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Estimation of occupancy, density, and abundance of larval lampreys in tributary river mouths upstream of dams on the Columbia River, Washington and Oregon

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Abstract: We estimated occupancy, density, and abundance of larval Pacific lamprey (*Entosphenus tridentatus*) and *Lampetra spp.* in tributary river mouths to impounded portions of the Columbia River, Washington and Oregon, using count data from deepwater electrofishing. Count data were analyzed by Bayesian methods using zero-inflated N-mixture models modified to include our experimentally-derived estimate of capture probability of 0.70 (95%: 0.63 – 0.77). *Lampetra spp.* were only collected in river mouths in Bonneville Reservoir, while Pacific lamprey were also captured from river mouths in The Dalles and John Day reservoirs. In occupied river mouths, average densities were commonly $0.2 - 0.3 \cdot \text{m}^{-2}$, but ranged from $0.18 \cdot \text{m}^{-2}$ to $1.72 \cdot \text{m}^{-2}$ for Pacific lamprey and $0.24 \cdot \text{m}^{-2}$ to $1.72 \cdot \text{m}^{-2}$ for *Lampetra spp.* Although there was spatial overlap, estimated density peaked in the Klickitat River mouth (556 600 larvae) for Pacific lamprey and in the Wind River mouth (544 800 larvae) for *Lampetra spp.* Our study demonstrates considerable larval rearing in river mouths to impounded portions of the Columbia River; however, information on survival is needed to evaluate the contribution of this production to population growth and conservation.

Introduction

World-wide, lampreys have experienced population declines (Renaud 1997; Maitland et al. 2015). A species of particular conservation concern is the anadromous Pacific lamprey (*Entosphenus tridentatus*) (Close et al. 2002; Wang and Schaller 2015). Pacific lamprey import and cycle nutrients in freshwater ecosystems and are prey for marine and freshwater predators (Beamish 1980; Close et al. 2002; Riemer et al. 2011). They are also important to Native American tribes for subsistence, spiritual, and medicinal purposes (Close et al. 2002; Wang and Schaller 2015; Noble et al. 2016). Pacific lamprey were historically distributed from Mexico to Japan (Ruiz-Campos and Gonzalez-Guzman 1996; Yamazaki et al. 2005); however, they do not exhibit natal homing and there is only limited genetic differentiation over their range (Goodman et al. 2008; Spice et al. 2012). The Columbia River Basin may serve as a region of high production for Pacific lamprey and therefore may be important for conservation of the species (Keefer et al. 2013; McIlraith et al. 2015). A better understanding of distribution and density of larval Pacific lamprey in the heavily modified Columbia River Basin would help identify and characterize larval rearing habitat and the potential value of spawning upstream of dams.

Similar freshwater habitat preferences have been documented for larvae of multiple lampreys (Slade et al. 2003; Smith et al. 2011; Ferreira et al. 2013; Aronsuu and Virkkala 2014). Once Pacific lamprey develop beyond the swim-up stage, larvae burrow and filter feed in fine sand when it is available (Torgersen and Close 2004; Stone and Barndt 2005). Larvae regularly disperse, usually moving in a downstream direction (Moser et al. 2015b). After the larval stage, Pacific lamprey metamorphose into juveniles and migrate to the Pacific Ocean where they are parasitic until they reach sexual maturity (Beamish 1980; Dawson et al. 2015). Larval western brook lamprey (*Lampetra richardsoni*) which are river resident, and larval river lamprey

(*Lampetra ayresii*) which are anadromous, are also found burrowed in fine sediments in the Columbia River Basin. To date, most larval lamprey sampling has been completed in wadeable streams (Moser et al. 2007). Although use of non-wadeable areas by larval sea lamprey (*Petromyzon marinus*) has been documented (Bergstedt and Genovese 1994; Lee and Weise 1989; Fodale et al. 2003), use by larvae of other lamprey species has received little study; it has been suggested that future research is needed to evaluate the importance of deeper-water habitat for lamprey rearing and production (Jolley et al. 2012; Dawson et al. 2015).

Our study quantified use of tributary river mouths in impounded areas of the Columbia River by larval lampreys. There are 14 large dams on the mainstem Columbia and Snake rivers that provide fish passage. Although Pacific lamprey and *Lampetra spp.* have been collected upstream of the fourth dam, McNary Dam (Moser and Close 2003; Meeuwig et al. 2005; Grote et al. 2014), larval use of tributary river mouths in impounded areas has not been studied. We sampled for larval lampreys using a deepwater electrofishing method designed by Bergstedt and Genovese (1994). In soft sediments, the perimeter of the deepwater electrofisher behaves like a cap, covering, stunning, and collecting burrowed lampreys in a known unit of area (Bergstedt and Genovese 1994). Because the area sampled is known and sampling can be conducted at a variety of depths, the deepwater electrofisher could be ideal for estimating density and abundance of larval lampreys, although the probability of capturing a burrowed lamprey must be incorporated into density and abundance estimation, which can be challenging. We had two specific objectives: 1) experimentally estimate the probability of capturing a larval lamprey by deepwater electrofishing; and 2) examine distribution and estimate the probability of occupancy, density, and abundance of larval Pacific lamprey and *Lampetra spp.* in tributary river mouths entering impounded portions of the Columbia River.

