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RESEARCH ARTICLE

Pacific lamprey recolonization of a Pacific Northwest river following dam removal

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Abstract

Recolonization of Pacific lampreys *Entosphenus tridentatus* into historically used freshwater habitats in the United States Pacific Northwest was evaluated in the White Salmon River basin after removal of Condit Dam. Pacific lamprey population declines are of concern, and passage barrier removal is often recommended for conservation. Condit Dam on the White Salmon River in Washington was a complete barrier to fish migrating upstream for nearly 100 years, was breached in 2011, and was removed by 2012. Distribution of larval Pacific lampreys was estimated before and after removal of Condit Dam using either backpack or deepwater electrofishing. Larval detection probabilities were calculated for the basin, and sample efforts were refined to ensure at least 80% confidence that larvae were absent when not detected. Pacific lampreys were not present upstream of Condit Dam before it was removed but were present in areas downstream of the dam. After dam removal, Pacific lamprey larvae were collected upstream of the former dam site from four reaches of the mainstem White Salmon River, indicating a recent recolonization event. Pacific lampreys were absent from the river mouth area before the dam was removed but were found in newly created habitat at the mouth after dam removal. Pacific lampreys naturally recolonized the White Salmon River basin within a few years after dam removal. Removing dams and providing passage opportunity can allow Pacific lampreys to distribute into vacant areas and may help reverse population declines.

KEYWORDS

dam removal, detection probability, *Entosphenus*, occupancy sampling, Pacific lamprey, recolonization

1 | INTRODUCTION

Anadromous Pacific lampreys *Entosphenus tridentatus* are ecologically significant and culturally important to Native American tribes (Docker, Hume, & Clemens, 2015). Their widespread decline has prompted conservation action, most notably in the Columbia River Basin (Close, Fitzpatrick, & Li, 2002; Luzier et al., 2011). Furthermore, worldwide declines in lamprey populations have created a broad conservation need (Renaud, 1997). Rigorous, empirical information on the causes of the Pacific lamprey population decline is mostly unavailable; however, adult passage impediments have been implicated as a major factor (Jackson & Moser, 2012; Keefer, Boggs, Peery, & Caudill, 2013). The response of the Pacific lampreys to dam removals is largely unknown.

Dams can have negative impacts on the ecology of watersheds by fragmenting habitats and impeding migration, as well as by altering temperature regime, nutrient flow, and hydrographs (Babbitt, 2002; Pringle, 2001). The number and scope of dam removals in the United States have been increasing, resulting in positive benefits to ecosystems (Poff & Hart, 2002). However, the thrust for many dam removals is socio-economic (Pejchar & Warner, 2001); an evaluation of ecological aspects is often lacking (Foley et al., 2017; Hart et al., 2002), and the data that exist are concentrated on small dams (Doyle, Stanley, Harbor, & Grant, 2003).

Information about how fish populations respond to dam removals can help inform conservation and management actions. Condit Dam was completed in 1913 and was the only dam on the 72-km mainstem White Salmon River of south-central Washington. It was 144-m long,

