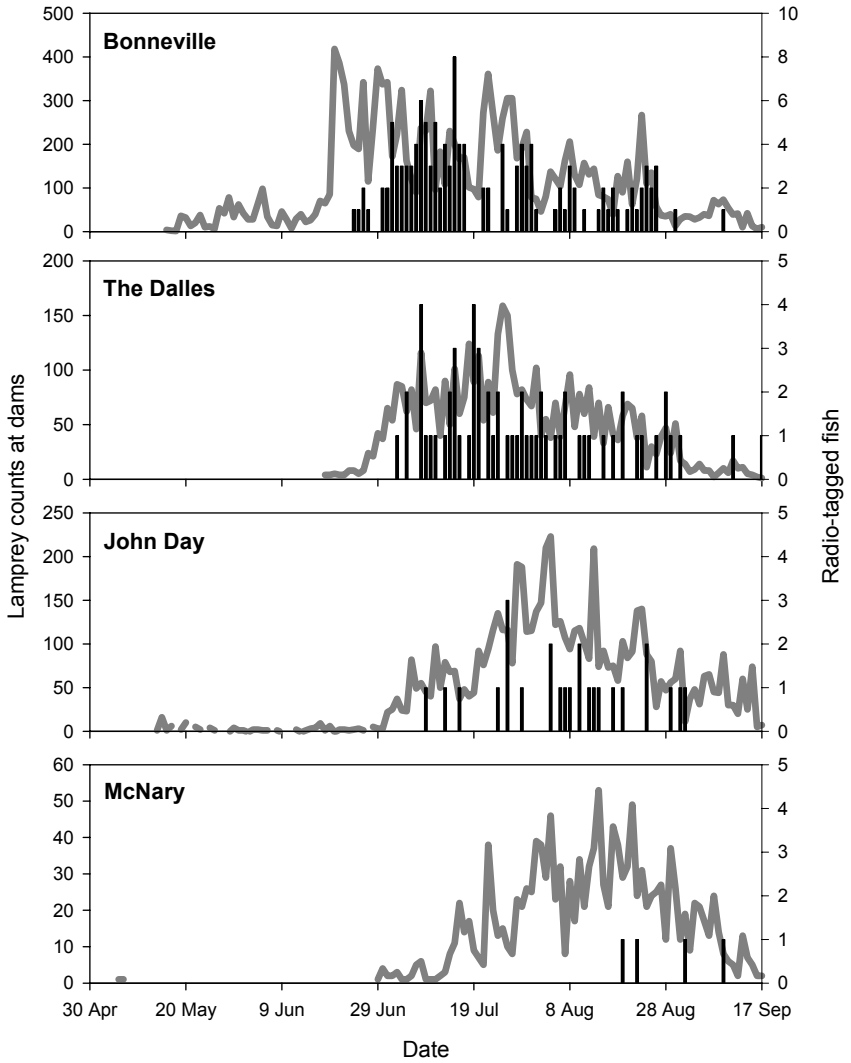

Figure 3. Daily numbers of adult Pacific lampreys counted passing dams via fish ladders (daytime only, gray lines) and the numbers of radio-tagged lampreys that were detected at top-of-ladder radiotelemetry antennas (black bars) in 2008.

Passage Times and Rates – Median radio-tagged lamprey passage times were 5.57 d from the release site to the top of Bonneville Dam, 5.76 d between Bonneville and The Dalles dams, 4.98 d between The Dalles and John Day dams, and 2.84 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 7). Median passage rates (upstream migration distance divided by passage time in days) in these reaches were < 1 km•d^{-1} (release-Bonneville top), 12.7 km•d^{-1} (Bonneville-The Dalles), 7.8 km•d^{-1} (The Dalles-John Day), and 43.3 km•d^{-1} (John Day-McNary). Passage rates through reservoirs only (i.e., from ladder exit at the downstream dam to upstream dam tailrace) were 22.8 km•d^{-1} in the Bonneville reservoir and 17.6 km•d^{-1} in The Dalles reservoir.

Median lamprey passage times through multiple dam-and-reservoir reaches were 14.04 d (5.5 km•d^{-1}) from release to the top of The Dalles Dam, 16.96 d (6.8 km•d^{-1}) from release to the top of John Day Dam, and 35.94 d (6.6 km•d^{-1}) from release to the top of McNary Dam (Table 7).

Lamprey migration times from release to first approach and from release to first enter Bonneville Dam fishways were weakly positively correlated (r = 0.02-0.10, P > 0.05) with lamprey size metrics, positively correlated with release date (r = 0.12, P < 0.05) and negatively correlated with river discharge (r = -0.14, P < 0.05) (Table 8). Passage times from release to exit into the Bonneville Dam forebay were more strongly correlated with the size metrics (r = 0.21-0.26, P < 0.05), with larger fish taking longer to pass, but less correlated with date and river discharge. Passage times from release to sites at dams upstream from Bonneville Dam were mostly positively correlated with lamprey size metrics. However, the only statistically significant (P < 0.05) correlation was that fish migrated faster from release to The Dalles tailrace as temperatures increased (r = -0.46) (Table 8). Significant passage time correlations between pairs of dams included larger fish migrating significantly faster through the Bonneville reservoir (r = -0.44, weight and r = -0.49, length) and faster passage later in the season between top-of-ladder sites at The Dalles and John Day dams (r = -0.46, date).

Table 6. Adult lamprey reach escapement estimates and antenna detection efficiencies for radio-tagged fish in 2008. Two estimates are provided for each site or reach, one that includes HDX-PIT detections of double-tagged fish and a second based only on radiotelemetry detections only. In addition, "Bonneville top A" includes 10 fish recaptured at the adult fish trap and released upstream from the Bonneville Dam; "Bonneville top B" excludes these fish. See Table 1 for antenna locations.

Site	Minimum past site (all tag types)	Radiotelemetry detections (%)	Minimum past site (telemetry only)	Telemetry detections (%)
Release	595		595	
Bonneville[1]	444	99.8%	443	100.0%
Bonneville top A[2]	156	84.0%	153	85.6%
Bonneville top B[2]	146	97.9%	143	91.6%
The Dalles[3]	95	97.9%	93	100.0%
The Dalles top[2]	63	96.8%	61	100.0%
John Day[3]	42	90.5%	38	100.0%
John Day top[2]	27	77.8%	21	100.0%
McNary[3]	8	62.5%	5	100.0%
McNary top[2]	7	57.1%	4	100.0%

	Reach escapement (%)		
	All tag types	Telemetry only	Difference
Release-Bonneville	74.6%	74.5%	0.1%
Release-Bonneville top A	26.2%	25.7%	0.5%
Release-The Dalles	16.0%	15.6%	0.4%
Release-The Dalles top	10.6%	10.3%	0.3%
Release-John Day	7.1%	6.4%	0.7%
Release-John Day top	4.5%	3.5%	1.0%
Release-McNary	1.3%	0.8%	0.5%
Release-McNary top	1.2%	0.7%	0.5%
Bonneville-Bonneville top A	35.1%	34.5%	0.6%
Bonneville top A-The Dalles top	40.4%	39.9%	0.5%
Bonneville top A-John Day top	17.3%	13.7%	3.6%
Bonneville top A-McNary top	4.5%	2.6%	1.9%
The Dalles top-John Day top	42.9%	34.4%	8.5%
The Dalles top-McNary top	11.1%	6.6%	4.5%
John Day top-McNary top	25.9%	19.0%	6.9%

[1] all antennas, except tailrace [2] top-of-ladder antennas [3] all antennas, including tailrace

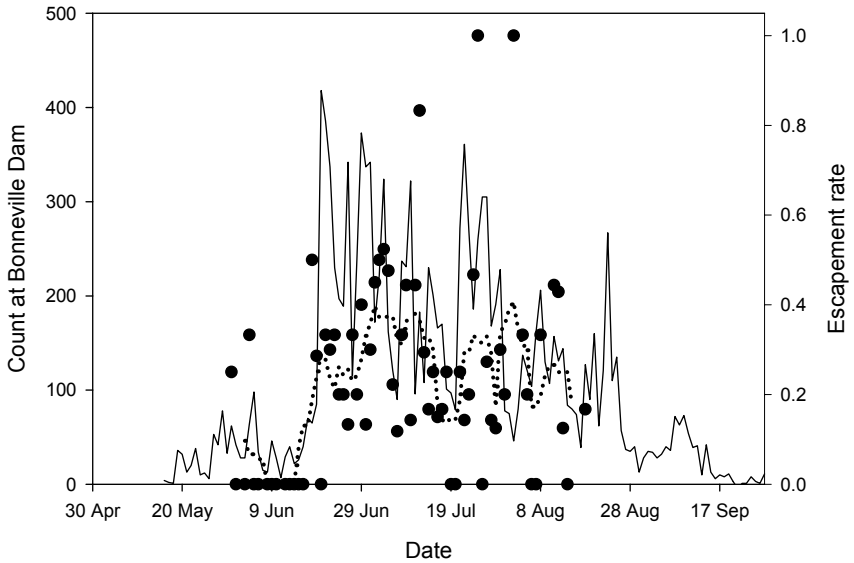

Figure 4. Daily radio-tagged lamprey escapement estimates (●) from release to the top of Bonneville Dam, by date of lamprey release near Hamilton Island or Tanner Creek in 2008. Dotted line shows 7-d moving average. Solid line shows daily daytime counts of lamprey at the dam.

Diel Passage – Lamprey passage distributions at top-of-ladder sites clearly showed that most passage occurred at night (Figure 5). This pattern was consistent at the four lower Columbia River dams (n = 4 at McNary Dam). The majority of passage events were between sunrise and sunset, though some fish passed during almost all hours. Daylight passage most often occurred between 0500 and 1100, suggesting that some fish that initiated dam passage at night continued migrating in the morning in an effort to exit fishways.

Detection Efficiency – Efficiencies described in this section were based on radiotelemetry data only (i.e., no HDX records). See the 'Evaluations Using Double-Tagged Lampreys' section for efficiencies calculated using double-tagged fish. Radiotelemetry-only detection efficiency estimates for the radio-tagged fish at Bonneville, The Dalles, and John Day dams indicated that fish that reached the dams were highly likely to be detected on one or more antennas (Table 5). At Bonneville Dam, 589 fish were recorded at one or more sites. Of these, 580 (98.5%) were detected on aerial tailrace antennas. A total of 443 fish were recorded at antennas upstream from the Bonneville tailrace (including approaching fishways) and 317 were recorded inside Bonneville fishways. Of the 317 recorded inside fishways, 232 (73.2%) were recorded passing an entrance antenna. A minimum of 153 lamprey were known to pass Bonneville Dam, of which 131 (85.6%) were detected at top-of-ladder antennas. However, only 143 of the fish known to pass had an opportunity to pass top-of-ladder antennas because ten fish were recaptured at the adult trap and released upstream from the dam. The resulting top-of-ladder efficiency was 91.6% (131/143, Table 5). Eight of the 12 that were not recorded passing top-of-ladder sites were last detected at antennas in the auxiliary channel near the lamprey bypass system at the top of the Bradford Island ladder; because these fish likely passed the dam via the bypass, this result suggests overall detection efficiencies was likely closer to 97.2% (139/143).