76

77 **Methods**78 **Study site**

79 We sampled for larval lampreys in river mouths of most substantial tributaries entering
80 the four lowest reservoirs in the Columbia River: Bonneville, The Dalles, John Day, and McNary
81 (Fig. 1). Included rivers ranged in stream order (1:100 000 scale) from fourth (Little White
82 Salmon River) to seventh (Yakima River; Table 1). Fine sediments in these rivers originate in
83 the Cascade and the Blue mountain ranges of Washington and Oregon (Wydoski and Whitney
84 2003). Tributary river mouths varied temporally and spatially in terms of flows, depths, and
85 sediments due to dynamic fluvial and alluvial processes, as well as hydrosystem operations. In
86 sampled river mouths, recorded ranges were 26 to 410 $\mu\text{S cm}^{-1}$ for ambient conductivity (average
87 = 102 $\mu\text{S cm}^{-1}$), 5.2 to 24.4 °C for temperature (average = 16.3 °C), and 0.2 to 23.8 m for depth
88 (average = 3.4 m). Five river mouths were sampled within Bonneville Reservoir, one within The
89 Dalles Reservoir, and two each within the John Day and McNary reservoirs (Table 1).

90 **Field methods**

91 We sampled for larval lampreys in tributary river mouths using a deepwater electrofisher
92 from March to November, 2011-2015. Field methods were similar to those used for sampling
93 larval Pacific lamprey in the Willamette River (Jolley et al. 2012). Each tributary river “mouth”
94 was defined by a 0.5 km semicircle from the point where the midchannel of the tributary
95 intersected the Columbia River based on orthophotography. A layer of 30 x 30 m quadrats
96 encompassing each mouth was created with ArcMap 9.3 (Environmental Systems Research
97 Institute, Redlands, California). We used a Generalized Random Tessellated Stratified (GRTS)
98 approach to select 11 – 38 quadrats from each mouth in a random, spatially balanced order to

sample each year (Stevens and Olsen 2004). In addition, in 2013, quadrats in the Klickitat and Wind rivers were sampled on up to three different dates. On each sampling date, each quadrat was sampled once by deepwater electrofishing (i.e., one drop). The deepwater electrofisher samples 0.42 m² of sediment in one drop. The number of quadrats sampled in each tributary river mouth in each year can be found in Table 1. Deepwater electrofishing sampling techniques are described in Jolley et al. (2012).

Genetic samples confirmed each collected larval lamprey as either an *Entosphenus spp.* or a *Lampetra spp.* (Spice et al. 2011; Docker et al. 2016). Each larvae was anesthetized in a bath of buffered MS-222 (tricaine methanesulfonate, 2:1), measured for total length (TL in mm), and a two x two mm tissue sample was clipped from the caudal fin and preserved in ethanol for genetic analysis. All *Entosphenus* were assumed to be Pacific lamprey as there are no other known species of that genus in the area, but *Lampetra spp.* could be either western brook lamprey *L. richardsoni* or western river lamprey *L. ayresii*. These two *Lampetra spp.* are “paired species” and their larvae cannot currently be distinguished by any method (Docker 2009).

Capture probability experiments

The probability of a Pacific lamprey being captured by deepwater electrofishing was estimated experimentally at Eagle Creek National Fish Hatchery in October 2011. Fiberglass troughs were subdivided with wooden dividers into chambers (n=23) that fit the electrofisher snugly. Five to seven cm of sediment and then water were added to each chamber. A known number of larval Pacific lamprey were seeded into each chamber and allowed 24 hours to acclimate prior to electrofishing. Each chamber was seeded at an abundance of five or 10 individuals of one of two length classes (either <70 mm TL or >80 mm TL). All larvae in the experiment were collected by backpack electrofishing in North Fork Eagle Creek (Clackamas

River Basin, Oregon). To estimate capture probability, the deepwater electrofisher was lowered into each chamber and one drop was completed according to electrofishing methods in Jolley et al. (2012). Total catch (C_i) from the one drop was recorded for each chamber (i). After one drop was conducted in each chamber, sediment from all chambers was thoroughly examined to locate any non-captured individuals. For analysis, the number of individuals (A_i) in each chamber (i) was considered the total number captured by electrofishing and those located through sediment examination. It was suspected that the individuals seeded into chambers, but not captured or found, had escaped or were consumed by predators during the acclimation period; these larvae were removed from analysis. Capture probability (p_i) was estimated by logistic regression:

$$C_i \sim \text{Binomial}(A_i, p_i)$$

The logit link was used to evaluate the relationship between p_i and two categorical covariates (full model), density class: either $12 \cdot \text{m}^{-2}$ or $24 \cdot \text{m}^{-2}$ (i.e., 5 or 10 individuals) and length class: either less than 70 mm TL or greater than 80 mm TL:

$$\text{Logit}(p_i) = I + b_1[\text{Density class}] + b_2[\text{Length class}]$$

where b_1 and b_2 are slopes for the two categorical covariates (i.e., density class and length class, respectively) and I represents the intercept. We modeled capture probability as a function of all combinations of the two covariates (i.e., full and reduced candidate models; See Table 2). We evaluated the importance of the two covariates using the Akaike's Information Criterion (AIC) and the candidate model with the lowest AIC score (i.e., appropriate tradeoff between fit and complexity) was selected as the best model (Burnham and Anderson 2002).

