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ARTICLE

Seasonal Migration Behaviors and Distribution of Adult Pacific Lampreys in Unimpounded Reaches of the Snake River Basin

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Abstract
Complex life histories render anadromous fishes particularly susceptible to environmental and anthropogenic change. Adult Pacific Lampreys *Entosphenus tridentatus* migrating in the Columbia River and its tributaries must ascend a series of dams to reach interior spawning sites. While considerable research has focused on improving dam passage for lampreys, little is known about adult Pacific Lamprey behavior and distribution patterns within free-flowing environments, particularly within the interior portions of their distribution. In this 3-year study, we monitored the movements of 146 adult Pacific Lampreys in the Snake River and its tributaries upstream from Lower Granite Dam, the eighth dam from the Pacific Ocean. Our objectives were to characterize migration and test several hypotheses about adult upstream movement after dam passage. A majority of radio-tagged adults, released above Lower Granite Dam, migrated upstream after release and many moved hundreds of kilometers upstream into Snake River tributaries. Of those with telemetry records after release, 59–70% were recorded in the Clearwater River, 16–25% were in the Snake River, and 13–16% were in the Salmon River. Lampreys that passed the Snake River–Clearwater River confluence were significantly more likely, in most years, to enter the lower-discharge Clearwater River. Adults moved primarily at night during the summer–fall migration and did not exhibit a consistent response to changes in water temperature or discharge. These findings highlight the importance of the Clearwater River to Pacific Lampreys in the lower Snake River basin and indicate that adults that successfully pass through the Columbia–Snake hydrosystem can continue upstream migration into many Snake River subbasins. This distribution suggests that improved passage efficiency at dams may increase the number of adult Pacific Lampreys available for spawning within the interior portions of their distribution.

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Complex life cycles make anadromous fishes particularly susceptible to environmental and anthropogenic change (Musick et al. 2000; Noonan et al. 2012). Anadromous lampreys (family: Petromyzontidae), for example, move over extensive spatial and temporal scales in order to successfully complete their life cycles. They use freshwater benthic habitats as larvae, freshwater streams and rivers as downstream-migrating juveniles, the ocean as parasitic adults, and then freshwater again during their upstream migration prior to spawning (Pletcher 1963; Beamish 1980; Clemens et al. 2010). Human impacts on habitats and ecological communities potentially affect these fish at each life history stage.

The Pacific Lamprey *Entosphenus tridentatus* is native to the Pacific Rim with a historical distribution from Japan to Baja California (Ruiz-Campos and Gonzalez-Guzman 1996; Yamazaki et al. 2005; Renaud 2008). This species is a culturally and ecologically significant part of river ecosystems throughout its range and provides subsistence opportunities for regional tribes, high-value forage opportunities for a variety of predators, and marine-derived nutrients to freshwater stream systems (Close et al. 2002; Petersen Lewis 2009; Miller et al. 2012). The Columbia River basin has historically provided extensive spawning and rearing habitat for the species. Much of this historic habitat is no longer accessible due to hydroelectric and low-head irrigation dams and diversions (Wallace and Ball 1978; Simpson and Wallace 1982; Luzier et al. 2011). There are few time series of Pacific Lamprey abundance in the interior Columbia River basin, but one index—daytime counts of Pacific Lampreys passing Ice Harbor Dam on the lower Snake River (the largest Columbia River tributary)—indicate a decline from tens of thousands of Pacific Lampreys in the 1960s to ~100 in 2010 (USACE 2012). Individuals still migrate from the Pacific Ocean through the Columbia River as far inland as the Salmon River in Idaho and the Okanogan River in northern Washington. These interior-basin fish have some of the longest known migrations of any lamprey species (Hardisty and Potter 1971; Renaud 2011), and their decline has stimulated considerable conservation and management attention (Close et al. 2002; Kostow 2002; CRITFC 2011; Luzier et al. 2011) especially from tribes of the interior Columbia River basin.

In 2003, a petition to list Pacific Lamprey under the U.S. Endangered Species Act (ESA) was denied by the U.S. Fish and Wildlife Service, primarily due to a lack of basic biological information (USFWS 2004). This decision emphasized the need to address critical, underresearched components of Pacific Lamprey life history including their distribution, population structure, and migration ecology. Since the listing petition, a series of genetic studies have indicated that the Pacific Lamprey has limited philopatry (Spice et al. 2012) but do exhibit some geographic population structuring (Lin et al. 2008) that may be related to traits like body size and migration timing and distance (Hess et al. 2013, 2014, 2015). There has also been a substantial research effort, primarily using radio- or PIT-tagged lampreys, into basic life history (e.g., Clemens et al. 2013), migration ecology (e.g., Keefer et al. 2009b; Starcevich et al. 2014), and the influence of migration obstacles (i.e., dams) on the distribution of adults (e.g., Moser et al. 2002; Mesa et al. 2003, 2010; Jackson and Moser 2012; Keefer et al. 2013b). The bulk of this work has been conducted in the lower Columbia River and its tributaries, including in the Willamette River basin in Oregon.

Very little is known about the prespawning behaviors or spawning distribution of adults at interior sites distant from the ocean. Specifically, there is concern that passage delay and/or the energetic demands of passing up to eight Columbia and Snake river hydroelectric dams and reservoirs may limit the ability of adult Pacific Lampreys to reach spawning sites and successfully reproduce. We used radiotelemetry to monitor adult Pacific Lampreys during a 3-year study in the unimpounded Snake River and its tributaries upstream from Lower Granite Dam, more than 700 km from the Pacific Ocean (Figure 1). Our goal was to test whether adult Pacific Lampreys would continue their migration to interior headwater sites after passing the impounded lower Snake River and thus evaluate the potential benefits of passage improvements at dams. Simultaneously, we characterized migration timing, migration rates, distribution patterns, and prespawn overwintering behaviors to test several hypotheses about the response of migrating adults to environmental conditions using our observational data.

METHODS

Study area.—The Snake River drains ~280,000 km^2 of Idaho as well as portions of Washington, Oregon, Montana, Nevada, and Wyoming. The upper and lower portions of the Snake River are separated by Hells Canyon Dam (river kilometer [rkm] 919 from the Pacific Ocean; Figure 1), which is impassable to upstream migrants. The lower Snake River is regulated by four hydroelectric dams that have fish passage facilities: Ice Harbor Dam (IHA, rkm 538), Lower Monumental Dam (LMO, rkm 589), Little Goose Dam (LGO, rkm 635), and Lower Granite Dam (LGR, rkm 695).

Upstream migrations of adult Pacific Lampreys were monitored in the Snake River and its tributaries upstream from LGR and below Hells Canyon Dam. This area includes four major tributaries: the Clearwater (rkm 746), Grande Ronde (rkm 793), Salmon (rkm 825), and Imnaha (rkm 830) rivers. The North Fork Clearwater River is a major Clearwater tributary, though fish passage is blocked by Dworshak Dam (rkm 811). Coldwater releases from Dworshak Reservoir strongly alter the thermal regime of the lower Clearwater River and the Snake River below the Snake–Clearwater confluence in the summer (Connor et al. 1998).