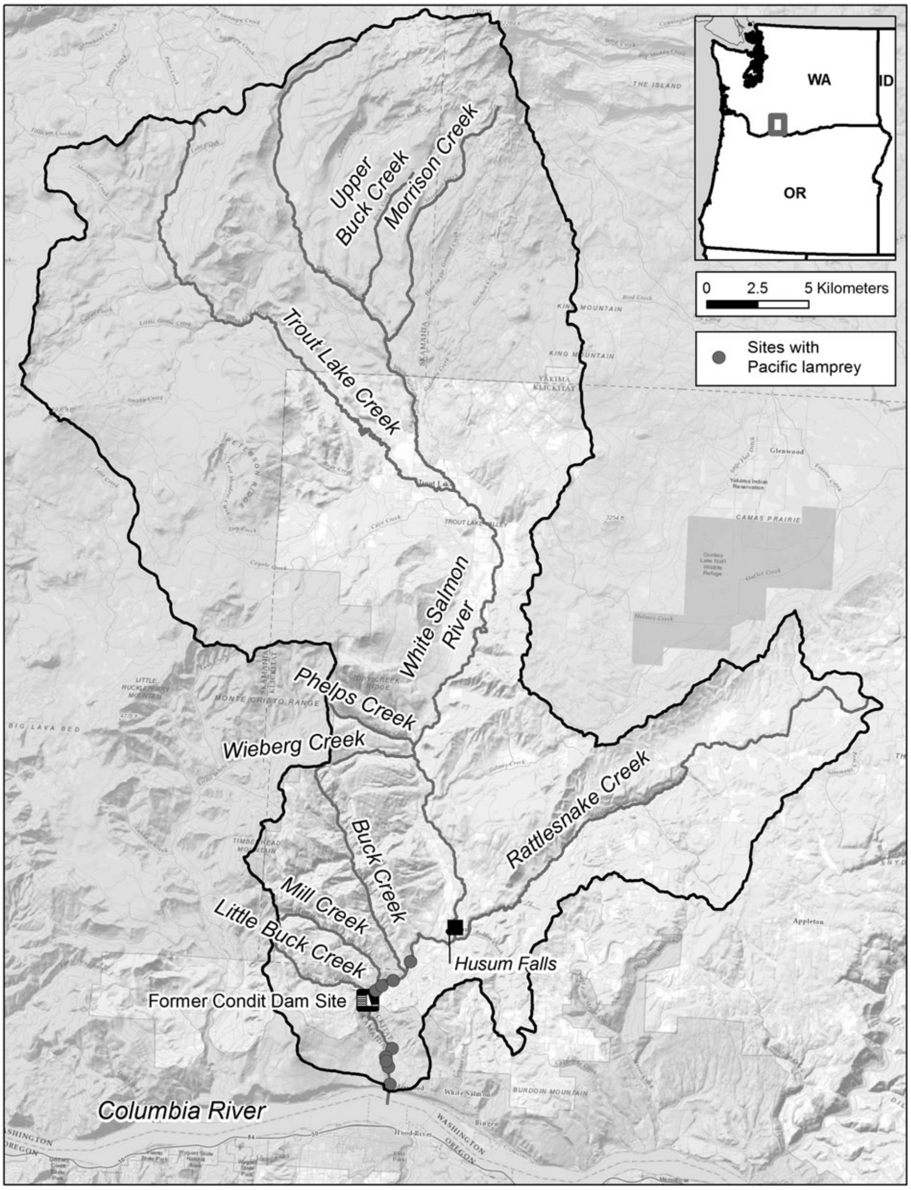

FIGURE 1 The White Salmon River basin in south central Washington and tributaries sampled for larval lampreys in 2007–2015

38-m high, and located 5.3 km upstream from the confluence of the White Salmon River and the Columbia River (Figure 1). The dam also created the 2.9 km long Northwestern Reservoir containing 1.8 million m^3 of accumulated sediment (Wilcox, O'Connor, & Major, 2014). Upstream fish passage was blocked, causing declines in anadromous fish production, and little fish production occurred downstream due to habitat loss and alteration of the natural flow regime (Lower Columbia Fish Recovery Board, 2004). Condit Dam was breached in October 2011 and was completely removed by September 2012. Sediment from the impounded Northwestern Reservoir was allowed to rapidly flush downstream after the breach and continues to redistribute during high winter and spring flows (Allen et al., 2016; Wilcox et al., 2014).

Pacific lampreys have multiple stages in their life history including larval, migratory juvenile, and adult marine phases (Scott & Crossman, 1973). After development beyond the swim-up stage, larvae burrow and filter-feed in sand and other fine sediments (Stone & Barndt, 2005; Torgersen & Close, 2004). Larvae regularly disperse, usually moving in a downstream direction (Moser, Jackson, Lucas, & Mueller, 2015). After the larval stage, Pacific lampreys metamorphose into juveniles and migrate to the Pacific Ocean where they are parasitic until they reach sexual maturity, finally returning to freshwater streams for spawning (Beamish, 1980; Dawson, Quintella, Almeida, Treble, & Jolley, 2015).