Occupancy, density, and abundance estimation

We used modified zero-inflated N-mixture models to estimate occupancy and local abundance of larval Pacific lamprey and *Lampetra spp.* in tributary river mouths in the Columbia

River upstream of Bonneville Dam (Royle 2004). An N-mixture (or binomial mixture) model is a hierarchical Poisson regression model. These models usually incorporate spatially and temporally replicated (i.e., multiple sites and multiple surveys at those sites) counts of organisms to estimate two parameters: site-specific abundances and capture probability (Royle 2004; Kéry and Schaub 2012). Sites and surveys at sites are considered random interchangeable samples of the area as a whole. There is an ecological process to assess spatial variability in local abundance (i.e., across sites) and an observational process that usually uses replicate sites and surveys to estimate capture probability (Kéry and Schaub 2012). Failure to account for the observational process can bias estimates, trends, variability, and relationships (Kéry et al. 2009). Zero-inflated models assess the probability of occupancy, as well as abundance, given occupancy (Wenger and Freeman 2008). Similar to the zero-inflated N-mixture model described in Kéry and Schaub (2012), our model for each lamprey (i.e., Pacific lamprey and *Lampetra spp.*) had three hierarchical levels: 1) probability that a tributary river mouth (i) is occupied; 2) true abundance from one electrofishing drop (j) given that it is in an occupied tributary river mouth (i); and 3) observed count from one electrofishing drop (j) in each tributary river mouth (i) given the true abundance in that drop and capture probability. For the first level, unobserved potential occupancy in each tributary river mouth (z_i) was estimated by a Bernoulli distribution:

$$z_i \sim \text{Bernoulli}(\Omega)$$

Where Ω is the overall probability that a tributary mouth is occupied. For the second level, the unobserved true abundance ($N_{i,j}$) in a drop for each tributary river mouth (i) and each electrofishing drop (j) was estimated using a Poisson distribution:

$$N_{i,j} \sim \text{Poisson}(\gamma_{i,j})$$

Where $\gamma_{i,j}$ is effective abundance for that tributary mouth (i) and drop (j). The Poisson model is often appropriate for modelling biological count data. Each effective abundance is the product of the expected abundance ($\lambda_{i,j}$) for that tributary mouth (i) and drop (j) given that the tributary is occupied and the probability that the tributary mouth is occupied (i.e., z_i):

$$\gamma_{i,j} = z_i \times \lambda_{i,j}$$

To allow for greater differences in true abundance (i.e., $N_{i,j}$) among occupied tributary mouths (i) and drops (j) than expected by the Poisson model, we used the log link to incorporate overdispersion, or variability greater than expected by the Poisson model:

$$\text{Log}(\lambda_{i,j}) = \alpha + e_{i,j}$$

with log of expected local abundance (α), and added variability ($e_{i,j}$) by tributary river mouth (i) and drop (j) distributed according to a normal distribution with mean zero and variance σ^2 . An estimate of σ^2 close to zero suggests minimal overdispersion. Accounting for variability is important because abundance of larval lamprey varies at multiple spatial scales (Torgersen and Close 2004; Stone and Barndt 2005). Abundance could vary temporally (i.e., sampling occurred on different calendar days and in different years) or spatially as a result of factors at the tributary level (i.e., number of dams to pass) and drop level (i.e., presence of appropriate sediment for burrowing). For the third level, each count ($y_{i,j}$) from a tributary (i) and drop (j) was a function of the true abundance ($N_{i,j}$) and capture probability (p):

$$y_{i,j} \sim \text{Binomal}(N_{i,j}, p)$$

This level allows for non-100% detection associated with the sampling process (i.e., it accounts for the fact that some individuals within the perimeter of the electrofisher will not be collected during the drop; Kéry and Schaub 2012). Usually, repeated sampling in the same location (i.e., multiple drops at the same spot) is completed to estimate capture probability and it is assumed

that $N_{i,j}$ does not change between the repeated surveys. However, larval lamprey exhibit very patchy distributions even at small spatial scales (Torgersen and Close 2004) and because our collection and identification methods required that larvae be removed from sediments, it was not possible to insure $N_{i,j}$ remained constant over multiple drops even within a quadrat. Thus, we estimated capture probability (p) using data from the experimental approach described above:

$$C_i \sim \text{Binomial}(A_i, p)$$

All models were evaluated by Bayesian analysis methods using OpenBUGs software (Spiegelhalter et al. 2010). All priors were selected to be uninformative: for each capture probability experiment logistic regression model, the intercept and any slope values were each estimated from a normal distribution with a mean of zero and a variance of 1000; priors for N-mixture models are listed in Table 3. Capture probability evaluations included two initial chains run for 20 000 iterations, with 10 000 iterations removed as burn-in and the remaining 10 000 used to produce posterior distributions. Both N-mixture models (i.e., one for Pacific lamprey and one for *Lampetra* spp.) were also run with two initial chains, but for 100 000 iterations with 50 000 iterations removed as burn-in, and the remaining 50 000 iterations saved to produce posterior distributions for all examined parameters. We report the median of the posterior distribution as a measure of central tendency (i.e., as the expected value) and 2.5% and 97.5% values in the posterior distribution as 95% credible intervals to illustrate precision. We assessed that convergence had occurred and that parameters had reached stable distributions by visually examining history and density plots (Spiegelhalter et al. 2010; Kéry 2010).

To assess larval production in tributary river mouths, we produced density and abundance estimates. We estimated the densities (i.e., larvae $\cdot$ m⁻²) of larval Pacific lamprey and *Lampetra* spp. in each electrofishing drop as $N_{i,j}$ divided by the area sampled by one drop (i.e., 0.42 m²).

To estimate the average density in each tributary river mouth, we divided the calculated mean of all $N_{i,j}$ in that mouth by the area of a drop. To estimate total abundance in each tributary river mouth, we multiplied the estimated average density for that tributary river mouth by an estimate of total area for that mouth. Total area for each tributary river mouth was the product of the number of quadrats in the mouth and the total area of one quadrat (i.e., 900 m²).

Spatial distribution

We mapped spatial distribution and evaluated spatial overlap for Pacific lamprey and *Lampetra spp.* in the Wind and Klickitat river mouths. We examined these two river mouths because they were extensively sampled (Table 1; Fig. 2) and had both Pacific lamprey and *Lampetra spp.* We mapped spatial distribution by plotting the average density (i.e., larvae·m⁻²) for each sampled quadrat (all years combined) using ArcMap 9.3 (Environmental Systems Institute, Redlands, California). Similar to other studies (Worischka et al. 2012; Wuenschel et al. 2012), we evaluated spatial overlap using Schoener’s index of proportion similarity (O) for the Wind and Klickitat river mouths separately (Schoener 1970):

$$O = 1 - 0.5 \times \left(\sum_j^{quad} |p_{x,j} - p_{y,j}| \right)$$

Where $p_{x,j}$ and $p_{y,j}$ were the average proportions of Pacific lamprey and *Lampetra spp.* collected in each quadrat. Schoener’s index values greater or equal to 0.6 are generally considered to indicate biologically significant resource overlap (Wuenschel et al. 2012).

Results

We conducted 23 trials to estimate larval lamprey capture probability using the deepwater electrofisher (Table 2). Of the 170 Pacific lamprey seeded into chambers, 112 were captured by

electrofishing and 47 were found by manually sorting sediment following the experiment; thus, 11 (of the 170) larvae were assumed to have escaped or be consumed by predators and were removed from analysis of capture probability. The capture probability model with the lowest AIC score did not include either measured covariate, although AIC scores for all models were relatively similar, suggesting some support for all models, especially the two top models since the ΔAIC for those were less than 2.0 (Table 2; Burnham and Anderson 2002). The full model, including a term for both length and density class had the highest ΔAIC score (i.e., lowest ranked model). For the full model, 95% credible intervals on coefficients for both length class and density class overlapped zero. Although a minimal decrease in capture probability was observed with higher density and larger size, our results suggest no substantial relationship (Table 2).

Including no covariates, capture probability (p) was estimated to be 0.70 (95%: 0.63 – 0.77).

We conducted 813 electrofishing drops in tributary river mouths, sampling 341 m² of sediment. In total, 145 collected larvae were identified as Pacific lamprey and 115 larvae were identified as *Lampetra spp.* In addition, 18 small larval lamprey (typically <20 mm TL) were observed to be lost through the mesh in the collection basket and thus were not identified. These individuals were not included in analyses. Larval Pacific lamprey ranged in size from 18 mm to 136 mm TL with 87% between 20 and 80 mm TL and a peak of 38% between 30 and 40 mm TL (Fig. 3). *Lampetra spp.* ranged in size from 14 to 152 mm TL with 85% between 20 and 90 mm TL and no distinct peak observed (Fig. 3).

