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SPECIAL SECTION

Native Lampreys: Research and Conservation of Ancient Fishes

Patterns in distribution and density of larval lampreys in the main-stem Columbia River, Washington–Oregon

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Abstract

Objective: This study compiled data sets from multiple research efforts from 2010 to 2018 to describe patterns in the presence and density of larval lampreys in deep water habitats across 430 river kilometers of the lower and middle main-stem Columbia River.

Methods: We used logistic regression to evaluate the influence of landscape-level factors on Pacific Lamprey *Enthosphenus tridentatus* and *Lampetra* spp. presence. Additionally, we used *N*-mixture models to estimate larval lamprey densities in six river mouths in the spring and fall of multiple years.

Result: At the landscape-level, the models suggested that the probability of presence for both Pacific Lampreys and *Lampetra* spp. decreased with increasing distance from the ocean, distance from the closest upstream tributary river mouth, and distance from the nearest main-stem riverbank. The probability of presence also varied by upstream tributary river mouth. The probability of larval presence in river mouths was an order of magnitude greater than in reservoir pools. Evaluating river mouth habitats, larval lamprey densities varied seasonally, annually, and among river mouths, ranging from 0.04 to 9.63 larvae/m^2. Results generally suggested broader distributions and higher densities within river mouths during spring when flows were high compared to the fall when flows were lower, although not in all river mouths or across all years. Larval densities increased in the Wind and Klickitat rivers (the most consistently examined tributary river mouths) over the study period.

Conclusion: Our findings suggest that the main-stem Columbia River supports larval lamprey rearing year-round. Probability of presence was highest and variable among river mouths, suggesting the importance of some river mouths as rearing habitats. Understanding shifts (seasonal, annual, and those as result of changes in environmental conditions) in lamprey presence and density could inform how specific management actions (e.g., dewatering for in-river work) and their timing could affect larval lampreys in rivers.

KEYWORDS

distribution, lampreys, large rivers, reservoir

INTRODUCTION

Impact statement

This research demonstrated that the main-stem river habitats provide year-round rearing for lampreys and tributary river mouth habitats are of particular importance. Understanding changes in seasonal and annual shifts in populations could inform management and conservation actions for lampreys in large rivers systems.

Native lamprey populations have declined worldwide (Renaud 1997, 2011; Maitland et al. 2015). Many anthropogenic factors have contributed to these declines, including decreased quality and quantity of larval rearing habitat, increased fragmentation of habitat, and passage barriers within migration corridors (Clemens et al. 2017, 2021). In the Columbia River basin, declines in the Pacific Lamprey *Entosphenus tridentatus* have generated conservation concerns (Close et al. 2002; Columbia River Inter-Tribal Fish Commission 2011; Luzier et al. 2011; Wang and Schaller 2015). Pacific Lamprey are culturally significant to many Native American tribes and are harvested in subsistence fisheries and used for spiritual and medicinal purposes (Close et al. 2002; Miller 2012). Pacific Lamprey and other native lampreys also provide ecological benefits in both freshwater and marine environments. Notably, lampreys improve habitat conditions for other species by filter feeding and burrowing in the benthos as larvae (Shirakawa et al. 2013; Boeker and Geist 2016; Nika et al. 2021) and by nest building and serving as a source of marine-derived nutrients as adults (Close et al. 2002; Hogg et al. 2014; Dunkle et al. 2020; Georgakakos 2020). Lampreys also serve as prey for numerous species throughout their life cycle (Beamish 1980; Cochran 2009; Riemer et al. 2011; Clemens et al. 2019; Arakawa and Lampman 2020; Dunkle et al. 2020).

Lampreys exhibit diverse life history strategies and occupy various habitats over the course of their lives. Larval lampreys rear in the fine benthos of small- and medium-sized streams for up to 10 years (Dawson et al. 2015; Docker and Potter 2019; Hess et al. 2022). As larvae, lampreys filter detritus and algae out of the water column (Moore and Mallatt 1980; Sutton and Bowen 1994; Evans et al. 2019) and usually disperse downstream, commonly with high flows (Potter 1980; Moser et al. 2015; Zvezdin et al. 2022). Anadromous lampreys transform from larvae into ectoparasitic juveniles and then migrate to the ocean to feed on host fishes and whales (Dawson et al. 2015; Clemens et al. 2019). Although the duration of ocean residence is not well known and may vary among lamprey species and individuals, it is thought that Pacific Lamprey reside in the ocean for several years (Beamish 1980; Hess et al. 2022; Weitkamp et al. 2023, this special section). Resident nonparasitic lampreys transform directly from larvae into adults. Adults typically build their nests in gravels and cobbles (Stone 2006; Gunckel et al. 2009) and die after spawning (Renaud 2011; Johnson et al. 2015). Both resident and anadromous lampreys require specific habitats throughout their life cycle, and connectivity between these habitats is essential.

