

Technical Report 2012-3

IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

**ADULT PACIFIC LAMPREY MIGRATION IN THE LOWER COLUMBIA
RIVER: 2011 HALF-DUPLEX PIT TAG STUDIES**

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

by

M. L. Keefer, C. C. Caudill, E. L. Johnson,
T. S. Clabough, M. A. Jepson, C. T. Boggs
Department of Fish and Wildlife Sciences and
Idaho Cooperative Fish and Wildlife Research Unit
University of Idaho, Moscow, ID 83844-1141

and

M. L. Moser
Northwest Fisheries Science Center, NOAA Fisheries
2725 Montlake Blvd. East, Seattle, WA 98112



For

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

2012

Report Documentation Page				Form Approved OMB No. 0704-0188	
Public reporting burden for the collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to a penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number.					
1. REPORT DATE 2012		2. REPORT TYPE		3. DATES COVERED 00-00-2012 to 00-00-2012	
4. TITLE AND SUBTITLE Adult Pacific Lamprey Migration in the Lower Columbia River: 2011 Half-Duplex Pit Tag Studies				5a. CONTRACT NUMBER	
				5b. GRANT NUMBER	
				5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S)				5d. PROJECT NUMBER	
				5e. TASK NUMBER	
				5f. WORK UNIT NUMBER	
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) University of Idaho, Department of Fish and Wildlife Sciences, Idaho Cooperative Fish and Wildlife Research Unit, Moscow, ID, 83844-1136				8. PERFORMING ORGANIZATION REPORT NUMBER	
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)				10. SPONSOR/MONITOR'S ACRONYM(S)	
				11. SPONSOR/MONITOR'S REPORT NUMBER(S)	
12. DISTRIBUTION/AVAILABILITY STATEMENT Approved for public release; distribution unlimited					
13. SUPPLEMENTARY NOTES					
14. ABSTRACT					
15. SUBJECT TERMS					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT Same as Report (SAR)	18. NUMBER OF PAGES 38	19a. NAME OF RESPONSIBLE PERSON
a. REPORT unclassified	b. ABSTRACT unclassified	c. THIS PAGE unclassified			

**ADULT PACIFIC LAMPREY MIGRATION IN THE LOWER COLUMBIA RIVER: 2011
HALF DUPLEX PIT-TAG STUDIES**

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

by

M. L. Keefer, C. C. Caudill, E. L. Johnson, T. S. Clabough, M. A. Jepson, C. T. Boggs
Department of Fish and Wildlife Sciences and
Idaho Cooperative Fish and Wildlife Research Unit
University of Idaho, Moscow, ID 83844-1141

and

M. L. Moser
Northwest Fisheries Science Center, NOAA Fisheries
2725 Montlake Blvd. East, Seattle, WA 98112

For

U.S. Army Corps of Engineers
Portland and Walla Walla Districts

2012

Acknowledgements

Many people assisted with the field work and data compilation for this report and its successful completion was made possible through their efforts. Steve Lee, Dan Joosten, Dennis Quaempts and Brandon Treloar were responsible for collecting and tagging lampreys. Charles Boggs, Travis Dick, Mark Morasch, Matt Knoff, and Steve Corbett maintained and downloaded the monitoring equipment. Ben Ho provided proximate analysis data used to estimate lipid content from the Distell Fatmeter. Staff at other agencies also provided lamprey detection data, including Matt Fox (Confederated Tribes of Warm Springs Reservation of Oregon), Nathan Jahns and Bryan Nass (LGL Northwest Research Associates), and Mike Clement (Grant County Public Utility District). We also thank the staff of Pacific States Marine Fisheries Commission's Kennewick Field Office, especially Darren Chase and Don Warf. The U.S. Army Corps of Engineers provided funding for this study; we thank Sean Tackley, David Clugston, Derek Fryer, Tammy Mackey, Jon Rerecich, Ben Hausmann, Kasey Welch, Miro Zyndol, Robert Cordie, Brad Eby, and Mark Plummer.

Table of Contents

Executive Summary	v
Introduction	1
Methods	1
Lamprey Collection and Tagging	1
Monitoring Sites	2
Data Analyses	2
Results	4
Lamprey Collection and Tagging	4
Detection Efficiency: Downstream release group	6
Detection Efficiency: Upstream release group	6
Downstream Release Group	7
Upstream Progression	7
Dam-to-Dam Escapement	7
Passage Times and Rates	7
Diel Passage	15
Last Detection Summary	15
Upstream Release Group	17
Dam-to-Dam Escapement	18
Passage Times and Rates	18
Diel Passage	18
Last Detection Summary	18
Final Detection Comparison for Downstream and Upstream Release Groups	18
Cascades Island Release Group	19
Detection of Lampreys Tagged in 2010	19
Discussion	22
Escapement	22
Passage Times	25
Final Distribution	25
HD Antenna Detection Efficiency	26
Lampreys Released Upstream from Bonneville Dam	27
Conclusions	27
References	29
Appendix A: 2011 Columbia River Discharge and Temperature Profiles	33

Executive Summary

We tagged adult Pacific lamprey (*Entosphenus tridentatus*) collected at Bonneville Dam with half duplex (HD) passive integrated transponder (PIT) tags and monitored their passage and migration behaviors at Bonneville, The Dalles, John Day, McNary, Ice Harbor, Lower Monumental, Lower Granite, and Priest Rapids dams. Our objectives were to calculate lamprey passage times, to estimate escapement past the monitored sites, and to evaluate potential physiological and environmental correlates with lamprey migration through the study area.

In total, we HD-PIT tagged 929 lampreys in 2011: 800 were released downstream from Bonneville Dam near Hamilton Island, 109 were released upstream from Bonneville Dam near Stevenson, WA, and 20 were released directly into the Cascades Island lamprey passage structure (LPS). An additional 85 lampreys were double-tagged with HD-PIT tags and acoustic transmitters (JSATS), and results from these fish are presented in a separate report.

The 2011 escapement estimate from release below Bonneville Dam past the dam was 56%, higher than estimates in the 2005-2009 HD-PIT studies (41-53%). Escapement from the top of Bonneville Dam to the top of The Dalles Dam (52%) and from the top of The Dalles Dam to the top of John Day Dam (80%) was also higher than or similar to previous estimates. Large lampreys in the downstream release group were significantly more likely than small lampreys to pass through most dam-to-dam reaches. As in previous years, lampreys last detected at upriver sites were significantly larger than those last recorded closer to the release site, indicating that size-dependent effects on migration distance and final distribution were likely.

Lamprey migration times were highly variable. The median passage time for the downstream-released fish was 10.2 days ($< 1 \text{ km} \cdot \text{d}^{-1}$) from release to the top of Bonneville Dam. Median times between top-of-ladder antennas were 4.3 days ($17 \text{ km} \cdot \text{d}^{-1}$) between Bonneville and The Dalles dams, 3.4 days ($11 \text{ km} \cdot \text{d}^{-1}$) between The Dalles and John Day dams, and 9.1 days ($14 \text{ km} \cdot \text{d}^{-1}$) between John Day and McNary dams. Each of the reaches upstream from Bonneville Dam included one reservoir and one dam. Median migration rates ranged from 5-18 $\text{km} \cdot \text{d}^{-1}$ in reservoir-plus-dam reaches upstream from McNary Dam that included portions of the Snake and upper Columbia rivers, including the unimpounded Hanford Reach. Lampreys generally migrated faster later in the summer through most reaches, coincident with increasing river temperatures and decreasing river discharge.

The sample released upstream from Bonneville Dam ($n = 109$) generally had lower reach escapement estimates, slower passage times, and fewer fish that reached sites upstream from McNary Dam than the downstream-released fish. However, several factors confounded direct comparison of these two samples. First, the upstream-released fish were the only tagged lampreys collected in the Cascades Island LPS trap. Second, these fish were tagged on relatively few dates, primarily in the second half of the migration (i.e., they were not sampled proportionately to the run). Third, they were smaller, on average, than the downstream-released fish that passed Bonneville Dam. Among-sample differences in behavior and distribution generally persisted even after statistically controlling for these factors inasmuch as possible. It is possible that handling, transport, or passage through the Cascades Island LPS affected the behavior or survival of the upstream-released sample.

The combined basin-wide results in 2011 indicated improved passage efficiency at Bonneville Dam and through some upstream reaches, despite river discharge that was well above average (typically associated with lower escapement). Recent modifications made to fishway operations and structures potentially improved lamprey passage at dams (especially Bonneville Dam).

Introduction

Pacific lamprey (*Entosphenus tridentatus*) is the largest lamprey species in the Columbia and Snake rivers. Pacific lampreys are anadromous, with parasitic adults spending 1-4 years in the ocean before returning to spawn in freshwater rivers (Beamish 1980; Close et al. 2002; Moser and Close 2003). Recent studies suggest that Pacific lamprey abundance has steadily declined in the Columbia River basin and in other regional rivers since the early 1960's (Kostow 2002; Clemens et al. 2010; USFWS 2010). 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. 2009a; Keefer et al. 2010a, 2011a).

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

The objectives of the 2011 studies described in this report were to use HD-PIT systems to: (1) calculate adult lamprey passage rates past multiple dams and reservoirs; (2) estimate lamprey escapement past multiple dams, through individual dam-to-dam reaches, and into tributaries; (3) examine potential physiological and environmental correlates with upstream passage. A more detailed description of JSATS-tagged lamprey behaviors and an evaluation of HD-PIT tagged lamprey use of lamprey passage systems (LPS, Moser et al. 2011) are presented in separate reports.

Methods

Lamprey Collection and Tagging

Lampreys used in this study were collected at night in traps at Bonneville Dam (Columbia River kilometer [rkm] 235). Traps were located near the Adult Fish Facility (AFF) and at the Washington-shore fishway entrance and additional fish were captured in a trap at the top of the Cascades Island LPS. In 2011, 929 lampreys were tagged with only half-duplex passive integrated transponder (HD-PIT) tags. Lampreys captured in the Cascades Island LPS ($n = 109$) were all released upstream from Bonneville Dam at the boat ramp near Stevenson, WA. Lampreys captured in all other locations were released downstream from Bonneville Dam near Hamilton Island at Columbia River rkm 232.5 ($n = 800$) or into the Cascades Island LPS ($n = 20$).

Before tagging, all fish were anaesthetized using 60 ppm (3 mL•50 L⁻¹) eugenol, measured (length and girth to the nearest mm), and weighed (nearest g). HD-PIT fish were then outfitted with a uniquely-coded, glass-encapsulated HD-PIT tag (Texas Instruments, 4×32 mm, 0.8 g). HD-PIT tags were surgically implanted in the body cavity of anaesthetized fish through a small incision (< 1 cm) along the ventral midline and in line with the anterior insertion of the first dorsal fin as described in Moser et al. (2006). An additional physiological measure, muscle lipid content (% lipid), was collected for most lampreys using a Distell fat meter (e.g., Crossin and Hinch 2005). Fat meter readings from 2011 were converted to estimated % lipid (wet weight basis) using the regression equation 'percent lipid' = 3.618 * reading – 2.436 ($P < 0.01$; $r^2 = 0.4808$; $n = 33$). The regression equation was developed by comparing Fatmeter readings taken in 2008 on live lamprey captured at Bonneville ($n = 20$) and McNary ($n = 13$) dams to lipid levels determined by biochemical proximate analysis on the same individuals following euthanasia (B. Ho, unpublished data). The 2008 proximate analysis was performed by the Wildlife Habitat Nutrition Laboratory, Washington State University, Pullman, Washington. Collection and tagging protocols were reviewed and approved by the University of Idaho Institutional Animal Care and Use Committee.

Monitoring Sites

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

Data Analyses

Reach escapement rates were calculated by dividing the number of lamprey known to pass an upstream HD site by those known to pass a site downstream or by the number released. Fish were treated as having passed a site if they were detected at the site or at a location further upstream. Escapement rates were calculated across all release dates. Lamprey sizes (length, weight, and girth) were compared for groups that passed through a reach and those that did not using general linear models (PROC GLM, SAS) and analysis of variance. Eleven lampreys were recaptured and these fish were transported to Stevenson, WA and released. Where appropriate, these fish were excluded from analyses of escapement and passage times.

Lamprey migration times (d) and passage rates (km•d⁻¹) were calculated from release to top-of-ladder HD-PIT antennas at dams and between monitored sites. Linear regression was used to evaluate relationships between log₁₀-transformed lamprey passage times and the following: length, girth, weight, release date or date fish entered upstream reaches, river discharge, and water temperature either on the release date or the date each fish passed top-of-ladder sites at dams. Analyses using environmental data should be considered conservative as environmental conditions were constantly changing during the passage periods and the temporal variance may have obscured associations between behavior and environmental factors.

Detection efficiencies for HD-PIT sites were estimated by dividing the number of fish detected at a site by the number that was detected upstream from that site. (Note: this method differs from

previous years, when double-tagged fish were used to estimate efficiencies.) These estimates were conservative because fish could pass via unmonitored routes at many locations (e.g., navigation locks or alternate routes in and adjacent to fishways) and thus represent minimum estimates of detection efficiency in most cases.

Table 1. Half-duplex PIT tag interrogation sites (antennas) used by UI/NMFS to monitor lamprey passage at lower Columbia and Snake river dams in 2011. See Appendix B for maps of antenna sites at individual dams. Note: additional HD monitoring sites were operated at Priest Rapids and Wanapum dams (LGL) and in Fifteenmile Creek and Shitike Creek (CTWSRO).

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

¹ did not operate in 2011

Results

Lamprey Collection and Tagging

The total adult lamprey count at Bonneville Dam in 2011 was 51,606 (daytime count station = 18,315; night video count = 18,957; LPS count = 14,334). This total was higher than in 2008-2010, but still well below historic counts. A total of 929 lampreys were HD-PIT-tagged, or approximately 1.8% of the combined day, night, and LPS count of adult lampreys at Bonneville Dam (Figure 1). The tagged sample included 800 lampreys released downstream from Bonneville Dam, 109 released upstream from the dam near Stevenson, WA, and 20 released directly into the Cascades Island LPS (Figure 1). These three groups were analyzed separately for most of the summaries provided below. Overall, sampling was generally proportional to daily counts, except that handling was restricted during a warm-water period from 12-24 August.