Collection and tagging.—Adult Pacific Lampreys were collected at LMO and LGO from salmonid juvenile bypass

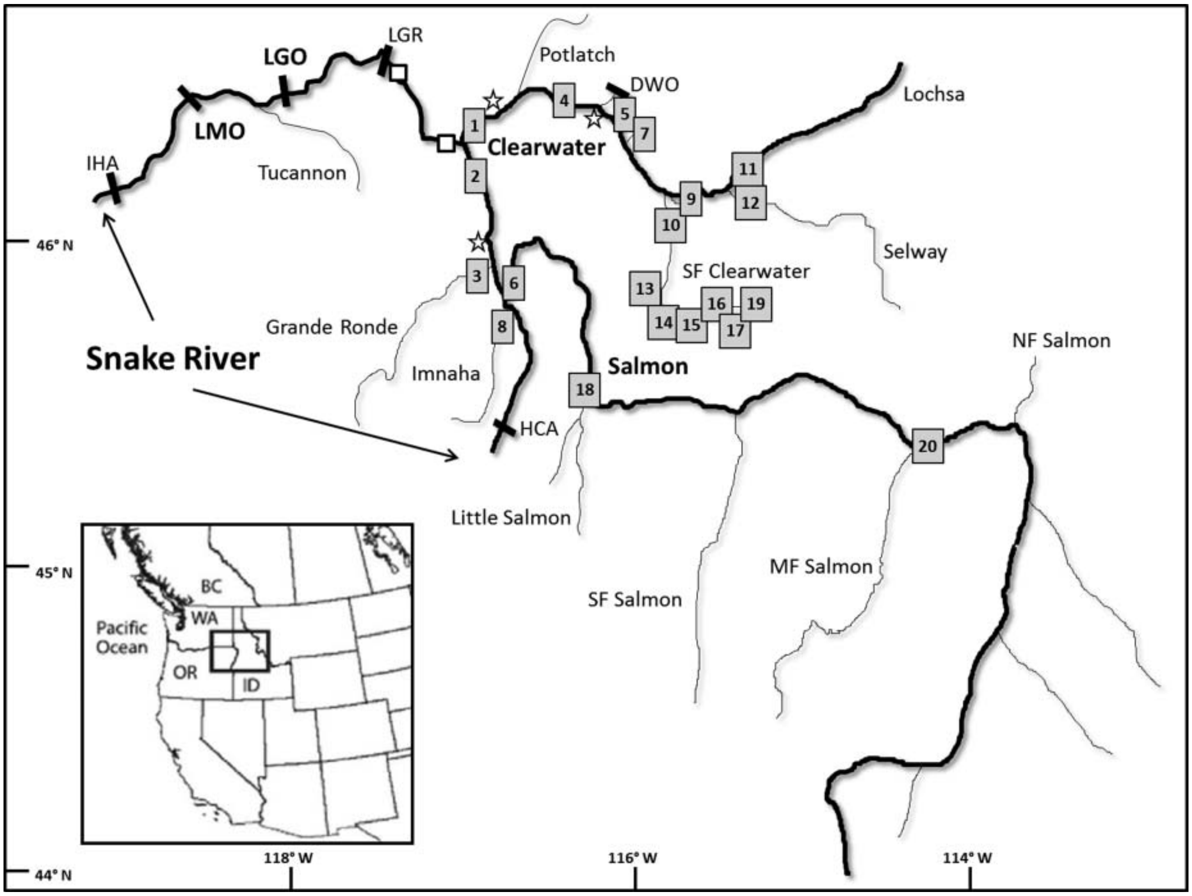

FIGURE 1. The lower Snake River and its major tributaries showing the Pacific Lamprey collection locations (LMO = Lower Monumental Dam; LGO = Little Goose Dam), release locations (white boxes), 20 fixed-site radiotelemetry antennas (boxed numbers), and USGS gauging stations (white stars). IHA = Ice Harbor Dam, LGR = Lower Granite Dam, HCA = Hells Canyon Dam, DWO = Dworshak Dam.

systems (JBSs) from July to October in 2006–2008. These locations were used because collection methods and effort were restricted over concerns for comigrating ESA-listed salmonids, and the collection methods (e.g., active trapping) used at other downstream locations were not feasible because lamprey counts in the Snake River were more than an order of magnitude lower than at Columbia River dams. Adults collected in JBSs presumably ascended the dam using adult fishways, entered the dam forebays, and were volitionally or involuntarily entrained in the JBS entrance on the upstream face of the dam prior to moving downstream to JBS sampling facilities. Few adult lampreys were observed in the LGR JBS in the years leading up to this study; therefore collection effort was focused at LMO and LGO JBSs. The JBSs at LMO and LGO provided adequate lamprey sample sizes while minimizing potential negative interactions with ESA-listed salmonids through active trapping inside the fishways. Once collected, adult lampreys were held in 190-L containers supplied with ambient river water. Adults were held until tagging and release, which occurred within 48 h of collection.

Before tagging, Pacific Lampreys were anesthetized with 60 ppm eugenol, measured (length and girth to the nearest millimeter), and weighed (nearest gram). Weight data were not collected in 2006. No fish with a girth <9 mm at the dorsal fin were radio-tagged to minimize tag effects. All fish were surgically implanted with uniquely coded radio transmitters (18.3 mm long × 8.3 mm in diameter, 2.1 g in water; model NTC-4-2 L, Lotek Wireless, Newmarket, Ontario) as described in Johnson et al. (2012). Sex was determined by examining the gonads during surgery and each individual was classified as female (eggs present), male (testes present), or undetermined (gonads not visible). Both ANOVA and pairwise *t*-tests were used to compare individual size metrics by year, collection location, release location, and sex.

After tagging, adults were placed in a 142-L cooler filled with oxygenated river water. Water temperature was maintained between 15°C and 20°C with the use of 4-L containers of frozen river water placed in the transport cooler. Fish were transported from their tagging locations and released a short distance upstream in the LGR forebay (rkm 696 or 700) or downstream from the Snake River–Clearwater River confluence near Red Wolf Crossing Bridge (rkm 743). The 2006 data indicated that just 42% of adults released within the LGR forebay (Figure 1) had postrelease detections. Thereafter, a majority of fish were released upstream from LGR reservoir to maximize telemetry data within unimpounded reaches of the Snake River basin.

Telemetry monitoring.—Lamprey movements were monitored using two methods. First, an extensive network of fixed-site radiotelemetry receivers was jointly maintained by the University of Idaho and the U.S. Fish and Wildlife Service. Fixed-site aerial antennas with receivers were placed at the mouths of the major Snake River tributaries, including the Clearwater, Grande Ronde, Imnaha, and Salmon rivers, as well as many secondary tributaries (Figure 1). Each receiver was equipped with one or more four-element Yagi antennas that faced downriver at a 45° angle offshore towards the thalweg. Data from fixed-site receivers were downloaded periodically (e.g., weekly to monthly). Second, mobile tracking by boat and automobile was used to locate transmitters between fixed-site receivers. The sections of the Snake, Salmon, and Clearwater rivers that were accessible by road were surveyed every 2 weeks from July to November or until it was determined that fish had stopped migrating. Surveys continued monthly from December to February during the presumed overwinter period until indications of movement were again observed. From March through June, the presumed final spawning migration period, surveys continued every 2 weeks until no actively transmitting tags were found. This period ranged from April to June of the following year, based on the reported transmitter battery life of 251 d. Mobile tracking by boat was conducted on portions of the Snake River upstream from Lewiston, Idaho, that did not have road access in October 2007 and February 2009. Latitudes and longitudes of mobile-track locations were recorded using a handheld GPS unit (Garmin GPS 76, Garmin International, Olathe, Kansas) and corresponding river kilometers were calculated.

Data analysis.—All data recovered from fixed-site receivers were electronically transferred to the Northwest Fisheries Science Center of the National Oceanic and Atmospheric Administration (NOAA) in Seattle, Washington, for processing. Each file was loaded into a database and processed according to the methods described in Moser et al. (2002). Once processed, we assigned first (F) and last (L) date–time stamps to blocks of telemetry records for unique transmitters at each fixed-site receiver. Coded fixed-site records (date, time, location) were combined with tagging data (size metrics, tagging and release date, and release location) and mobile-track data (date, time, latitude, longitude, rkm) to create individual Pacific Lamprey migration histories. Detection efficiencies at fixed-site receivers were estimated using combined fixed-site and mobile-track data by dividing the number of transmitters detected at a specific receiver by the number detected at any location upstream from the site.