In the Columbia River basin, large, main-stem hydropower dams and their operations have altered and reduced connectivity among habitats, which has negatively impacted native lampreys (Close et al. 2002; Kostow 2002; Clemens et al. 2017; Wicks-Arshack et al. 2018). The management of the hydrosystem (e.g., spill) has altered historical hydrologic patterns, changed the timing and magnitude of flow from runoff, transitioned fluvial habitat into reservoirs, increased out-migration travel times, and dramatically reduced longitudinal and lateral aquatic connectivity for native fishes (McCoy et al. 2018). Water levels over larval rearing habitats within reservoirs of the Columbia River can fluctuate daily and become dewatered (McMichael et al. 2005; Liedtke et al. 2015; Mueller et al. 2015). These fluctuations are driven by hydroelectric power generation, navigational requirements, and other hydrosystem operations, which are designed in part to facilitate the downstream passage of juvenile salmonids. These fluctuations can be particularly impactful on shallow-water delta habitats that form at tributary river mouths. The river mouth deltas are lower energy environments where fine sediment settles out, making them areas of potentially high-quality larval lamprey habitat. Additionally, maintenance of navigation channels through dredging activities can alter the benthos at both at the dredging and instream disposal locations, thus posing a threat to burrowed larval lampreys (Luzier et al. 2011; Maitland et al. 2015; Clemens et al. 2021). The Columbia River has the potential to provide extensive rearing habitat for larval lampreys; thus, an understanding of larval lamprey utilization of these main-stem environments across time is needed.

Studies to assess the distribution and density of native larval lampreys have mainly been completed using backpack electrofishing methods (Clemens et al. 2022). Due to limitations of the sampling method, studies have generally been restricted to wadeable habitats. However, Bergstedt and Genovese (1994) developed a boat-mounted electrofisher for sampling larval Sea Lamprey *Petromyzon marinus* in larger systems with deepwater habitats. From 2010 to 2018 (no sampling in 2017), multiple studies on larval lamprey biology and distribution were conducted using a deepwater electrofisher in over 430 river kilometers (rkm) of the lower and middle main-stem Columbia River. Temporal sampling in these studies ranged from March to November. Results from some but not all of these studies have been published (Jolley et al. 2011, 2014, 2016; Harris and Jolley 2017); however, they have not been fully compiled or evaluated for landscape-scale patterns across space or any patterns across time. Additionally, data collected in 2018 have not previously been reported. Our objective was to compile these studies into one long-term data set and use that data set to assess spatial and temporal patterns in the presence and density of larval lampreys within riverine and reservoir habitats in the lower and middle Columbia River. Our study describes the basic life history of larval lampreys in deep and shallow habitats in a large-river environment and explores how distribution patterns may be affected by natural seasonal patterns and hydrosystem management, which could be used to aid the conservation of native lampreys.

METHODS

Study area

The study area spans 430 rkm of the lower and middle Columbia River from the Kalama River mouth (rkm 117) to upstream of the Yakima River mouth (rkm 547; Figure 1). This section of the river contains four hydropower dams and their respective reservoirs: Bonneville Dam (rkm 235), The Dalles Dam (rkm 308), John Day Dam (rkm 347), and McNary Dam (rkm 470; Figure 1). Sampling was conducted in two main-stem habitats: tributary river mouths (hereafter, "river mouths") and main-stem reservoir pool sites (hereafter, "pools"). The river was discretized into 30- × 30-m quadrats in both river mouths and pools by using ArcGIS version 10.1 (Esri 2012; Figure 2). Quadrats to be sampled were selected using a generalized random tessellation stratified (GRTS) approach to ensure that surveys provided an unbiased representation of the study area (Stevens and Olsen 2004). At 14 river mouths, the sampled area was defined by a semicircle with a 500-m radius, centered where the mid-channel of the tributary intersected the Columbia River based on orthophotography and encompassing the wetted area within the main-stem Columbia River (Figure 2A). For the pools, a grid was overlaid on the main-stem river National Hydrography Dataset layer from rkm 235 to rkm 547 (U.S. Geological Survey 2006; Figure 2B).