Lamprey size metrics and lipid content were positively correlated in the combined 2011 HD-PIT sample (Figure 2). Percent lipid was more variable than the other metrics, perhaps in part because of the relatively weak relationship ($r^2 = 0.48$) between Fatmeter estimates and true lipid content (as measured by proximate analysis in 2008; see Methods). For example, the coefficient of variation (CV) for mean %lipid was 33% versus 19% for weight, 7% for girth, and 6% for length for the total sample (Table 2). In general, release date was weakly, but significantly negatively correlated with lamprey length, girth, weight, and %lipid ($-0.20 < r < -0.11$, $P \leq 0.05$).

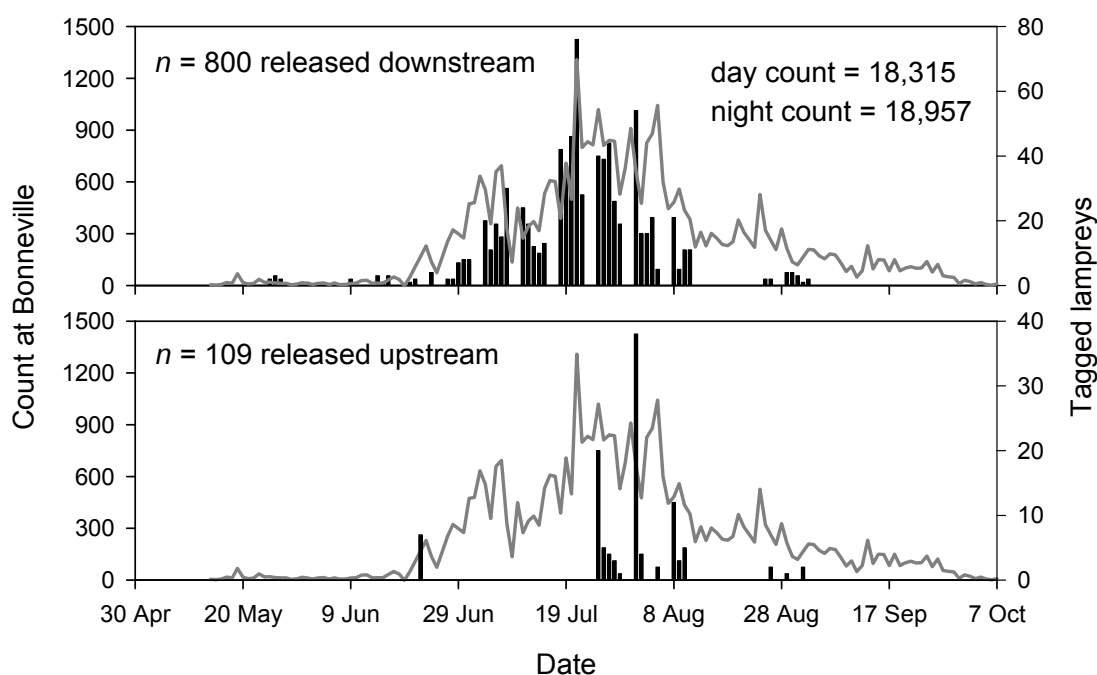


Figure 1. Number of adult Pacific lamprey counted passing Bonneville Dam during the day and night (solid line) and the numbers that were collected and HD-PIT tagged (bars) in 2011. Top panel shows fish released downstream from Bonneville Dam near Hamilton Island and bottom panel shows fish released upstream from the dam near Stevenson, WA.

Table 2. Length, girth, weight, and percent lipid of adult Pacific lampreys collected and tagged with HD-PIT tags and released downstream from Bonneville Dam near Hamilton Island (HAM), upstream from the dam near Stevenson, WA (STE), or in the Cascades Island LPS (CI) in 2011. Lipid estimates were based on four readings per fish.

Type	Length (cm)			Girth (cm)			Weight (g)			Percent lipid (%)		
	<i>n</i>	Mean	<i>sd</i>	<i>n</i>	Mean	<i>sd</i>	<i>n</i>	Mean	<i>sd</i>	<i>n</i>	Mean	<i>sd</i>
PIT-HAM	800	64.8	4.1	795	10.8	0.8	737	437.0	84.2	704	24.8%	8.1%
PIT-STE	109	64.8	3.9	109	10.7	0.8	105	431.3	78.7	109	23.5%	7.1%
PIT-CI	20	64.1	4.4	20	10.5	0.8	14	400.9	82.9	20	25.2%	9.9%
All fish	929	64.8	4.1	924	10.8	0.8	856	435.7	83.7	833	24.6%	8.1%

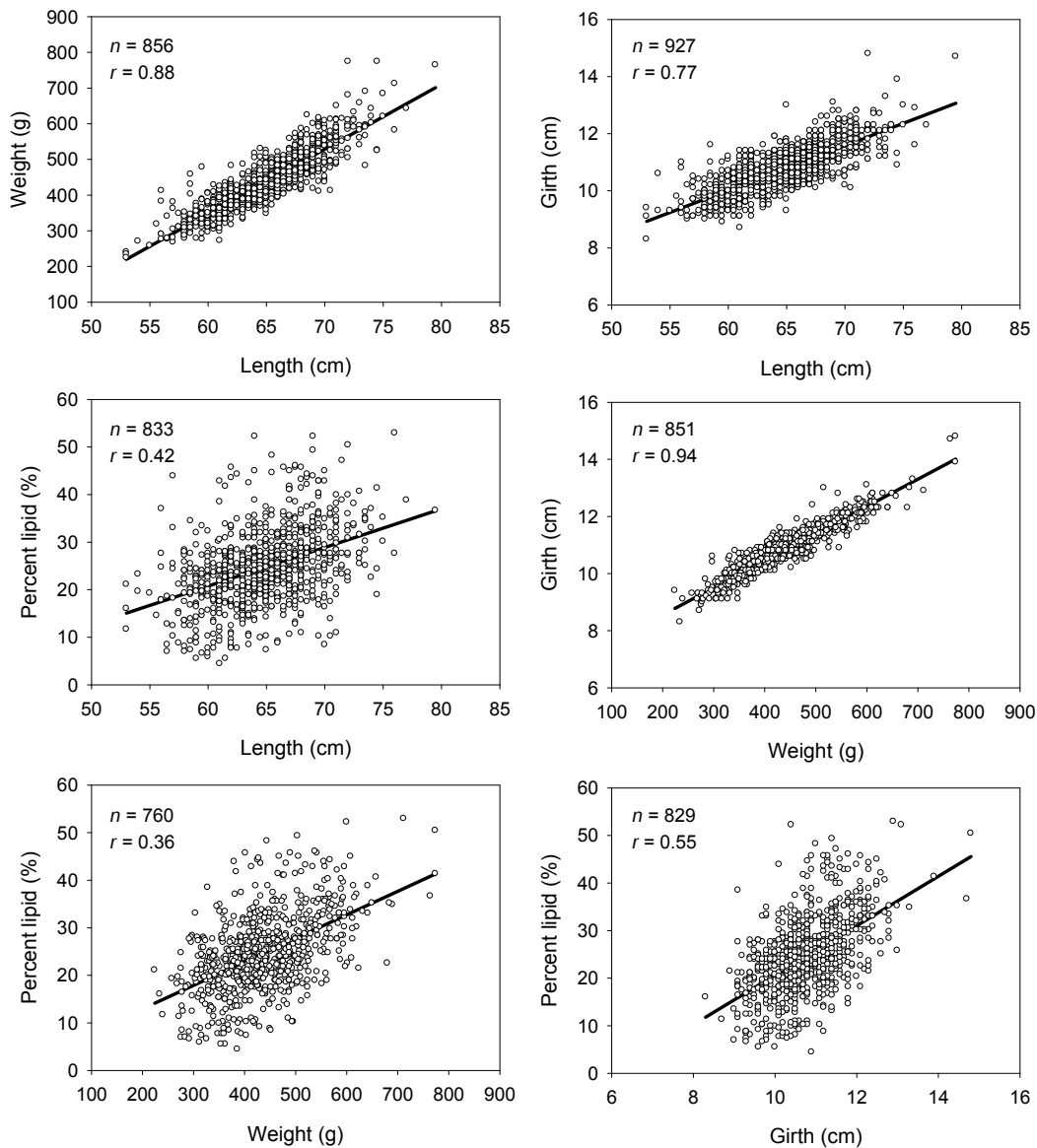


Figure 2. Linear relationships between length, weight, girth, and %lipid metrics for adult lampreys HD-PIT tagged in 2011. Note: all release groups combined.

Detection Efficiency: Downstream Release Group – Efficiencies described in this section were based on HD-PIT data only (i.e., no records from double-tagged fish; see Noyes et al. (2012) for additional details derived from lampreys double-tagged with HD-PIT tags and acoustic transmitters).

A total of 323 lampreys were detected at antennas upstream from Bonneville Dam. Of these, 282 (87.3%) were detected at one or more Bonneville HD antennas and 201 (62.2%) were detected at top-of-ladder or top-of-LPS antennas (includes fish that were recaptured at Bonneville Dam and released upstream). Based on inspections of individual fish histories, most lampreys that passed top-of-ladder sites undetected were last recorded in the Washington-shore or Cascades Island fishway. Of the 122 fish that passed Bonneville Dam without detection at an exit site, 23 (19%) had records (censored) that suggested they passed the Washington-shore fish ladder prior to release (i.e., there was a data error related to fish release time or with the time recorded on the exit antenna). Another 26 (21%) were last recorded at Bonneville Dam by antennas in the Cascades Island fishway or LPS. Thirty-five fish (29%) were last recorded at Bonneville Dam on an antenna inside the Washington-shore fishway or fish ladder and 40 (33%) were not detected at any site.

A total of 194 lampreys were detected at antennas upstream from The Dalles Dam. Of these, 146 (75.3%) were detected at one or more antennas at The Dalles Dam. We did not estimate efficiency for the top-of-ladder antennas separately because the antenna at the top of the east ladder was not operated in 2011. Seventy-four lampreys were detected upstream from John Day Dam, of which 71 (95.9%) were detected at the top-of-ladder antennas at John Day Dam.

Fifty-seven lampreys were detected at sites upstream from McNary Dam, of which 44 (77.2%) were detected at one or more McNary antennas and 15 (26.3%) were detected at McNary top-of-ladder antennas. Of the 42 that passed top-of-ladder sites undetected, 12 (29%) likely circumvented the top-of-ladder antennas via the juvenile channels adjacent to the upper south fishway, 16 (38%) were last detected on antennas inside the two fishways, and 14 (33%) were not detected at any McNary site.

Sample sizes at the Snake River dams were small (≤ 15) and there were limited upstream detection sites. Eleven lampreys were detected upstream from Ice Harbor Dam, of which 11 (100%) were detected at an Ice Harbor antenna; 8 of the 11 (72.7%) were detected at top-of-ladder antennas. Three lampreys were detected at Lower Granite Dam, all of which were detected at Lower Monumental Dam (100%). No estimate was calculated for the Lower Granite antenna site.

A total of 35 lampreys were detected at either University of Idaho or LGL antennas at Wanapum Dam, of which 34 (97.1%) were detected at Priest Rapids ladder antennas. No estimate was calculated for Wanapum Dam.

Detection Efficiency: Upstream Release Group – Antenna detection efficiency at combined HD antennas at The Dalles Dam was 61.3% (19 lampreys were detected at The Dalles of 31 detected at upriver locations). All 4 of the fish detected upstream from John Day Dam were detected at John Day Dam top-of-ladder antennas (efficiency = 100%). Two lampreys were detected upstream from McNary Dam and neither was detected at McNary top-of-ladder antennas (efficiency = 0%); however, one of the two was detected at the McNary south juvenile channel.

Downstream Release Group

Upstream Progression – Of the 800 lampreys released downstream from Bonneville Dam, 568 (71.0%) were subsequently recorded at one or more Bonneville Dam HD antennas inside fishways, at LPS systems, or at dams further upstream (Table 3). A total of 451 fish passed Bonneville Dam (56.4% of the 800 released, and 79.4% of the 568 detected at one or more sites after release). Another 11 (1.4%) were recaptured in traps and were released upstream. (Note: release time and recapture data for 28 lampreys were unknown due to a clock error at the AFF trap. Data for these fish were unaffected upstream from Bonneville Dam and we only used records we considered reliable.)

The median tag date for HD-PIT tagged lampreys released downstream was 21 July (*mean* = 21 July). Median recorded passage dates at top-of-ladder sites were 4 August at Bonneville Dam (*n* = 327), 9 August at The Dalles Dam (*n* = 103), 9 August at John Day Dam (*n* = 187), 6 September at McNary Dam (*n* = 21), 9 September at Priest Rapids Dam (*n* = 34), 5 September at Wanapum Dam (*n* = 22), 25 August at Ice Harbor Dam (*n* = 11), 2 September at Lower Monumental Dam (*n* = 11), and 29 August at Lower Granite Dam (*n* = 3). Additional fish passed each dam without detection at top-of-ladder (or LPS) antennas (i.e., passage date was uncertain). Top-of-ladder dates of detection for the HD-PIT tagged fish indicated relative underrepresentation early in the run at Bonneville and The Dalles dams (Figure 5) and this carried over into the Snake River (Figure 6). Distributions of tagged fish at McNary, Priest Rapids, and Wanapum dams more closely approximated the daytime counts, though we note that tagged-fish sample sizes at all dams upstream from John Day Dam were small.