Diel timing of Pacific Lamprey movements was determined using unique detections at all fixed-site receivers. Migration timing and seasonal movements were estimated using the detections of each unique fish at the fixed-site receivers. We classified movements into summer–fall (July 1 to December 31) and winter–spring (January 1 to June 30). Pearson's χ^2 tests were used to test whether the proportions of radio-tagged adults using the Snake River versus the Clearwater River (the first major confluence lampreys encountered after release) were random with respect to an equal (1 : 1) distribution or were proportional to the ratio of average discharge of the two drainages during the monitoring period (July–June) for each annual sample (~7 : 3 = Snake : Clearwater).

Daily mean water temperature and discharge data as well as daytime counts of adult Pacific Lampreys passing fishways at all lower Snake River dams were provided by the U.S. Army Corps of Engineers (DART 2010). Similar temperature and discharge data for the Clearwater and Snake rivers were provided by U.S. Geological Survey (USGS) gauging stations near Spalding, Idaho (13342500; rkm 767), Anatone, Washington (13334300; rkm 791), and Orofino, Idaho (13340000; rkm 820). These data were used to assess the environment experienced by upstream-migrating adult lampreys detected at the lower Clearwater (antennas 1 and 4), Snake (antenna 2), and upper Clearwater (antenna 9) fixed-site locations (Figure 1).

Migration rates (rkm/d) and passage times (d) were calculated using date–time stamps from fixed-site telemetry records. Reaches were defined as the area between release location (REL) and upstream fixed-site (FS) receivers (REL–FS reaches), downstream and upstream fixed-site receivers (FS–FS reaches), or mobile-tracked location and an upstream receiver (MBT–FS reaches). Winter–spring movements were not calculated due to variability in starting locations within long reaches, overwinter holding behavior, and limited FS–FS detections. Migration rates and passage times were calculated using the last record at the downstream location and the first record at the upstream location. Rates and passage times are reported as medians due to right-skewed passage time distributions.

RESULTS

Sample Summary

A total of 146 adult Pacific Lampreys were collected and radio-tagged from late July through early October in 2006–2008 (Table 1; Figure 2). Median tag dates at LMO and LGO were later than median dam passage dates as indexed by the visual daytime counts, except at LGO in 2007. A majority (68–86%) of each annual sample was collected at LGO. Sex ratios (male : female : undetermined) were 19 : 29 : 2 in 2006, 17 : 20 : 9 in 2007, and 23 : 20 : 7 in 2008. A majority (82%)

TABLE 1. Numbers of radio-tagged adult Pacific Lampreys by sex, collection location (LMO = Lower Monumental Dam, LGO = Little Goose Dam), and release location (RWC = Red Wolf Crossing, LGF = Lower Granite Dam forebay), with corresponding means and SDs for lamprey size metrics. Different letters accompanying values indicate significant differences between mean lengths among study years (a, b, c) and size metrics among sex categories in 2007 (z, y) and 2008 (d, e). M = male, F = female, U = sex undetermined, NA = data not available.

			Collection location		Release location				
Year	Sex	*n*	LMO	LGO	RWC	LGF	Mean length (SD)	Mean girth (SD)	Mean weight (SD)
2006	M	19	6	13	12	7	67.3 (4.4)	10.6 (0.9)	NA
	F	29	10	19	12	17	68.1 (3.4)	10.9 (0.6)	NA
	U	2		2	2		69.3 (1.8)	11.0 (0.4)	NA
	Total	50	16	34	26	24	67.8 (3.7) a	10.8 (0.7)	NA
2007	M	17	2	15	17		63.9 (4.5) y	10.8 (0.6) y	431 (65) y
	F	20	5	15	20		66.9 (2.6) z	11.3 (0.7) z	493 (84) z
	U	9	3	6	7	2	63.7 (4.2) y	10.5 (0.8) y	415 (82) y
	Total	46	10	36	44	2	65.1 (4.0) c	10.9 (0.7)	455 (83)
2008	M	23	2	18	20		65.9 (2.6)	10.9 (0.6)	431 (37) e
	F	20	3	20	23		66.8 (3.6)	11.2 (0.6)	471 (64) d
	U	7	2	5	7		65.9 (4.4)	10.7 (0.8)	410 (91) e
	Total	50	7	43	50		66.3 (3.3) b	11.0 (0.6)	447 (62)

of the total sample was released at Red Wolf Crossing, and the remainder (18%) were released in the LGR forebay (mostly in 2006). There was some variation in Pacific Lamprey size metrics among year, collection site, and sex categories (Table 1). Mean lamprey lengths differed among years (ANOVA: F = 5.90, P = 0.004), ranging from a mean of 65.1 cm in 2007 to 67.8 cm in 2006. In 2007, Pacific Lampreys collected at LGO were larger (girth and weight: 11.1 cm versus 10.5 cm; 468.1 g versus 406.5 g) than those collected at LMO (girth: $F = 4.27$, $P = 0.045$; weight: $F = 4.68$, $P = 0.037$). In almost all within-year comparisons, females were larger (lengths, weights, and girths) than males and undetermineds with differences in all size metrics in 2007 (F = 4.60–5.38, P = 0.008–0.011) and weight in 2008 ($F = 4.34$, $P = 0.020$). There were no within-year differences in lamprey size among release locations (ANOVA: $0.07 \geq F \leq 3.53$, df = 1, $P > 0.05$).

Postrelease Detections

Postrelease detection rates differed among years and release locations. In 2006, 81% of the lampreys released at Red Wolf Crossing had postrelease detections versus 42% of those released in the LGR forebay. Patterns were similar for the 2007 release groups: rates were 82% (Red Wolf Crossing) and 50% (LGR forebay). In 2008, all fish were released at Red Wolf Crossing and 98% had postrelease detections.

Estimated antenna detection efficiencies at the Clearwater River (antenna 1) and the Snake River (antenna 2) fixed-site locations were 95% and 78% in 2006, 31% and 64% in 2007, and 97% and 88% in 2008, respectively. Mean annual detection efficiencies at upstream Clearwater River sites (antennas 4, 9, 10, 11, and 12) ranged from 69% to 92% (grand mean = 81%). The Salmon River location (antenna 18) had no valid detections despite four (2006), five (2007), and eight (2008) lampreys detected upstream from this site. We did not estimate efficiency for the Imnaha River location (antenna 8; n = 1 lamprey detected).

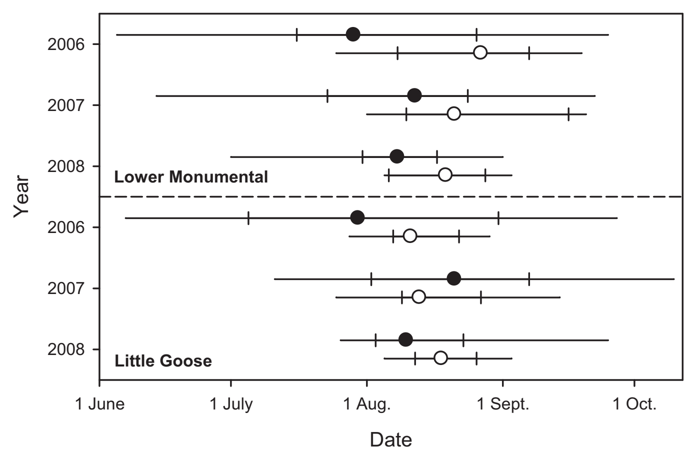

FIGURE 2. Adult Pacific Lamprey run-timing distributions (solid circles) at Lower Monumental Dam (annual n = 139–175 fish counted) and Little Goose Dam (n = 73–124 counted) and the timing distributions of those that were collected inside the juvenile bypass system and radio-tagged (open circles) in 2006–2008. The run-timing data were from daytime-only counts inside fish ladders and are considered a minimum index of upstream passage. Circles = median dates, vertical lines = 25th and 75th percentile dates, ends of horizontal lines = 5th and 95th percentiles.