Pacific lamprey were found in tributary river mouths of Bonneville, The Dalles, and John Day reservoirs (Table 4; Fig. 1). Pacific lamprey were detected in 7 of 10 sampled tributary river mouths and the probability of occupancy for a tributary river mouth was estimated to be 0.70 (95%: 0.41 – 0.93). For river mouths in which no Pacific lamprey were collected, estimated

probabilities of occupancy were 0.11. Larval Pacific lamprey were collected at depths ranging from 0.6 to 8.5 m. Estimated larval densities varied both within and among tributary river mouths and the 95% credible interval on variance (σ^2) did not include zero, indicating heterogeneity (Table 3). Estimated average densities in occupied river mouths ranged from $0.18 \cdot \text{m}^{-2}$ to $1.72 \cdot \text{m}^{-2}$; however, in five of seven occupied river mouths, estimated densities were $0.18 \cdot \text{m}^{-2}$ to $0.26 \cdot \text{m}^{-2}$ (Table 4). The maximum estimated density from a drop was 33.33 (95%: 23.81 – 47.62) larvae $\cdot \text{m}^{-2}$. For tributary river mouths determined to be occupied by Pacific lamprey, larval abundance ranged from 11 530 (95%: 7689 – 23 070) in the John Day River mouth to 556 600 (95%: 448 700 – 651 600) in the Klickitat River mouth (Table 4).

Lampetra spp. were collected from all five sampled tributary river mouths to Bonneville Reservoir and none upstream of The Dalles Dam (Table 4; Fig. 1). The mean probability of tributary river mouth occupancy was 0.51 (95%: 0.24 – 0.78). The model suggested very small probabilities of potential occupancy for tributary river mouths in which no *Lampetra spp.* were collected; the probability was lower for the Deschutes River (<0.01) which was sampled by 72 drops, than for all other tributaries in which no individuals were collected (0.03) since those were sampled by 34 drops (Table 4). Larval *Lampetra spp.* were collected at depths of 0.3 to 8.5 m. Similar to Pacific lamprey, the 95% credible interval on variance (σ^2) was substantially above zero, suggesting higher variability in drop counts than expected by the Poisson model (Table 3). Average estimated density in an occupied tributary river mouth was $0.24 - 1.72 \cdot \text{m}^{-2}$ (Table 4). Similar to Pacific lamprey, maximum average density was $1.72 \cdot \text{m}^{-2}$, but in most river mouths average densities were lower (Table 4). For both lamprey species, average densities in tributary river mouths were most commonly $0.2 - 0.3 \cdot \text{m}^{-2}$ (Table 4). The maximum estimated density of *Lampetra spp.* observed from a drop was 38.10 (95%: 28.57 – 54.76) larvae $\cdot \text{m}^{-2}$. For tributary

river mouths known to be occupied, abundance of *Lampetra spp.* ranged from 95 030 (95%: 67 880 – 131 200) in the mouth of the Klickitat River to 544 800 (95%: 477 300 – 634 900) in the mouth of the Wind River (Table 4).

Pacific lamprey and *Lampetra spp.* overlapped spatially, although the highest densities and abundances were found in different tributary river mouths (Table 4). Density and abundance were highest for Pacific lamprey in the Klickitat River mouth, whereas they were highest for *Lampetra spp.* in the Wind River mouth, although both lampreys were found in both systems (Table 4). A total of 83 of the 338 drops completed in the Klickitat and Wind river mouths combined contained at least one lamprey and 26 of those 83 occupied drops (31%) contained at least one individual of both species. Thus, nearly a third of the occupied drops in the Klickitat and Wind river mouths contained both species of lamprey, suggesting spatial overlap, at least at the scale of a drop. For both lampreys, quadrats with high densities appeared to correspond to areas in the river mouth that were more directly impacted by discharge from the tributary river (Fig. 4). While distribution overlapped in both tributary river mouths, areas of highest density differed somewhat (Fig. 4). Schoener's index of proportion similarity (O) was 0.41 in the Klickitat River mouth and 0.58 in the Wind River mouth indicating similarity in spatial resource use, but suggesting that overlap may not be biologically significant (i.e., both were <0.6).

Discussion

We produced the first estimates of density and abundance of larval Pacific lamprey and *Lampetra spp.* in tributary river mouths in an impounded river. In most occupied river mouths, average densities were 0.2 to $0.3 \cdot \text{m}^{-2}$, although in some river mouths average densities were much higher (up to $1.72 \cdot \text{m}^{-2}$) and there was considerable variability. Average and maximum

larval densities in river mouths appear generally lower than those within streams (Ojutkangas et al. 1995; Torgersen and Close 2004; Stone and Barndt 2005), which may be a function of distance from spawning areas, habitat quantity or quality, or sampling differences. Todd and Kelso (1993) observed larval *Geotria australis* in New Zealand freshwater streams from headwaters to sea, but noted that a higher percentage were collected from small tributaries (<10 m wide) as compared to larger downstream channels (>20 m wide). Some small larvae (i.e., <20 mm TL) escaped our collection basket, which would bias our density and abundance estimates low. Despite potential differences in density in different freshwater environments, we collected larval lampreys at depths up to 8.5 m and our estimates illustrate considerable rearing in deepwater tributary river mouths upstream of dams in the Columbia River Basin, suggesting the potential importance of these areas to population status and conservation.