Dam-to-Dam Escapement – Of 800 fish released, 57.8% (*n* = 462) were known to have passed Bonneville Dam (including the 11 that were recaptured and released upstream), 29.8% (*n* = 238) passed The Dalles Dam, 23.8% (*n* = 190) passed John Day Dam, 8.1% (*n* = 65) passed McNary Dam, 4.4% (*n* = 35) passed Priest Rapids Dam, and 2.8% (*n* = 22) passed Wanapum Dam (Tables 3 and 4). A total of 1.9% (*n* = 15) passed Ice Harbor Dam, 1.4% (*n* = 11) passed Lower Monumental Dam, and 0.3% (*n* = 3) passed Lower Granite Dam. Escapement from the top of Bonneville Dam was 51.7% to the top of The Dalles Dam, 41.3% to the top of John Day Dam, and 13.9% to the top of McNary Dam. Escapements were 79.8% between ladder tops at The Dalles and John Day dams and 33.7% between ladder tops at John Day and McNary dams. Of 64 lampreys that passed McNary Dam, 15 (23.4%) passed Ice Harbor Dam and 35 (54.7%) passed Priest Rapids Dam (Tables 3 and 4).

In almost all reaches, lamprey that passed upstream sites were significantly ($P < 0.05$) larger than those that did not pass (Table 5). This pattern was less evident upstream from John Day Dam. Escapement through a reach was not significantly associated with the date that lampreys were released downstream from Bonneville Dam, except that lampreys that passed John Day Dam were tagged 3 d earlier, on average, than those that did not pass John Day Dam ($P = 0.049$). Lampreys that passed The Dalles Dam had passed Bonneville Dam earlier and encountered higher river discharge, on average, than those that did not pass The Dalles Dam (Table 6). We also found significant water temperature effects in The Dalles-John Day and John Day-McNary reaches, but these effects were in opposite directions. We also note that many lampreys passed The Dalles Dam without being detected on the most upstream antenna, reducing the statistical power of these tests.

Passage Times and Rates – Median HD-PIT tagged lamprey passage times were 10.2 d from the release site to the top of Bonneville Dam, 4.3 d between Bonneville and The Dalles dams, 3.4 d between The Dalles and John Day dams, and 9.1 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 7). Median passage rates in these reaches were $< 1 \text{ km} \cdot \text{d}^{-1}$ (release-Bonneville top), $17.0 \text{ km} \cdot \text{d}^{-1}$ (Bonneville-The Dalles), $11.4 \text{ km} \cdot \text{d}^{-1}$ (The Dalles-John Day), and 13.5

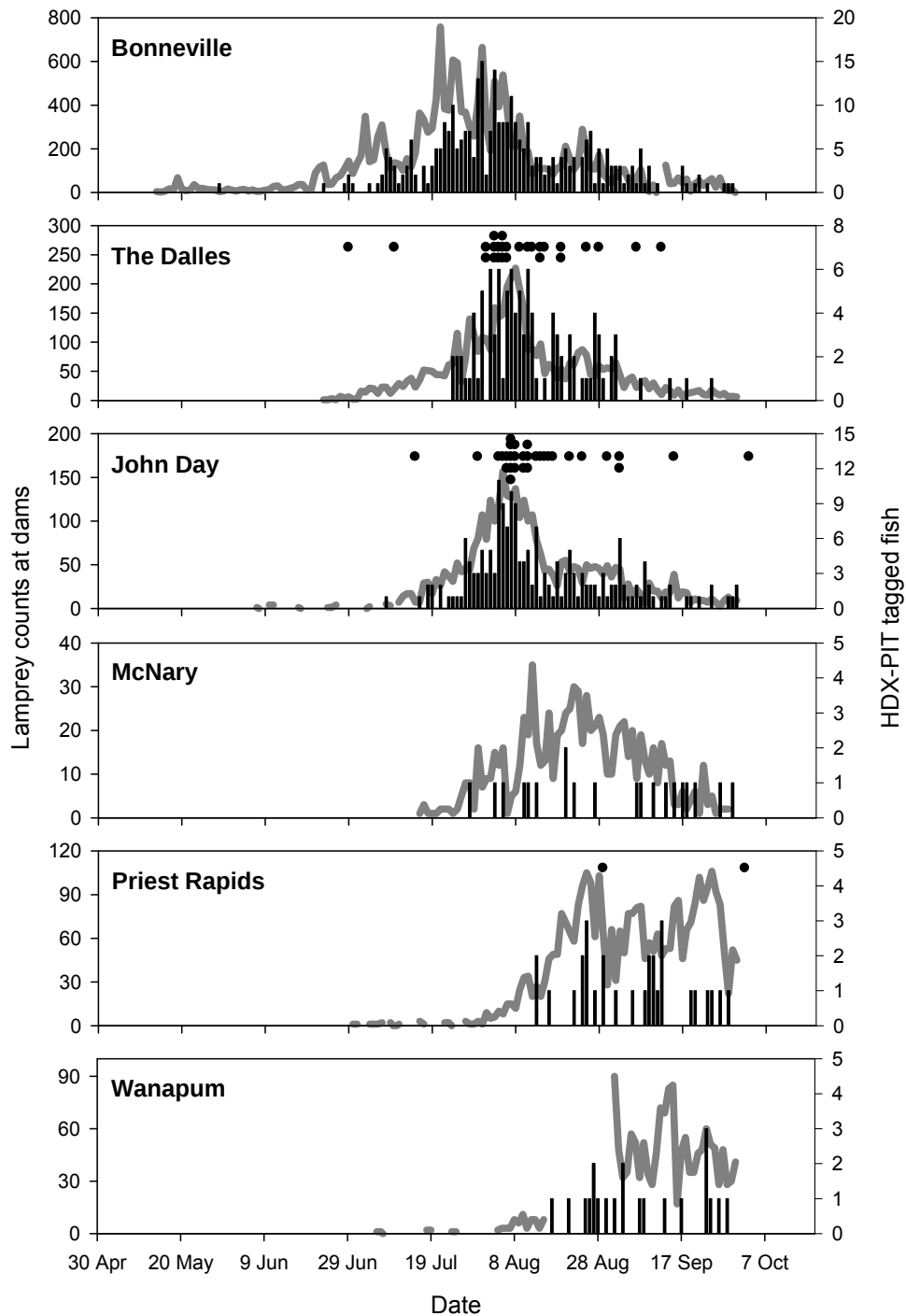


Figure 3. Daily numbers of adult Pacific lamprey counted passing Columbia River dams via fish ladders (gray lines) and the numbers of HD-PIT tagged fish that were detected at top-of-ladder antennas (black bars = detections from fish released downstream from Bonneville; • = detections from fish **released upstream from Bonneville Dam**) in 2011. Note: many lampreys passed dams undetected, particularly at The Dalles and McNary dams, and count data were unavailable at Wanapum Dam for 16 d in August.

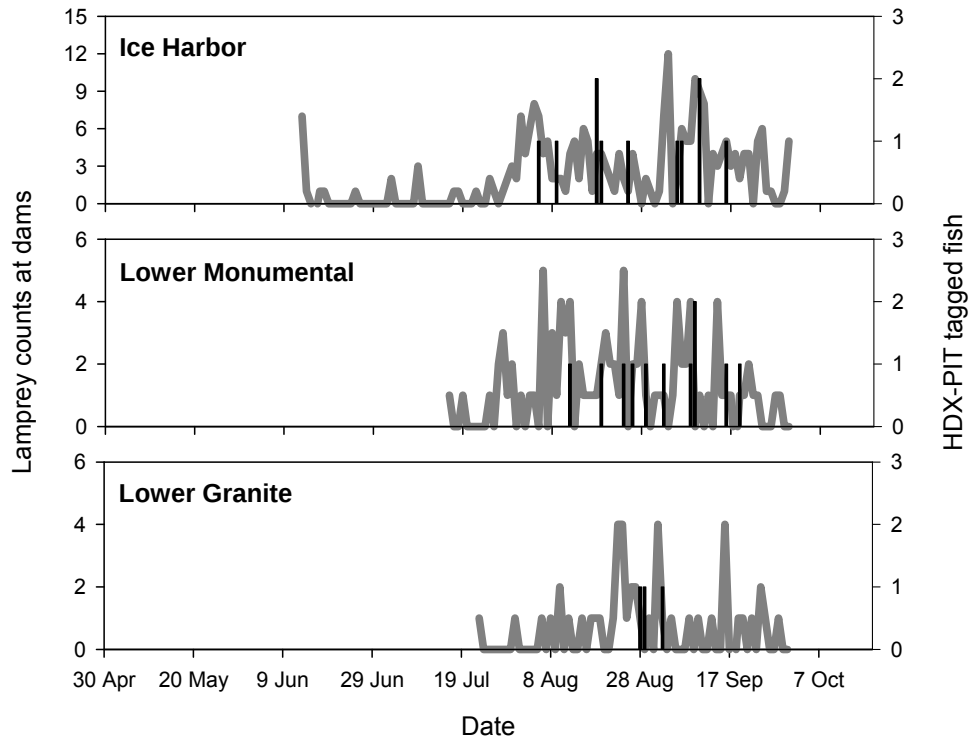


Figure 4. Daily numbers of adult Pacific lamprey counted passing Snake River dams via fish ladders (gray lines) and the numbers of HD-PIT tagged fish that were detected at top-of-ladder antennas (black bars = detections from **fish released downstream from Bonneville**) in 2011. No fish released upstream from Bonneville Dam were detected at the Snake River dams.

$\text{km} \cdot \text{d}^{-1}$ (John Day-McNary). Above McNary Dam, median passage times were 9.2 d ($18.4 \text{ km} \cdot \text{d}^{-1}$) between McNary and Priest Rapids dams, 5.1 d ($13.3 \text{ km} \cdot \text{d}^{-1}$) between McNary and Ice Harbor dams, 5.6 d ($5.4 \text{ km} \cdot \text{d}^{-1}$) between Priest Rapids and Wanapum dams, and 4.2 d ($12.1 \text{ km} \cdot \text{d}^{-1}$) between Ice Harbor and Lower Monumental dams (Table 7).

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

Table 3. Minimum numbers of adult lampreys that passed each site estimated as the number of adult HD-PIT tagged lamprey detected at dam antennas or inferred to pass sites based on upstream detections in 2011. Lampreys were released **downstream from Bonneville Dam near Hamilton Island or upstream from the dam near Stevenson, WA**. See Table 2 for antenna locations.

Release: Hamilton Island (n =800)		Release: Stevenson (n = 109)	
Site	Minimum past (n)	Site	Minimum past (n)
Release	800	Release	109
Bonneville ¹	568		
Bonneville top ²	451-462 ⁴		
The Dalles ¹	302	The Dalles ¹	54
The Dalles top ²	238	The Dalles top ²	47
John Day top ²	190	John Day top ²	31
McNary ¹	73	McNary ¹	4
McNary top ²	65	McNary top ²	2
Ice Harbor ¹	15	Ice Harbor ¹	-
Ice Harbor top ²	15	Ice Harbor top ^{2,3}	-
L. Monument top ^{2,3}	11	L. Monumental top	-
L. Granite top ^{2,3}	3	L. Granite top	-
Priest Rapids ⁵	42	Priest Rapids ⁵	2
Priest Rapids top ⁵	35	Priest Rapids top ⁵	2
Wanapum ⁵	24	Wanapum ⁵	-
Wanapum top ⁵	22	Wanapum top ⁵	-

¹ all fishway antennas, including LPS at Bonneville

² top-of-ladder antennas, including LPS at Bonneville

³ no or limited upstream sites to assess missed detections

⁴ higher number includes 11 fish recaptured in Bonneville traps and released upstream

⁵ combined detections at UI and LGL antennas

Table 4. Adult HD-PIT tagged lamprey escapement estimates for fish released downstream from Bonneville Dam near Hamilton Island and upstream from the dam near Stevenson, WA in 2011. Estimates exclude double-tagged fish. See Table 2 for antenna locations.

Reach	Escapement	Reach	Escapement
Release-Bonneville	71.0%		-
Release-Bonneville top ¹	56.3-57.8%		-
Release-The Dalles	37.8%		-
Release-The Dalles top	29.8%		-
Release-John Day top	23.8%		-
Release-McNary	9.1%		-
Release-McNary top	8.1%		-
Release-Ice Harbor top	1.9%		-
Release-Lower Monumental top	1.4%		-
Release-Lower Granite top	0.4%		-
Release-Priest Rapids top	4.4%		-
Release-Wanapum top	2.8%		-
Bonneville-Bonneville top ¹	79.4-81.3%		-
Bonneville top-The Dalles top	51.5%	Release-The Dalles top	43.1%
Bonneville top-John Day top	41.1%	Release-John Day top	28.4%
Bonneville top-McNary top	14.1%	Release-McNary top	1.8%
Bonneville top-Ice Harbor top	3.2%	Release-Ice Harbor top	-
Bonneville top-L. Monum. top	2.4%	Release-L. Monum. top	-
Bonneville top-L. Granite top	0.6%	Release-L. Granite top	-
Bonneville top-Pr. Rapids top	7.6%	Release-Priest Rapids top	1.8%
Bonneville top-Wanapum top	4.8%	Release-Wanapum top	-
The Dalles top-John Day top	79.8%	The Dalles top-John Day top	66.0%
The Dalles top-McNary top	26.9%	The Dalles top-McNary top	4.3%
The Dalles top-Ice Harbor top	6.3%	The Dalles top-Ice Harbor top	-
The Dalles top-L. Monum. top	4.6%	The Dalles top-L. Monum. top	-
The Dalles tops-L. Granite top	1.3%	The Dalles tops-L. Granite top	-
The Dalles top-Pr. Rapids top	14.7%	The Dalles top-Pr. Rapids top	4.3%
The Dalles top-Wanapum top	9.2%	The Dalles top-Wanapum top	-
John Day top-McNary top	33.7%	John Day top-McNary top	6.5%
John Day top-Ice Harbor top	7.8%	John Day top-Ice Harbor top	-
John Day top-L. Monum. top	5.8%	John Day top-L. Monum. top	-
John Day top-L. Granite top	1.6%	John Day top-L. Granite top	-
John Day top-Priest Rapids top	18.4%	John Day top-Priest Rapids top	6.5%
John Day top-Wanapum top	11.6%	John Day top-Wanapum top	-
McNary top-Ice Harbor top	23.1%	McNary top-Ice Harbor top	-
McNary top-L. Monum. top	16.9%	McNary top-L. Monum. top	-
McNary top-L. Granite top	4.6%	McNary top-L. Granite top	-
McNary top-Priest Rapids top	53.8%	McNary top-Priest Rapids top	100.0%
McNary top-Wanapum top	33.8%	McNary top-Wanapum top	-