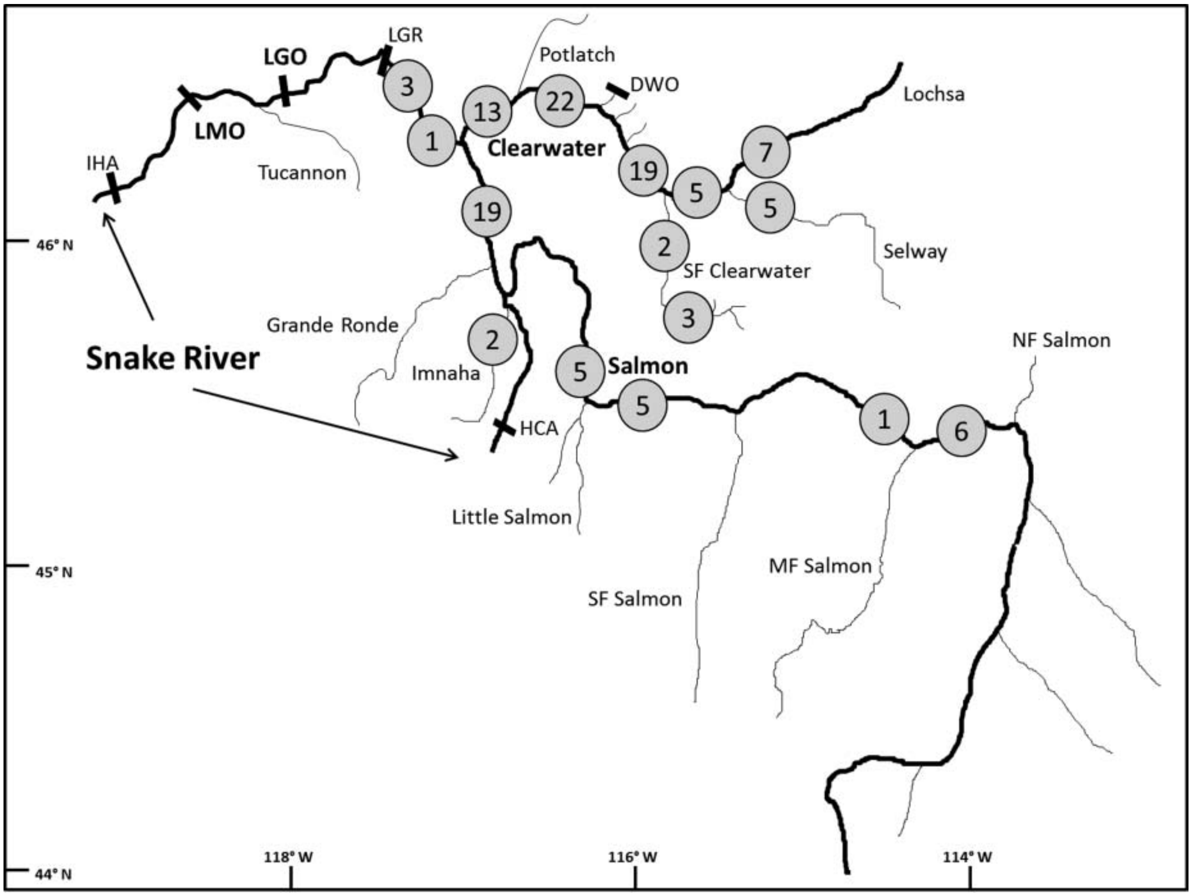

FIGURE 3. Final detection locations for radio-tagged Pacific Lampreys in 2006 (n = 32), 2007 (n = 37), and 2008 (n = 49). Gray circles show the number of fish per reach. An additional number of lampreys—18 in 2006, 9 in 2007, and 1 in 2008—had no postrelease detections.

Final Distribution

Radio-tagged Pacific Lampreys were last detected throughout much of the Clearwater, Snake, and Salmon river basins in all study years (Figure 3). Of those with telemetry records after release (annual n = 32–49), 59–70% were in the Clearwater River, 16–25% were in the Snake River, 13–16% were in the Salmon River, and 0–3% were in the Imnaha River. Within the more intensively monitored Clearwater River basin, fish were detected in the Selway (n = 5), South Fork Clearwater (n = 5), Middle Fork Clearwater (n = 5), and Lochsa rivers (n = 7). In the Salmon River basin, six lampreys were detected upstream from the Middle Fork Salmon River above rkm 1,144.

Lampreys that passed the Snake River–Clearwater River confluence were more likely to enter the Clearwater River than the Snake River in 2007 ($\chi^2 = 6.08$, $P = 0.01$) and 2008 ($\chi^2 = 3.45$, $P = 0.06$) when we tested for a uniform (50 : 50) distribution to the two rivers. When assuming a Snake–Clearwater ratio of 66 : 34, proportional to the mean daily discharges of the two rivers during the study period, more lampreys entered the Clearwater River than expected in all 3 years (χ^2 = 12.60–24.18, all $P < 0.001$). There were no indications that collection site (ANOVA: $0.18 \geq F \leq 2.19$, df = 1, $P > 0.05$), tagging metrics (e.g., length, girth, release date) (Wilcoxon rank-sum tests: $0.11 \geq P \leq 0.80$), or release sites (ANOVA: $0.05 \geq F \leq 0.24$, df = 1, $P > 0.10$) were related to the river drainage that the lampreys entered (Snake versus Clearwater rivers).

Movement Timing and Overwintering

Most (88–94%) lamprey detections at the fixed-site antennas were at night in all years (Figure 4). Seasonal movements varied among locations. At the most downstream Clearwater River location (antenna 1), 67–73% of first detections were in summer–fall (mostly August–September) and the rest (27–33%) were in winter–spring (mostly February–April). Summer–fall percentages were 40–100% at the second upstream Clearwater River location (antenna 4) and 86–100% at the Snake River location (antenna 2), and most fish were detected in August–September. Fewer lampreys were recorded at sites farther upstream (1–9 fish per site per year; Figure 4) and these detections were primarily after the overwintering