The specific objectives of the various discrete projects dictated sampling locations and time frames, but all sampling occurred between March and November in 2010–2018. No sampling was conducted in 2017 (Table 1). Quadrat samples were collected at both river mouths and pools during 2011–2015 and at only river mouths in 2016 and 2018 (Table 1). In some locations, repeated sampling events (hereafter, "site visits") were made. Most of the site visits were completed over two consecutive days, but due

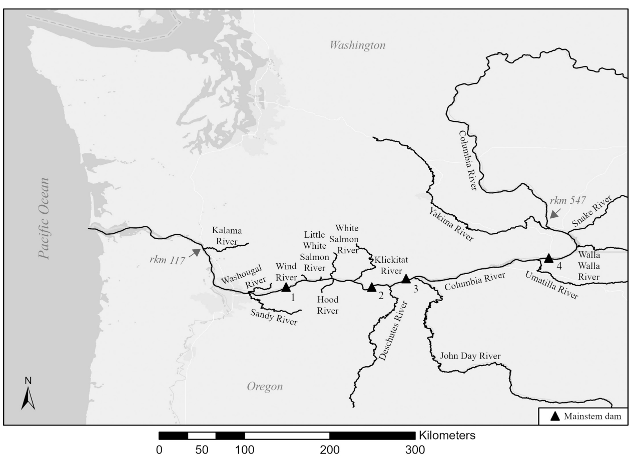

FIGURE 1 Map of the study area in Washington and Oregon. Data collection began at river kilometer (rkm) 117 on the Columbia River, continuing upstream to rkm 547. Tributaries where river mouth surveys were conducted at the confluence with the Columbia River are labeled. Four main-stem hydroelectric dams within the project site are labeled (black triangles with numbers): (1) Bonneville Dam (rkm 235), (2) The Dalles Dam (rkm 308), (3) John Day Dam (rkm 347), and (4) McNary Dam (rkm 470).

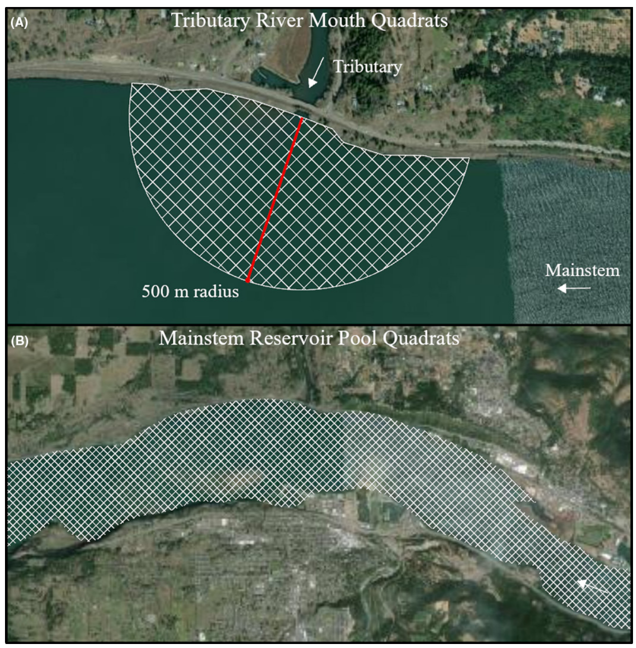

FIGURE 2 Example diagram of 30- × 30-m grid layout for (A) tributary river mouth quadrats and (B) main-stem reservoir pool quadrats in the Columbia River. Random quadrats within the grids were selected for lamprey sampling using a generalized random tessellation stratification approach to ensure unbiased and spatially balanced representation within the study area.

TABLE 1 Summary of lamprey sampling efforts compiled across multiple projects that were included in this synthesis. Reservoir pool sites were sampled from 2010 to 2015; river mouth sites were sampled from 2010 to 2018 (sampling was not conducted in 2017).

Year	River mouth site visits	River mouth quadrats	Reservoir pool quadrats	Total quadrats sampled
2010	1	6	110	116
2011	4	133	31	164
2012	4	140	33	173
2013	6	342	67	409
2014	3	66	196	262
2015	2	46	207	253
2016	6	200	–	200
2018	12	424	–	424
Total	38	1357	644	2001

to the dynamic weather conditions in this area, a single site visit could occur over several days. For example, a total of 286 quadrats in the Klickitat River mouth were sampled over six different site visits, which occurred over the course of 8 years (2011–2018). In other locations, quadrats were sampled only during a single site visit. For example, the John Day River mouth was only sampled during the late summer of 2014, resulting in 40 quadrats sampled.