Table 7. Summary of radio-tagged adult lamprey passage times through dam-to-dam and multi-dam reaches of the lower Columbia River.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to approach Bonneville fishway	396	1.63	5.24	0.55	4.55
Release to enter Bonneville fishway	199	3.81	8.93	0.67	8.47
Release to pass Bonneville Dam	131	5.57	9.60	2.58	12.67
Release to The Dalles tailrace	26	10.05	22.61	6.53	17.48
Release to pass The Dalles Dam	60	14.04	20.35	9.75	23.24
Release to John Day tailrace	26	14.60	21.58	11.72	27.15
Release to pass John Day Dam	21	16.96	22.15	12.87	30.54
Release to McNary tailrace	1	33.49	33.49	-	-
Release to pass McNary Dam	4	35.94	36.56	32.71	39.79
Bonneville top to The Dalles tailrace	22	3.06	12.95	2.81	4.87
Bonneville top to pass The Dalles Dam	55	5.76	8.01	4.06	8.11
Bonneville top to John Day tailrace	24	8.95	9.38	6.14	11.70
Bonneville top to pass John Day Dam	19	9.08	10.53	7.64	11.23
Bonneville top to McNary tailrace	1	23.00	23.00	-	-
Bonneville top to pass McNary Dam	4	25.31	24.62	22.40	27.54
The Dalles tailrace to pass The Dalles Dam	14	2.94	3.20	1.89	3.81
The Dalles top to John Day tailrace	25	2.10	3.58	1.19	5.78
The Dalles top to pass John Day Dam	20	4.98	5.61	3.01	6.24
The Dalles top to McNary tailrace	1	18.47	18.47	-	-
The Dalles top to pass McNary Dam	4	18.65	17.68	15.12	21.21
John Day tailrace to pass John Day Dam	9	2.84	4.61	1.86	4.56
John Day top to McNary tailrace	1	16.82	16.82	-	-
John Day top to pass McNary Dam	9	2.84	4.61	1.86	4.56
McNary tailrace to pass McNary Dam	1	1.99	1.99	-	-

Table 8. Correlation coefficients (*r*) for log-transformed radio-tagged lamprey passage times (d) in 2008. Predictor variables included size metrics (length, weight, girth) recorded at the time of tagging and date, and Columbia River flow and temperature on the date fish were released or passed the top-of-ladder sites at Bonneville or The Dalles dams for each reach. Gray shading indicates $P < 0.05$.

			Correlation coefficient (*r*)					
Reach start	Reach end	*n*	Length	Weight	Girth	Date	Flow	Temp.
Release	Bonneville approach	396	0.02	0.04	0.04	0.12	-0.14	0.07
Release	Bonneville entry	199	0.10	0.10	0.08	0.09	-0.14	0.06
Release	Bonneville top	131	0.24	0.26	0.21	0.01	0.02	-0.10
Release	The Dalles tailrace	26	-0.10	-0.07	-0.08	-0.33	0.38	-0.46
Release	The Dalles top	60	0.17	0.18	0.02	0.10	-0.06	-0.00
Release	John Day tailrace	26	0.19	0.26	0.11	0.04	-0.00	-0.03
Release	John Day top	21	0.39	0.34	0.14	-0.27	0.24	-0.29
Bonneville top	The Dalles tailrace	22	-0.49	-0.44	-0.38	-0.28	0.40	-0.34
Bonneville top	The Dalles top	55	0.01	-0.07	-0.08	0.19	-0.13	0.16
Bonneville top	John Day tailrace	24	-0.04	0.12	0.06	-0.13	0.06	-0.10
Bonneville top	John Day top	19	0.12	-0.06	-0.14	-0.40	0.03	-0.23
The Dalles top	John Day tailrace	25	-0.17	-0.09	-0.15	0.04	-0.17	0.11
The Dalles top	John Day top	20	-0.10	-0.18	-0.19	-0.46	0.17	-0.31

A total of 93 fish were detected at The Dalles Dam. Thirty-five of the 93 (37.6%) were recorded on aerial tailrace antennas. Ninety fish were recorded at antennas monitoring fishway entrances or inside fishways. Seventy-seven were recorded inside fishways, all of which (100%) were recorded passing fishway entrance antennas. Sixty-one fish (65.6% of 93) were known to pass The Dalles Dam, and all were recorded at top-of-ladder antennas (Table 5).

Thirty-eight lampreys were recorded at John Day Dam antennas, with 31 (81.6%) recorded on aerial tailrace antennas (five only after dam passage and subsequent fallback). The only additional antennas at John Day Dam were at the top-of-ladder sites, where 21 (55.3% of 38) fish were recorded. Five fish were recorded at McNary Dam. Two of these (40%) were recorded at aerial antennas. Four fish were recorded inside McNary fishways, of which 3 (75%) were recorded at fishway entrance antennas. Four lampreys were recorded at McNary top-of-ladder sites.

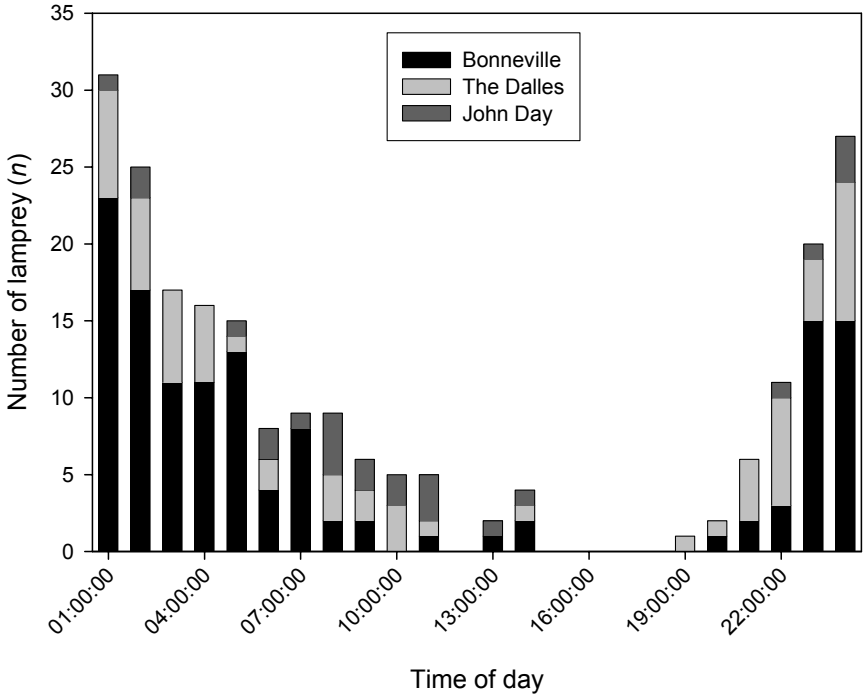

Figure 5. Distributions of the times that radio-tagged lamprey were detected passing top-of-ladder sites at Bonneville, The Dalles, and John Day dams in 2008.

Last Detection Summary – More than half (52.8%) of the 595 radio-tagged lampreys were last recorded at Bonneville tailrace antennas and another 23.9% were last recorded at Bonneville fishway antennas, including fishway approach sites (Table 9). Nine fish (1.5%) were last recorded downstream from the release sites, including one in the Willamette River.

Upstream from Bonneville Dam, eight fish (1.3%) were recorded in Bonneville reservoir tributaries and 13 (2.2%) were last recorded in the Deschutes River. Another 37 (6.2%) were last recorded at The Dalles Dam, 27 (4.5%) were at John Day Dam, five (0.8%) were at McNary Dam, and two (0.3%) were at Priest Rapids Dam (all tailrace, fishway, and ladder sites combined, Table 9).

Table 9. Last recorded locations for 595 radio-tagged adult Pacific lampreys in 2008.

Site	*n*	%	Site	*n*	%
Willamette River	1	0.2%	At The Dalles Dam	27	4.5%
			The Dalles ladder exits	10	1.7%
Columbia R. below release	8	1.3%			
Release site	4	0.7%	Deschutes River	13	2.2%
Bonneville tailrace	314	52.8%	At John Day Dam	15	2.5%
At Bonneville Dam	142	23.9%	John Day ladder exits	12	2.0%
Bonneville ladder exits	16	2.7%			
Bonneville forebay	18	3.0%	At McNary Dam	1	0.2%
			McNary Dam ladder exits	4	0.7%
Wind River	1	0.2%			
Klickitat River	5	0.8%	Priest Rapids ladder exits	2	0.3%
Fifteenmile Creek	2	0.3%			

HDX PIT-Tagged Lampreys (No Double-Tagged Fish)

Upstream Progression – Of the 608 lampreys released downstream from Bonneville Dam with only HDX-PIT tags, 369 (60.7%) were subsequently recorded at one or more Bonneville Dam HDX antennas inside fishways, at LPS systems, or at dams further upstream. A total of 318 fish passed Bonneville Dam (52.3% of the 608 released, and 86.2% of the 369 detected at one or more HDX antennas).

The median tag date for HDX-PIT tagged lampreys was 10 July. Median recorded passage dates at top-of-ladder sites were 21 July at Bonneville Dam (n = 277), 29 July at The Dalles Dam (n = 110), 29 July at John Day Dam (n = 109), 5 August at McNary Dam (n = 25), 24 July at Ice Harbor Dam (n = 5), and 31 July at Priest Rapids Dam (n = 3). Additional fish passed each dam without detection at top-of-ladder antennas. Top-of-ladder migration timing distributions for the HDX-PIT tagged fish indicated relative under-sampling early in the run at Bonneville and The Dalles dams and during migration peaks at all sites; samples were very small at Ice Harbor and Priest Rapids dams (Figure 6).

Dam-to-Dam Escapement – Of 608 fish released, 52.3% (n = 318) were known to have passed Bonneville Dam, 27.3 % (n = 166) passed The Dalles Dam, 17.9% (n = 109) passed John Day Dam, 4.6% (n = 28) passed McNary Dam, 0.8% (n = 5) passed Ice Harbor Dam, and 0.5% (n = 3) passed Priest Rapids Dam (Table 10). Escapement estimates from the top of Bonneville Dam were 52.2% to the top of The Dalles Dam, 34.3% to the top of John Day Dam, and 9.1% to the top of McNary Dam. Escapements were 65.7% between ladder tops at The Dalles Dam and John Day dams and 25.7% between ladder tops at John Day to McNary dams. Five lampreys were recorded passing Ice Harbor Dam, representing 0.8% of the total sample and 17.9% of the fish that passed McNary Dam. Three fish were recorded passing Priest Rapids Dam, 10.7% of those that passed McNary Dam (Table 10). Daily escapement rates from release past Bonneville Dam decreased with increasing release date but were highly variable (Figure 7).

In almost all reaches, lamprey that passed upstream sites were significantly ($P < 0.05$) larger than those that did not pass (Table 11). Escapement was also significantly associated with the date that lamprey were released downstream from Bonneville Dam, with mean dates earlier for fish that passed most reaches. Mean dates lampreys passed upstream antenna sites were generally earlier for fish that passed through dam-to-dam reaches, with a significant difference between groups ($P = 0.023$) from Bonneville to The Dalles (Table 12). Temperature and discharge conditions lampreys encountered on the dates they entered upstream reaches also differed significantly between fish that

did or did not pass through the Bonneville–The Dalles reach; those that passed The Dalles Dam encountered higher flow and lower temperature than those that did not pass (Table 12, $P \leq 0.019$).