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

Table 5. Mean HD-PIT tagged lamprey size metrics and tag dates in relation to their escapement through the monitored reaches, **for fish released downstream from Bonneville Dam** in 2011. Top-of-ladder sites were used for the upper end of each reach. *F* and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Length (n)	Weight (n)	Girth (n)	%Lipid (n)	Tag date (n)
Release - Bonneville top	No	64.2 (340)	425.5 (310)	10.7 (328)	23.5 (300)	22 Jul (340)
	Yes	65.3 (460)	445.4 (427)	10.9 (457)	25.8 (404)	21 Jul (460)
	<i>F</i>	14.73	10.09	10.16	13.53	1.76
	<i>P</i>	<0.001	0.002	0.002	<0.001	0.185
Release - The Dalles top	No	64.1 (562)	421.2 (515)	10.6 (559)	23.9 (500)	22 Jul (562)
	Yes	66.5 (238)	473.8 (222)	11.2 (236)	27.1 (204)	20 Jul (238)
	<i>F</i>	58.81	65.78	70.43	23.04	2.30
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	0.130
Release - John Day top	No	64.2 (610)	424.0 (560)	10.7 (605)	23.9 (540)	22 Jul (610)
	Yes	66.7 (190)	478.4 (177)	11.2 (190)	27.6 (164)	19 Jul (190)
	<i>F</i>	58.36	60.68	66.47	27.13	3.89
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	0.049
Release - McNary top	No	64.6 (736)	433.4 (679)	10.7 (731)	24.6 (649)	21 Jul (736)
	Yes	66.8 (64)	479.3 (58)	11.2 (64)	27.2 (55)	23 Jul (64)
	<i>F</i>	16.70	16.14	19.67	5.46	1.05
	<i>P</i>	<0.001	<0.001	<0.001	0.020	0.305
Bonneville top - The Dalles top	No	64.0 (222)	414.6 (205)	10.6 (221)	27.9 (200)	21 Jul (222)
	Yes	66.5 (238)	473.8 (222)	11.2 (236)	30.7 (204)	20 Jul (238)
	<i>F</i>	47.13	65.74	68.20	10.86	0.89
	<i>P</i>	<0.001	<0.001	<0.001	0.001	0.346
Bonneville top - John Day top	No	64.3 (270)	422.0 (250)	10.6 (267)	24.5 (240)	21 Jul (270)
	Yes	66.7 (190)	478.4 (177)	11.2 (190)	27.6 (164)	19 Jul (190)
	<i>F</i>	46.54	57.00	60.85	15.28	2.36
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	0.126
Bonneville top - McNary top	No	65.0 (396)	440.1 (369)	10.8 (393)	25.5 (349)	20 Jul (164)
	Yes	66.8 (64)	479.3 (58)	11.2 (64)	27.2 (55)	23 Jul (8)
	<i>F</i>	10.97	12.09	14.89	2.14	2.03
	<i>P</i>	0.001	<0.001	<0.001	0.145	0.155
The Dalles top - John Day top	No	65.4 (48)	455.7 (45)	11.0 (46)	24.7 (40)	22 Jul (48)
	Yes	66.7 (190)	478.4 (177)	11.2 (190)	27.6 (164)	19 Jul (190)
	<i>F</i>	5.11	3.08	3.45	4.69	2.08
	<i>P</i>	0.025	0.081	0.065	0.031	0.150
The Dalles top - McNary top	No	66.3 (174)	471.9 (164)	11.1 (172)	27.0 (149)	19 Jul (174)
	Yes	66.8 (64)	479.3 (58)	11.2 (64)	27.2 (55)	23 Jul (64)
	<i>F</i>	0.76	0.39	0.78	0.04	4.62
	<i>P</i>	0.389	0.535	0.379	0.838	0.033
John Day top - McNary top	No	66.7 (126)	478.0 (119)	11.2 (126)	27.8 (109)	18 Jul (126)
	Yes	66.8 (64)	497.3 (58)	11.2 (64)	27.2 (55)	23 Jul (64)
	<i>F</i>	0.04	0.01	0.13	0.21	0.09
	<i>P</i>	0.847	0.914	0.722	0.646	0.768

Note: overwintering fish not included

Table 6. Mean HD-PIT tagged lamprey migration dates (release date or top-of-ladder date), water temperature (°C) and discharge (kcfs) in relation to their passage through the monitored reaches, **for fish released downstream from Bonneville Dam** in 2011. Environmental data were assigned on the date each fish was recorded passing the lower end of each reach (fish that passed downstream dams undetected were excluded because environmental data could not be assigned). *F* and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Date (<i>n</i>)	Temperature (<i>n</i>)	Discharge (<i>n</i>)
Release - Bonneville top	No	22 Jul (340)	18.01 (340)	289.1 (340)
	Yes	21 Jul (460)	17.85 (460)	297.9 (460)
	<i>F</i>	1.76	2.58	2.87
	<i>P</i>	0.185	0.109	0.091
Bonneville top - The Dalles top	No	11 Aug (180)	19.34 (167)	215.5 (180)
	Yes	3 Aug (147)	19.14 (145)	239.1 (147)
	<i>F</i>	11.96	1.60	9.45
	<i>P</i>	<0.001	0.207	0.002
The Dalles top - John Day top	No	14 Aug (43)	20.25 (43)	184.8 (43)
	Yes	10 Aug (60)	19.92 (58)	190.4 (60)
	<i>F</i>	2.27	4.79	0.97
	<i>P</i>	0.135	0.031	0.327
John Day top - McNary top	No	15 Aug (126)	19.92 (115)	192.7 (126)
	Yes	14 Aug (61)	20.26 (61)	185.4 (61)
	<i>F</i>	0.01	4.79	0.97
	<i>P</i>	0.934	0.030	0.327

Note: overwintering fish not included

Table 7. Summary of HD-PIT tagged adult lamprey passage times (d) through monitored reaches of the lower Columbia River, **for fish released downstream from Bonneville Dam** in 2011. Shaded rows show comparable available data **for fish released upstream from Bonneville Dam**.

Reach	n	Passage time (d)			
		Median	Mean	Quartile 1	Quartile 3
Release to pass Bonneville Dam	326	10.23	17.03	4.16	23.12
Release to pass The Dalles Dam	102	16.22	20.68	10.18	28.41
Release to pass John Day Dam	187	22.43	25.97	14.09	33.00
Release to pass McNary Dam	21	36.15	42.04	24.36	53.31
Release to pass Priest Rapids Dam	34	44.80	47.59	32.45	57.51
Release to pass Wanapum Dam	22	45.02	48.13	34.42	59.27
Release to pass Ice Harbor Dam	11	29.44	38.44	27.23	50.44
Release to pass L. Monumental Dam	11	42.44	42.84	29.13	52.53
Release to pass L. Granite Dam	1	37.09	37.09	-	-
Bonneville top to pass The Dalles Dam	57	4.30	6.54	2.91	7.86
Stevenson release to pass The Dalles Dam	26	6.26	8.39	4.22	11.70
Bonneville top to pass John Day Dam	115	10.05	13.92	6.63	17.35
Stevenson release to pass John Day Dam	26	11.60	12.76	8.29	15.45
Bonneville top to pass McNary Dam	14	25.60	23.56	14.98	29.71
Bonneville top to pass Priest Rapids Dam	23	29.62	35.28	24.76	47.34
Stevenson release to pass P. Rapids Dam	2	32.71	32.71	31.89	33.53
Bonneville top to pass Wanapum Dam	12	29.75	33.04	25.08	37.18
Bonneville top to pass Ice Harbor Dam	5	24.44	21.97	17.31	24.44
Bonneville top to pass L. Monumental Dam	6	23.25	25.09	18.92	28.50
Bonneville top to pass L. Granite Dam	1	53.75	53.75	-	-
The Dalles top to pass John Day Dam	60	3.42	5.95	2.06	5.44
The Dalles top to pass John Day Dam	11	4.95	9.99	3.27	8.36
The Dalles top to pass McNary Dam	7	8.76	15.71	7.18	13.49
The Dalles top to pass Priest Rapids Dam	10	23.97	25.25	21.72	30.73
The Dalles top to pass Wanapum Dam	9	34.36	33.30	25.85	40.00
The Dalles top to pass Ice Harbor Dam	3	20.85	19.00	10.08	26.07
The Dalles top to pass L. Monumental Dam	1	34.97	34.97	-	-
John Day top to pass McNary Dam	19	9.13	12.12	4.93	15.21
John Day top to pass Priest Rapids Dam	33	20.99	27.68	15.83	37.35
John Day top to pass Priest Rapids Dam	2	15.43	15.43	14.33	16.53
John Day top to pass Wanapum Dam	22	24.02	29.15	20.42	32.25
John Day top to pass Ice Harbor Dam	10	12.10	15.18	7.05	18.21
John Day top to pass L. Monumental Dam	10	18.82	22.05	12.98	34.45
John Day top to pass L. Granite Dam	3	17.91	21.20	14.70	31.00
McNary top to pass Priest Rapids Dam	9	9.20	12.49	7.29	13.99
McNary top to pass Wanapum Dam	5	17.10	18.24	13.77	18.08
McNary top to pass Ice Harbor Dam	3	5.08	7.09	2.90	13.28
McNary top to pass L. Monumental Dam	2	27.18	27.18	26.95	27.40
Priest Rapids top to pass Wanapum Dam	22	5.62	7.94	3.12	12.99
Ice Harbor top to pass L. Monumental Dam	7	4.20	7.88	3.55	10.03
Ice Harbor top to pass L. Granite Dam	1	10.05	10.05	-	-
L. Monumental top to pass L. Granite Dam	1	7.77	7.18	-	-

Note: overwintering fish not included

Table 8. Correlation coefficients (r) for log-transformed HD-PIT tagged lamprey passage times (d), **for fish released downstream from Bonneville Dam** in 2011. Predictor variables included size metrics (length, weight, girth) recorded at the time of tagging and date, river discharge, and water temperature at the start of each reach. Gray shading indicates $P < 0.05$. Italicized rows show comparable available data **for fish released upstream from Bonneville Dam**. Samples with $n < 10$ not included.

Reach start	Reach end	n^1	Length	Correlation coefficient (r)				
				Weight	Girth	Date	Flow	Temp.
Release	Bonneville top	326	0.08	0.09	0.07	-0.29	0.28	-0.29
Release	The Dalles top	102	0.11	0.18	0.22	-0.56	0.56	-0.54
Release	John Day top	187	0.01	0.07	0.10	-0.38	0.39	-0.37
Release	McNary top	21	0.17	0.07	0.06	-0.32	0.36	-0.27
Release	Priest Rapids top	34	0.01	0.12	0.17	-0.22	0.31	-0.28
Release	Wanapum top	22	0.11	0.21	0.26	-0.31	0.33	-0.29
Release	Ice Harbor top	11	-0.13	0.15	0.40	-0.51	0.48	-0.47
Release	L. Monumental top	11	-0.20	0.04	0.14	-0.70	0.75	-0.72
Bonneville top	The Dalles top	57	-0.17	-0.16	-0.14	-0.37	0.47	-0.48
<i>Stevenson release</i>	<i>The Dalles top</i>	26	-0.13	-0.24	-0.18	-0.16	0.16	-0.19
Bonneville top	John Day top	115	0.03	0.05	0.07	-0.28	0.35	-0.32
<i>Stevenson release</i>	<i>John Day top</i>	31	0.19	-0.05	-0.13	-0.41	0.40	-0.52
Bonneville top	McNary top	14	0.13	0.23	0.11	0.24	-0.28	0.26
Bonneville top	Priest Rapids top	23	0.22	0.09	0.01	-0.25	0.26	-0.32
Bonneville top	Wanapum top	12	0.64	0.35	0.07	-0.28	0.53	-0.33
The Dalles top	John Day top	60	-0.09	0.01	0.13	0.05	0.06	0.04
<i>The Dalles top</i>	<i>John Day top</i>	11	0.28	0.07	0.04	-0.94	0.89	-0.85
The Dalles top	Priest Rapids top	10	0.30	0.06	-0.10	0.38	-0.18	0.39
John Day top	McNary top	19	0.05	0.05	0.07	0.25	-0.21	0.32
John Day top	Priest Rapids top	33	0.08	0.07	-0.02	-0.23	0.12	-0.13
John Day top	Wanapum top	22	0.42	0.28	0.16	-0.19	0.30	-0.15
John Day top	Ice Harbor top	10	-0.39	-0.23	0.05	-0.31	0.24	-0.08
John Day top	L. Monumental top	10	-0.69	-0.86	-0.44	-0.49	0.43	-0.29
Priest Rapids top	Wanapum top	22	0.34	0.26	0.14	0.43	-0.53	-0.06

¹ sample size varied slightly among variables

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

Last Detection Summary – A total of 232 (29.0%) of the 800 lampreys released near Hamilton Island were not subsequently detected (Table 9). Another 108 (13.5%) were last recorded at HD antennas inside Bonneville Dam fishways and 129 (16.1%) were at top-of-ladder exit sites or LPS sites. Twenty-eight fish (3.5%) were last recorded at antennas maintained by the Confederated Tribes of Warm Springs Reservation of Oregon (CTWRSO) in Fifteenmile Creek, 107 (13.8%) were at The Dalles Dam, 120 (15.0%) were at John Day Dam, 17 (2.1%) were at McNary Dam, 15 (1.9%) were at Snake River dams, and 43 (5.4%) were at Priest Rapids or Wanapum dams (Table 9). The remaining two fish were detected by CTWRSO biologists at Sherars Falls and Shitike Creek sites in the Deschutes River basin.

When lampreys were grouped based on final recorded location, median release dates varied only slightly among groups (Figure 6). In contrast, there were clear among-group differences in lamprey size (Figure 7). On median, lampreys were largest in the Snake River (524 g), upper Columbia River (468 g), John Day Dam (471 g), and McNary Dam (464 g) groups. Lampreys were smallest in the groups last recorded in Fifteenmile Creek (378 g) and at the top of Bonneville Dam (394 g).