In addition to density and abundance, we estimated the probability that a tributary river mouth was occupied, if no larvae were collected. This is particularly important for Pacific lamprey, since status is currently more commonly assessed by distribution, rather than by abundance (Jolley et al. 2012; Dunham et al. 2013; Reid and Goodman 2015). Our results suggest that the probability of occupancy in river mouths in which no Pacific lamprey were detected would be fairly low at 0.11 with 34 drops. For *Lampetra spp.*, the probability of occupancy where no larvae were collected was even lower at 0.03 with 34 drops. Although both Pacific lamprey and *Lampetra spp.* have been found upstream of McNary Dam (Moser and Close 2003; Grote et al. 2014; Meeuwig et al. 2005), we did not find any Pacific lamprey in river mouths in McNary Reservoir and we collected no *Lampetra spp.* upstream of The Dalles Dam. Reduced occupancy in upstream areas may partially be a function of impeded adult migration at dams for the anadromous Pacific lamprey and western river lamprey (Moser et al. 2002).

Western river lamprey can be common in estuaries (Vladykov and Follett 1958; Weitkamp et al. 2015), but records from upstream of Bonneville Dam are scarce (Vladykov and Follett 1958; Jolley et al. 2016). Western brook lamprey are not highly migratory (Moser et al. 2015a) and there may be multiple highly localized riverine populations in the Columbia River Basin that may not use tributary river mouths (USFWS unpublished data).

Although considerable spatial overlap occurred, there were differences in distribution of Pacific lamprey and *Lampetra spp.* within and among occupied tributary river mouths. Adult spawning site selection may affect large-scale larval distribution; thus, variation among river mouths may result from differences in spawning habitat preferences and migration patterns (especially anadromous vs. resident). Generally, western brook lamprey produce smaller redds in areas characterized by shallower depths, slower water velocities, and smaller substrates, as compared to Pacific lamprey, which are much larger in size as adults (Stone 2006; Gunckel et al. 2009; Hayes et al. 2013). Spatial distribution patterns could also result from dissimilarities in larval habitat preferences as suggested by Taverny et al. (2012) for *Petromyzon* and *Lampetra*; although, various species of larval lamprey appear to prefer fine sand for burrowing (Stone and Barndt 2005; Sugiyama and Goto 2002; Smith et al. 2011; Ferreira et al. 2013). We observed spatial overlap in the Klickitat and Wind river mouths; however, average densities were different and Schoener's index values were not greater than 0.6 (although 0.58 in the Wind River) potentially indicating that the spatial resource overlap was not biologically significant. Perhaps, habitat preferences for larvae affect distribution at a small scale (such as in a drop) and adult behaviors affect distribution at a larger scale (such as in a tributary unit).

To appropriately estimate density and abundance from count data, it is essential to correctly account for the capture probability of an individual (Kéry et al. 2009). Often, capture

probability is estimated in an N-mixture model by the pattern of counts collected by multiple surveys at multiple sites (Kéry and Schaub 2012); however, our sampling methods and larval lamprey biology made it impossible for us to ensure that we could sample the same individuals during multiple surveys in the wild (i.e., it was impossible to assume closure). As a result, we estimated capture probability experimentally. Closure may be impossible in some studies, especially when the target species must be captured (or handled) to confidentially identify or is highly mobile; thus, estimating capture probability experimentally can make abundance estimation by N-mixture model analysis possible. We estimated capture probability to be 0.70 (95% credible interval: 0.63 – 0.77), which is only slightly lower than the 0.75 (95% confidence interval: 0.63 – 0.93) estimated by Bergstedt and Genovese (1994) using the same electrofishing method to collect sea lamprey. Small differences in capture probability between the two studies may be a result of differences between species, estimation methods, or experimental settings. Our estimates were made in relatively cold, low conductivity water, which may lower the response rate of larval lampreys to electric stimuli (Bowen et al. 2003). However, expected values were generally similar and intervals overlapped among the two studies, corroborating results from both studies. Deepwater electrofishing capture probability for larval lampreys appears high, which is beneficial since higher capture probability can result in increased accuracy and precision of abundance estimates from N-mixture models (Veech et al. 2016). Recent experimental work suggests that larval Pacific lamprey burrow close to the sediment surface (Liedtke et al. 2015); thus, it is likely that most, if not all, burrowed individuals are available for capture by deepwater electrofishing.

If capture probability is substantially impacted by environmental or individual covariates, estimates of length distribution and density could be biased (Breton et al. 2013; Veech et al.

2016). In our experiments, the selected capture probability model did not include either larval length or density as a covariate. However, Bergstedt and Genovese (1994) modeled length as a continuous parameter and found that capture probability decreased as size increased for larval sea lamprey and our experimental results illustrated some support for a capture probability model that included larval length. Our selected model may not have included larval length due to small sample sizes or because we recorded length as a categorical variable instead of a continuous variable. Similar to other types of electrofishing (Millar et al. 2016), capture probability of the deepwater electrofisher could be impacted by local environmental factors such as water conductivity, temperature, and depth, as well as sediment type. Research to examine deepwater electrofishing capture probability as a function of local environmental parameters would be valuable. Incorporating environmentally-based estimates of capture probability would improve estimates of density and abundance.