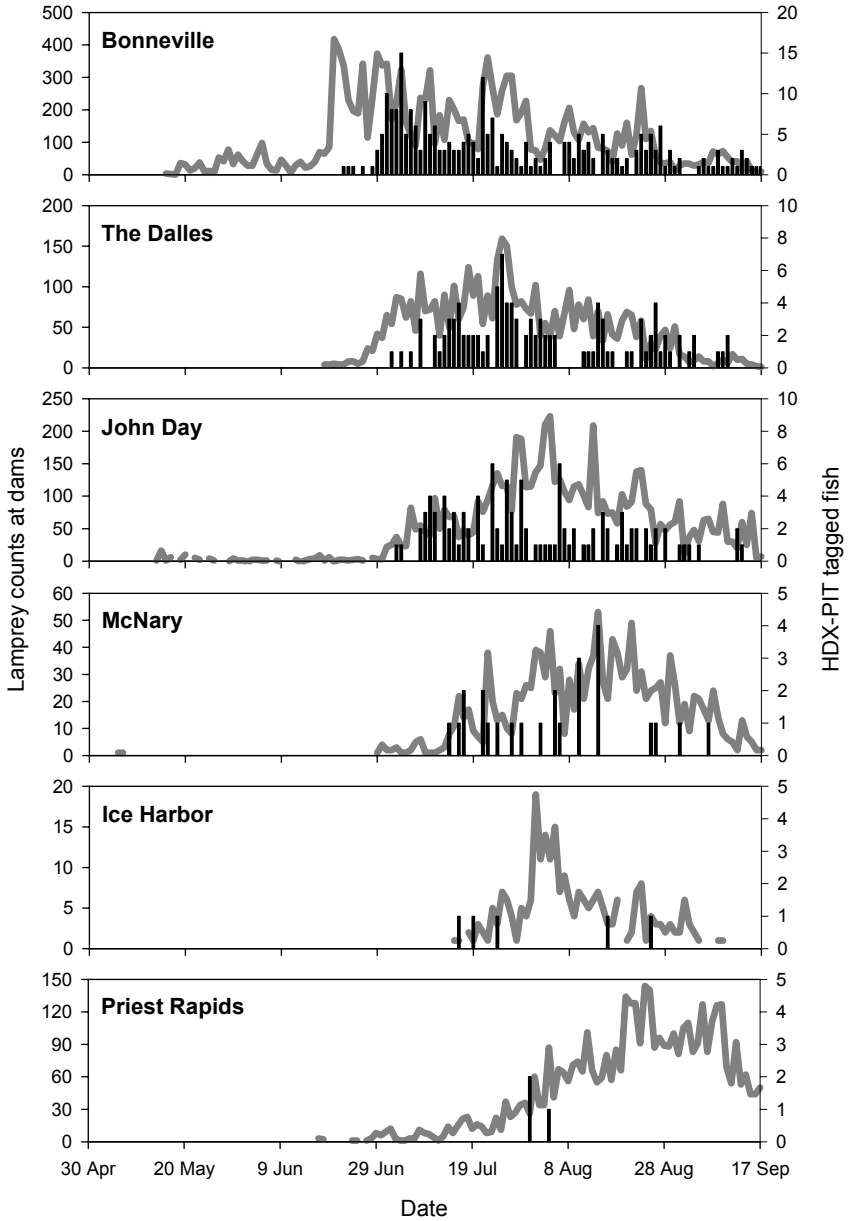

Figure 6. Daily numbers of adult Pacific lamprey counted passing dams via fish ladders (gray lines) and the numbers of HDX-PIT tagged (no double-tagged) fish that were detected at top-of-ladder antennas (black bars) in 2008.

Passage Times and Rates – Median HDX-PIT tagged lamprey passage times were 7.7 d from the release site to the top of Bonneville Dam, 4.9 d between Bonneville and The Dalles dams, 3.7 d between The Dalles and John Day dams, and 5.4 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 13). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 15.0 km•d^{-1} (Bonneville-The Dalles), 10.5 km•d^{-1} (The Dalles-John Day), and 22.9

km•d^{-1} (John Day-McNary). Rates over multi-dam reaches were: 11.6 km•d^{-1} (Bonneville-John Day), 13.9 km•d^{-1} (Bonneville-McNary) and 19.9 km•d^{-1} (Bonneville-Ice Harbor).

Lamprey migration times were not significantly correlated with fish size metrics through any of the analyzed study reaches (Table 14). In contrast, seasonal effects on lamprey migration times were evident in most reaches, with faster passage as water temperature and date increased and flow decreased. Passage times were positively correlated with flow and negatively correlated with temperature and date through all four reaches that started at the release site (i.e., slower migration rates at higher flow, Table 14). Overall, however, the selected predictor variables explained relatively small proportions of the variability in lamprey passage times.

Table 10. Adult HDX-PIT tagged lamprey escapement estimates for 2008. No double-tagged fish were included and one outlier was excluded. "Bonneville top A" includes 11 fish recaptured at the adult fish trap and released upstream from the Bonneville Dam; "Bonneville top B" excludes these fish. See Table 2 for antenna locations.

Site	Minimum past (*n*)	Detected (%)	Reach escapement Reach	(%)
Release	608		Release-Bonneville	60.7%
Bonneville[1]	369	94.6%	Release-Bonneville top A	52.3%
Bonneville top A[2]	318	87.1%	Release-The Dalles	31.1%
Bonneville top B[2]	307	90.2%	Release-The Dalles top	27.3%
The Dalles[1]	189	87.3%	Release-John Day top	17.9%
The Dalles top[2]	166	66.3%	Release-McNary	5.8%
John Day top[2]	109	100.0%	Release-McNary top	4.6%
McNary[1]	35	100.0%	Release-Ice Harbor	1.3%
McNary top[2]	28	89.3%	Release-Ice Harbor top	0.8%
Ice Harbor[1]	8	100.0%	Release-Priest Rapids top	0.5%
Ice Harbor top[2,4]	5	100.0%		
Priest Rapids top[2]	3	100.0%	Bonneville-Bonneville top A	86.2%
			Bonneville top A-The Dalles top	52.2%
			Bonneville top A-John Day top	34.3%
			Bonneville top A-McNary top	9.1%
			Bonneville top A-Ice Harbor top	1.6%
			Bonneville top A-Priest Rapids top	0.9%
			The Dalles top-John Day top	65.7%
			The Dalles top-McNary top	16.7%
			The Dalles top-Ice Harbor top	3.0%
			The Dalles top-Priest Rapids top	1.8%
			John Day top-McNary top	25.7%
			John Day top-Ice Harbor top	4.6%
			John Day top-Priest Rapids top	2.8%
			McNary top-Ice Harbor top	17.9%
			McNary top-Priest Rapids top	10.7%

[1] all fishway antennas, including LPS at Bonneville
[2] top-of-ladder antennas, including LPS at Bonneville
[3] all antennas, including tailrace
[4] No upstream site to assess missed detections

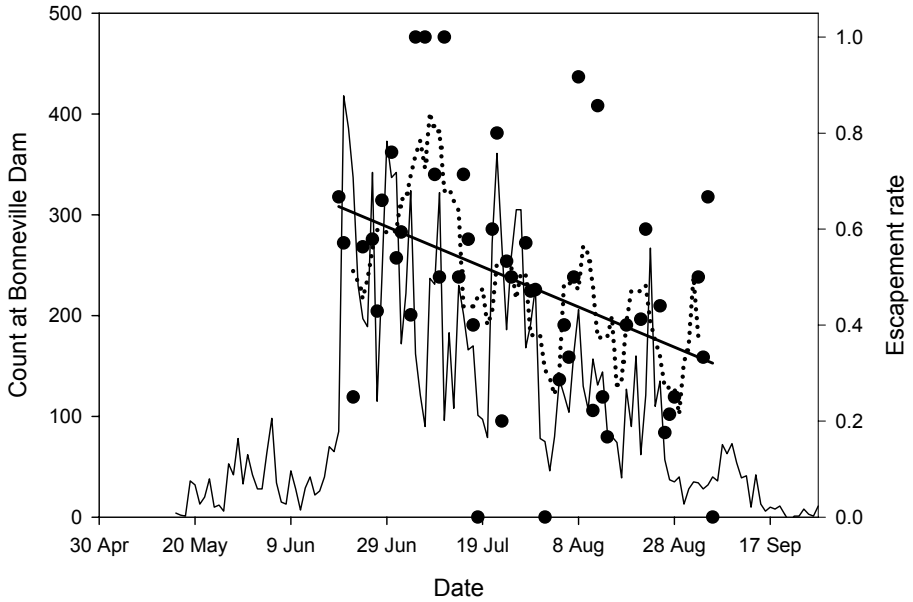

Figure 7. Daily HDX-PIT tagged lamprey escapement estimates (●) from release to the top of Bonneville Dam, by date of lamprey release in 2008. Dotted line shows 7-d moving average. Solid line shows daily lamprey counts at the dam. Trend line shows linear regression between release dates and daily escapement estimates (r^2 = 0.15).

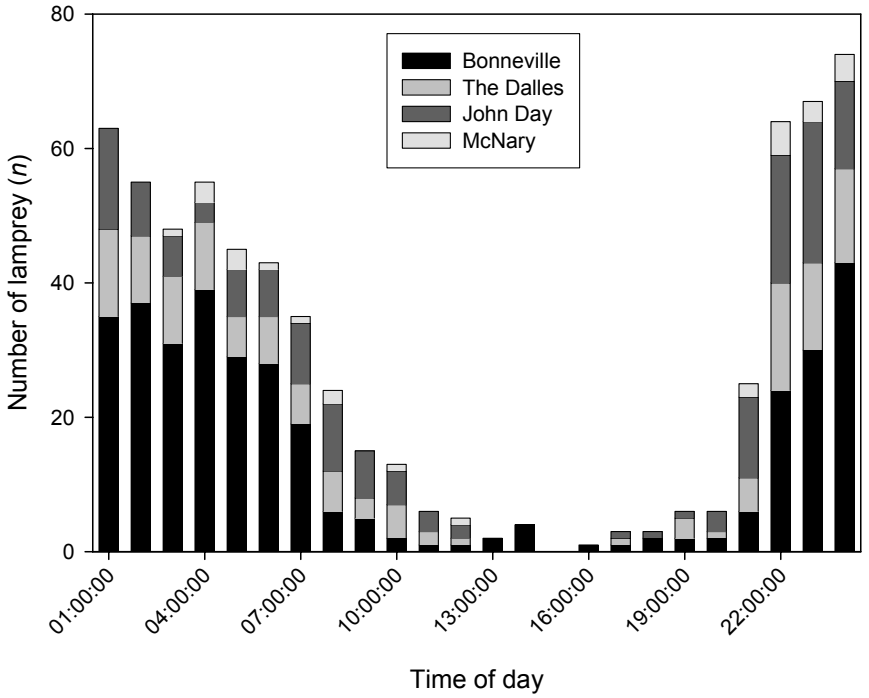

Figure 8. Distributions of the times that HD PIT-tagged lampreys were detected passing top-of-ladder sites at Bonneville, The Dalles, John Day, and McNary dams in 2008. No double-tagged fish were included.

Table 11. Mean HDX-PIT tagged lamprey size metrics and tag dates in relation to their escapement through the monitored reaches in 2008. Top-of-ladder sites were used for the upper end of each reach. *F* and *P* values are from analysis of variance tests (ANOVA). No double-tagged fish were included and one outlier was excluded.

Reach	Passed	Length (*n*)	Weight (*n*)	Girth (*n*)	%Lipid (*n*)	Tag date (*n*)
Release - Bonneville top A	No	64.1 (290)	420.8 (290)	10.5 (290)	27.6 (221)	23 Jul (290)
	Yes	65.2 (317)	446.5 (317)	10.8 (317)	29.4 (279)	15 Jul (318)
	F	10.06	13.20	12.01	6.30	18.01
	P	**0.002**	**<0.001**	**<0.001**	**0.012**	**<0.001**
Release - The Dalles top	No	63.9 (442)	419.5 (442)	10.5 (442)	27.6 (345)	21 Jul (442)
	Yes	66.7 (165)	473.8 (165)	11.0 (165)	30.5 (155)	11 Jul (166)
	F	48.35	49.82	45.72	17.57	25.40
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Release - John Day top	No	64.1 (498)	423.8 (498)	10.5 (498)	28.0 (398)	20 Jul (499)
	Yes	67.2 (109)	481.7 (109)	11.1 (109)	30.8 (102)	10 Jul (109)
	F	43.49	41.56	37.96	12.57	18.41
	P	<0.001	<0.001	<0.001	<0.001	<0.001
Release - McNary top	No	64.5 (579)	431.1 (579)	10.6 (579)	28.3 (472)	19 Jul (580)
	Yes	68.2 (28)	499.0 (28)	11.2 (28)	33.4 (28)	6 Jul (28)
	F	18.59	16.44	13.14	11.98	8.49
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.004**
Bonneville top A - The Dalles top	No	63.7 (152)	416.8 (152)	10.5 (152)	27.6 (124)	19 Jul (152)
	Yes	66.7 (165)	473.8 (165)	11.0 (165)	30.5 (155)	11 Jul (166)
	F	39.13	36.31	34.43	11.44	11.63
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Bonneville top A - John Day top	No	64.2 (208)	428.0 (208)	10.6 (208)	28.3 (177)	17 Jul (209)
	Yes	67.2 (109)	481.7 (109)	11.1 (109)	30.8 (102)	10 Jul (109)
	F	33.11	28.54	26.83	7.44	8.50
	P	**<0.001**	**<0.001**	**<0.001**	**0.007**	**0.004**
Bonneville top A - McNary top	No	64.9 (289)	441.4 (289)	10.7 (289)	29.0 (251)	16 Jul (290)
	Yes	68.2 (28)	499.0 (28)	11.2 (28)	33.4 (28)	6 Jul (28)
	F	13.65	11.14	8.85	9.18	5.14
	P	**<0.001**	**<0.001**	**0.003**	**0.003**	**0.024**
The Dalles top - John Day top	No	65.7 (56)	458.3 (56)	10.9 (56)	30.1 (53)	13 Jul (57)
	Yes	67.5 (109)	481.7 (109)	11.1 (109)	30.8 (102)	10 Jul (109)
	F	5.35	3.42	3.54	0.38	0.84
	P	**0.022**	0.066	0.062	0.540	0.360
The Dalles top - McNary top	No	66.4 (137)	468.6 (137)	11.0 (137)	30.1 (127)	12 Jul (138)
	Yes	68.2 (28)	499.0 (28)	11.2 (28)	33.4 (28)	6 Jul (28)
	F	5.54	3.65	2.66	4.67	2.42
	P	**0.020**	0.058	0.105	**0.032**	0.122
John Day top - McNary top	No	66.8 (81)	475.7 (81)	11.1 (81)	30.1 (74)	11 Jul (81)
	Yes	68.2 (28)	499.0 (28)	11.2 (28)	33.4 (28)	6 Jul (28)
	F	3.72	2.52	1.72	4.43	1.92
	P	0.056	0.115	0.193	**0.038**	0.169

Table 12. Mean HDX-PIT tagged lamprey migration dates and encountered water temperature and discharge in relation to their passage through the monitored reaches in 2008. Environmental data were from the dates fish were recorded passing the lower end of each reach (i.e., 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). No double-tagged fish were included and one outlier was excluded.