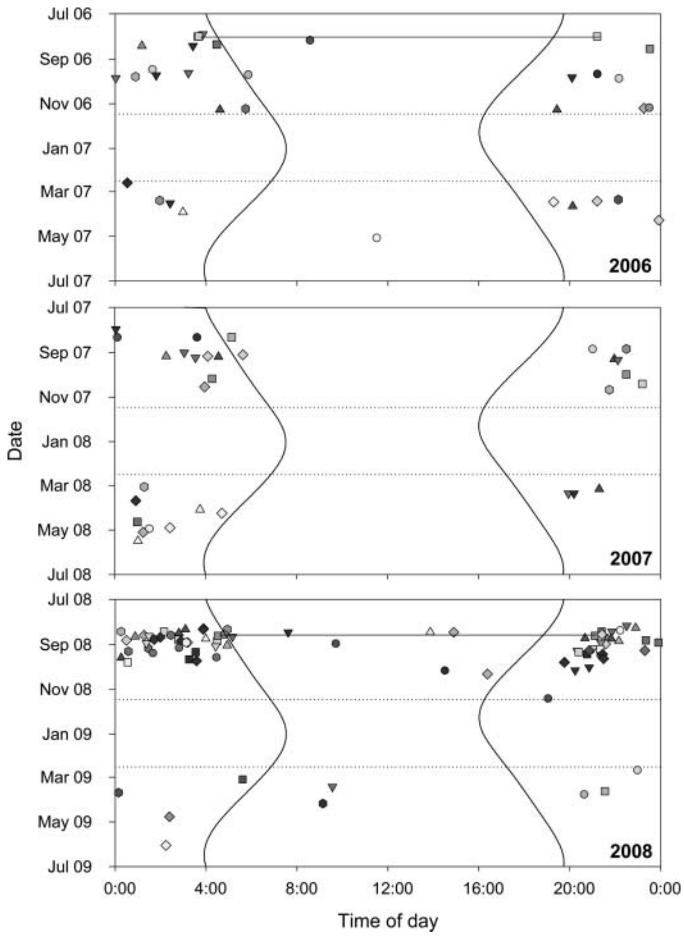

FIGURE 4. Date (month and year) and time of day that radio-tagged Pacific Lampreys were detected at fixed-site antennas in 2006–2009 from individuals released in 2006–2008. Hourglass lines represent sunrise and sunset near Lewiston, Idaho. Dotted horizontal lines represent periods of no lamprey detections at the fixed-site antennas. Each unique symbol represents an individual Pacific Lamprey, and many were observed at multiple sites. Solid horizontal lines represent two individuals that held positions near receivers during daylight.

period. Of 27 unique lamprey detections at the Middle Fork Clearwater, South Fork Clearwater, Lochsa, Selway, and Imnaha river antennas, 25 (93%) were in the winter–spring (mostly March–May).

We noted that several ($n = 19$) Pacific Lampreys were located only during mobile tracking and had no summer–fall or winter–spring fixed-site detections. Seasonal movement timing for these fish was somewhat ambiguous, but there was no evidence that their behaviors differed markedly from the population detected at fixed sites. The combined detection data suggest that most overwintering occurred in lower to middle reaches of the larger rivers.

Migration Rates and Passage Times

A total of 111 reach migration rates and passage times were calculated for 66 Pacific Lampreys during summer–fall movements: 22 in 2006, 19 in 2007, and 70 in 2008. Migration rates and passage times were calculated for 15 reaches varying in length from 9 to 127 rkm. Most fish migrated upstream at rates between 1 and 20 rkm/d, and some observed rates were >35.0 rkm/d in all years. Annual median migration rates across reaches ranged from 1.9 rkm/d in 2006 to 10.6 rkm/d in 2008. On average, lamprey migration rates were lower in REL–FS reaches (mean of annual medians = 4.2 rkm/d) than FS–FS (mean of annual medians = 14.9 rkm/d), perhaps due to recovery of the REL lampreys from collection, tagging, and transport. The fastest individual rates were in the reaches that started at the Red Wolf Crossing release site. Migration rates were considerably slower in the winter–spring, when medians were mostly <3 rkm/d.

River Environment Effects

In the summer–fall period, coldwater releases from Dworshak Reservoir resulted in much cooler conditions in the lower Clearwater River than in the Snake River (Figure 5). Although tagged lampreys entered the two rivers at approximately the same time each summer–fall, mean USGS gauge temperatures on the date of lamprey detection in the Snake River (antenna 2) were 20.6–22.0°C versus 10.3–12.1°C for those detected in the lower Clearwater River (antenna 1). Frequent use of both rivers during this period suggested little active selection for one over the other based on temperature or discharge preference. An exception was that a high discharge event in November 2006 coincided with numerous lamprey detections at antenna 1 on the lower Clearwater River when temperatures were below 6°C in both rivers (Figure 5).

In the winter–spring period, mean temperatures on the dates that lampreys passed into the lower Clearwater River (antenna 1) were 5.0–5.8°C, suggesting that this temperature range may act as a cue for upstream movement following overwintering. Discharge was more variable in the winter–spring period and was characterized by multiple peaks, some of which coincided with pulses of lamprey movement. Winter–spring movements within the Clearwater River were weakly associated with increasing discharge (Figure 5).

DISCUSSION

Pacific Lamprey Distribution

A majority of the radio-tagged Pacific Lampreys migrated upstream after release and many moved hundreds of kilometers upstream into Snake River tributaries supporting the hypothesis that adult Pacific Lampreys would continue migration to interior headwater sites after passing the impounded lower Snake River. Those lampreys last recorded in the upper reaches of the Clearwater and Salmon rivers migrated 900 to >1,100 rkm from the Pacific Ocean, among the longest freshwater migration distances recorded for any lamprey species

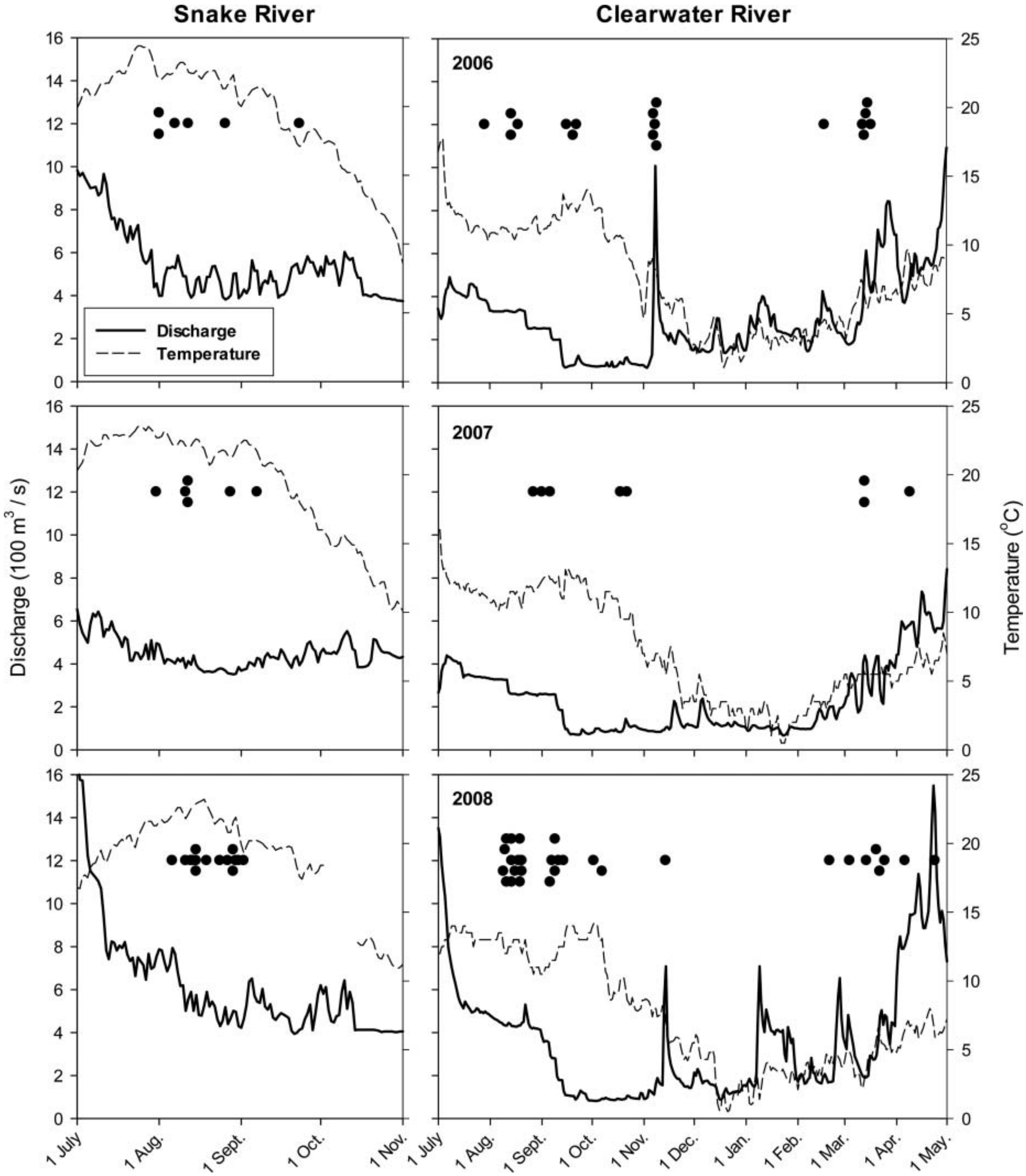

FIGURE 5. Date of first Pacific Lamprey detections at the Snake (antenna 2) and Clearwater (antenna 1) river fixed-site antennas in 2006–2008 in relation to mean daily discharge (solid lines) and mean daily water temperature (dashed lines). Each solid circle represents an individual lamprey. Two fish were first detected at the SNR site in the spring (not shown).