Our research suggests that evaluating catch data from a deepwater electrofisher using an N-mixture model is an effective method for estimating abundance of larval lampreys. Data for N-mixture models are counts (which are often sparse) from multiple sites (Royle 2004). These models assume that abundance at each site is an independent random variable from a distribution, such as the Poisson distribution. These models incorporate capture probability, so counts are scaled up to estimate abundance (Kéry and Schaub 2012). N-mixture models generally produce accurate and precise estimates of abundance when capture probability is above 0.5 (Veech et al. 2016), as it appears to be for larval lampreys collected by a deepwater electrofisher. Other techniques to estimate abundance, such as mark-recapture and distance sampling (Williams et al. 2002), are logistically difficult to implement for larval lampreys in large, open systems such as tributary river mouths; in contrast, collecting count data by

deepwater electrofishing is feasible (Jolley et al. 2012). Assessing periodic trends or how environmental factors may impact occupancy and density could be evaluated with only minimal changes to the model structure (Wenger and Freeman 2008; Kéry et al. 2009), although such analyses would require additional sampling effort.

Our results quantify considerable use of upstream tributary river mouths for rearing, but the extent to which these areas currently contribute to the Pacific lamprey population across its range is still unclear. Once upstream of impediments in the Columbia River Basin, adult Pacific lamprey can migrate up to hundreds of river kilometres before spawning (McIlraith et al. 2015). However, research is still required to assess the contribution of larvae reared upstream of impediments because mortality rates may be higher there, particularly during emigration periods, than for individuals spawned downstream of dams. We also do not know how larval growth and survival rates in these deeper-water tributary river mouths compare to those in wadeable streams; however, recent work in the Great Lakes suggests that larval sea lamprey exhibit slower growth, but slightly higher survival, in lentic areas as opposed to streams (Johnson et al. *In Press*). Since Pacific lamprey and western river lamprey are anadromous, connectivity within rivers is vital. Our study illustrated the value of using count data from deepwater electrofishing analyzed by N-mixture models to estimate density and abundance of larval lampreys and provided abundance estimates for tributary river mouths upstream of dams. In combination with our results, additional studies similar to Keefer et al. (2013) to evaluate downstream passage efficiency and passage limitations at dams in the Columbia River would help assess the actual and potential contribution of larvae reared in upstream tributary river mouths to the conservation of Pacific lamprey across the species range.

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Table 1. Stream order at the mouth (at the 1:100 000 scale), river kilometre (“Rkm”) for the Columbia River, and estimated total area (in m²) of each mouth, as well as the number of quadrats sampled (i.e., number of drops completed) during each year (labelled by the year) for each tributary river mouth in the Columbia River basin upstream of Bonneville Dam sampled by deepwater electrofishing.

Reservoir	Tributary name	Stream order	Rkm	Area	2011	2012	2013	2014	2015
Bonneville	Wind River	5	249	317 700	32	34	102		
	Little White Salmon River	4	262	346 500			34		
	White Salmon River	5	269	380 700		34	34		
	Hood River	5	273	462 600	34		35		
	Klickitat River	5	290	323 100	34	34	102		
The Dalles	Deschutes River	6	330	380 700		38	34		
John Day	John Day River	6	352	54 900				34	
	Umatilla River	6	466	397 800				34	
McNary	Walla Walla River	6	506	588 600					34
	Yakima River	7	539	432 900				23	11

Note: Locations of all tributary river mouths are in Fig. 1.

Table 2. Experiment information and model selection to estimate capture probability of larval Pacific lamprey using deepwater electrofishing: A) number of trials, average ambient water conductivity and temperature (with ranges), and expected proportions captured (with 95% credible intervals) as estimated by the full model, by density in the chamber (i.e., five or 10 larvae) and total length class; and B) number of parameters (k) and Akaike's Information Criterion (AIC) results for all examined capture probability models (Δ AIC indicates the difference in AIC between the listed model and the model with the lowest AIC value).

A)

Length (mm)	Density (m ⁻²)	# of trials	Ambient conductivity (μ S cm ⁻¹)	Temperature (°C)	Proportion captured
<70	12	6	34.3 (32.3 – 37.7)	7.5 (7.2 – 7.6)	0.77 (0.63 – 0.87)
<70	24	5	34.9 (34.3 – 35.6)	8.7 (8.6 – 8.8)	0.74 (0.62 – 0.84)
>80	12	6	33.4 (33.1 – 34.3)	10.0 (9.9 – 10.2)	0.69 (0.53 – 0.82)
>80	24	6	34.5 (33.1 – 36.1)	10.9 (10.8 – 11.1)	0.66 (0.54 – 0.76)

B)

Model	Estimated parameters	Mean of deviance	k	AIC	Δ AIC
No covariates	I	72.25	1	74.25	0
Length class	I, b_2	71.48	2	75.48	1.23
Density class	I, b_1	73.11	2	77.11	2.86
Full model	I, b_1, b_2	72.39	3	78.39	4.14

Table 3. Prior distributions and posterior estimates (with 95% credible intervals) for the N-mixture models to estimate density and total abundance of larval Pacific lamprey and *Lampetra spp.* in tributary river mouths to the impounded portion of the Columbia River basin including the probability of occupancy (Ω), log of expected local abundance (α), variance on local abundance as a function of differences in tributary river mouth and drop (σ^2), and capture probability as estimated by an experimental approach (p).