Reach	Passed	Date (*n*)	Temperature (*n*)	Flow (*n*)
Release - Bonneville top A	No	23 Jul (290)	18.79 (290)	222.7 (290)
	Yes	15 Jul (318)	18.31 (318)	250.9 (318)
	F	18.01	10.31	14.84
	P	<0.001	0.001	<0.001
Bonneville top - The Dalles top	No	31 Jul (132)	19.48 (129)	183.4 (132)
	Yes	25 Jul (145)	19.11 (144)	209.0 (145)
	F	5.24	5.58	7.74
	P	0.023	0.019	0.006
The Dalles top - John Day top	No	5 Aug (57)	19.93 (56)	154.0 (57)
	Yes	1 Aug (53)	19.78 (52)	165.1 (53)
	F	1.15	0.87	1.96
	P	0.287	0.353	0.164
John Day top - McNary top	No	4 Aug (81)	20.13 (79)	151.1 (81)
	Yes	27 Jul (28)	19.97 (28)	163.3 (28)
	F	3.50	0.49	1.43
	P	0.064	0.487	0.235

Table 13. Summary of HDX-PIT tagged adult lamprey passage times through monitored reaches of the lower Columbia River. No double-tagged fish were included and one outlier was excluded.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to pass Bonneville Dam	277	7.70	12.37	3.60	15.48
Release to pass The Dalles Dam	110	19.58	21.92	12.37	26.48
Release to pass John Day Dam	109	20.54	23.12	13.48	28.44
Release to pass McNary Dam	25	26.63	30.21	23.41	36.24
Release to pass Ice Harbor Dam	5	21.61	21.13	20.80	23.34
Release to pass Priest Rapids Dam	3	33.39	33.80	33.00	34.40
Bonneville top to pass The Dalles Dam	90	4.87	6.79	3.14	9.04
Bonneville top to pass John Day Dam	93	9.67	11.76	6.92	14.31
Bonneville top to pass McNary Dam	24	16.85	18.37	11.56	21.89
Bonneville top to pass Ice Harbor Dam	5	15.19	17.23	13.85	20.88
Bonneville top to pass Priest Rapids Dam	3	29.98	28.63	27.44	30.50
The Dalles top to pass John Day Dam	53	3.68	5.42	2.40	6.80
The Dalles top to pass McNary Dam	3	13.96	13.05	10.30	16.26
The Dalles top to pass Ice Harbor Dam	1	12.32	12.32	-	-
The Dalles top to pass Priest Rapids Dam	-	-	-	-	-
John Day top to pass McNary Dam	25	5.36	7.96	4.00	8.58
John Day top to pass Ice Harbor Dam	5	8.27	8.69	6.56	10.36
John Day top to pass Priest Rapids Dam	3	15.98	15.68	15.04	16.46
McNary top to pass Ice Harbor Dam	3	2.49	4.60	2.28	5.87
McNary top to pass Priest Rapids Dam	2	7.46	7.46	-	-

Table 14. Correlation coefficients (*r*) for log-transformed HDX-PIT tagged lamprey passage times (d) in 2008. Predictor variables included size metrics (length, weight, girth) recorded at the time of tagging and date, Columbia River flow, and temperature at the downstream site for each reach. Gray shading indicates $P < 0.05$.

			Correlation coefficient (*r*)					
Reach start	Reach end	*n*	Length	Weight	Girth	Date	Flow	Temp.
Release	Bonneville top	277	0.062	0.059	0.066	-0.135	0.137	-0.159
Release	The Dalles top	110	0.117	0.148	0.143	-0.359	0.370	-0.388
Release	John Day top	109	0.095	0.095	0.064	-0.272	0.190	-0.243
Release	McNary top	25	0.066	0.101	0.107	-0.472	0.462	-0.450
Bonneville top	The Dalles top	90	-0.071	-0.012	0.007	-0.082	0.155	-0.172
Bonneville top	John Day top	93	0.150	0.154	0.107	-0.206	0.142	-0.186
Bonneville top	McNary top	24	0.022	0.073	0.068	-0.317	0.390	-0.351
The Dalles top	John Day top	53	0.220	0.103	-0.036	-0.228	0.132	-0.218
John Day top	McNary top	25	0.054	0.138	0.065	-0.040	0.165	-0.060

Diel Passage – As with the radiotelemetry-only data, lamprey passage distributions at top-of-ladder sites clearly showed that most dam passage occurred at night (Figure 8). This pattern was consistent across the four lower Columbia River dams. The majority of passage events were between sunrise and sunset, though some fish passed during all hours.

Detection Efficiency – Efficiencies described in this section were based on HDX-PIT data only (i.e., no radiotelemetry records or records from double-tagged fish). See 'Evaluations Using Double-Tagged Lampreys' section for efficiencies calculated using double-tagged fish. Estimating detection efficiencies for the HDX-PIT sites was difficult due to a lack of antenna redundancy in individual fishways and lamprey passage structures (Bonneville only). A total of 369 lampreys were either recorded at Bonneville detection antennas or passed the dam and were detected at upstream dams. Of the 369, 349 (94.6%) were detected on a Bonneville HDX-PIT antenna (Table 10). A total of 307 lampreys were recorded passing Bonneville Dam or were recorded at upstream sites. Of these, 277 (90.2%) were detected at top-of-ladder antennas or in lamprey passage systems where exit to the forebay was likely. Of the 30 fish that passed Bonneville Dam without detection at an exit site, 10 (33.3%) were recorded on antennas in the Washington-shore or Cascades Island fishways and 20 (66.6%) were not detected at any site. It was not possible to determine if these fish passed undetected or via unmonitored routes (e.g., the navigation lock or UMT channel).

A total of 189 lampreys were detected at HDX-PIT antennas at The Dalles Dam or at sites upstream from The Dalles. Of the 189, 165 (87.3%) were detected at The Dalles antennas. A total of 166 fish were known to have passed The Dalles Dam, of which 110 (66.3%) were detected at top-of-ladder antennas. Of the 56 fish that passed but were not recorded at top-of-ladder antennas, 32 (57.1%) were recorded at an antenna above the count window in the East ladder.

At John Day Dam, all of 129 lamprey (100.0%) known to pass the dam were detected at John Day Dam top-of-ladder antennas.

At McNary Dam, 35 fish were detected at HDX-PIT antennas; no additional fish were detected upstream at Ice Harbor or Priest Rapids dams (Table 10). Twenty-eight lampreys passed McNary Dam, all of which (100.0%) were detected at top-of-ladder antennas. Eleven fish were recorded exiting via the Washington-shore ladder, of which 8 (72.7%) were also detected at the Washington-

shore transition pool antenna. Fourteen fish were recorded exiting the Oregon-shore ladder, and 11 (78.6%) were also recorded at the antennas in the Oregon-shore transition pool area.

Eight lampreys were detected at Ice Harbor HDX-PIT antennas, with five recorded at top-of-ladder sites (Table 10). The five that passed were also detected at antennas near fishway entrances and/or in transition pools.

Last Detection Summary – More than a third (37.3%) of the 608 lampreys with only HDX-PIT tags were not detected after release near Hamilton Island (Table 15). Another 31.7% were last recorded at HDX antennas at Bonneville Dam, including at top-of-ladder exit sites, LPS sites, and sites near the Washington-shore fishway entrance and inside ladders. Eighty fish (13.1%) were last recorded at The Dalles Dam, 74 (12.2%) were at John Day Dam, 24 (3.9%) were at McNary Dam, 8 (1.3%) were at Ice Harbor Dam, and 3 (0.5%) were at Priest Rapids Dam (Table 15).

Table 15. Last recorded locations for 595 radio-tagged adult Pacific lampreys in 2008. No double-tagged fish were included and one outlier was excluded. WA = Washington shore; LPS = lamprey passage structure.

Site	*n*	%	Site	*n*	%
Release site	227	37.3%	At The Dalles Dam	23	3.8%
			The Dalles ladder exits	57	9.4%
Bonneville Dam - WA fishway entry	17	2.8%			
Bonneville Dam - Cascade Island	28	4.6%	John Day ladder exits	74	12.2%
Bonneville Dam - WA ladder	17	2.8%			
Bonneville Dam - Adult Facility	4	0.7%	At McNary Dam	6	1.0%
Bonneville Dam - WA LPS	8	1.3%	McNary Dam ladder exits	18	3.0%
Bonneville Dam - WA ladder exit	63	10.4%			
Bonneville Dam - Bradford LPS	23	3.8%	At Ice Harbor Dam	3	0.5%
Bonneville Dam - Bradford ladder exit	32	5.3%	Ice Harbor Dam ladder exits	5	0.8%
			Priest Rapids ladder exits	3	0.5%

Evaluations Using Double-Tagged Lampreys

Reach escapement and passage time details for the double-tagged lampreys (radio and HDX-PIT) were included in the radiotelemetry section of this report that included all radio-tagged fish. However, the 2008 objectives also included comparing results for the double-tagged fish with fish that only received radio tags and those with only HDX-PIT tags and estimation of detection efficiencies for both radiotelemetry and HDX-PIT antennas using only the double-tagged fish.

Dam-to-Dam Escapement – In general, the double-tagged fish performed similarly to those with only radio tags (Table 16). When passage by fish that were only detected on HDX-PIT antennas was included, double-tagged lampreys had higher reach escapement estimates in nine of ten reach comparisons with fish tagged with only radio tags. When we excluded the HDX-PIT detections, double-tagged fish had higher escapement in about half of the reaches and lower escapement estimates in the remaining reaches (Table 16). Overall, these results suggest that double tagging did not adversely affect escapement compared to radio-only tagging. Instead, double tagging allowed us to identify a small number of additional dam passages (3-6 fish per dam) that would have been missed without the HDX-PIT tag.

As described in previous sections, the PIT-tag only group had significantly higher escapement estimates than either radio-only or double-tagged fish across all study reaches (Table 16).

Table 16. Comparison of lamprey reach escapement estimates (*n* in parentheses) for the radiotelemetry, double-tag and HDX-PIT tag groups. Reaches were limited to release sites and top-of-ladder sites to accommodate paired radiotelemetry and PIT tag antenna locations. "Bonneville top A" includes fish recaptured at the adult fish trap and released upstream from Bonneville Dam. See Table 2 for antenna locations.