Sampling was conducted across variable water conditions and at various river discharge levels in the tributaries and main-stem Columbia River. The hydrology within the tributaries was characterized by high discharge in the winter and spring, associated with individual winter storms and spring snowmelt runoff (hereafter, "high-flow periods"). Low-discharge conditions occurred in late summer and early fall, typically August and September (hereafter, "low-flow periods"). River mouths in higher elevation watersheds, such as the Hood and Klickitat rivers, typically have high-flow conditions extending later into the spring, corresponding with snowmelt, as compared to river mouths in lower elevation watersheds like the Kalama and Washougal rivers. Hydrologic patterns in the main-stem Columbia River are influenced by similar annual high spring flows due to precipitation and snowmelt, with peak flows typically occurring in May and June. Additionally, changes in discharge within the regulated reaches of the main stem are dictated by seasonal water management actions, including spill (to assist juvenile salmonid downstream migration) and daily hydroelectric power demand. These demands result in largely consistent river levels throughout the year, except for peak streamflows in the spring. However, demands also result in rapid changes to water levels at hourly and daily time scales. Areas downstream of Bonneville Dam experience twice-daily fluctuations due to tides.

Field sampling

Each 30- × 30-m quadrat that was selected via GRTS was sampled once using a boat-mounted deepwater electrofishing unit, which was described in detail by Bergstedt and Genovese (1994). The boat navigated to the quadrat coordinates and idled in place. The 0.65-m^2 fiberglass suction bell, with the attached cathode and anode, was lowered to sit flush with the riverbed. The electrofishing unit delivered direct current at a rate of 3 pulses/s with a 10% duty cycle and a 2:2 burst pulse train (two pulses on, followed by two pulses off). The voltage was adjusted at each quadrat to maintain a peak voltage gradient of 0.6–0.8 V/cm between the electrodes. Concurrent with shocking, a hydraulic eductor provided suction and prevented the larval lampreys from being conveyed through the pump. Larvae were suctioned up through a hose as they emerged from the sediment under the bell and were deposited in a collection basket on the boat. Shocking was performed for 60 s, and suction continued for an additional 60 s to ensure that the hose was cleared of lampreys. Samples were collected in quadrats with water depths between 0.2 and 14.3 m (median = 1.8 m). At the time of sampling, if the quadrat was located where the water depth was >21 m, then the quadrat was not sampled due to pump limitations and the next sequential GRTS-selected quadrat was sampled instead. Likewise, if the GRTS-selected quadrat was on an area that was dry during the site visit, that quadrat was not sampled and the next sequential GRTS-selected quadrat was sampled instead.

After collection, larvae were anesthetized in a tricaine methanesulfonate solution buffered with sodium bicarbonate. All lampreys were measured for total length (TL), and larvae greater than 65 mm were identified either as Pacific Lamprey or as *Lampetra* spp. based on tail morphological characteristics (Goodman et al. 2009; Docker et al. 2016). In the Columbia River, *Lampetra* spp. include the Western River Lamprey *L. ayresii* and Western Brook Lamprey *L. richardsoni*, which are not genetically distinct (Carim et al. 2023), and the Pacific Brook Lamprey *L. pacifica*, which appears to be currently limited to the Willamette River basin (Reid et al. 2011; Carim et al. 2023) and thus was outside our study area. Like Pacific Lamprey, Western River Lamprey are anadromous (Weitkamp et al. 2015, 2023). Tissue was sampled from a subset of larvae for future genetic confirmation of morphological identification. After data collection, larvae were allowed to recover and were released near the point of capture.

Landscape characteristics

Landscape characteristics derived using ArcGIS for each quadrat location included distance from the ocean, distance from the closest tributary, and distance from the nearest riverbank ("bank"). Distance from the ocean (O_i), measured in kilometers, was derived as the shortest distance between the quadrat and the middle of the river where the Columbia River meets the Pacific Ocean (rkm 0). The distance (m) from the closest tributary river mouth (T_i) was measured from the quadrat to the midpoint of the tributary river's confluence with the Columbia River. For river mouth sampling, the closest river mouth was the specific river mouth from which the sample was collected; however, for pool samples, the nearest river mouth was the closest upstream tributary river on the same side of the river or reservoir. Distance from the nearest main-stem bank (B_i) was derived using a water surface polygon representing the transition from riverine habitat to riparian or upland habitat. The shortest distance to the nearest edge of the polygon from the quadrat was calculated as the distance to the bank. This value represents a consistent distance to the riverbank and not the distance to the water's edge at the time of sampling.