We assessed whether Pacific lampreys recolonized the White Salmon River after the removal of Condit Dam. We evaluated larval distribution in the basin before and after the removal of Condit Dam, in areas upstream and downstream of the dam site. The larval stage is often targeted for sampling to identify occupancy and assess status (Cowx, Harvey, Noble, & Nunn, 2009; Moser, Butzerin, & Dey, 2007). We surveyed both wadable and non-wadable habitats for larval lamprey. Wadable streams of 3rd order (hereafter 1:100,000 scale) or lower (Stone & Barndt, 2005; Torgersen & Close, 2004) were sampled because larvae commonly distribute in areas containing depositional material typical in these streams. Non-wadable habitats were also sampled as larvae that are known to occur in the depositional materials of deeper habitats and presence could indicate production upstream

(Harris & Jolley, 2017; Jolley, Silver, & Whitesel, 2012a). The presence of western brook lamprey *Lampetra richardsoni* in some areas above the dam site suggested spawning and rearing habitat was available for Pacific lampreys (Silver, Jolley, & Whitesel, 2010). We expected to find increased distribution of larvae in the basin after the dam was removed. Our specific objectives were to determine occupancy of Pacific lamprey larvae (a) in wadable tributaries upstream of the historic dam site, (b) in wadable areas downstream of the historic dam site, and (c) and in non-wadable areas of the White Salmon River mainstem and river mouth downstream of the historic dam site.

2 | METHODS

2.1 | Study area

The White Salmon River is a 5th order river with a basin of 1,000 km^2 that enters the Columbia River at Rkm 269 (Figure 1). It originates from Mount Adams in the Cascade Mountain Range of south-central Washington that is the source of fine sediments that would provide adequate rearing habitats for larval lamprey. Condit Dam was 5.3 km upstream from the confluence of the White Salmon and Columbia rivers.

2.2 | Distribution assessment

We assessed larval Pacific lamprey occupancy both upstream and downstream of the Condit Dam site, before and after dam removal. We used an adaptive probabilistic framework to identify the number and specific location of sampling sites needed to assess occupancy (Jolley, Silver, & Whitesel, 2012b). When individuals are observed in a unit, occupancy is known with a probability of 1; however, when no individuals are observed, the unit could be truly unoccupied or it could be occupied but with no individuals detected within it. The posterior probability of unit occupancy if no larval lampreys are observed, $P(F|C_o)$, can be estimated by a model developed by Peterson and Dunham (2003):

$$p(F|C_o) = \frac{p(C_o|F)P(F)}{p(C_o|F)p(F) + p(C_o|{\sim}F)p({\sim}F)}. \quad (1)$$

$p(F)$ is the prior probability of larval lamprey presence and $P({\sim}F)$ is the prior probability of absence (i.e., 1- $p(F)$). We set $P(F) = p({\sim}F) = .5$ (uninformed) because larval lamprey's presence in each unit was considered unknown. $p(C_o|F)$ is the probability of not detecting a larval lamprey when it occurs (C_0 = no detection; Peterson & Dunham, 2003) and is a function of detection probability and the number of sites sampled, n. Detection probability, or the probability of detecting a larval lamprey from a site within an occupied unit, d_{unit}, is influenced by sampling method and gear. For practical purposes we assumed d_{unit} was the proportion of sampled sites in which lamprey were observed. $p(C_o|F)$ is then estimated as $(1- d_{unit})^n$. Thus, identifying n requires a unit-and gear-specific detection probability (assumed or estimated) and a predetermined acceptably low level for $p(F|C_o)$, the posterior probability of unit occupancy if no larval lamprey are observed. On the basis of this model, we always chose a sampling effort that would result in at least 80% confidence that larvae were absent, if not detected (Jolley et al., 2012a).

We used a generalized random tessellation stratified approach to select sampling sites in a random, spatially-balanced order, from all possible sites in a unit of interest (Stevens & Olsen, 2004). This sample design allows proper estimation of detection probabilities. A sampling site was defined as a 50-m stream reach for wadable areas and a 30-m × 30-m quadrat for non-wadable areas.