Parameter	Prior Distribution	Pacific lamprey	<i>Lampetra spp.</i>
Ω	Uniform (0,1)	0.70 (0.41 – 0.93)	0.51 (0.24 – 0.78)
α	Normal(0,10 ³)	-4.21 (-5.48 – -3.42)	-3.54 (-4.56 – -2.80)
σ^2	Uniform (0,10)	2.71 (2.21 – 3.48)	2.31 (1.83 – 2.96)
p	Uniform (0,1)	0.70 (0.63 – 0.77)	

Table 4. Estimates of occupancy probability, density, and abundance of Pacific lamprey (upper panel) and *Lampetra spp.* (lower panel) in tributary river mouths to the Columbia River, Oregon and Washington, Bonneville Reservoir to McNary Reservoir.

Pacific lamprey

Tributary name	Occupancy probability	# of larvae	# of drops	Density (m ⁻²)	Abundance
Wind River	1	40	168	0.79 (0.67 – 0.96)	252 100 (211 600 – 306 200)
Little White Salmon River	0.11	0	34	0.00 (0.00 – 0.07)	0 (0 – 24 260)
White Salmon River	1	3	68	0.18 (0.11 – 0.35)	66 650 (39 990 – 133 300)
Hood River	1	4	69	0.21 (0.14 – 0.38)	95 780 (63 850 – 175 600)
Klickitat River	1	89	170	1.72 (1.51 – 2.02)	556 600 (488 700 – 651 600)
Deschutes River	1	5	72	0.26 (0.17 – 0.46)	100 700 (62 950 – 176 300)
John Day River	1	2	34	0.21 (0.14 – 0.42)	11 530 (7 689 – 23 070)
Umatilla River	1	2	34	0.21 (0.14 – 0.42)	83 570 (55 710 – 167 100)
Walla Walla River	0.11	0	34	0.00 (0.00 – 0.07)	0 (0 – 41 220)
Yakima River	0.11	0	34	0.00 (0.00 – 0.07)	0 (0 – 30 320)

Table 4 Continued

Lampetra spp.

Tributary name	Occupancy probability	# of larvae	# of drops	Density (m ⁻²)	Abundance
Wind River	1	89	168	1.72 (1.50 – 2.00)	544 800 (477 300 – 634 900)
Little White Salmon River	1	4	34	0.42 (0.28 – 0.70)	145 600 (97 060 – 242 600)
White Salmon River	1	5	68	0.28 (0.18 – 0.46)	106 600 (66 650 – 173 300)
Hood River	1	4	69	0.24 (0.14 – 0.41)	111 700 (63 850 – 191 600)
Klickitat River	1	13	170	0.29 (0.21 – 0.41)	95 030 (67 880 – 131 200)
Deschutes River	<0.01	0	72	0.00 (0.00 – 0.00)	0 (0 – 0)
John Day River	0.03	0	34	0.00 (0.00 – 0.00)	0 (0 – 0)
Umatilla River	0.03	0	34	0.00 (0.00 – 0.00)	0 (0 – 0)
Walla Walla River	0.03	0	34	0.00 (0.00 – 0.00)	0 (0 – 0)
Yakima River	0.03	0	34	0.00 (0.00 – 0.00)	0 (0 – 0)

Note: “# of larvae” is the total number of larval lamprey collected in that tributary river mouth and “# of drops” is the total number of quadrats sampled by a drop in that tributary river mouth.

Fig.1. Map of study area in the Columbia River Basin, Washington (WA) and Oregon (OR). The location of each tributary river sampled is shown and indicated (“LWS” = Little White Salmon, “WS” = White Salmon, and “Walla” = Walla Walla) and the location of each dam is indicated by a diamond and letter (“B” = Bonneville, “D” = The Dalles, “J” = John Day, and “M” = McNary).

Fig 2. Number of drops completed in each quad (quad located at white circle center) in the Wind (left panel) and Klickitat (right panel) river mouths.

Fig.3. Total length distribution for Pacific lamprey and *Lampetra* spp. collected in tributary river mouths in the Columbia River basin.

Fig. 4. Average density (m^{-2}) for Pacific lamprey (upper panels) and *Lampetra* spp. (lower panels) estimated by N-mixture models incorporating experimentally-derived estimates of capture probability in the Wind (left panels) and Klickitat (right panels) river mouths.