	Tag group				
	Radio-all[1]	Radio-only	Double[1]	Double[2]	PIT-only
Release-Bonneville top A	26.2% (595)	23.6% (296)	28.8% (299)	27.8% (299)	52.3% (608)
Release-The Dalles top	10.6% (595)	8.1% (296)	13.0% (299)	12.4% (299)	27.3% (608)
Release-John Day top	4.5% (595)	3.7% (296)	5.4% (299)	3.3% (299)	17.9% (608)
Release-McNary top	1.2% (595)	0.7% (296)	1.7% (299)	0.7% (299)	4.6% (608)
Bonneville top A-The Dalles top	40.4% (156)	34.3% (70)	45.3% (86)	44.6% (83)	52.2% (318)
Bonneville top A-John Day top	17.3% (156)	15.7% (70)	18.6% (86)	12.0% (83)	34.3 (318)
Bonneville top A-McNary top	4.5% (156)	2.9% (70)	5.8% (86)	2.4% (83)	9.1% (318)
The Dalles top-John Day top	42.9% (63)	45.8% (24)	41.0% (39)	27.0% (37)	65.7% (166)
The Dalles top-McNary top	11.1% (63)	8.3% (24)	12.8% (39)	5.5% (37)	16.7% (166)
John Day top-McNary top	25.9% (27)	18.2% (11)	31.3% (16)	20.0% (10)	25.7% (109)

[1] includes passage identified from only HDX-PIT detections
[2] excludes passage identified from only HDX-PIT detections

Passage Times – There were no significant ($P > 0.05$) differences in mean or median reach passage times for double-tagged versus radio-only lamprey groups (Table 17). The double-tagged fish migrated from release to past Bonneville Dam and through the Bonneville reservoir more slowly than the radio-only group; this pattern was reversed for mean times through The Dalles reservoir.

In other passage time comparisons among tag groups, HDX-PIT-only fish migrated significantly more slowly ($P < 0.05$) than the radio-only and radio-all groups from release past Bonneville Dam (Table 17). This difference was likely related – at least in part – to the smaller mean size of the HDX-PIT-only fish at tagging. In the reservoirs, HDX-PIT-only fish migrated faster than the double-tagged and radio-only groups in some comparisons and more slowly in others (Table 17). No other significant differences were detected at these sites.

Detection Efficiency – We calculated detection efficiencies for both radio and HDX-PIT antennas at top-of-ladder sites at all four lower Columbia River dams using the double-tagged lampreys (Table 18). Efficiencies at the radiotelemetry sites ranged from 50% at the McNary south ladder to 100% at The Dalles south ladder (mean = 78.9%). Radiotelemetry efficiencies were lowest at John Day and McNary dams. However, the radiotelemetry data suggested that several of the undetected transmitters at these sites were either shed or stopped functioning because these transmitters missed all radiotelemetry sites, not just top-of-ladder sites. Shed or failed transmitters would result in underestimation of radiotelemetry detection efficiency.

The HDX-PIT detection efficiencies ranged from 36.7% at The Dalles south ladder to 100% at several sites (mean = 78.9%, Table 18). The low efficiency at The Dalles south was related to the size of the opening. Most of the missed fish at this site were recorded at the antenna installed

downstream from the ladder top near the count window. The lower HDX-PIT site did not have a radiotelemetry equivalent.

Table 17. Comparison of mean and median lamprey passage times among tag-type groups. 'Radio-all' includes double-tagged and radio-only fish. Times with the same superscript notation were significantly different ($P < 0.05$, ANOVAs for means and Kruskal-Wallis tests for medians). No tests were run comparing radio-all to radio-only or radio-all to double-tagged groups.

	Time to pass (d)					
	Release to Bonneville top			Bonneville top to The Dalles top		
	n	Mean	Median	*n*	Mean	Median
Radio-all	131	[a] 9.60	[a] 5.57	55	8.01	5.76
Radio-only	60	[b] 7.93	[b] 5.48	22	6.28	4.73
Double	71	11.02	6.71	33	9.16	5.83
PIT-only	277	[ab] 12.37	[ab] 7.70	90	6.79	4.87
	The Dalles top to John Day top					
Radio-all	20	5.61	4.99			
Radio-only	10	6.09	4.53			
Double	10	5.12	4.99			
PIT-only	53	5.41	3.68			

Table 18. Detection efficiencies at top-of-ladder antennas calculated using double-tagged lampreys in 2008. Only includes fish detected on at least one monitoring system.

			Detection efficiency	
Dam	Ladder	Total detected	Radiotelemetry	HDX-PIT
Bonneville	South (Bradford)[1]	24	91.7%	100.0%
	North (WA-shore)	38	94.7%	63.2%
The Dalles	South (East)	30	100.0%	36.7%
	North	8	87.5%	100.0%
John Day	South	13	61.5%	100.0%
	North	3	66.6%	100.0%
McNary	South	4	50.0%	50.0%
	North	0	-	-

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

Tagging and Handling Effects

We tested for differences in tagging and handling effects among HDX-PIT tagged and radio-tagged fish (including double-tagged fish) by comparing logistic regression models that included tag type, tag date, release time, and fish weight predictor variables in various combinations. Using AIC, the model that included tag type, fish weight, and tag date was the most parsimonious (Table 19). In this model, HDX-PIT tagged fish were more likely than radio-tagged fish to pass Bonneville Dam (χ^2 = 97.6, $P < 0.0001$). In addition, larger fish (χ^2 = 13.1, P = 0.0003), and earlier migrants (χ^2 = 9.2, P = 0.0024) were more likely to pass the dam across tag types. Importantly, this model statistically adjusted for the larger mean size of radio-tagged fish (~ 1.5 cm and 30.3 g). Models that included tag date, release time, and/or weight — but not tag type — explained much smaller portions of the variability in escapement past Bonneville Dam (Table 19). These results indicate a negative radio-tagging effect.

Table 19. Model comparison results for logistic regression models where the dependent variable was passage of Bonneville Dam and independent variables were tagtype (radio, HDX-PIT), tag date, release time, and fish weight (g). ∆AIC = the change in AIC relative to the most parsimonious model.

Model	*df*	AIC	∆AIC
Tagtype + Weight + Tagdate	**3**	**1505.6**	**0.0**
Tagtype + Weight +Tagdate + Reltime	4	1507.0	1.4
Tagtype + Weight + Reltime	3	1511.2	5.6
Tagtype + Weight	2	1512.9	7.3
Tagtype + Tagdate	2	1518.5	12.9
Tagtype + Tagdate + Reltime	3	1519.5	14.0
Tagtype + Reltime	2	1526.6	21.0
Tagtype	1	1530.2	24.7
Weight + Tagdate	2	1608.0	102.4
Weight	1	1609.6	104.1
Weight + Tagdate + Reltime	3	1609.9	104.4
Weight + Reltime	2	1610.8	105.2
Tagdate	1	1612.1	106.6
Tagdate + Reltime	2	1614.0	108.5
Reltime	1	1615.8	110.2

Discussion

The 2008 adult lamprey studies had multiple objectives at a variety of scales and used multiple technologies. The results summarized in this report primarily address reach-scale and system-wide migration questions and compare results among tag-type groups. A companion report (Johnson et al. *in review*) provides results for fine-scale behavioral questions at the lower Columbia River dams, including fishway entrance use, response to an experimental fishway velocity test at Bonneville Dam, and passage efficiencies through a variety of fishway segments. A third report will summarize behaviors of the tagged fish in and near Bonneville lamprey passage structures (LPS).

Escapement. – The 2008 reach-scale and system-wide escapement results can be used for several evaluations. First, the results can be compared among tag types. This requires similar start and end points of each passage segment or reach. Because dam tailraces and fishway entrances can not be efficiently monitored with PIT systems, comparisons between tag types are necessarily limited to release and top-of-ladder sites. Table 20 shows release to top-of-ladder escapement metrics for the 1997-2002 and 2007-2008 radiotelemetry studies and the 2005-2008 HDX-PIT studies. Second, it is important to compare lamprey escapement estimates at Bonneville Dam upstream from the tailrace. Evaluations of fishway modifications at Bonneville Dam, including development of lamprey passage structures, are most instructive if events that occur in the tailrace can be excluded (i.e., the effects of predation or other mortality and migration downstream out of the study area). Table 21 presents radiotelemetry study escapement estimates – synonymously termed 'passage efficiency' in previous years – from lamprey approach at Bonneville Dam fishway antennas to top-of-ladder antennas. No comparable metric was possible with the HDX-PIT data.

Using the escapement estimate from release to top-of-ladder sites at Bonneville Dam, the 2008 radiotelemetry estimate of 26% was considerably lower than in the 1997-2002 radiotelemetry studies (33-46%) and was lower than the HDX-PIT estimates from 2005-2008 (41-53%) (Table 20). However, the radiotelemetry result for 2008 was higher than the 2007 radiotelemetry estimate (21%), which was

the most directly comparable radiotelemetry study year. We note that the 2008 estimate of 26% was minimally inflated (perhaps 1-2%) by the fish that were recaptured in the ladder and released into the forebay. Multi-dam escapement estimates across lamprey passage studies in the lower Columbia River also suggest that the 2008 escapement estimates for radio-tagged fish were broadly lower than for the 1997-2002 radiotelemetry studies but were somewhat higher than the 2007 results. Differences in comparisons with 2002 and earlier studies reflect the smaller mean lamprey size in the 2008 radiotelemetry sample and the very consistent pattern of lower passage success for smaller radio-tagged fish (see Daigle et al. 2008 and Keefer et al. 2009). The mean fork length for radio-tagged lampreys in 2008 (66 cm) was 4-11 cm (6-17%) smaller than in the 1997-2002 samples. Similarly, the mean weight in 2008 (465 g) was 80-147 g (18-31%) smaller than means in 2002 and earlier radiotelemetry samples. Fish sizes in the 2008 sample were much more similar to those in 2007 (Table 21).

Table 20. Summary of reach escapement estimates for radio-tagged and HDX-PIT tagged (only) lampreys released downstream from Bonneville Dam and recorded at or known to pass top-of-ladder sites at lower Columbia River dams. 1997-2002 data are from radiotelemetry study annual reports (e.g., Ocker et al. 2001) and 2005-2007 HDX-PIT data are from Daigle et al. (2008) and Keefer et al. (2009).

	Escapement estimates Radiotelemetry							
	1997	1998	1999	2000	2001	2002	2007	2008
Release	147	205	199	299	298	201	398	595
Top BO	0.33 (49)	0.36 (73)	0.41 (82)	0.41 (123)	0.43 (129)	0.46 (92)	0.21 (83)	0.26 (156)
Top TD	0.11 (16)	0.12 (24)	0.13 (25)	0.23 (70)	0.23 (68)	0.23 (46)	0.05 (21)	0.11 (63)
Top JD	0.02 (3)	0.01 (3)	0.02 (3)	0.08 (23)	0.09 (27)	0.08 (17)	0.02 (9)	0.05 (27)

	HDX-PIT (only)			
	2005	2006	2007	2008
Release	841	2000	757	608
Top BO	0.53 (446)	0.41 (822)	0.52 (393)	0.52 (318)
Top TD	-	0.28 (558)	0.33 (246)	0.27 (166)
Top JD	-	0.19 (382)	0.17 (129)	0.18 (109)
Top MN	0.05 (40)	0.04 (80)	0.05 (35)	0.05 (28)

Comparisons across radiotelemetry study years also indicate that the 2008 escapement estimate from release to approach Bonneville Dam fishways (i.e., through the tailrace) was considerably lower (75%) than in the 1997-2002 radiotelemetry studies (87-96%), but was higher than in 2007 (68%) (Table 21). It is not clear whether the lower return to Bonneville Dam in 2007-2008 was primarily size related, or to what extent other factors (i.e., increased pinniped predation, Tackley et al. [2008], the use of different transmitters, antenna arrays or different tagging protocols) were important. When we limited the return-to-Bonneville analysis to fish with girth ≥ 11.5 cm (the cutoff in pre-2007 radiotelemetry studies), estimates were 75% in 2007 and 78% in 2008. These large-fish results indicate an improvement over the full samples, but were still lower than the 1997-2002 results. This suggests that some of the other factors listed above were important. We note again the larger transmitters used in most of the early study years (i.e., with longer read ranges) and the more extensive antenna arrays in those years (i.e., more Bonneville fishway entrances were open and monitored).