For both Pacific Lamprey and *Lampetra* spp., we examined models including only a linear term (i.e., β_B) and models including both a linear term (β_B) and a quadratic term (β_{B^2}) for distance from the nearest bank. Including a quadratic term allowed us to evaluate whether presence was highest at an intermediate distance from the bank; areas closest to the bank would potentially be closer to tributary sources but would also experience a higher probability of dewatering due to changes in flow and water management in the Columbia River. Regular and prolonged dewatering could result in lower densities or absence of larval lampreys in these nearshore habitats.

Analysis methods

For our first analysis, we used logistic regression to examine the presence of larval Pacific Lamprey and larval *Lampetra* spp. separately in the main-stem Columbia River as a function of landscape-level factors and variability associated with the closest river mouth. As described in the preceding section, the landscape factors examined were distance from the quadrat (i) to the ocean (O_i), distance from the quadrat to the closest river mouth (T_i), and distance from the quadrat to the nearest bank (B_i); all were modeled as continuous factors. In addition, we included a categorical factor ($j = 14$ for the 14 examined river mouths) to account for variability associated with the river mouth closest to the quadrat (D_i):

$$\text{Logit}(\phi_i) = \alpha + \beta_O(O_i) + \beta_T(T_i) + \beta_B(B_i) + \beta_{B^2}(B_i^2) + \beta_{D,j}(D_i),$$

where β_O, β_T, β_B, β_{B^2}, and $\beta_{D,j}$ are the slopes for the effects and ϕ_i is the expected probability of presence at quadrat i. The expected probability of presence was estimated from a Bernoulli distribution of presence (Y_i) data from field collections of either Pacific Lamprey or *Lampetra* spp.:

$$Y_i \sim Bernoulli(\phi_i).$$

We included the nearest river mouth as a factor to assess and account for variability in larval presence among river mouths (j) as a function of differences in the number of spawning adults, seasonal spawning period, sampling periods, habitat, and other characteristics among river mouths in the Columbia River. Because we were mainly interested in assessing and accounting for variation among river mouths as opposed to identifying specific differences between the included river mouths (i.e., river mouths were considered to represent a sample of all possible river mouths), we assumed that all estimated slopes (i.e., all 14 $\beta_{D,j}$) were from a normal distribution with a mean of zero and an estimated standard deviation σ:

$$\beta_{D,j} \sim Normal(0, \sigma).$$

Thus, σ is intended to account for and identify variation in presence among the 14 river mouths (j). Quadrat-specific habitat characteristics within a river mouth (e.g., water depth, substrate size, and water velocity) would also be expected to affect the probability of presence in a quadrat (Dawson et al. 2015). Quadrat-specific habitat characteristics were collected during some but not all of the studies, so they were not included in this landscape-scale analysis that encompassed all studies combined.

We evaluated logistic models including all combinations of the four examined factors (β_O, β_T, β_B, and σ). All models that included distance from the bank were evaluated with only a linear term (i.e., β_B) and with both linear and quadratic terms (i.e., β_B and β_{B^2}). We compared all models using the deviance information criterion (DIC) and considered the best model to be the one with the lowest DIC score (Spiegelhalter et al. 2002; Wilberg and Bence 2008). Although the model with the lowest DIC score is considered the best performing model (Spiegelhalter et al. 2002; Wilberg and Bence 2008), we also made note of the factors included in all models that had DIC scores within 10 units of the best model (i.e., DIC difference [ΔDIC] $\le$ 10), as this could provide information on the importance of those factors. Using the DIC-selected model for each Pacific Lamprey and *Lampetra* sp., we calculated the expected probabilities of presence for a deepwater electrofishing sample collected from a river mouth and from a pool by using the average T_i of all river mouth samples (356 m) or pool samples (48,193 m), respectively, and the average O_i of all samples (295 rkm).