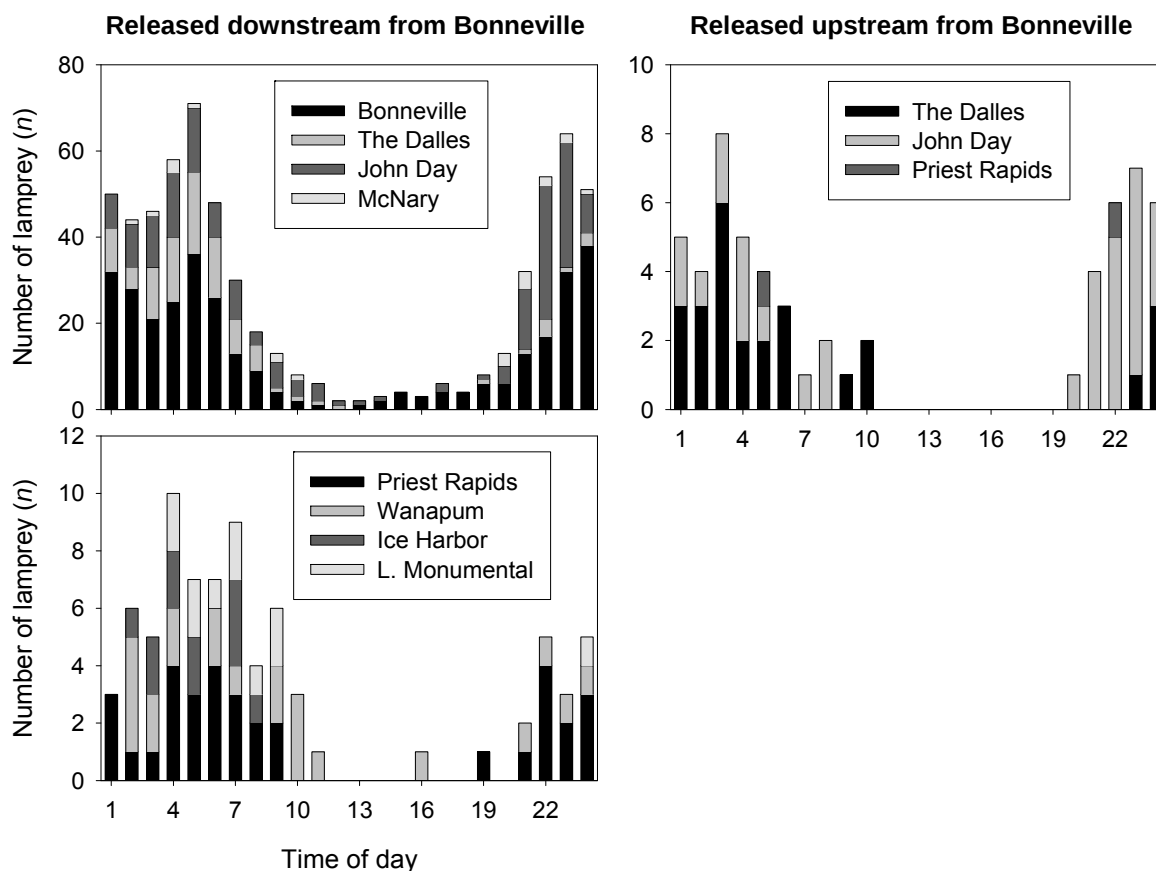


Figure 5. Distributions of the times (binned by hour) that HD PIT-tagged lampreys were detected passing top-of-ladder or LPS sites at Bonneville, The Dalles, John Day, McNary, Priest Rapids, Wanapum, Ice Harbor, and Lower Monumental dams in 2011. Left panels are for fish released downstream from Bonneville Dam and right panels are for fish released upstream from the dam near Stevenson, WA in 2011

Table 9. Last recorded locations for HD-PIT-only tagged adult Pacific lampreys in 2011 **released downstream from Bonneville Dam near Hamilton Island and upstream from the dam near Stevenson, WA**. WA = Washington shore; LPS = lamprey passage structure.

Release: Hamilton Island (n =800)			Release: Stevenson (n = 109)		
Site	n	%	Site	n	%
Release site	232	29.0%	Release site	49	45.4%
Bonneville Dam - WA fishway entry	4	0.5%			
Bonneville Dam – Casc. Is. entrance	37	4.6%			
Bonneville Dam – Casc. Is. flow cont.	19	2.4%			
Bonneville Dam – Casc. Is. LPS ¹	1	0.4%			
Bonneville Dam - WA ladder ²	48	6.0%			
Bonneville Dam - WA LPS	11	1.4%			
Bonneville Dam - WA ladder exit	57	7.1%			
Bonneville Dam - Bradford LPS	20	2.5%			
Bonneville Dam - Bradford ladder exit	40	5.0%			
Fifteenmile Creek	28	3.5%	Fifteenmile Creek	6	5.6%
At The Dalles Dam	63	7.9%	At The Dalles Dam	7	6.4%
The Dalles ladder exits	44	5.5%	The Dalles ladder exits	15	13.8%
Sherars Falls (Deschutes)	2	0.2%	Sherars Falls (Deschutes)	-	-
Shitike Creek (Deschutes)	-	-	Shitike Creek (Deschutes)	1	0.9%
John Day ladder exits	120	15.0%	John Day ladder exits	27	24.8%
At McNary Dam	9	1.1%	At McNary Dam	2	1.8%
McNary Dam ladder exits	7	0.9%	McNary Dam ladder exits	-	-
Ice Harbor Dam	4	0.5%	Ice Harbor Dam	-	-
Lower Monumental Dam	8	1.0%	Lower Monumental Dam	-	-
Lower Granite Dam	3	0.4%	Lower Granite Dam	-	-
Priest Rapids ladder exits	19	2.4%	Priest Rapids ladder exits	1	0.9%
Wanapum Dam	24	3.0%	Wanapum Dam	1	0.9%

¹ includes 1 recaptured fish; ² includes 3 recaptured fish

Upstream Release Group

The 109 HD-PIT tagged lampreys released near Stevenson, WA were collected from the Cascades Island LPS trap on 15 days from 22 June to 1 September (*mean* = 30 July). Almost 90% of these fish were tagged between 25 July and 9 August, and the group was not tagged in proportion to the run (Figure 1). Mean size metrics for the upstream release group were very similar to those for the downstream release group at the time of release (Table 2).

Top-of-ladder detections at The Dalles and John Day dams were concentrated in the middle and later portion of the run at these sites, reflecting the relatively late collection-date distribution at the Cascades Island LPS (Figure 3). Very few lampreys from the upstream release group were detected at McNary Dam, none were detected at Snake River dams, and two were at Priest Rapids Dam.

Dam-to-Dam Escapement – Of 109 fish released, 43.1% ($n = 47$) were known to have passed The Dalles Dam, 28.4% ($n = 31$) passed John Day Dam, 1.8% ($n = 2$) passed McNary Dam, and 1.8% ($n = 2$) passed Priest Rapids Dam (Tables 3 and 4). Escapement from the top of The Dalles Dam was 66.0% to the top of John Day Dam and 4.3% to the top of McNary and Priest Rapids dams. Escapement was 6.5% between the top of John Day Dam and both McNary and Priest Rapids dams.

As with the downstream release group, there was a tendency among upstream-released lampreys for higher reach escapement for larger fish (Table 10). However, fewer comparisons were statistically significant, at least in part due to smaller sample sizes. Lamprey girth and %lipid were higher ($P < 0.05$) for fish that passed the release-John Day reach, and %lipid was higher for those that passed from the top of The Dalles Dam to the top of John Day Dam. Escapement through a reach was not significantly associated with the date that lampreys were released downstream from Bonneville Dam, although there was a tendency for higher passage success for earlier releases (Table 10).

Passage Times and Rates – Median passage times were 6.3 d from the Stevenson release site to the top of The Dalles Dam and 5.0 d between The Dalles and John Day dams (Table 7). Median passage rates in these reaches were $11.7 \text{ km} \cdot \text{d}^{-1}$ (Release-The Dalles) and $7.8 \text{ km} \cdot \text{d}^{-1}$ (The Dalles-John Day). In general, fish released upstream from Bonneville Dam migrated more slowly than fish released downstream from the dam, but this may have been an artifact of release date and post-release recovery near the Stevenson release site for reaches that started at this location (Table 7).

As with the downstream release group, upstream-released lamprey migration times were not generally correlated with fish size metrics ($P > 0.05$ in all tests, Table 8). Seasonal effects on lamprey migration times were significant in the Release-John Day and The Dalles-John Day reaches, with faster passage as water temperature and date increased and discharge decreased (Table 8). Note small sample sizes in these analyses.

Diel Passage – Top-of-ladder passage times at The Dalles, John Day and Priest Rapids dams were primarily at night with a few lampreys passing in the morning hours, consistent with results for the downstream release group (Figure 5). No upstream-released fish were detected passing these sites from 11:00 to 19:00.

Last Detection Summary – A total of 49 (45.4%) of the 109 lampreys released near Stevenson were not detected after release (Table 9). Final detections at upstream sites included 6 (6%) in Fifteenmile Creek, 22 (20%) at The Dalles Dam, 1 (1%) in the Deschutes River, 27 (25%) at John Day Dam, 2 (2%) at McNary Dam, and 1 each at Priest Rapids and Wanapum dams. None were recorded at Snake River dams.

Final Detection Comparison for Downstream and Upstream Release Groups

Release of lampreys upstream from Bonneville Dam allowed us to indirectly assess the effects of release location and Cascades Island LPS passage on upstream movement. We compared the final records of downstream-released fish that passed Bonneville Dam to the final records of fish released at Stevenson. To minimize the effects of collection and dam passage date, we limited the sample of downstream-released fish to those that passed the dam on the same dates as fish were released at Stevenson. The resulting sub-samples included 101 lampreys released at Stevenson (14 dates, median = 31 July) and 118 lampreys released downstream from Bonneville Dam that passed on those

same 14 dates (*median* = 1 August). Note that 7 Stevenson-released fish were excluded because no downstream-released fish passed on the same date (June 22) .

Despite controlling for date, the downstream-released sample was larger on average (65.6 cm, 447 g) than the upstream-released sample (64.5 cm, 425 g) (ANOVA $F = 4.2$ for both comparisons, $0.041 \leq P \leq 0.43$). This resulted primarily from the greater likelihood of Bonneville passage for larger fish.

Forty-eight of the 101 (48%) Stevenson-released fish were not detected at any upstream sites versus 23 (19%) of the 118 that passed Bonneville Dam (Figure 8, top panel). Percentages last detected at sites from Fifteenmile creek to the top of John Day Dam were generally similar for the two groups. In contrast, far more of the downstream-released fish (23%) than the upstream-released fish (1%) were recorded upstream from McNary Dam. We also examined lampreys with records above Stevenson to minimize potential effects of short-term handling effects in the Stevenson release group (Figure 8, bottom panel) and found a similar pattern, with 28% of downstream-released fish last recorded above McNary versus 2% of upstream-released fish (2×2 contingency test, $\chi^2 = 15.0$, $P < 0.001$). This effect was less pronounced among the percentage that passed John Day Dam, with 67% for downstream-released fish versus 53% for upstream-released fish ($\chi^2 = 2.9$, $P = 0.086$) and there was minimal difference in the percentage past The Dalles Dam (80% versus 82%, $\chi^2 = 0.1$, $P = 0.731$).

Cascades Island Release Group

Twenty HD-PIT tagged lampreys were experimentally released into the Cascades Island LPS in 2011. Releases occurred on five dates from 22 June to 25 August (*mean* = 4 August). These lampreys were slightly smaller, on average, than those in the Hamilton Island and Stevenson release groups (Table 2).

Six of these fish were eventually recaptured in the LPS and were released upstream. Two were recorded passing Bonneville Dam via other routes (WA-shore fishway and WA-shore LPS). Another six were detected at sites upstream from Bonneville Dam, without definitive records at Bonneville. Six fish did not pass Bonneville Dam and were not recaptured in the LPS or detected elsewhere.

Final detections for the 20 fish were: 6 (30%) at the release site, 1 (5%) at the top of the WA-shore LPS, 2 (10%) at the release site upstream from Bonneville Dam, 1 (5%) in Fifteenmile Creek, 3 (15%) inside The Dalles fishways, 4 (20%) at the top of John Day Dam, 2 (10%) at Wanapum Dam fishways or exits, and 1 (5%) at the top of Lower Monumental Dam.

Detection of Lampreys Tagged in 2010

A total of six lampreys tagged in 2010 were detected on HD antennas in 2011, including three from the 2010 radiotelemetry study (1% of 312 released) and three from the JSATS study (10% of 30 released). Overwintering fish from the radiotelemetry study were detected at Bonneville's Cascades Island fishway entrance (18 May), the Bonneville Washington-shore fishway exit (27 June), and at both Priest Rapids (26 June) and Wanapum (14 August) dams. Those from the JSATS study were detected at Fifteenmile Creek (25 July), Priest Rapids Dam (11 June), and at both Priest Rapids (29 August) and Wanapum (13 September) dams.