(Hardisty and Potter 1971; Renaud 2011). The behaviors and final distributions of radio-tagged fish were consistent with completed migrations to potential spawning areas. While these data show that some adult Pacific Lampreys have the energetic reserves to reach the interior Snake River after passing multiple hydroelectric dams, documenting spawning activity and reproductive success were beyond the study scope. Questions regarding the relationship between multiple dam and reservoir passage events and possible fitness effects remain unresolved.

The Pacific Lampreys that enter the Snake River have been a very small percentage (often <1%) of those counted at Bonneville Dam (rkm 235), the primary population index site for the Columbia River basin (Luzier et al. 2011; USACE 2012). For a species such as Pacific Lamprey, with relatively minimal population structuring, their reduction or extirpation in the Snake River basin could be considered a range contraction rather than an extinction of a locally adapted population. However, there is accumulating evidence that the interior Columbia River basin population, including the Snake River group, is phenotypically distinct with an earlier migration timing and larger body size (e.g., Keefer et al. 2009a) than those that enter sites closer to the Pacific Ocean (e.g., Clemens et al. 2012, 2013). It is unclear if this phenotypic cline is a natural occurrence or a consequence of the difficult passage environment that exists in the Columbia–Snake hydrosystem (i.e., smaller lampreys may be selected out during dam passage). The observed genetic associations with phenotypic and morphological variation among Pacific Lampreys collected at different sites across their range also suggest that there is adaptive significance associated with the morphological variation (Hess et al. 2013), as has been shown in Pacific salmon *Oncorhynchus* spp. (e.g., Kinnison et al. 2003; Crossin et al. 2004). While our understanding of the basis for the observed phenotypic variation has not advanced enough to definitively integrate this information with conservation and management decisions, the extirpation of interior populations may still represent the loss of important adaptive phenotypic variation.

The hypothesis that adult Pacific Lampreys would use the Snake and Clearwater river drainages in proportion to discharge experienced at the confluence was not supported by the data. Within the Snake River, Pacific Lampreys entered the Clearwater River at higher-than-expected rates based on an expectation of a null random distribution or random distribution weighted by the relative discharge of the Snake and Clearwater rivers at the confluence. This result was in contrast to the behavior of lampreys at the Columbia River–Snake River confluence (rkm ~521) with respect to discharge, but not temperature, where both radio-tagged and untagged adults are several times more likely to continue up the higher-discharge Columbia River than the smaller Snake River (USACE 2012; Keefer et al. 2013a). The Clearwater and upper Columbia rivers are similar in that both are cooler, on average, than the Snake River at their confluences, and it is possible that Pacific Lampreys preferentially select the cooler sites. A lower temperature may provide a physiological benefit such as reduced energetic costs or slowed maturation (e.g., Clemens et al. 2009). We note, however, that many lampreys entered the warmer Snake River when much cooler water was available in the Clearwater River, indicating that other factors affected route selection.

Pacific Lamprey distributions among Snake River sites may have resulted, at least in part, from olfactory cues produced by conspecifics. Pheromones released by larvae and juveniles are used by upstream-migrating adult lampreys of several species (Wagner et al. 2009; Vrieze et al. 2010) and can elicit behavioral responses by adult Pacific Lampreys (Yun et al. 2011). Differences in the quality or concentration of pheromones may explain the route selection decisions we recorded; however, it remains unclear how Pacific Lampreys might use these chemical cues in guiding upstream migrations. The higher entry rate to the Clearwater River by adults observed in this study is consistent with the pheromone-distribution hypothesis because recent surveys have shown that larval Pacific Lamprey densities, from a limited number of comparable sites, are 3–4 times higher in the Clearwater River than in the Salmon River (Hyatt et al. 2007; Cochnauer and Claire 2009), but alternative explanations are possible.

Behavioral Ecology

Almost all of the Pacific Lamprey detections in this study occurred at night, supporting the hypothesis that adults generally exhibit nocturnal movements throughout their spawning migration. This was consistent with results from adult Pacific Lamprey studies in Oregon's John Day and Willamette rivers (Robinson and Bayer 2005; Mesa et al. 2010) and in a variety of Columbia River fishway, reservoir, and main-stem habitats (Keefer et al. 2013c). In fact, many lamprey species are predominantly nocturnal during migration (e.g., Hardisty and Potter 1971; Almeida et al. 2002), during which upstream movements occur at night and refuge seeking or inactivity occurs during the day. This pattern presumably provides a survival benefit, perhaps through predator avoidance. We did not find evidence for reduced nocturnality coincident with sexual maturation in the spring, a pattern that has been reported in other lamprey studies (e.g., Binder and McDonald 2007), though small-scale movement patterns during the day, near the time of spawning, would have been difficult to detect.

Pacific Lamprey migration speeds (i.e., rates) varied with season and river reach, but were broadly similar to those reported at other sites. Typical summer–fall rates in our study were in the 5–15-rkm/d range with maximum rates >35 rkm/d. By comparison, radio-tagged lampreys migrated about 11 rkm/d in the John Day River in the summer–fall (Robinson and Bayer 2005), ~5–7 rkm/d in the Willamette River (Clemens et al. 2012), and ~2–12 km/d in the coastal Smith River, Oregon (Starcevich et al. 2014). The fastest migrants in the Snake and Clearwater rivers moved at rates that were similar to those of Pacific Lampreys passing through lower Columbia River reservoirs in summer (median rates = 23–30 rkm/d: Moser et al. 2013). We collected fewer detection data after the overwintering period, but migration rates during this period were mostly <5 km/d, consistent with reduced scope for activity at lower water temperatures (Brett 1971; Beamish 1974). Prespawn staging behaviors and proximity to spawning grounds also may have contributed to slower movement in spring.

It was not possible to pinpoint which habitats were used by overwintering Pacific Lampreys, but telemetry detections during this period suggested that deep, low-velocity areas with coarse substrate were used by some fish. Similar overwintering habitats were reported for the radio-tagged Pacific Lampreys in Clemens et al. (2012), Robinson and Bayer (2005), and Starcevich et al. (2014). Resumption of upstream movement in the Snake and Clearwater rivers coincided with water temperatures in the 4–7°C range and rain or snowmelt freshets. Both increasing temperature and increasing discharge (Almeida et al. 2002; Binder et al. 2010) have been associated with adult migratory activity in Sea Lamprey *Petromyzon marinus*. Most of the first movements we recorded were in March each year, and it is possible that rapidly increasing photoperiod played a role as well. Many anadromous steelhead *Oncorhynchus mykiss* also overwinter in the Snake River habitats used by lampreys, and Keefer et al. (2008) hypothesized that the combination of increasing photoperiod, water temperature, and discharge in March similarly stimulates steelhead movement to spawning sites.