2.3 | Wadable areas

All watersheds up to 3rd order in size are generally wadable and were classified as potential adult lamprey spawning and early larval rearing areas. Because spawning substrates of Pacific lampreys and anadromous steelhead trout *Oncorhynchus mykiss* overlap, (Bjornn & Reiser, 1991; Scott & Crossman, 1973) we used the anadromous steelhead intrinsic spawning habitat potential in the White Salmon River Basin (Burnett et al., 2007) to refine the number of watersheds (i.e., sample units) likely to support spawning and early rearing for Pacific lampreys. We also eliminated seasonally dewatered or inaccessible areas (Silver, Hudson, & Whitesel, 2011) from our sample framework. A watershed was defined as a sample unit for which we would evaluate Pacific lamprey occupancy (i.e., d_{unit}) in wadable streams. An additional sample unit, the White Salmon River mainstem, downstream of the Condit Dam site, was included to assess occupancy in the portion of the subbasin that Pacific lampreys had access to prior to dam removal (Figure 1).

Ten sample units were identified and samples from 2007 to 2009 (Table 1). We initiated this work in Buck Creek and Trout Lake Creek in 2007 and assumed a conservative detection probability (i.e., d_{unit} = .065; Jolley et al., 2012b) resulting in a high sample effort (i.e., n = 21 sample reaches) to achieve at least 80% certainty of larval lamprey absence when they were not detected in wadable streams. We also derived a specific detection probability for the wadable streams of the subbasin. We expected the derived d_{unit} to be higher than our assumed value and the ability to reduce our sample effort accordingly. We applied the explicit d_{unit} value to the remainder of the watersheds and targeted the minimum number of sampled reaches to achieve at least 80% confidence, an acceptable level used previously (Jolley et al., 2012a). Lastly, five wadable reaches of the mainstem White Salmon River, identified mainly by accessibility, were opportunistically sampled downstream of the Condit Dam site.

Many watersheds were eliminated for our post-dam sampling in 2015 due to the identification of suspected impassable barriers and ephemeral streams. Although Pacific lampreys are known to climb vertically (Frick, Corbett, & Moser, 2017; Reinhardt, Eidietis, Friedl, & Moser, 2008), it is unknown what conditions preclude passage. Because Pacific lampreys do not have jumping ability, any barrier that had a perched ledge was deemed impassable. In 2015, four remaining watersheds and the White Salmon River mainstem downstream of the historic dam location were sampled in wadable areas. In addition, newly accessible wadable areas of the White Salmon River mainstem upstream of the dam site to Husum Falls (Rkm 13) were also sampled.

TABLE 1 Subbasins of the White Salmon River sampled and occupied with Pacific lampreys from backpack electrofishing surveys, 2007–2015. Pre-dam removal sampling occurred in 2007–2009 and post-dam removal sampling occurred in 2015

	Before Condit Dam removal			After Condit Dam removal		
Sample unit	Reaches sampled	Pacific lamprey detected (number of reaches)	d_{unit}	Reaches sampled	Pacific lamprey detected (number of reaches)	d_{unit}
Buck Creek	21	0	.00	6	0	.00
Trout Lake Creek	21	0	.00	6	0	.00
Rattlesnake Creek	21	0	.00	3	0	.00
Little Buck Creek	8	0	.00	–	–	–
Mill Creek	7	0	.00	10	0	.00
Morrison Creek	5	0	.00	–	–	–
Phelps Creek	4	0	.00	–	–	–
Wieberg Creek	3	0	.00	–	–	–
Upper Buck Creek	2	0	.00	–	–	–
White Salmon River above Condit	–	–	–	6	4	.67
White Salmon River below Condit	5	1	.20	6	5	.83

2.4 | Non-wadable areas

Two non-wadable areas, the Lower White Salmon River mainstem (1.4 km section upstream from the mouth) and the White Salmon River mouth (0.5 km semicircle from the point intersection of the White Salmon River channel and the edge of Bonneville Reservoir; Figure 1) were sampled. We developed a layer of 30 m × 30 m quadrats using ArcMap 9.3 (Environmental Systems Research Institute, Redlands, California) that was overlaid on each of these units of interest. The Universal Trans Mercator coordinates representing the centre point of each quadrat were determined. In other mainstem habitats, we have previously found detection rates ranging from .02 to .32 (Jolley et al., 2012a; Jolley, Silver, & Whitesel, 2012c) using a deepwater electrofisher. We assumed detection probability was at least .04, resulting in the need to sample 34 quadrats to be 80% certain an area was not occupied, if no individuals were collected. Quadrats that could not be feasibly sampled due to dewatered conditions or excessive velocity were eliminated from the sampling frame and all subsequent quadrats increased in priority.