The escapement estimate from Bonneville fishway approach to exit from the top of a Bonneville fishway was also lower in 2008 (35%) than in the 1997-2002 radiotelemetry studies (38-47%) but higher than in 2007 (31%) (Keefer et al. 2009). Detailed analyses of lamprey movements through entrance areas, collection channels, transition pools, and up ladders and past count stations suggest

that the radio-tagged lamprey in 2008 performed similarly to radio-tagged fish in 2007 and at similar or slightly lower efficiencies than in 1997-2002 in most fishway segments (Johnson et al. 2009 and *in review*).

Table 21. Number of radio-tagged lampreys released below Bonneville Dam from 1997-2002 and in 2007-2008, mean lamprey length and weight, number of lampreys detected approaching fishway antennas at Bonneville Dam, percentage of tagged fish recorded passing the dam (escapement rate or passage efficiency), and the median travel time (days) to pass the dam from release. Pre-2008 data are from Moser et al. (2002, 2003, 2004 and 2005) and Keefer et al. (2009). The navigation lock was unmonitored in 2007-2008.

	Year							
	1997	1998	1999	2000	2001	2002	2007	2008
# Released	147	205	199	299	298	201	398	595
Mean Length (cm)	70	70	71	70	77	72	66	66
Range	60-80	59-79	65-78	62-80	62-82	60-80	53-86	49-79
Mean Weight (g)	-	545	571	570	588	612	466	465
Range	> 450	420-830	475-755	405-825	380-880	440-790	256-810	284-706
Detected at BON	88%	89%	92%	87%	93%	96%	68%	75%
Escapement rate[1]	38%	40%	45%	47%	46%	48%	31%	26%
Median BON Passage	4.9 d	5.7 d	5.5 d	4.4 d	11.0 d	9.0 d	3.0 d	5.6 d

[1]'passage efficiency' in previous years

Individual dam escapement estimates for HDX-PIT tagged fish in 2005-2007 were 41-53% from release below Bonneville Dam to pass the dam, and 62-76% from detection in a McNary Dam fishway to the top of McNary Dam (Daigle et al. 2008). The 2008 HDX-PIT results were very similar to these earlier HDX-PIT study results, with escapements of 52% at Bonneville Dam and 82% at McNary Dam. HDX-PIT escapement estimates from the release site past upstream dams in 2008 were also similar to or just slightly lower (~1-6%) than in 2005-2007 (Table 20). As of this writing, data were unavailable for lampreys that may have overwintered in the lower Columbia River as these fish typically do not resume upstream migration until late spring or early summer. Based on the 2005-2007 HDX-PIT results, we expect escapement estimates described here would increase by a few percentage points when the overwintering data are included.

Both the radiotelemetry and HDX-PIT escapement data in 2008 consistently indicated higher passage rates for larger fish. This pattern held across study reaches and did not appear to be related to migration timing as there were limited size×timing correlations (except that there was a slight tendency for later-time HDX-PIT tagged fish to be smaller). This finding was consistent with the HDX-PIT results first described in Daigle et al. (2008) and more fully examined in Keefer et al. (*in press b*). In 2008, the relationship between fish size and upstream escapement was not statistically significant in all reaches, but this may have been due (at least in part) to sample size limitations for the radio-tagged group. 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). Fourth, handling and tagging effects may have been greater for smaller lampreys.

Importantly, these hypotheses are not mutually exclusive. It is possible, for example, that higher escapement rates by larger fish was related to swimming ability, energetic or maturation status, and/or some underlying stock structure. Regardless of the mechanism, efforts to increase adult lamprey passage at dams should consider operations or structures that can accommodate smaller individuals. As an example, the high velocity areas near adult fishway entrances have been an area of difficult lamprey passage (Moser et al. 2002b), and such velocity barriers may be especially difficult for smaller fish. An experimental flow reduction from Bonneville fishway entrances at night significantly improved lamprey entrance efficiency in 2007, presumably by allowing weaker swimmers to enter more easily (Johnson et al. 2009). Preliminary results from a continuing study in 2008 showed that reduction to zero fishway discharge at night had a negative impact on lamprey entrance success (Johnson et al. *in review*). Lamprey passage structures (LPS) installed adjacent to fish ladders at Bonneville Dam also allow lampreys to circumvent high velocity areas in serpentine weir sections of ladders. In these examples, both operational (fishway entrance velocity) and structural (bypass systems) changes potentially increase overall dam passage for adult lamprey.

We found some evidence in 2008 for broad-scale environmental effects on dam and multi-reach escapement rates. In general, escapement was higher for fish released early in the season, corresponding with relatively higher river discharge and relatively lower water temperature. This pattern was primarily evident in the HDX-PIT tag data. This finding was somewhat in contrast with the 2007 study results, which showed relatively limited, but mixed, environmental effects that included higher escapement by fish that encountered slightly warmer temperatures in the Bonneville-The Dalles reach and slightly higher discharge in the John Day-McNary reach (Keefer et al. 2009). The lack of escapement patterns at a broad scale across years does not imply that environmental conditions were unimportant. Proximate conditions such as water velocity and volume near fishway entrances or near spillways likely impact lamprey energy use and behaviors, with consequent effects on escapement rates. Broad metrics like total river discharge may poorly represent the specific conditions encountered by individual fish. We also emphasize that the strong correlations among discharge, water temperature and date of migration make it difficult to isolate cause and effect at these scales.

Dam-to-dam and longer reach escapement estimates are valuable for making generalizations about lamprey passage, identifying potential problem areas, and comparing migrations across years. However, a more informative interpretation of escapement estimates will require a better understanding of the distribution and size of Pacific lamprey spawning populations in the Columbia basin. Pacific lamprey historically coincided spatially with anadromous salmonids in the basin (Close et al. 1995), but there has been little systematic study of current populations (see Cochnauer and Claire 2002; Moser and Close 2003; Graham and Brun 2005). The PIT tag data from 2005-2008 suggests that relatively large proportions of the runs may enter tributaries between John Day and McNary dams (i.e., the John Day and Umatilla rivers). The relatively high escapements between The Dalles-John Day dams (~66%) suggest that more modest numbers of fish likely entered the Deschutes River. Radiotelemetry results in the 1997-2002 Moser et al. studies indicated that ~25-30% of lamprey that passed The Dalles Dam entered the Deschutes River, but there was little apparent use of Bonneville reservoir tributaries in those studies. The radiotelemetry data in 2008 presented a similar picture: about 20% of the fish that passed The Dalles Dam were subsequently reported in the Deschutes River, whereas only eight fish were recorded in Bonneville reservoir tributaries (5% of those that passed Bonneville Dam). A more complete accounting of fish fates, including better discrimination between mortality, harvest and tributary turn-off will be needed to fully interpret escapement estimates (e.g., Keefer et al. 2005).

Passage Rates. – HDX-PIT tagged lamprey took a median of 26 days to pass from release near Hamilton Island to the top of McNary Dam in 2008 which is at the low end of the range of estimates

from similar studies in 2005-2007 (Daigle et al. 2008; Keefer et al. 2009). These times were 2-5 times longer than those recorded for radio-tagged summer Chinook salmon (*O. tshawytscha*) and sockeye salmon (*O. nerka*) migrating during the same season (summer) over approximately the same distance in previous years of radiotelemetry studies (Keefer et al. 2004; Naughton et al. 2005).

Lamprey passage times at dams are typically much longer than those recorded for salmonids. In the several lamprey radiotelemetry studies (including 2008), median passage times at dams were 4-8 d at Bonneville, 2-4 d at The Dalles and ~ 2 d at McNary (Moser et al. 2002b; Cummings 2007; Boggs et al. 2008; Keefer et al. 2009). Dam passage times in the earlier (1997-2002) radiotelemetry studies were generally calculated from the first detection at a receiver in a fishway, thus excluding time fish initially spent in tailrace areas searching for passage routes.

The 2008 radio-tagged lamprey passed relatively quickly through reservoirs, as has been reported in previous studies. Median times in 2008 were ~3 d through the Bonneville reservoir and ~2 d through The Dalles reservoir. These times are approximately twice as long as those recorded for summer Chinook salmon (Keefer et al. 2004), and slightly faster than radio-tagged lampreys in 2007 (Keefer et al. 2009). Both lamprey and salmonid results indicate that fish moved relatively rapidly through reservoirs but were significantly slowed while passing dams.

Median HDX-PIT tagged lamprey passage rates through reaches with a single dam and reservoir ranged from 10-23 $km \bullet d^{-1}$ and were 12-20 $km \bullet d^{-1}$ through multi-dam reaches. Maximum rates past multiple dams were > 35 $km \bullet d^{-1}$. Overall, these rates were higher than median (11 $km \bullet d^{-1}$) and maximum (21 $km \bullet d^{-1}$) passage rates recorded for radio-tagged lampreys in the unimpounded John Day River (Robinson and Bayer 2005) and were consistent with those for radio-tagged lampreys in the Columbia River in 2008 and in previous years (e.g., Moser and Close 2003). The fastest-migrating lamprey passed at about the same rate as an average summer Chinook or sockeye salmon (Keefer et al. 2004; Naughton et al. 2005).

We did not find strong correlations between migration rates and lamprey size, either through single dam-to-dam reaches or over longer reaches. However, there was evidence for increased passage rates later in the migration seasons and slower passage when Columbia River flow was high. Because flow decreased through the migrations in both years, separating migration timing and environmental effects was difficult. Robinson and Bayer (2005) found similar seasonal patterns of faster migration late in the season for lampreys in the John Day River. Similarly, Moser et al. (2004) Daigle et al. (2008), and Keefer et al. (*in press a*) found lamprey passage rates at dams and over longer migration reaches were positively (if weakly) correlated with both temperature and date of year and negatively correlated with total river discharge.

Overall, environmental conditions and lamprey size explained only small proportions of the variability in lamprey passage time in 2008. This is consistent with previous lamprey summaries and suggests that other factors were important. The underlying challenges associated with dam passage for lamprey — independent of river environment or migration timing — may be the primary drivers behind the considerable passage time variability we recorded. These potential factors include nocturnal behaviors, among-population differences, individual physiology, sex, or maturation status, and a relatively flexible migration timetable. Quantifying physiological attributes (e.g., energetic reserves or maturation status), tributary entrances, and final fates of lampreys may improve our understanding of their migration behaviors.

Tagging and Handling Effects and Tag Performance

A concern in the 2007-2008 studies was that radio-tagged fish had significantly lower reach escapement estimates than HDX-PIT tagged fish through almost all study reaches (see Table 20). In contrast, passage times for the two groups were generally similar, with radio-tagged fish passing more rapidly in some reaches and HDX-PIT tagged fish passing faster in others (see Table 17). Other patterns, such as higher escapement estimates for larger fish, were also consistent across tag types, including for double-tagged fish.

The a plausible explanation for the escapement differences between tag types is that radio tagging and associated handling and anesthesia effects negatively affected survival relative to HDX-PIT tagging. Total handling time (including anesthetized time) for radio-tagged lampreys averaged about 10 minutes versus about three minutes for HDX-PIT tagging. In addition, the incision was larger for radio transmitter insertion, sutures were required, and the diameter of the transmitter was twice that of the HDX-PIT tag (8 mm versus 4 mm, respectively). Although we have not identified problems associated with the trailing radio antenna in adult salmonids, the antenna may also be a concern for lamprey given their swimming behavior and attachment to surfaces. Greater handling of radio-tagged fish may also induce downstream movement after release at Bonneville Dam in some fish, a hypothesis that is testable in future studies by increasing radio radiotelemetry coverage downstream and/or by implanting acoustic tags in a sample of adults.

As in 2007, the majority of the radio-tagged fish that did not pass Bonneville Dam in 2008 were last recorded in the tailrace or approached, but did not enter fishways. These results provide some spatial resolution on the non-passing fish but do not help identify the cause for relatively low escapement for radio-tagged fish as final fates were unknown.