There are very few reliable locations for collecting adult Pacific Lampreys for research and monitoring in the Snake River basin, and it is not known what study biases may have been introduced by using lampreys collected in the JBSs at Snake River dams. Collection at these locations required translocation prior to release, essentially bypassing 60–154 rkm of migration distance and 1–2 dam passage events. Thus, the translocations may have resulted in some overestimation of postrelease migration distances. The collected sample from the JBSs may have simply been a random subset of those lampreys migrating upstream. However, it is also possible that this group was moving downstream because they had difficulty locating suitable olfactory cues or because they were compromised in some way (e.g., weaker swimmers may have been more likely to be entrained in a JBS). Such effects could have resulted in altered behaviors or underestimated postrelease distances for study fish relative to the runs at large. Given the long postrelease distances moved by most lampreys, especially those released at the head of LGR reservoir, we do not think that the study sample was substantively compromised by selectivity of the JBS.

Management Considerations

Our results demonstrate that Pacific Lampreys can continue upstream migration into many Snake River subbasins after successfully passing through the Columbia–Snake hydrosystem. Although adult passage has not been evaluated at the lower Snake River dams, annual fish counts suggest that adults do migrate upstream from Lower Granite dam (DART 2010). However, it is unclear how the lower Snake River dams have altered the population density and distribution of lampreys in the lower Snake River. There is extensive suitable habitat available, including large wilderness tracts, where Pacific Lampreys were once relatively abundant (Luzier et al. 2011). It is widely acknowledged that hydroelectric dams are one of the primary drivers of declining interior populations. It is possible that substantially improved up- and downstream lamprey passage efficiency at dams and through reservoirs may contribute to repopulating the Snake River basin still accessible to anadromous fishes. There is considerable uncertainty, however, about whether improved adult passage alone can achieve restoration goals for the species in the interior Columbia and Snake river basins. Pacific Lamprey translocation and hatchery programs (e.g., Close et al. 2009; Ward et al. 2012) are underway or are being considered at various Columbia River basin locations in an effort to stem population declines and maintain the presence of Pacific Lampreys within their inland distribution. Such programs may be suitable for the Snake River basin, but a critical remaining uncertainty is how dams affect survival of out-migrating juveniles. Additionally, uncertainty regarding the potential genetic and demographic effects of interbasin transfers should be understood and resolved as much as possible, particularly given the recent evidence for a genetic basis for phenotypic differences and the presence of adaptive variation in Pacific Lamprey (Hess et al. 2013). Thus, we encourage careful monitoring and evaluation of the source populations used for such efforts, which may include using genetic parentage analysis to monitor and evaluate adult spawning, juvenile out-migration, and adult returns.

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REFERENCES

Almeida, P. R., B. R. Quintella, and N. M. Dias. 2002. Movement of radio-tagged anadromous Sea Lamprey during the spawning migration in the River Mondego (Portugal). Hydrobiologia 483:1–8.

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 tridentata*) from the Pacific coast of Canada. Canadian Journal of Fisheries and Aquatic Sciences 37:1906–1923.

Binder, T. R., and D. G. McDonald. 2007. Is there a role for vision in the behaviour of sea lampreys (*Petromyzon marinus*) during their upstream spawning migration? Canadian Journal of Fisheries and Aquatic Sciences 64:1403–1412.

Binder, T. R., R. L. McLaughlin, and D. G. McDonald. 2010. Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase Sea Lampreys in Lake Ontario. Transactions of the American Fisheries Society 139:700–712.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of Sockeye Salmon (*Oncorhynchus nerka*). American Zoologist 11:99–113.

Clemens, B., S. van de Wetering, J. Kaufman, R. Holt, and C. Schreck. 2009. Do summer temperatures trigger spring maturation in Pacific Lamprey, *Entosphenus tridentatus*? Ecology of Freshwater Fish 18:418–426.

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 35:580–594.

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.

Clemens, B. J., S. van de Wetering, S. A. Sower, and C. B. Schreck. 2013. Maturation characteristics and life-history strategies of the Pacific Lamprey, *Entosphenus tridentatus*. Canadian Journal of Zoology 91:775–788.

Close, D. A., K. P. Currens, A. Jackson, A. J. Wildbill, J. Hansen, P. Bronson, and K. Aronsuu. 2009. Lessons from the reintroduction of a noncharismatic, migratory fish: Pacific Lamprey in the upper Umatilla River, Oregon. Pages 233–253 *in* L. Brown, S. Chase, M. Mesa, R. Beamish, and P. Moyle, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Bethesda, Maryland.

Close, D. A., M. S. Fitzpatrick, and H. W. Li. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific Lamprey. Fisheries 27(7):19–25.

Cochnauer, T., and C. Claire. 2009. Evaluate status of Pacific Lamprey in the Clearwater River and Salmon River drainages, Idaho. Annual Report to the Bonneville Power Administration, Project 2008-028-00, Portland, Oregon.

Connor, W. P., H. L. Burge, and D. H. Bennett. 1998. Detection of PIT-tagged subyearling Chinook Salmon at a Snake River dam: implications for summer flow augmentation. North American Journal of Fisheries Management 18:530–536.

CRITFC (Columbia River Inter-Tribal Fish Commission). 2011. Tribal Pacific Lamprey restoration plan for the Columbia River basin. Nez Perce, Umatilla, Warm Springs, and Yakama tribes. Available: http://www.critfc.org/wp-content/uploads/2012/12/lamprey_plan.pdf. (December 2014).

Crossin, G. T., S. G. Hinch, A. P. Farrell, D. A. Higgs, A. G. Lotto, J. D. Oakes, and M. C. Healey. 2004. Energetics and morphology of Sockeye Salmon: effects of upriver migratory distance and elevation. Journal of Fish Biology 65:788–810.

DART (Data Access in Real Time). 2010. Columbia River DART (data access in real time). Available: http://www.cbr.washington.edu/dart/. (December 2014).

Hardisty, M., and I. Potter. 1971. The general biology of adult lampreys. Pages 127–206 *in* M. W. Hardisty and I. C. Potter, editors. The biology of lampreys, volume 1. Academic Press, London.

Hess, J. E., N. R. Campbell, D. A. Close, M. F. Docker, and S. R. Narum. 2013. Population genomics of Pacific Lamprey: adaptive variation in a highly dispersive species. Molecular Ecology 22:2898–2916.

Hess, J. E., N. R. Campbell, M. F. Docker, C. Baker, A. Jackson, R. Lampman, B. McIlraith, M. L. Moser, D. P. Statler, W. P. Young, A. J. Wildbill, and S. R. Narum. 2015. Use of genotyping by sequencing data to develop a high-throughput and multifunctional SNP panel for conservation applications in Pacific Lamprey. Molecular Ecology Resources 15:187–202.

Hess, J. E., C. C. Caudill, M. L. Keefer, B. J. McIlraith, M. L. Moser, and S. R. Narum. 2014. Genes predict long distance migration and large body size in a migratory fish, Pacific Lamprey. Evolutionary Applications 7:1192–1208.

Hyatt, M. W., T. Cochnauer, and C. Claire. 2007. Evaluate status of Pacific Lamprey in the Clearwater River drainage, Idaho. Annual Report to the Bonneville Power Administration, Project 2008-028-00, Portland, Oregon.

Jackson, A., and M. L. Moser. 2012. Low-elevation dams are impediments to adult Pacific Lamprey spawning migration in the Umatilla River, Oregon. North American Journal of Fisheries Management 32:548–556.

Johnson, E. L., C. C. Caudill, M. L. Keefer, T. S. Clabough, C. A. Peery, M. A. Jepson, and M. L. Moser. 2012. Movement of radio-tagged adult Pacific Lampreys during a large-scale fishway velocity experiment. Transactions of the American Fisheries Society 141:571–579.