2.5 | Field sampling methods

Larval lampreys were collected using electrofishing (described below). A stream reach or quadrat was considered occupied when one individual was captured. Field sampling for larval lampreys in wadable areas was conducted using an AbP-2 backpack electrofisher (ETS Electrofishing, Verona, WI) specifically designed for capturing larval lamprey (Weisser & Klar, 1990) and widely used (Harris, Jolley, Silver, Yuen, & Whitesel, 2016; Torgersen & Close, 2004). Sampling for larval lampreys in non-wadable areas was conducted using a deepwater electrofisher/suction dredge combination (Bergstedt & Genovese, 1994) in a 30 m × 30 m quadrat (Jolley et al., 2012a). If a given reach or quadrat in a sample unit could not be electrofished (e.g., dewatered or inaccessible), the reach or quadrat was omitted from the sample unit and the next highest priority reach was added.

Collected lampreys were anaesthetized in a solution of tricaine methanesulfonate (MS-222), and those that were 50 mm total length (TL) or greater were identified as Pacific lampreys or *Lampetra* spp. according to caudal pigmentation (Docker, Silver, Jolley, & Spice, 2016; Goodman, Kinzinger, Reid, & Docker, 2009), and classified according to developmental stage (i.e., larvae, juvenile, or adult). Lamprey that were less than 50 mm total length cannot be reliably identified visually, thus, a sample of caudal fin tissue was removed and stored in ethanol for genetic identification of genus. Lampreys were measured (TL in mm), allowed to recover in fresh river water, and released after resuming active swimming behaviour. Genetic analyses for the identification of genus were performed using both the *Hae*III restriction fragment length polymorphism assay (see Goodman et al., 2009) and the Etr-1 microsatellite locus (see Spice, Whitesel, McFarlane, & Docker, 2011).

2.6 | Statistical analyses

Patterns of occupancy before and after Condit Dam removal were compared using Chi-square tests (for paired before-after data) for differences in probability of detection (Conover, 1999). In addition, unit detection probabilities were compared before and after the removal of Condit Dam using Fisher's Exact Test with a multivariate technique for multiple comparisons (for three years of comparisons; Brown & Fears, 1981). Significance level for all statistical tests was $\alpha = 0.05$

3 | RESULTS

Prior to the removal of Condit Dam, Pacific lampreys were not detected in any sampled reaches ($N = 92$) above the dam (Table 1). A suspected impassable waterfall likely blocked 16 reaches in Trout Lake Creek. Suspected natural passage barriers were also identified in Rattlesnake Creek (Rattlesnake Falls) and Buck Creek (Buck Creek Falls) although no larvae were captured in these subbasins. Little Buck, Morrison, Phelps, Wieberg, Gotchen, and Upper Buck creeks were sampled but eliminated from future consideration upon discovering they were likely inaccessible to fish, became dewatered in the summer, or had barriers at or near the confluence with the White Salmon River. We estimated with over 80% confidence that larval lampreys were absent in the watersheds where we failed to detect them, based on high detectability of larval western brook lamprey in Trout Lake Creek (d_{unit} = 0.80; Silver et al., 2010) assumed to be similar in other White Salmon River watersheds.

After Condit Dam removal, we did detect Pacific lampreys above the former dam site. Specifically, 13 larval Pacific lampreys (26–67 mm TL; Table 2) were found in four reaches in the White Salmon River mainstem above the former Condit Dam site. In the White Salmon River mainstem downstream of the former dam site, we detected Pacific lampreys in five reaches. After the removal of Condit Dam, Pacific lampreys were not detected in any reach of Trout Lake Creek, Mill Creek, Rattlesnake Creek, or Buck Creek (Table 1), areas accessible to migratory adult Pacific lampreys. Larval Pacific lampreys were detected in wadable areas of the mainstem White Salmon River downstream of Condit Dam both before the removal in one of five reaches (d_{unit} = .20) and after the removal in five of six reaches (d_{unit} = .83; Table 1). Five Pacific lamprey larvae (size range 57–91 mm TL) were captured prior to dam removal. Forty three Pacific lamprey larvae (10–107 mm TL; Table 2) were captured after dam removal. There was no change in the detection rate (p = .24) in the White Salmon mainstem below the dam.