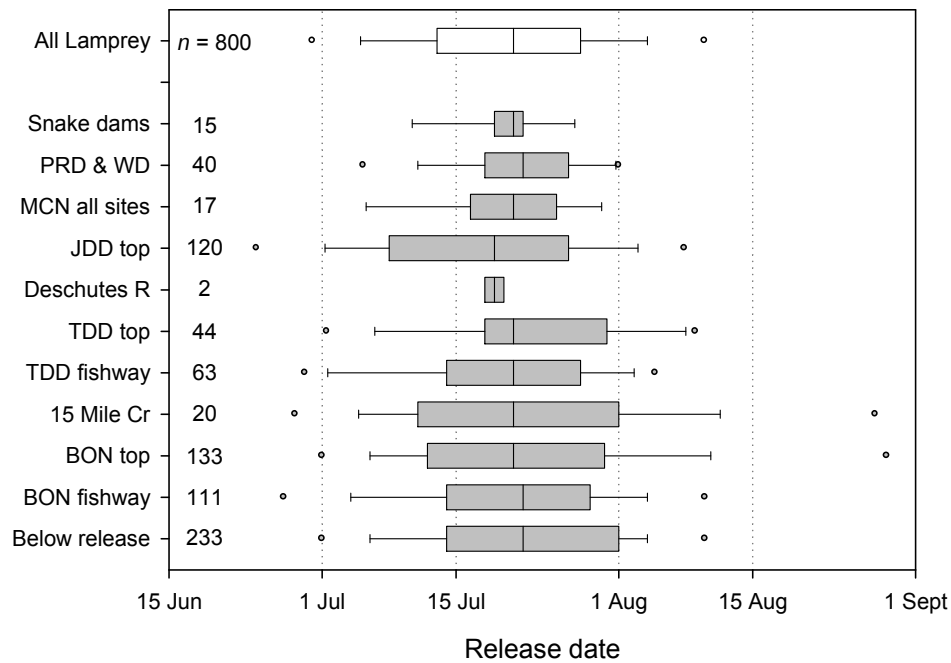


Figure 6. Distributions of **lamprey release dates downstream from Bonneville Dam** by the final recorded locations for each fish. Fishway locations include fish last recorded inside fishways without evidence of passing. Box plots show 5th, 25th, 50th, 75th and 95th percentiles.

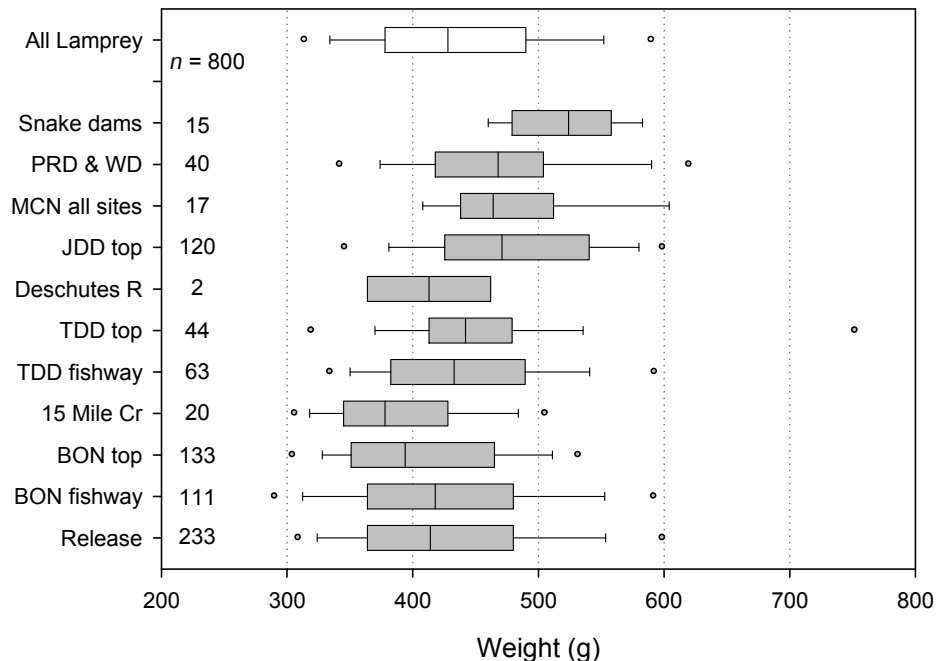


Figure 7. Distributions of of lamprey weights (g) for adults entering each reach (white boxes) and by the final recorded locations for each fish (grey boxes). Data shown are for of **lamprey released downstream from Bonneville Dam**. Tailrace locations include fish last recorded at fishway entrances or inside fishways without passing. Box plots show 5th, 25th, 50th, 75th and 95th percentiles. Note: weight was not collected for 63 (8%) of the sample.

Table 10. Mean HD-PIT tagged lamprey size metrics and tag dates in relation to their escapement through the monitored reaches, **for fish released upstream from Bonneville Dam near Stevenson, WA** in 2011. Top-of-ladder sites were used for the upper end of each reach. *F* and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Length (<i>n</i>)	Weight (<i>n</i>)	Girth (<i>n</i>)	%Lipid (<i>n</i>)	Tag date (<i>n</i>)
Release - The Dalles top	No	64.7 (62)	424.8 (59)	10.6 (62)	22.5 (62)	31 Jul (62)
	Yes	64.9 (47)	439.6 (46)	10.8 (47)	24.8 (47)	30 Jul (47)
	<i>F</i>	0.12	0.90	1.76	2.81	0.10
	<i>P</i>	0.725	0.346	0.187	0.097	0.758
Release - John Day top	No	64.5 (78)	422.3 (74)	10.6 (78)	22.2 (78)	1 Aug (610)
	Yes	65.6 (31)	452.8 (31)	11.0 (31)	26.7 (31)	27 Jul (190)
	<i>F</i>	1.88	3.32	4.223	9.54	2.28
	<i>P</i>	0.173	0.071	0.042	0.003	0.134
The Dalles top - John Day top	No	63.7 (16)	412.3 (15)	10.6 (16)	21.1 (16)	4 Aug (16)
	Yes	65.6 (31)	452.8 (31)	11.0 (31)	26.7 (31)	27 Jul (31)
	<i>F</i>	2.71	2.96	2.92	9.36	2.64
	<i>P</i>	0.106	0.093	0.095	0.004	0.111

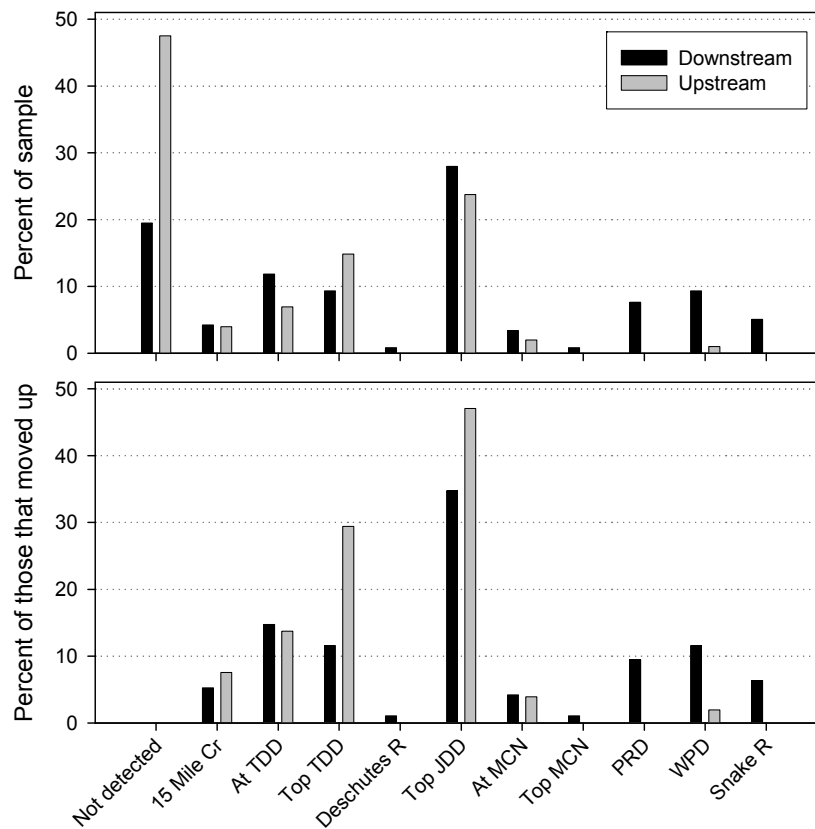


Figure 8. Final detection locations for 101 lampreys released upstream from Bonneville Dam near Stevenson, WA (gray bars) and 118 lampreys released downstream from Bonneville Dam that passed the dam on the same dates as the Stevenson-released fish (black bars). Top panel shows percentages for the full sample (*n* = 101 and 118, respectively). Bottom panel shows percentages only for the sub-samples (*n* = 51 and 95, respectively) that were detected at one or more sites upstream from the Stevenson release site.

Discussion

The 2011 adult lamprey studies used an integrated set of technologies to address multiple questions about lamprey migration in the Columbia River Hydrosystem at a variety of scales. The results summarized in this report primarily address reach-scale and system-wide migration using HD-PIT detection data. Companion 2011 study reports provide results from lampreys tagged with acoustic transmitters (JSATS) and released both upstream and downstream from Bonneville Dam (Noyes et al. 2012), behaviors of the HD-PIT tagged fish in and near Bonneville lamprey passage structures (Moser et al. *in review*), and results from the pilot study using dual frequency identification sonar (DIDSON) to monitor adult lampreys inside and near fishways at Bonneville Dam (Johnson et al. 2012b).

Escapement. – The 2011 reach-scale and system-wide escapement results from the HD-PIT samples can be used for several evaluations. These include comparisons of passage performance among years, among lampreys of different sizes and tagged at different times during the migration, and among lampreys released upstream and downstream from Bonneville Dam. The migration-scale summaries generated by the 2005-2011 HD-PIT studies provide some of the most consistently collected baseline monitoring data for the species in the Columbia basin.

Lamprey escapement for the downstream release group from release past Bonneville Dam (56%) was higher than estimates in HD-PIT samples from 2005-2009 (41-53%, Table 11) and similar to the 2010 estimate of 58% (note: 2010 $n = 13$). Similarly, a higher percentage passed John Day Dam (24%) and McNary Dam (8%) in 2011 than in previous studies, where previous estimates were 14-19% past John Day Dam and 2-5% past McNary Dam. Dam-to-dam estimates in 2011 were also higher than in previous years for the The Dalles-John Day (80%) and John Day-McNary (34%) reaches (Table 11). These estimates were higher than we anticipated given the high-flow conditions.

Several environmental and management-related factors likely contributed to increased upstream escapement compared to recent years. On the environmental side, very high river discharge during most of the 2011 lamprey migration (Appendix Figure 1) resulted in increased discharge through Powerhouse 1 at Bonneville Dam. This operation provides additional attraction flow to the Bradford Island fishway, which has historically had relatively higher lamprey passage efficiency than the Washington-shore and Cascades Island fishways (Moser et al. 2002a; Clabough et al. 2011b). Thus attracting more lampreys to Powerhouse 1 likely contributed to more fish passing Bonneville Dam. Additionally, water temperatures in 2011 were well below ($\sim 1-3$ °C) recent mean temperatures throughout the summer, and it is likely that the cool 2011 conditions extended the upstream migration period. In other years, we have seen a sharp reduction in upstream passage in late summer when water temperatures reach annual highs. This has been particularly evident in reaches upstream from John Day Dam (e.g., Keefer et al. 2012). The significant loss of body mass and energetic reserves reported for adult Pacific lamprey at high water temperatures (i.e., > 20 °C, Clemens et al. 2009) is consistent with this hypothesis. The relatively high 8% escapement from release past McNary Dam in 2011 was likely due, at least in part, to the favorable migration temperatures.

Positive operations-related effects on passage include increased fishway entrance efficiency at Bonneville Dam as a result of night-time fishway velocity reductions at Powerhouse 2 (Johnson et al. 2012a). A variety of other incremental improvements inside Bonneville fishways, auxiliary water supply (AWS) channels, and LPSs have increased overall dam passage efficiency at Bonneville Dam (Clabough et al. 2010a; Moser et al. *in review*). Upstream from Bonneville Dam, the USACE has implemented operational and structural changes to fishways to benefit lampreys (e.g., orifice

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

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

¹ 0.62 ($n = 8$); ² 0.58 ($n = 460$) when recaptures were treated as passing the dam; ³ includes recaptured fish

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

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

rounding, diffuser plating, weir modifications, adding ramps to raised orifices, raising picket leads, blocking access to routes without exits, etc.) at lower Columbia and lower Snake River dams. The cumulative effects of these changes presumably contributed to the higher reach escapement estimates in 2011. A broader analysis that accounts for among- and within-year variability in river conditions and fish size will be necessary to put the 2011 results in broader context; meta-analyses will be included in an in-progress data synthesis.

The 2011 escapement data for the downstream release group consistently indicated higher passage efficiency for larger fish at a variety of spatial scales. The pattern was also evident, though with fewer statistically significant results, for the upstream release group. The size effect is consistent with results from HD-PIT tagged lampreys described in Keefer et al. (2009c), and also reported in the 2007-2010 radiotelemetry studies (e.g., Keefer et al. 2010b). Several hypotheses may explain the higher escapement of larger fish. First, larger fish may be stronger swimmers and more able to ascend through the difficult passage environments at dams (e.g., Beamish 1974; Mesa et al. 2003). Second, larger fish may have greater energetic reserves, allowing for longer upstream passage distances before they seek spawning areas or initiate overwintering behavior. Third, larger fish may be disproportionately from upriver populations, though this would be at odds with a general consensus that anadromous lampreys (Pacific and other species) lack strong geographic stock structure (Bryan et al. 2005; Almada et al. 2008; Goodman et al. 2008; Spice et al. 2012). Fourth, negative handling and tagging effects may have been greater for smaller lampreys (e.g., Moser et al. 2007). However, handling effects almost certainly cannot fully account for the significant size effects reported across all our recent studies because the size effect has been evident regardless of tag type and size (i.e., HD vs. radiotelemetry) and handling time (i.e., longer for radiotelemetry).

Importantly, the size-related hypotheses are not mutually exclusive. It is possible, for example, that higher escapement rates by larger fish were related to swimming ability, energetic or maturation status, migration timing effects, and/or some underlying phenotypic stock structure. Regardless of the mechanism, efforts to increase adult lamprey passage at dams should consider operations or structural modifications that can accommodate smaller individuals. As an example, the high velocity areas near fishway entrances have been an area of difficult lamprey passage (Moser et al. 2002b; Clabough et al. 2010a, 2011a; Keefer et al. 2011a), and such velocity barriers may be especially difficult for smaller fish. Experimental velocity reductions from Bonneville fishway entrances at night has significantly improved lamprey entrance efficiency, presumably by allowing weaker swimmers to enter more easily (Johnson et al. 2012a). 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. Lamprey use of LPS's at the dam has increased in each year since installation (Moser et al. 2011). Therefore, both operational (i.e., fishway entrance velocity) and structural (i.e., LPS bypass systems, the Cascades Island entrance redesign) changes have potentially increased overall Bonneville Dam passage for adult lamprey of all size classes.