For our second analysis, we estimated the density of larvae using a modified *N*-mixture model that was explicitly developed to estimate larval lamprey density based on data collected from a deepwater electrofisher (Harris and Jolley 2017). This *N*-mixture model included two hierarchical levels: (1) a binomial model to estimate the capture probability (p) of the deepwater electrofisher and (2) a Poisson model to estimate average abundance (λ) as well as the abundance for each sample. We assumed that the quadrat location was occupied when the median estimate of abundance was 1 larval lamprey or greater, and we assumed that it was unoccupied when the median estimate of abundance was zero. Estimates of abundance were corrected for the bell size (0.65 m^2) to estimate density in larvae per square meter (see Harris and Jolley 2017 for more details on this analysis). We focused this analysis on six river mouths where multiple site visits were conducted over the study time frame, and we evaluated all of the site visits for these river mouths. The Kalama, Washougal, Sandy, and Hood rivers each had three site visits conducted, and the Wind and Klickitat rivers each had six site visits conducted. At each site visit, we sampled from at least 31 quadrats. We estimated site average and quadrat densities during the late-summer and early-fall low-flow periods (late August to late September) of 2013, 2016, and 2018 for all six river mouths: three below Bonneville Dam (Kalama, Washougal, and Sandy rivers) and three above Bonneville Dam (Wind, Klickitat, and Hood rivers). We also estimated densities for the spring high-flow period (April) in 2018 for five river mouths (Hood River was not sampled during this seasonal period) and for the spring high-flow period in 2011 and 2012 for the Wind and Klickitat rivers. We estimated densities for (1) all larval lampreys, (2) larvae that were 31 mm or greater, and (3) larvae that were 30 mm or less. High variability in length at age exists for larval lampreys, although research suggests that length frequency data can potentially be used to assess age for age-1 and younger Sea Lamprey larvae (Jones et al. 2003; Dawson et al. 2009). Results from statolith aging suggested that most larval Western Brook Lampreys under 30 mm TL were age 0 (Meeuwig and Bayer 2005; Schultz et al. 2017). Thus, although larval lampreys grow at different rates and emigrate from spawning locations after different periods of time, we assumed for these analyses that 30-mm-TL and smaller individuals could represent young of the year (hereafter, "presumed age 0"). Evaluating presumed age-0 larval densities in isolation is advantageous, as they could represent migrants from a single spawning season, a single larval dispersal event, and a single year of high-flow conditions. We combined Pacific Lamprey, *Lampetra* spp., and lampreys that were unidentified to species because sample sizes were small, especially for presumed age-0 larvae.

Models were evaluated by Bayesian methods. We used the package jagsUI (Kellner 2015) in JAGS software (Plummer 2003) called from R (R Core Team 2013). We used three chains, adaptation and burn-in values of 10,000 replicates, and an iteration interval of 50,000, and we saved enough iterations to meet convergence ($\hat{R}$ scores <1.1 for all estimated parameters; Gelman and Hill 2007; Kéry and Schaub 2012). The median of the posterior distributions was considered to be the estimate, and we used the 95% credible interval (95% CI) to describe variability. Non-overlapping 95% CIs were considered to potentially indicate "substantial differences" among estimates. For each logistic model of larval lamprey presence, we used noninformative normal distributions (mean = 0; standard deviation = 1000) as priors for slopes and intercepts and we used a uniform distribution (range = 0–10) for σ (when included in the model). For each *N*-mixture model, the prior distribution for λ was uniform (range = 0–20) and the prior distribution for p was uniform (range = 0–1).

RESULTS

Larval lamprey presence

All logistic models evaluating the presence of larval Pacific Lamprey as a function of examined landscape factors converged (Table 2). All models with ΔDIC scores of 10 or less included distance from the closest river mouth and variability among river mouths (Table 2). The best model as selected by DIC incorporated all examined factors, including the quadratic term for distance from the nearest bank (Table 2). The DIC-selected model suggested that the probability of larval Pacific Lamprey presence decreased as the distance from the ocean increased ($\beta_O = -0.79$; 95% CI = −1.60 to −0.20) and as the distance from the closest river mouth increased ($\beta_T = -0.07$; 95% CI = −0.15 to −0.03); the probability of presence also varied among river mouths ($\sigma = 0.80$; 95% CI = 0.36–1.76). The DIC-selected model also suggested a decline in the probability of presence with distance from the nearest bank over most of the range ($\beta_B = -3.91$; 95% CI = −7.10 to −1.22), but the quadratic term suggested that presence peaked at around 70 m from the bank and then declined at distances further from the bank (Figure 3). Although the quadratic term for distance from the bank was included in the DIC-selected model and had a negative slope ($\beta_{B^2} = -12.82$), the 95%

TABLE 2 Factors included in each examined logistic model, the deviance information criterion (DIC) score for the model, and the difference between the model's DIC score and the lowest DIC score (ΔDIC) among all examined logistic models. The models examined factors affecting the presence of larval Pacific Lamprey in the Columbia River basin. For model factors, O_i is the distance from the ocean, T_i is the distance from the closest tributary river mouth, B_i is the distance from the riverbank, B_i^2 is the quadratic term for distance from the riverbank, and σ accounts for variation associated with the specific tributary river mouth that was closest.