Larval Pacific lampreys were not found in the White Salmon River mouth before but were detected after the dam removal (Table 3). Most notably, the proportion of sites occupied increased in the river mouth 2 years after the dam removal, although detection rates did not change (Fisher's Exact Test, p = .067). Larval Pacific lampreys occupied the lower river before and after the dam removal. Detection probabilities of Pacific lampreys were higher before compared with after the dam removal in the lower White Salmon River (Fisher's Exact Test, $p < .01$). Pacific lamprey larvae ranged in size from 22 to 138 mm. Small sample sizes precluded statistical analyses of TL data (Table 2). Depths sampled ranged from .3 to 19.5 m, and larvae were detected in depths ranging from 1 to 8.5 m.

TABLE 2 Mean total length (TL) in mm, standard error (SE), and sample size (n) of Pacific lamprey larvae collected in the White Salmon River Basin, 2007–201

Year	Reach	Mean TL	SE	*n*
2007	White Salmon River below Condit	73	7	5
2015	White Salmon River above Condit	52	3	13
	White Salmon River below Condit	58	4	43
2011	Lower white Salmon River	85	9	12
	Lower Klickitat River	86	8	12
	Lower Wind River	82	9	8
	Wind River mouth	72	5	16
2012	Lower Klickitat River	99	-	1
	Lower Wind River	71	14	6
	Klickitat River mouth	62	20	4
	Wind River mouth	67	10	9
2013	White Salmon River mouth	61	19	3
	Klickitat River mouth	80	5	3
	Wind River mouth	97	31	3

Note. Values of "-" indicate no larvae were collected at that site at that time.

4 | DISCUSSION

This is one of the first directed studies to report natural recolonization by Pacific lampreys following removal of an impassable dam. In 2015, Pacific lamprey larvae were found in several areas of the White Salmon River basin that were inaccessible or unusable prior to the removal of Condit Dam, indicating recolonization occurred after less than 4 years. Pacific lamprey larvae were detected in four reaches above the former dam site and also in newly created habitats at the river mouth. Similarly, Hess et al. (2015) documented a likely Pacific lamprey recolonization in the nearby Hood River after the removal of Powerdale Dam; they surmised that the small larvae collected (<46 mm) were progeny from a recent colonization event less than 2 years after the dam removal. In other studies, Pacific lampreys were observed naturally, recolonizing the North Fork Toutle River following the eruption of Mount St. Helens that largely exterminated aquatic communities through volcanic debris and ash (Lin et al., 2008) and to recolonize Babine Lake in British Columbia after the removal of a rockslide that was a suspected barrier (Farlinger & Beamish, 1984). There are also reports of Pacific lampreys present in Indian Creek of the Elwha River Basin following the removal of Elwha Dam in 2012 (Witze, 2015). Sea lampreys, *Petromyzon marinus*, have also been shown to rapidly recolonize portions of stream basins following dam removals when they were already present downstream of the dam (Hogg, Coghlan, & Zydlewski, 2013; Lasne, Sabatié, Jeannot, & Cucherousset, 2015).

Recolonization above the Condit Dam site likely resulted from spawning events that occurred shortly after dam removal as evidenced by the small size of the larvae (26–67 mm TL). Although adult Pacific lamprey spawning migrations are protracted (Clemens, van de Wetering, Kaufman, Holt, & Schreck, 2009), adults typically enter river basins in spring (Beamish, 1980) and continue spawning activities into the summer (Stone, 2006); thus, there were three full migration seasons for adults to potentially enter the basin. Meeuwig and Bayer (2005) reported a mean length of 46 and 51 mm for age 1 and age 2 Pacific lamprey larvae, respectively. Quintella, Andrade, and Almeida (2003) reported that sea lamprey larvae were 50 mm at 12 months, and Potts, Dawson, and Jones (2015) reported that age 1 sea lampreys

TABLE 3 Quadrats sampled by deepwater electrofishing and occupied with larval lampreys in the lower White Salmon River and mouth in 2011–2013

Year	Sample unit	Quadrats sampled	Pacific lamprey detected	d_{unit}
2011	Lower White Salmon River	34	8	.24
	White Salmon River mouth	34	0	.00
2012	Lower White Salmon River	34	0	.00
	White Salmon River mouth	34	0	.00
2013	White Salmon River mouth	34	3	.09

were 30–60 mm. Although size-at-age for larval lamprey can be highly variable (Hess et al., 2015), the sizes of the Pacific lamprey larvae we captured suggest that they were likely age 2 or younger and thus produced after Condit Dam removal. The White Salmon River likely has an abundant source of adults as those fish only need to pass Bonneville Dam on the mainstem Columbia River to access the river. The potential for successful recolonization after barrier removal in areas above multiple passage impediments may be reduced or may take longer because fewer adults may be available to recolonize (Moser, Ocker, Stuehrenberg, & Bjornn, 2002).