Environmental effects on lamprey escapement have been mixed across years. In some years, escapement has been higher for fish released earlier in the season, when river discharge was relatively high and water temperature was relatively low (e.g., Keefer et al. 2011b). In other years, escapement was higher for fish released later in the summer (e.g., Keefer et al. 2010b). We found few statistically significant relationships between river environment and escapement in 2011, and those that were significant were not all in agreement regarding the effect. This may reflect the generally cool conditions and higher discharge throughout the 2011 migration, compared to previous years. To date, we do not have a clear explanation for the varying results within and among years. However, the lack of consistent environmental correlates with escapement 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 (e.g., Keefer et al. 2011a), with consequent effects on escapement. Broad metrics like total river

discharge may poorly represent the specific conditions encountered by individual fish, particularly near and inside fishways. We also emphasize that the strong correlations among discharge, water temperature and date of migration make it difficult to isolate cause and effect with our observational data.

Passage Times. – Lamprey migration times through dam-to-dam study reaches generally fell within the ranges reported in previous HD-PIT study years (Table 12). Because HD-PIT monitoring was limited to dam fishways, it was not possible to separate the time lampreys spent passing dams versus migrating through reservoirs. Median migration rates from ladder top to ladder top (i.e., past one reservoir + one dam) were mostly 11-18 km•d⁻¹. These rates were similar to the median (11 km•d⁻¹) and maximum (21 km•d⁻¹) passage rates recorded for radio-tagged lampreys in the unimpounded John Day River (Robinson and Bayer 2005) and were faster than rates recorded for radio-tagged lampreys in the Willamette River (Clemens et al. 2012). Radio and acoustic telemetry results from the lower Columbia studies have shown that lamprey pass quickly through reservoirs (*median* rates often > 20 km•d⁻¹), but can take several days or weeks to pass single dams (Moser et al. 2002b; Boggs et al. 2008; Keefer et al. 2009a; Johnson et al. 2009a, 2009b; Naughton et al. 2011).

In 2011, as in other study years, lampreys migrated faster later in the summer when water temperatures were higher and discharge was lower. Because discharge decreases and temperature increases through the lamprey migrations, separating migration timing and environmental effects is 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. (2009b, 2009d) found lamprey passage rates at dams and over longer migration reaches were positively (if weakly) correlated with both temperature and date and negatively correlated with total river discharge. There was very little evidence for a lamprey size effect on migration speed.

Overall, environmental conditions and lamprey size explained relatively small proportions of the variability in lamprey passage times in 2011. This is consistent with previous lamprey summaries and suggests that other factors were important. The foremost effect on migration speed over long distances in the lower river appears to be dam passage. Slow passage associated with fishway passage bottlenecks, entrance velocity barriers, and other features seem to be the primary drivers behind the considerable among- and within-year variability in passage time we have recorded. Additional contributing factors may include diel cycles in activity level, confusing orientation and navigation cues at the dams, distribution and density of predators (esp. white sturgeon), individual physiology, sex, or maturation status, and the lampreys' relatively flexible migration timetable.

Final Distribution. – More locations were monitored with HD-PIT antennas in 2011 than in any previous year. In addition to new sites we installed at Lower Monumental and Lower Granite dams, LGL and Grant County PUD increased monitoring effort at Priest Rapids and Wanapum dams and CTWSRO increased monitoring at Fifteenmile Creek and in the Deschutes River. We think these new sites helped with a final accounting for fish that would not have been possible previously. For example, several lampreys last recorded at Snake and upper Columbia dams had passed McNary Dam undetected and would have been assigned to the John Day reservoir reach in previous years. Similarly, the 37 lampreys recorded by CTWSRO biologists in Fifteenmile Creek and the Deschutes River basin represent new high percentages of our samples at those HD-PIT detection sites; most of these fish would have been assigned to the Bonneville or The Dalles reservoirs in previous years. We note that the addition of new monitoring sites complicates direct inter-annual comparisons of reach escapement and final distribution estimates.

Nonetheless, monitoring tributary entry remains a critical challenge for adult lamprey tagging studies, and particularly for HD-PIT studies. In the Columbia River radiotelemetry studies, tributary

detection has occurred primarily at the Deschutes, Klickitat, and John Day rivers plus Fifteenmile Creek – none of which are easily monitored with HD-PIT antennas. However, transmitter battery life has precluded spring-time monitoring and only a fraction of the lampreys that entered tributaries were likely detected. In 2011, the JSATS acoustic telemetry study that was companion research to this HD-PIT monitoring provides some additional reservoir use and tributary entry data (Noyes et al. 2012).

As in previous HD-PIT studies, lampreys last recorded in the Snake River, upper Columbia River, and other upriver sites were considerably larger at time of tagging than those last recorded at more downstream locations. Unlike in some previous years, there was only limited evidence in 2011 that lampreys released early in the migration were more likely to migrate further. The underlying mechanisms producing these patterns remain unknown and may be primarily related to environmental factors (e.g., suitable tributary temperatures at the time adults were passing confluences) or to lamprey physiology (e.g., lipid reserves, condition, age, maturation status).

About 44% of HD-PIT tagged adults did not pass Bonneville Dam in 2011. While this is a lower percentage than in previous study years, it continues to be cause for concern. The underlying reasons for failed passage and the ultimate fate of these adults remain unknown. These fish may have been lost to the reproductive population (true migration and reproductive failure), moved upstream without detection, and/or they may have moved into downstream tributaries or used the tailrace for spawning. Identifying the fate of non-passing fish remains an important question and will begin to be addressed by the small sample of JSATS-tagged fish released in the Bonneville tailrace in 2011.

HD Antenna Detection Efficiency. – There was no radiotelemetry component to the 2011 adult lamprey studies, and therefore no opportunity to directly estimate HD-PIT antenna detection efficiency using double-tagged fish. Instead, efficiencies were estimated using a combination of fish detections at individual dams (or combined top-of-ladder sites) in combination with detections at upstream antenna sites. This is an imperfect method for several reasons. First, there is a risk of underestimating detection efficiency when fish pass a dam via unmonitored routes (e.g., navigation locks or off-fishway routes that do not pass through antennas) but are subsequently detected upstream. Second, sample sizes for individual sites are limited to the number of fish detected upstream from that site. For example, 74 lampreys were detected upstream from John Day Dam and were used to estimate detection efficiency, but at least 190 passed John Day Dam (i.e., 116 fish detected at John Day antennas were excluded from efficiency estimates at the dam).

As in past years, the highest detection efficiencies at HD-PIT antennas were at the top-of-ladder sites at John Day Dam (~96%). The fishways at these sites have relatively small cross-sections and there are no alternative routes. Efficiencies were also high at the combined antenna sites at Ice Harbor (100%), Lower Monumental (100%) and Priest Rapids (97%) dams. However, the samples were small at the Snake River sites. More lampreys were detected at Priest Rapids Dam than in any other HD-PIT study year. This may have been related to increased monitoring effort there, including new antennas maintained by LGL and Grant County PUD.

Several combined sites had lower detection efficiency in 2011 than in previous years (note: estimation techniques differed in previous years). At Bonneville Dam, efficiency at the combined top-of-ladder sites (including LPSs) was 62%. We have not identified the reason(s) for reduced efficiency in 2011 at Bonneville Dam, but the problem appears to have been associated primarily with the Washington-shore top-of-ladder or LPS antennas and/or errors associated with recapture and release dates. Detection efficiency at McNary Dam top-of-ladder antennas in 2011 (26%) was also lower than in previous years. At least three factors appear to have played a role in the reduction at McNary Dam:

first, proportionately more lampreys were recorded at the juvenile salmon passage channels than in previous years suggesting more passed the dam via this route; second, increased detection opportunity at Priest Rapids and the Snake River dams in 2011 may have increased the likelihood of identifying fish that went undetected at McNary Dam that would have been undetected at both McNary and upriver sites in previous years; third, there were some problems maintaining power in the batteries that supplied the south-shore fishway antennas. The principal challenge at The Dalles Dam continues to be the large volume of the East ladder at the HD top-of-ladder antenna site. It is possible for lampreys to swim through this antenna (when operated) and yet be out of detection range.

Improving efficiency for the HD-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 arrays. In the meantime, detection efficiencies for HD-PIT antenna sites will remain lower than we have reported for radiotelemetry antennas simply as a function of much greater detection range for active radio tags versus passive HD-PIT tags.

Lampreys Released Upstream from Bonneville Dam. – Lampreys captured in the Cascades Island LPS trap were treated as an experimental group because these fish could not volitionally exit the trap. There has been no directly comparable study group in previous HD-PIT or radiotelemetry studies. The most similar group was the 30 JSATS-tagged lampreys tagged in the 2010 pilot study, although those fish were trapped at the traditional sites. A majority (77%) of the JSATS fish in 2010 were detected at an acoustic array near the Klickitat River, but only 23% were recorded upstream from The Dalles Dam (Naughton et al. 2011) – lower than the 39% past The Dalles Dam in the 2011 HD-PIT evaluation.

More importantly, the upstream release group appeared to migrate shorter distances upstream than the most comparable sub-sample from the downstream release group in 2011. The most likely explanation for this was that lampreys from the downstream comparison group were significantly larger than those that were in the upstream release group (mean weight = 447 g vs. 425 g, respectively). However, other factors may also have also been important.

Conclusions. – A pressing gap in our understanding of adult lamprey migration in the Columbia system is the lack of information about lamprey distribution and fate. A majority of the tagged fish in radiotelemetry and HD-PIT studies has failed to pass Bonneville Dam in most years, and almost nothing is known about where these fish go or whether they spawn. There is little evidence to assess whether large numbers return to tributaries downstream from the dam because monitoring at these sites has been limited with the exception of the Willamette River. We have mobile-tracked radio-tagged lampreys in the main stem Columbia downstream from Bonneville into the late fall, and some fish may spawn in main stem, tailrace or off-channel habitats or hold in the main channel prior to tributary entry in the spring after expiration of radio-tags. Radio transmitter life has precluded monitoring in these locations during the spring spawning period. Signal attenuation for radio transmitters has also limited monitoring in deep water habitats below Bonneville Dam, as well as in reservoirs upstream. The addition of HD-PIT monitoring sites in Fifteenmile Creek, some Deschutes River locations, and in the Snake River have reduced this information gap, as will planned HD-PIT installations at the Hood River and other tributary sites. The JSATS acoustic telemetry research, begun as a pilot in 2010 (Naughton et al. 2011) and continued with a modest sample in 2011 (Noyes et al. 2012) also has the potential to resolve some questions related to lamprey movement and distribution to spawning areas.

The multi-year HD-PIT and radiotelemetry monitoring studies have provided a wealth of information about lamprey behavior near dams and inside fishways as well as at the full migration

scale. Study results have directly informed many of the operational and structural changes applied at the USACE dams. The 2011 and earlier results suggest that many of these modifications may have incrementally improved adult lamprey passage, especially at Bonneville Dam. Continued investments in fishway improvements that can benefit lampreys will likely further improve passage metrics at Bonneville and at upstream dams. We anticipate that continued active (e.g., radio or acoustic telemetry) or passive (e.g., video or DIDSON) monitoring of difficult passage areas will provide important information about the selection and design of fishway modifications. Such integrated, multi-scale approaches are needed given Pacific lamprey population declines.

Lastly, some additional evaluation of Columbia River lamprey swimming behavior/performance and population demographics is probably warranted. The 2011 results and earlier PIT-tag study results (e.g., Keefer et al. 2009b, 2009c) indicate possible size- and timing-related population structuring and potential environmental cues for tributary entry. Understanding the mechanism(s) generating the consistent higher passage probability for larger adults may aid in the identification of passage bottlenecks at fishways and inform design of improvements. It may be possible, for example, to experimentally test whether larger lampreys can more successfully pass through velocity barriers or if they have more stamina than smaller lampreys. The population structure and demographics of Pacific lamprey, two central areas of knowledge used to manage fish populations, are not fully understood (structure) or are largely unknown (demographics). Improved understanding using genetic tools, spawning ground sampling, demographic modeling, or other methods may prove beneficial. 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 2005-2011 suggest that relatively large percentages of the runs may enter tributaries between John Day and McNary dams (especially the John Day River). Lampreys have also been relatively abundant in the Deschutes River. Radiotelemetry study results have shown that there is limited use of the Bonneville reservoir tributaries other than the Klickitat River and Fifteenmile Creek, at least in summer and fall when transmitters remain active. Similarly, sampling adults downstream from Bonneville Dam would help characterize the adult population present before fish enter the Hydrosystem, which is known to be selective for lamprey traits such as size.