Model factors	DIC	ΔDIC
$\beta_O, \beta_T, \beta_B, \beta_{B^2}, \sigma$	741.5	0.0
$\beta_O, \beta_T, \beta_B, \sigma$	742.7	1.2
$\beta_T, \beta_B, \beta_{B^2}, \sigma$	746.5	5.0
β_O, β_T, σ	746.6	5.1
β_T, β_B, σ	748.4	7.0
β_T, σ	751.5	10.0
$\beta_B, \beta_{B^2}, \sigma$	753.2	11.7
$\beta_O, \beta_B, \beta_{B^2}, \sigma$	754.1	12.7
β_B, σ	756.4	15.0
β_O, β_B, σ	757.1	15.7
$\beta_O, \beta_T, \beta_B, \beta_{B^2}$	763.7	22.2
$\beta_O, \beta_T, \beta_B$	765.0	23.5
β_O, σ	773.0	31.6
$\beta_T, \beta_B, \beta_{B^2}$	773.7	32.2
β_O, β_T	775.8	34.4
β_T, β_B	778.1	36.6
$\beta_O, \beta_B, \beta_{B^2}$	781.5	40.1
β_O, β_B	787.1	45.7
β_T	791.7	50.3
β_B, β_{B^2}	805.3	63.8
β_O	806.3	64.8
β_B	814.1	72.7

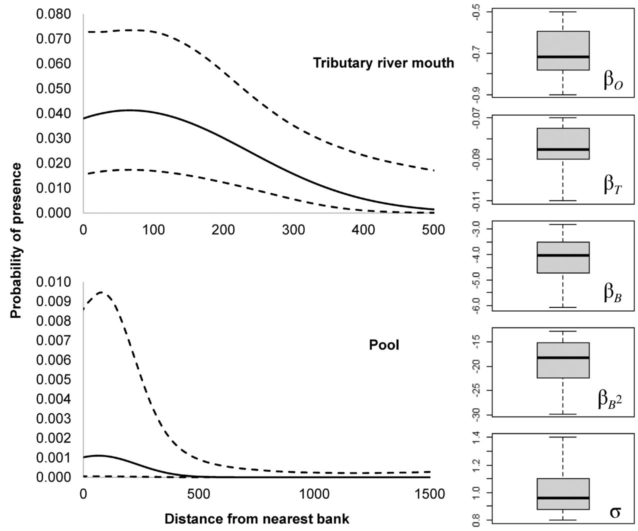

FIGURE 3 Predicted probability of presence (with dashed lines illustrating 95% credible intervals) of larval Pacific Lamprey sampled by a deepwater electrofisher in tributary river mouth and pool habitats in the Columbia River as a function of distance (m) from the nearest riverbank ("bank"). Probabilities were predicted using the deviance information criterion-selected model (see Table 2) and were calculated at the average distance from a tributary river mouth for either a tributary river mouth sample (356 m; upper panel) or a pool sample (48,193 m; lower panel) and the average distance from the ocean for all samples (295 rkm). Box plots illustrate the median (horizontal line within box), the first and third quartiles (ends of box), and range (extent of whiskers) for slope estimates of parameters in all evaluated models (see Table 2). The symbol β_O represents the slope for distance from the Pacific Ocean, β_T is the slope for distance from the closest tributary river mouth, β_B is the slope for distance from the nearest bank (β_{B^2} is the slope for the squared term), and σ is the standard deviation for variation among tributary river mouths. The *x*-axis and *y*-axis ranges differ between the two panels.

CI for the quadratic term was wide and overlapped zero (−30.62 to 1.40), and a similar DIC score was obtained for a model that included the four main factors without the quadratic term; thus, we suggest caution when interpreting the value of 70 m (Table 2). For all models evaluated, slope estimates suggested negative relationships between the probability of larval Pacific Lamprey presence and the examined landscape factors (i.e., distance from the ocean, distance from the nearest river mouth, and distance from the nearest bank; Figure 3). Evaluating the expected probabilities of presence using the DIC-selected model with the average factor values indicated that expected probabilities were an order of magnitude larger in river mouth habitats than in pool habitats (Figure 3).