Double-tagging with radio and HDX-PIT tags did not appear to have a greater negative effect than radio-tagging only. In the most direct comparisons (i.e., radio-only versus double-tagging), the two groups had similar escapement rates and migration times. Differences between the two groups tended to favor the double-tagged fish in that they had higher escapement and lower passage times, though we note that they also averaged slightly larger than radio-only fish. Overall, use of the secondary PIT tag was beneficial in that it helped identify several additional dam passage events that would have been missed with the radiotelemetry data only.

In general, detection efficiencies were lower for HDX-PIT antenna sites than for radiotelemetry antennas. This was expected given the much greater detection range for active radio tags versus passive HDX-PIT tags. The lowest HDX-PIT detection efficiency was at the top of The Dalles south fishway, a site with a large exit opening that is difficult to monitor with the HDX antennas. An additional antenna downstream in this fishway detected almost all of the fish that were missed at the top-of-ladder site. Improving efficiency for the HDX-PIT system can likely be achieved by building antenna redundancy into the most important monitoring sites, as has been done for the highly efficient full duplex (FDX) arrays. Detection on the radiotelemetry receivers was consistently high across top-of-ladder sites, as we have seen with adult salmonid studies. Only a few lampreys passed these sites without detection, and several of these appeared to have shed transmitters or had non-functioning transmitters because they were not detected on any sites after apparent loss dates. This suggests that top-of-ladder radiotelemetry efficiencies were likely near 100% at the study dams.

In conclusion, the HDX-PIT and radiotelemetry results provided complimentary adult lamprey migration data, and the combination provides both fine-scale and system-wide information. At this time, active radiotelemetry remains an essential tool for fine-scale behavioral evaluations and for monitoring tailraces, fishway entrance areas, reservoirs, and tributaries. Results from 2007 and 2008 suggest that use of radio transmitters likely has some negative effects on adult performance. In

comparison, the HDX tags are cost-effective for system-wide evaluations and their use appears to have fewer negative handling effects. However, the HDX system is relatively limited in its applications because only constricted sites are readily monitored.

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Appendix A. Maps of monitoring sites in 2008. See report Tables 1 and 2 for more detailed descriptions.

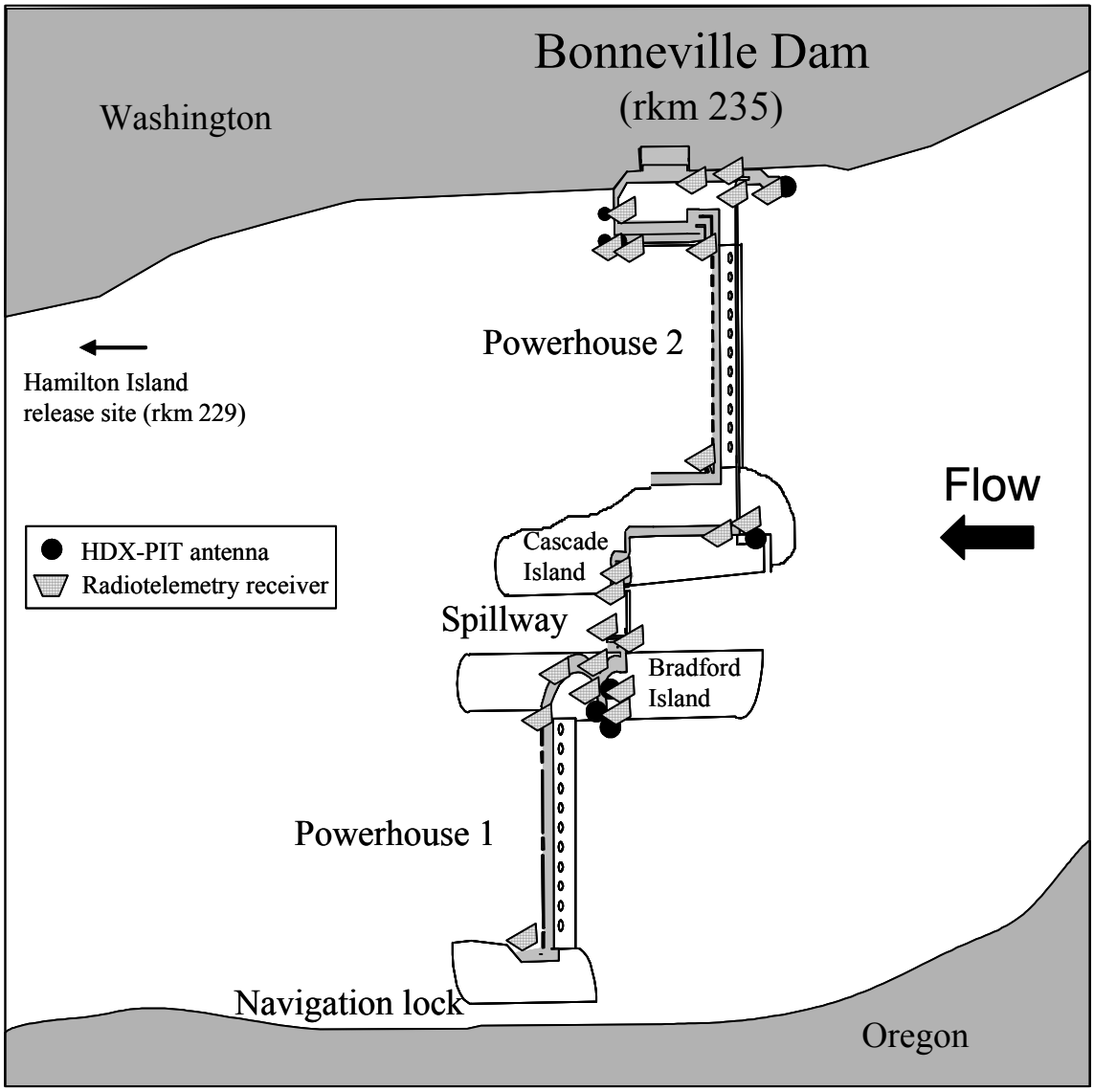


Figure 1. Study area at Bonnevillle Dam on the Columbia River in 2008. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Radiotelemetry sites supported multiple antennas.

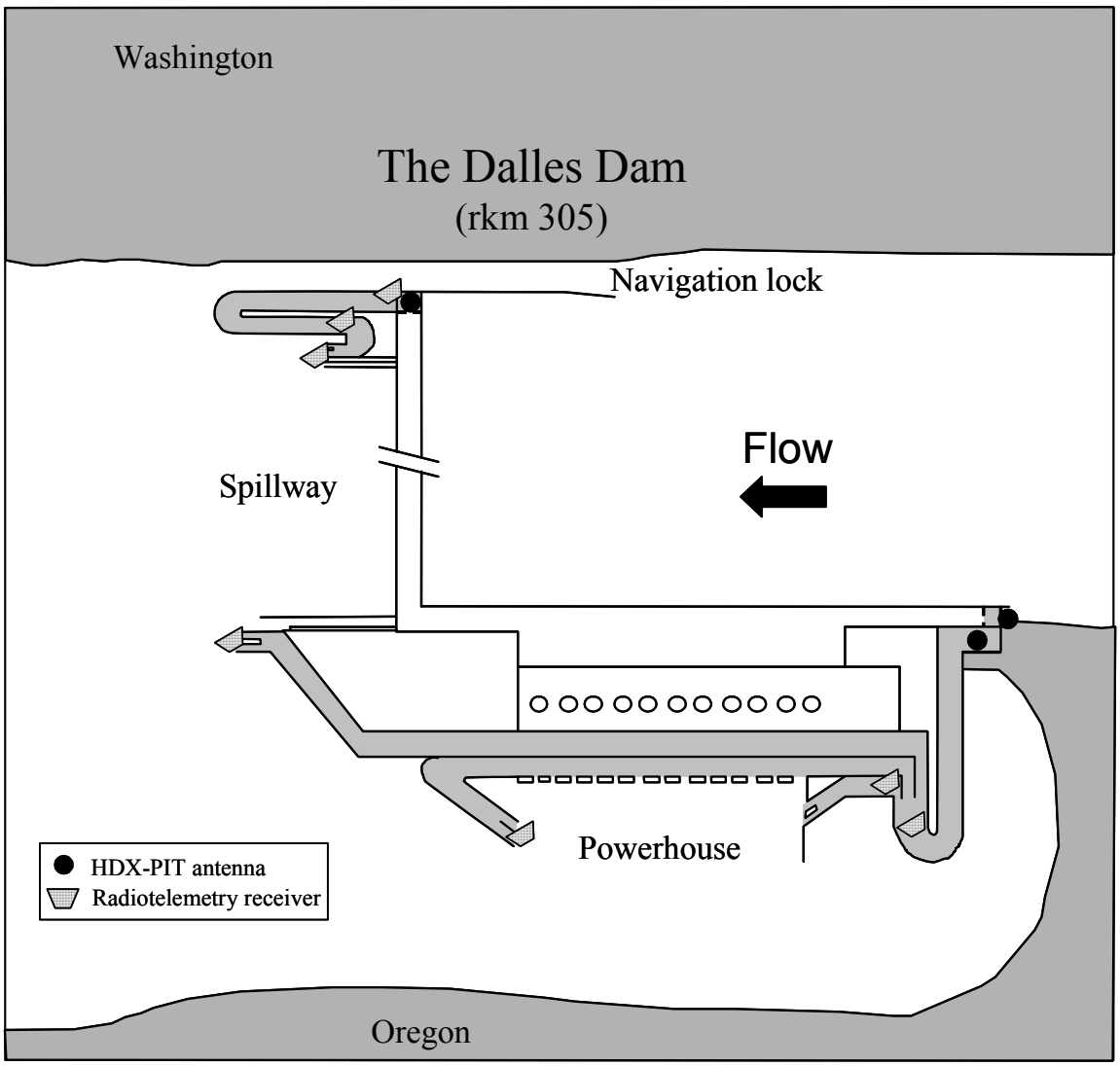


Figure 2. Study area at The Dalles Dam on the Columbia River in 2008. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Radiotelemetry sites supported multiple antennas.

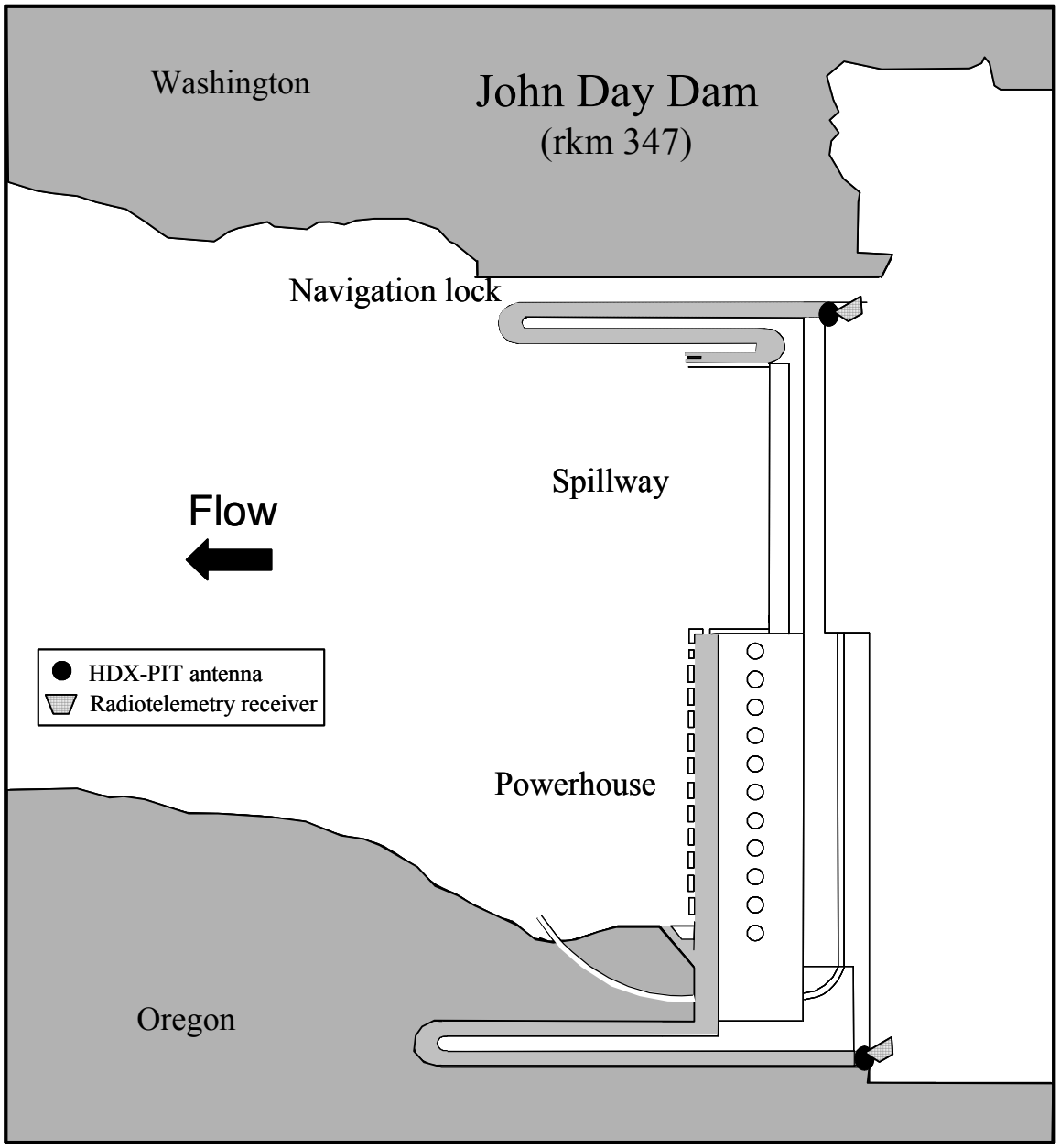


Figure 3. Study area at John Day Dam on the Columbia River in 2008. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Radiotelemetry sites supported multiple antennas.