References

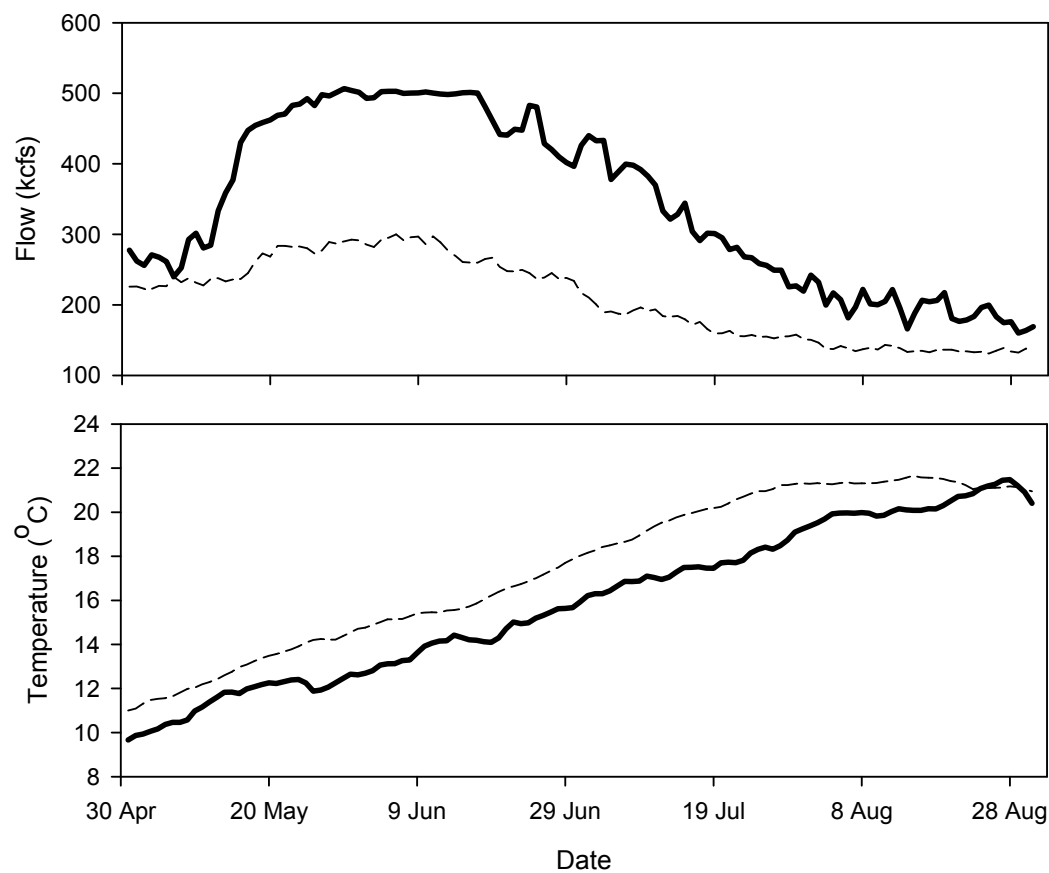
- Almada, V. C., J. I. Periera, J. P. Fonseca, A. Levy, C. Maia, and A. Valente. 2008. Mitochondrial DNA fails to reveal genetic structure in sea-lampreys along European shores. *Molecular Phylogenetics and Evolution* 46(1):391-396.
- Beamish, F. W. H. 1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. *Transactions of the American Fisheries Society* 103:355-358.
- Beamish, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentate*) from the Pacific coast of Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1906-1923.
- Boggs, C. T., M. L. Keefer, C. A. Peery, and M. L. Moser. 2008. Evaluation of adult Pacific lamprey migration and behavior at McNary and Ice Harbor dams, 2007. Technical Report 2008-9 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Walla Walla District.
- Bryan, M. B., D. Zalinski, K. B. Filcek, S. Libants, W. Li, and K. T. Scribner. 2005. Patterns of invasion and colonization of the sea lamprey (*Petromyzon marinus*) in North America as revealed by microsatellite genotypes. *Molecular Ecology* 14:3757-3773.
- Clabough, T., E. Johnson, D. Joosten, and C. Peery. 2008. Evaluating adult Pacific lamprey dam passage counting methodology at Bonneville and The Dalles dams – 2007. Letter Report of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Clabough, T. S., E. L. Johnson, M. L. Keefer, C. C. Caudill, and M. L. Moser. 2010a. Evaluation of adult Pacific lamprey passage at the Cascades Island fishway after entrance modifications, 2009. Technical Report 2010-2 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Clabough, T. S., E. L. Johnson, M. L. Keefer, C. C. Caudill, and M. L. Moser. 2010b. General passage and fishway use summaries for adult Pacific lamprey at Bonneville, The Dalles and John Day dams, 2009. Technical Report 2010-5 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Clabough, T. S., E. L. Johnson, M. L. Keefer, C. C. Caudill, and M. L. Moser. 2011a. Evaluation of adult Pacific lamprey passage at the Cascades Island fishway after entrance modifications, 2010. Technical Report 2011-3 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Clabough, T. S., E. L. Johnson, M. L. Keefer, C. C. Caudill, and M. L. Moser. 2011b. General passage and fishway use summaries for adult Pacific lamprey at Bonneville, The Dalles, and John Day Dams, 2010. Technical Report 2011-5 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Clemens, B. J., T. R. Binder, M. F. Docker, M. L. Moser, and S. A. Sower. 2010. Similarities, differences, and unknowns in biology and management of three parasitic lampreys of North America. *Fisheries* 35(12):580-594.

- Clemens, B. J., M. G. Mesa, R. J. Magie, D. A. Young, and C. B. Schreck. 2012. Pre-spawning migration of adult Pacific lamprey, *Entosphenus tridentatus*, in the Willamette River, Oregon, U.S.A. *Environmental Biology of Fishes* 93:245-254.
- Close, D., M. Fitzpatrick, H. W. Li, B. Parker, D. Hatch, and G. James. 1995. Status report of the Pacific lamprey (*Lampetra tridentata*) in the Columbia River Basin. Portland, Oregon, Bonneville Power Administration: 1-35.
- Close, D., M. Fitzpatrick, and H. W. Li. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries* 27(7):19-24.
- Cochnauer, T., and C. Claire. 2002. Evaluate status of Pacific lamprey in the Clearwater River drainage, Idaho. Bonneville Power Administration, 2001 Annual Report, Portland, OR.
- Crossin, G. T., and S. G. Hinch. 2005. A nonlethal, rapid method for assessing the somatic energy content of migrating adult Pacific salmon. *Transactions of the American Fisheries Society* 134:184-191.
- Daigle, W. R., M. L. Keefer, C. A. Peery, and M. L. Moser. 2008. Evaluation of adult Pacific lamprey passage rates and survival through the lower Columbia River Hydrosystem: 2005-2006 PIT-tag studies. Technical Report 2008-12 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland and Walla Walla Districts.
- Goodman, D. H., S. B. Reid, M. F. Docker, G. R. Haas, and A. P. Kinziger. 2008. Mitochondrial DNA evidence for high levels of gene flow among populations of a widely distributed anadromous lamprey *Entosphenus tridentatus* (Petromyzontidae). *Journal of Fish Biology* 72:400-417.
- Graham, J., and C. Brun. 2005. Determining lamprey species composition, larval distribution, and adult abundance in the Deschutes River, Oregon, subbasin. Bonneville Power Administration, 2004-2005 Annual Report, DOE/BP-00009553-3, Portland, OR.
- Johnson, E. L., C. A. Peery, M. L. Keefer, C. C. Caudill, and M. L. Moser. 2009a. Effects of lowered nighttime velocities on fishway entrance success by Pacific lamprey at Bonneville Dam and fishway use summaries for lamprey at Bonneville and The Dalles dams, 2007. Technical Report 2009-2 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Johnson, E. L., T. S. Clabough, M. L. Keefer, C. C. Caudill, C. A. Peery, and M. L. Moser. 2009b. Effects of lowered nighttime velocities on fishway entrance success by Pacific lamprey at Bonneville Dam and fishway use summaries for lamprey at Bonneville and The Dalles dams, 2008. Technical Report 2009-10 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Johnson, E. L., C. C. Caudill, M. L. Keefer, T. S. Clabough, C. A. Peery, M. A. Jepson, and M. L. Moser. 2012a. Movement of radio-tagged adult Pacific lampreys during a large-scale fishway velocity experiment. *Transactions of the American Fisheries Society* 141:571-579.
- Johnson, E. L., T. S. Clabough, M. L. Keefer, C. C. Caudill, P. N. Johnson, W. T. Nagy, and M. A. Jepson. 2012b. Evaluation of dual frequency identification sonar (DIDSON) for monitoring Pacific lamprey passage behavior at fishways of Bonneville Dam, 2011. Technical Report 2012-5 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.

- Keefer, M. L., C. T. Boggs, C. A. Peery, M. L. Moser. 2009a. Adult Pacific lamprey migration in the lower Columbia River: 2007 radiotelemetry and half-duplex PIT tag studies. Technical Report 2009-1 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Keefer, M. L., M. L. Moser, C. T. Boggs, W. R. Daigle, and C. A. Peery. 2009b. Variability in migration timing of adult Pacific lamprey (*Lampetra tridentata*) in the Columbia River, U.S.A. *Environmental Biology of Fishes* 85:253-264.
- Keefer, M. L., M. L. Moser, C. T. Boggs, W. R. Daigle, and C. A. Peery. 2009c. Effects of body size and river environment on the upstream migration of adult Pacific lampreys (*Lampetra tridentata*). *North American Journal of Fisheries Management* 29:1214-1224.
- Keefer, M. L., C.A. Peery, C. C. Caudill, E. L. Johnson, C. T. Boggs, B. Ho, and M. L. Moser. 2009d. Adult Pacific lamprey migration in the lower Columbia River: 2008 radiotelemetry and half-duplex PIT tag studies. Technical Report 2009-8 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Keefer, M. L., W. R. Daigle, C. A. Peery, H. T. Pennington, S. R. Lee, and M. L. Moser. 2010a. Testing adult Pacific lamprey performance at structural challenges in fishways. *North American Journal of Fisheries Management* 30:376-385.
- Keefer, M. L., C. C. Caudill, E. L. Johnson, C. T. Boggs, B. Ho, T. S. Clabough, M. A. Jepson, and M. L. Moser. 2010b. Adult Pacific lamprey migration in the lower Columbia River: 2009 radiotelemetry and half-duplex PIT tag studies. Technical Report 2010-3 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Keefer, M. L., C. A. Peery, S. R. Lee, W. R. Daigle, E. L. Johnson, and M. L. Moser. 2011a. Behavior of adult Pacific lampreys in near-field flow and fishway design experiments. *Fisheries Management and Ecology* 18:177-189.
- Keefer, M. L., C. C. Caudill, E. L. Johnson, T. S. Clabough, M. A. Jepson, and M. L. Moser. 2011b. Adult Pacific lamprey migration in the lower Columbia River: 2010 radiotelemetry and half-duplex PIT tag studies. Technical Report 2011-4 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Keefer, M. L., C. T. Boggs, C. A. Peery, and C. C. Caudill. 2012. Factors affecting dam passage and upstream distribution of adult Pacific lamprey in the interior Columbia River basin. *Ecology of Freshwater Fish*.
- Kostow, K. 2002. Oregon lampreys: natural history, status, and analysis of management issues. Oregon Department of Fish and Wildlife, Information report 2002-01, Portland, OR.
- Mesa, M. G., J. M. Bayer, and J. G. Seelye. 2003. Swimming performance and physiological responses to exhaustive exercise in radio-tagged and untagged Pacific lamprey. *Transactions of the American Fisheries Society* 132:483-492.
- Moser, M., A. Matter, L. Stuehrenberg, and T. Bjornn. 2002a. Use of an extensive radio receiver network to document Pacific lamprey (*Lampetra tridentata*) entrance efficiency at fishways in the Lower Columbia River, USA. *Hydrobiologia* 483:45-53.

- Moser, M., P. Ocker, L. Stuehrenberg, and T. Bjornn. 2002b. Passage efficiency of adult Pacific lampreys at hydropower dams on the lower Columbia River, USA. *Transactions of the American Fisheries Society* 131:956-965.
- Moser, M. L, and D. A. Close. 2003. Assessing Pacific lamprey status in the Columbia River basin. *Northwest Science* 77:116-125.
- Moser, M. L, R. W. Zabel, B. J. Burke, L. C. Stuehrenberg, and T. C. Bjornn. 2004. Factors affecting adult Pacific lamprey passage rates at hydropower dams: using "time to event" analysis of radiotelemetry data. *In Aquatic telemetry: advances and applications*. M.T. Spedicato, G. Marmella, and G. Lembo (Eds.). FAO-COISPA, Rome.
- Moser, M., D. Ogden, and C. Peery. 2005. Migration behavior of adult Pacific lamprey in the lower Columbia River and evaluation of Bonneville Dam modifications to improve passage, 2002. Seattle, Northwest Fisheries Science Center, National Marine Fisheries Service: 59.
- Moser, M., D. Ogden, D. Cummings, and C. Peery. 2006. Development and evaluation of a lamprey passage structure in the Bradford Island auxiliary water supply channel, Bonneville Dam, 2004. Seattle, Northwest Fisheries Science Center, National Marine Fisheries Service.
- Moser, M. L., D. A. Ogden, and B. P. Sandford. 2007. Effects of surgically implanted transmitters on anguilliform fishes: lessons from lamprey. *Journal of Fish Biology* 71:1847-1852.
- Moser, M. L., M. L. Keefer, H. T. Pennington, D. A. Ogden, and J. E. Simonson. 2011. Development of lamprey-specific fishways at a hydropower dam. *Fisheries Management and Ecology* 18:190-200.
- Moser, M. L., D. A. Ogden, H. T. Pennington, M. L. Keefer, and C. C. Caudill. *In review*. Development of passage structures for adult Pacific lamprey at Bonneville Dam, 2009-2010. Draft Report of National Marine Fisheries Service to U.S. Army Corps of Engineers, Portland District.
- Naughton, G. P. D. C Joosten, T. S. Clabough, M. A. Jepson, E. L. Johnson, and C. C. Caudill. 2011. Evaluation of adult Pacific lamprey behavior in Bonneville Reservoir using the Juvenile Salmon Acoustic Telemetry system, 2010. Technical Report 2011-6 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Noyes, C. J., C. C. Caudill, T. S. Clabough, D. C. Joosten, E. L. Johnson, M. L. Keefer, and G. P. Naughton . 2012. Adult Pacific lamprey migration behavior and escapement in the Bonneville reservoir and lower Columbia River monitored using the Juvenile Salmonid Acoustic Telemetry System (JSATS), 2011. Technical Report 2012-4 of Idaho Cooperative Fish and Wildlife Research Unit to U.S. Army Corps of Engineers, Portland District.
- Robinson, T. C., and J. M. Bayer. 2005. Upstream migration of Pacific lampreys in the John Day River, Oregon: behavior, timing, and habitat use. *Northwest Science* 79:106-119.
- US FWS. 2010. Pacific lamprey (*Lampetra tridentata*) draft assessment and template for conservation measures. U.S. Fish and Wildlife Service, Portland, OR.

Appendix A. 2011 Columbia River discharge and temperature profiles.



Appendix Figure 1. Mean daily Columbia River flow (kcfs) and temperature (°C) at Bonneville Dam in 2011 (solid line) and the 2001-2010 average (dashed line).