Habitat in the lower river and at the river mouth of the White Salmon River changed due to the release of impounded sediments from the dam era. In the lower river, the larval detection rate was lower in 2012 than in 2011, likely due to the changes in sediment composition as well as the unstable condition of the newly deposited sediments. In 2012, there was larger cobble and gravel upstream from the mouth than there was in 2011. Because the dam removal sediment has redistributed in this area and has been in a constant state of flux (Jolley et al., 2012c; Jolley, Silver, & Whitesel, 2013). Before dam removal, the mouth area was deep, swift, and scoured. Suitable substrates (i.e., fine sediment) for larval lamprey were scarce to non-existent (Jolley et al., 2012b), and no lampreys were detected. Due to the sediment influx after dam removal, a newly formed delta of fine sediments was present at the mouth (Wilcox et al., 2014). Multiple Pacific lamprey larvae were detected in 2013. Although the source of the larvae detected in the mouth area is unknown (i.e., whether the larvae were from the White Salmon River itself, or moving downstream within the Columbia River mainstem), this area now provides potential rearing habitat that was not present during the dam era.

The full extent of the White Salmon River subbasin that could be available and colonized by Pacific lampreys remains unclear. Rattlesnake Creek, Mill Creek, and Buck Creek are all accessible to Pacific lampreys now that Condit Dam has been removed, and no other major passage impediments remain. The White Salmon River mainstem up to at least Husum Falls is also available. It is also unclear what constitutes a natural passage barrier for adult Pacific lampreys. They can climb some structures (Close et al., 2002; Kemp, Tsuzaki, & Moser, 2009), but detailed evaluations of their full passage capabilities have not been conducted. There are a series of waterfalls on the mainstem White Salmon River including Husum Falls (Rkm 12.6) Other anadromous fish, including steelhead trout and Chinook salmon *O. tshawytscha* (Allen et al., 2016), have rapidly recolonized the basin up to Husum Falls. The occupancy-based sampling techniques outlined in this study can be adapted to assess potential passage barriers (Jolley et al., 2012b) or within-basin distribution.

Adopting a probabilistic sampling scheme that utilizes concepts of occupancy and detection probability has shown to be an efficient and valuable method for rapidly evaluating occupancy after a dam removal. This study design is adaptable and efficient because larval lampreys are highly detectable (Dunham, Chelgren, Heck, & Clark, 2013; Harris et al., 2016). Our methods of occupancy sampling could be expanded to include abundance estimation (Harris & Jolley, 2017) and modelling the effects of habitat covariates (Gu & Swihart, 2004; Krishna, Krishnaswamy, & Kumar, 2008), which could both be useful in assessing the benefit of dam removal to Pacific lamprey production.

Removing dams and providing passage opportunity can allow Pacific lampreys to distribute into vacant areas and may help reverse declines in their abundance. How rapidly Pacific lampreys naturally recolonized the White Salmon River basin after a dam removal was remarkable. Additional monitoring will be important to document the extent, rate, and pattern of lamprey expansion in the basin. Occupancy-based methods provide an efficient tool for investigating these types of topics. Recolonization of naturally producing aquatic animal populations can be a positive outcome of dam removals including reestablishing marine derived nutrients (Tonra, Sager-Fradkin, Morley, Duda, & Marra, 2015). The literature of the effects of dam removal is large (reviewed in Hart et al., 2002), and fish passage barrier removal is often recommended among a suite of conservation actions for Pacific lampreys (Clemens et al., 2017). Our findings provide yet another example for dam removal having a positive conservation value on fishes by allowing recolonization of a behaviourally unusual and understudied migratory fish.

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