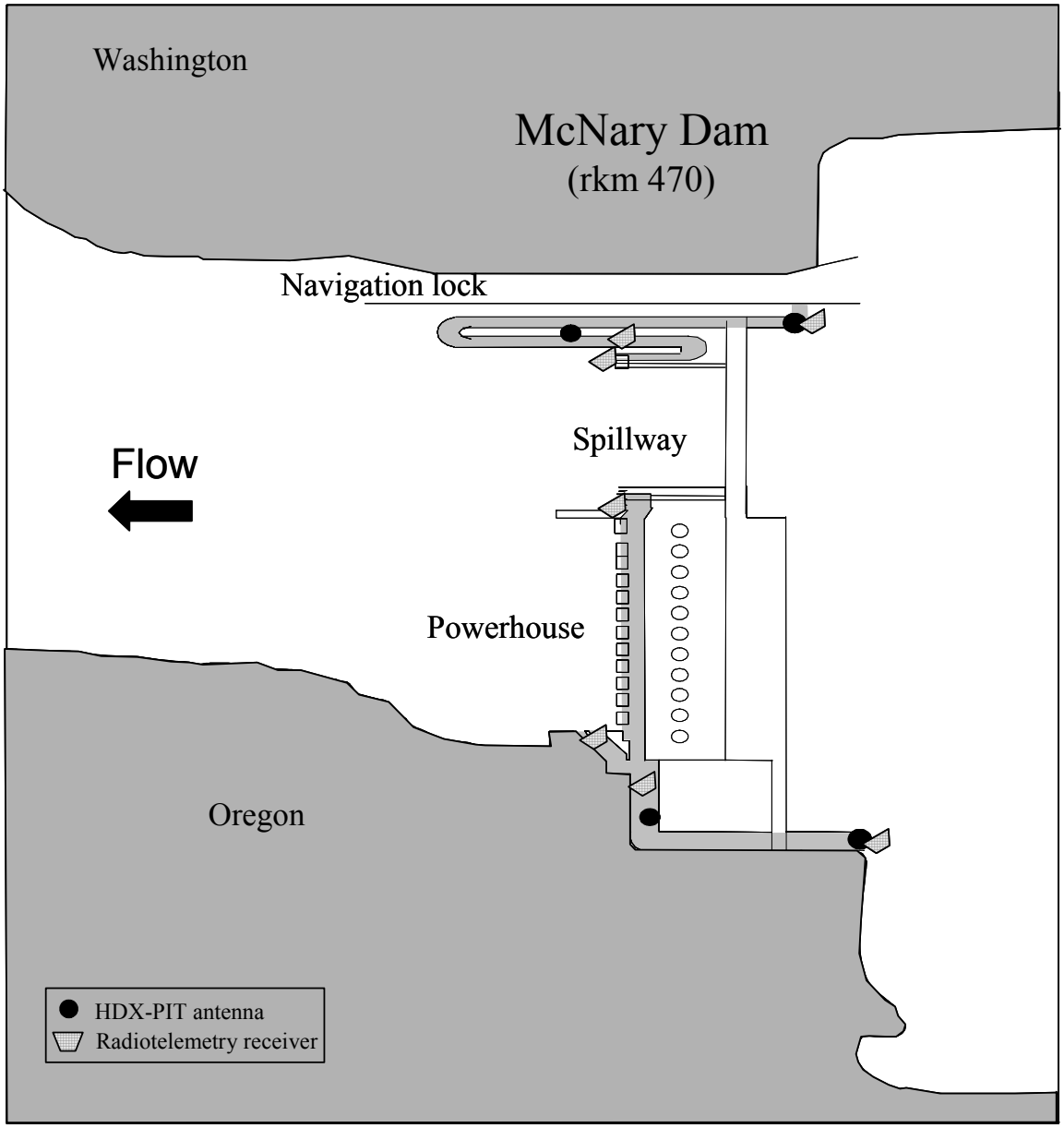


Figure 4. Study area at McNary Dam on the Columbia River in 2008. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Radiotelemetry sites supported multiple antennas.

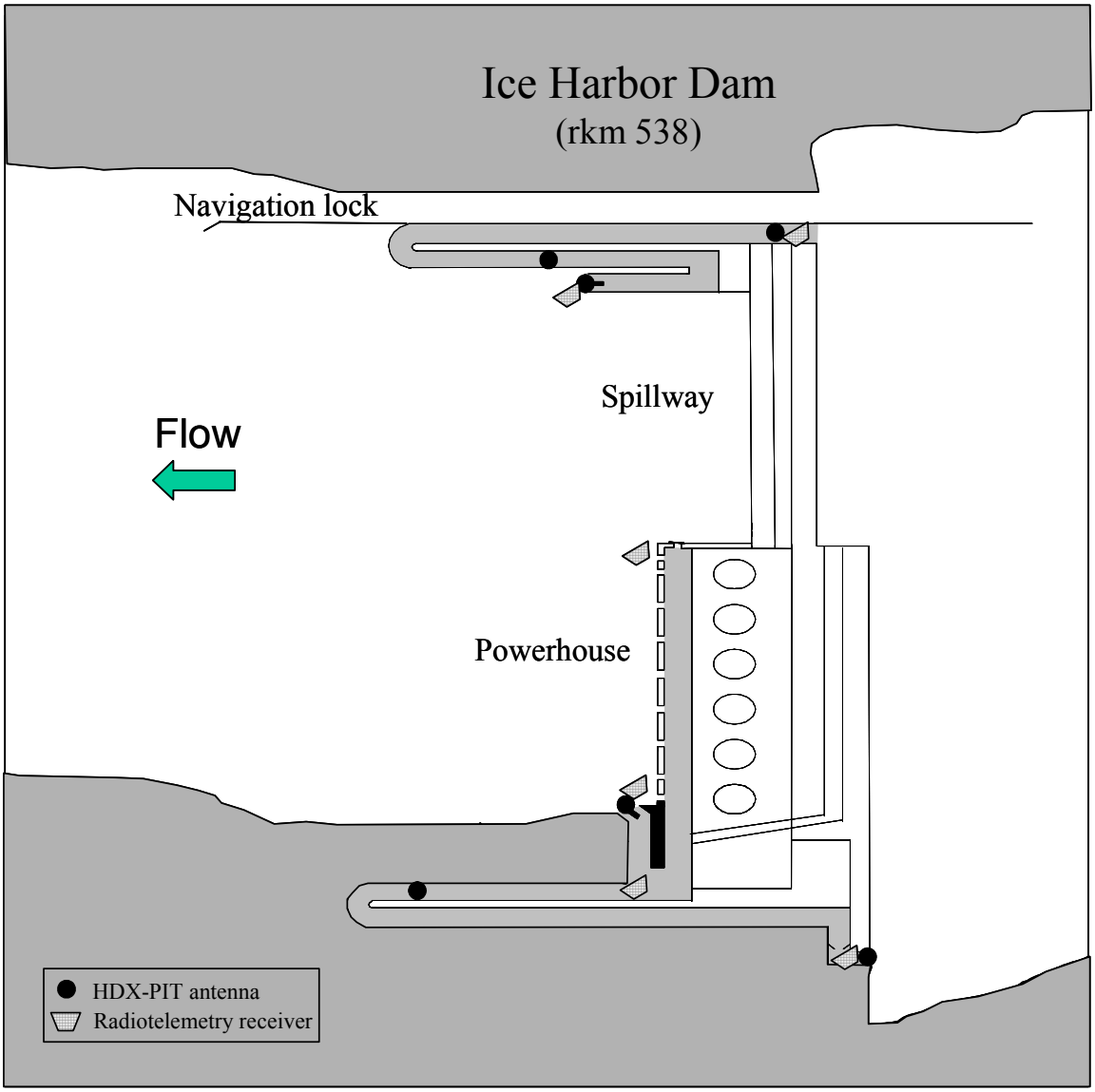
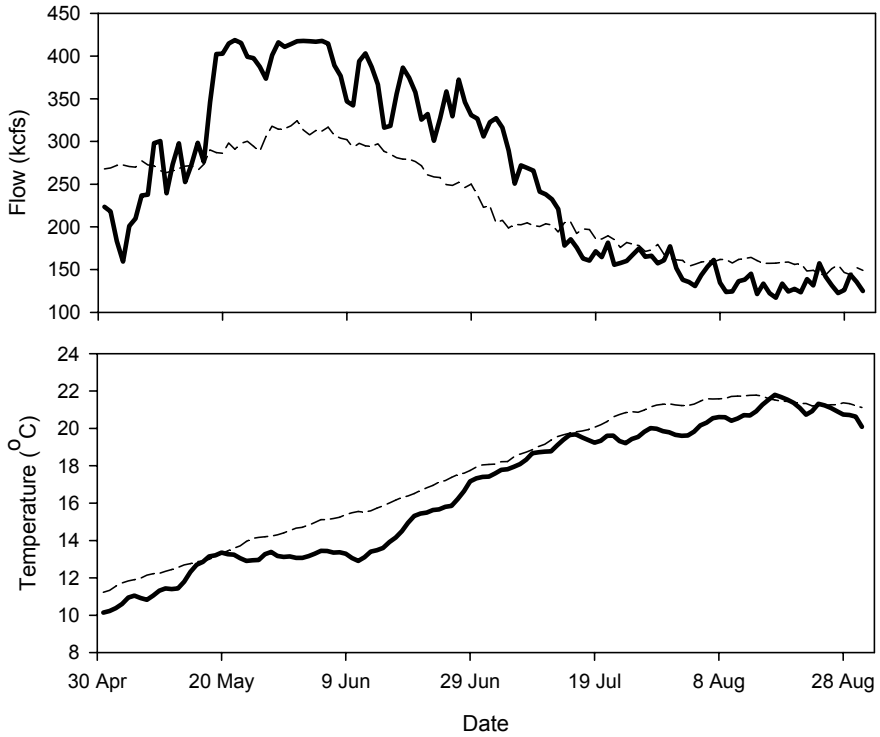


Figure 5. Study area at Ice Harbor Dam on the Snake River in 2008. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Radiotelemetry sites supported multiple antennas.

Appendix B. 2008 Columbia River flow and temperature profiles.



Appendix Figure 1. Mean daily Columbia River flow (kcfs) and temperature (°C) at Bonneville Dam in 2008 (solid line) and for the 1997-2006 average (dashed line).