Keefer, M. L., C. T. Boggs, C. A. Peery, and C. Caudill. 2008. Overwintering distribution, behavior, and survival of adult summer steelhead: variability among Columbia River populations. North American Journal of Fisheries Management 28:81–96.

Keefer, M. L., C. T. Boggs, C. A. Peery, and C. C. Caudill. 2013a. Factors affecting dam passage and upstream distribution of adult Pacific Lamprey in the interior Columbia River basin. Ecology of Freshwater Fish 22:1–10.

Keefer, M. L., C. C. Caudill, T. S. Clabough, M. A. Jepson, E. L. Johnson, C. A. Peery, M. D. Higgs, and M. L. Moser. 2013b. Fishway passage bottleneck identification and prioritization: a case study of Pacific Lamprey at Bonneville Dam. Canadian Journal of Fisheries and Aquatic Sciences 70:1551–1565.

Keefer, M. L., C. C. Caudill, C. A. Peery, and M. L. Moser. 2013c. Context-dependent diel behavior of upstream-migrating anadromous fishes. Environmental Biology of Fishes 96:691–700.

Keefer, M. L., M. L. Moser, C. T. Boggs, W. R. Daigle, and C. A. Peery. 2009a. Effects of body size and river environment on the upstream migration of adult Pacific Lampreys. North American Journal of Fisheries Management 29:1214–1224.

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, USA. Environmental Biology of Fishes 85:253–264.

Kinnison, M. T., M. J. Unwin, and T. P. Quinn. 2003. Migratory costs and contemporary evolution of reproductive allocation in male Chinook Salmon. Journal of Evolutionary Biology 16:1257–1269.

Kostow, K. E. 2002. Oregon lampreys: natural history, status and analysis of management issues. Oregon Department of Fish and Wildlife, Portland.

Lin, B., Z. Zhang, Y. Wang, K. P. Currens, A. Spidle, Y. Yamazaki, and D. A. Close. 2008. Amplified fragment length polymorphism assessment of genetic diversity in Pacific Lamprey. North American Journal of Fisheries Management 28:1182–1193.

Luzier, C. W., H. A. Schaller, J. K. Brostrom, C. Cook-Tabor, D. H. Goodman, K. Nelle, and B. Strief. 2011. Pacific Lamprey (*Entosphenus tridentatus*) assessment and template for conservation measures. U.S. Fish and Wildlife Service, Portland, Oregon.

Mesa, M. G., J. M. Bayer, and J. G. Seelye. 2003. Swimming performance and phyiological responses to exhaustive exercise in radio-tagged and untagged Pacific Lampreys. Transactions of the American Fisheries Society 132:483–492.

Mesa, M. G., R. J. Magie, and E. S. Copeland. 2010. Passage and behavior of radio-tagged adult Pacific Lampreys (*Entosphenus tridentatus*) at the Willamette Falls project, Oregon. Northwest Science 84:233–242.

Miller, J. 2012. Lamprey "eels" in the greater northwest: a study of tribal sources, experiences, and sciences. Journal of Northwest Anthropology 46:65–84.

Moser, M. L., M. L. Keefer, C. C. Caudill, and B. J. Burke. 2013. Migratory behavior of adult Pacific Lamprey and evidence for effects of individual temperament on migration rate. Pages 130–149 *in* H. Ueda and K. Tsukamoto, editors. Physiology and ecology of fish migration. CRC Press, Boca Raton, Florida.

Moser, M. L., P. A. Ocker, L. C. Stuehrenberg, and T. C. Bjornn. 2002. Passage efficiency of adult Pacific Lampreys at hydropower dams on the lower Columbia River, USA. Transactions of the American Fisheries Society 131:956–965.

Musick, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund, L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, S. J. Parker, S. G. Poss, E. Sala, T. W. Schmidt, G. R. Sedberry, H. Weeks, and S. G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries 25(11):6–30.

Noonan, M. J., J. W. A. Grant, and C. D. Jackson. 2012. A quantitative assessment of fish passage efficiency. Fish and Fisheries 13:450–464.

Petersen Lewis, R. S. 2009. Yurok and Karuk traditional ecological knowledge: insights into Pacific Lamprey populations of the lower Klamath Basin. Pages 1–40 *in* L. Brown, S. Chase, M. Mesa, R. Beamish, and P. Moyle, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Bethesda, Maryland.

Pletcher, F. T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. Master's thesis. University of British Columbia, Vancouver.

Renaud, C. B. 2008. Petromyzontidae, *Entosphenus tridentatus*: southern distribution record, Isla Clarión, Revillagigedo Archipelago, Mexico. Check List [online serial] 4:82–85.

Renaud, C. B. 2011. Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. Food and Agriculture Organization of the United Nations, FAO Species Catalogue for Fisheries Purposes 5, Rome.

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.

Ruiz-Campos, G., and S. Gonzalez-Guzman. 1996. First freshwater record of Pacific Lamprey, *Lamptera tridentata*, from Baja California, Mexico. California Fish and Game 82:144–146.

Simpson, J. C., and R. L. Wallace. 1982. Fishes of Idaho. University of Idaho Press, Moscow.

Spice, E. K., D. H. Goodman, S. B. Reid, and M. F. Docker. 2012. Neither philopatric nor panmictic: microsatellite and mtDNA evidence suggests lack of natal homing but limits to dispersal in Pacific Lamprey. Molecular Ecology 21:2916–2930.

Starcevich, S. J., S. L. Gunckel, and S. E. Jacobs. 2014. Movements, habitat use, and population characteristics of adult Pacific Lamprey in a coastal river. Environmental Biology of Fishes 97:939–953.

USACE (U.S. Army Corps of Engineers). 2012. Annual fish passage report. USACE, Portland, Oregon. Available: http://www.nwp.usace.army.mil/Missions/environment/Fish/Data.aspx. (December 2014).

USFWS (U.S Fish and Wildlife Service). 2004. Endangered and threatened wildlife and plants; 90-day finding on a petition to list three species of lamprey as threatened or endangered. Federal Register 69:247(27 December 2004):77158–77167.

Vrieze, L. A., R. Bjerselius, and P. W. Sorensen. 2010. Importance of the olfactory sense to migratory Sea Lampreys *Petromyzon marinus* seeking riverine spawning habitat. Journal of Fish Biology 76:949–964.

Wagner, C., M. Twohey, and J. Fine. 2009. Conspecific cueing in the Sea Lamprey: do reproductive migrations consistently follow the most intense larval odour? Animal Behaviour 78:593–599.

Wallace, R. L., and Ball, K. W. 1978. Landlocked parasitic Pacific Lamprey in Dworshak Reservoir, Idaho. Copeia 1978:545–546.

Ward, D. L., B. J. Clemens, D. Clugston, A. D. Jackson, M. L. Moser, C. Peery, and D. P. Statler. 2012. Translocating adult Pacific Lamprey within the Columbia River basin: state of the science. Fisheries 37:351–361.

Yamazaki, Y., N. Fukutomi, N. Oda, K. Shibukawa, Y. Niimura, and A. Iwata. 2005. Occurrence of larval Pacific Lamprey (*Entosphenus tridentatus*) from Japan, detected by random amplified polymorphic DNA (RAPD) analysis. Icthyological Research 52:297–301.

Yun, S.-S., A. J. Wildbill, M. J. Siefkes, M. L. Moser, A. H. Dittman, S. C. Corbett, W. Li, and D. A. Close. 2011. Identification of putative migratory pheromones from Pacific Lamprey (*Lampetra tridentata*). Canadian Journal of Fisheries and Aquatic Sciences 68:2194–2203.