For the evaluation of larval *Lampetra* spp., some models with a quadratic term for the effect of distance from the nearest bank on the presence of larval lampreys, including the model selected by DIC for Pacific Lamprey, did not converge and were not considered (Table 3). All models with a ΔDIC of 10 or less included distance from the nearest bank and variability among river mouths (Table 3). The best model as selected by DIC included all four factors (Table 3). The DIC-selected model suggested that the probability of larval *Lampetra* spp. presence decreased as the distance from the ocean increased ($\beta_O = -1.74$; 95% CI = −3.91 to −0.56), as the distance from the closest river mouth increased ($\beta_T = -0.06$; 95% CI = −0.12 to −0.02), and as the distance from the nearest bank increased ($\beta_B = -13.13$; 95% CI = −18.41 to −8.86); the probability of presence also varied among river mouths (σ = 1.39; 95% CI = 0.68–3.43; Figure 4). Similar to models for the Pacific Lamprey, in all models evaluated, slope estimates suggested negative relationships between the probability of larval *Lampetra*

TABLE 3 Factors included in each examined logistic model, the deviance information criterion (DIC) score for the model, and the difference between the model's DIC score and the lowest DIC score (ΔDIC) among all examined logistic models. The models examined factors affecting the presence of larval *Lampetra* spp. in the Columbia River basin. For model factors, O_i is the distance from the ocean, T_i is the distance from the closest tributary river mouth, B_i is the distance from the riverbank, B_i^2 is the quadratic term for distance from the riverbank, and σ accounts for the variation associated with the specific tributary river mouth that was closest. Abbreviation: NC, model did not converge.

Model factors	DIC	ΔDIC
$\beta_O, \beta_T, \beta_B, \sigma$	466.3	0.0
β_O, β_B, σ	471.9	5.5
β_T, β_B, σ	473.2	6.9
β_B, σ	474.6	8.2
β_O, β_T, σ	516.2	49.9
$\beta_O, \beta_T, \beta_B$	522.5	56.2
β_T, σ	524.0	57.7
β_O, σ	527.6	61.3
β_O, β_B	529.5	63.1
β_T, β_B	542.8	76.5
β_B	562.2	95.8
β_O, β_T	572.4	106.1
β_O	585.1	118.8
β_T	594.8	128.5
$\beta_T, \beta_B, \beta_{B^2}, \sigma$	1250.0	783.7
$\beta_O, \beta_B, \beta_{B^2}, \sigma$	1275.1	808.8
$\beta_T, \beta_B, \beta_{B^2}$	1302.8	836.5
$\beta_O, \beta_B, \beta_{B^2}$	1324.0	857.7
β_B, β_{B^2}	1382.2	915.9
$\beta_O, \beta_T, \beta_B, \beta_{B^2}, \sigma$	NC	
$\beta_O, \beta_T, \beta_B, \beta_{B^2}$	NC	
$\beta_B, \beta_{B^2}, \sigma$	NC	

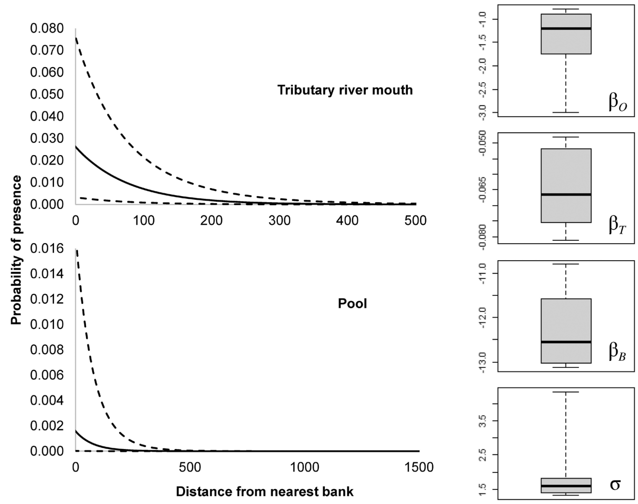

FIGURE 4 Predicted probability of presence (with dashed lines illustrating 95% credible intervals) of larval *Lampetra* spp. sampled by a deepwater electrofisher in tributary river mouth and pool habitats in the Columbia River as a function of distance (m) from the nearest riverbank ("bank"). Probabilities were predicted by the deviance information criterion-selected model (see Table 3) and were calculated at the average distance from a tributary river mouth for a tributary river mouth sample (356 m; upper panel) or a pool sample (48,193 m; lower panel) and the average distance from the ocean for all samples (295 rkm). Box plots illustrate the median (horizontal line within box), the first and third quartiles (ends of box), and range (extent of whiskers) for slope estimates of parameters in all evaluated models that converged (see Table 3). The symbol β_O represents the slope for distance from the Pacific Ocean, β_T is the slope for distance from the closest tributary river mouth, β_B is the slope for distance from the nearest bank, and σ is the standard deviation for variation among tributary river mouths. The *x*-axis and *y*-axis ranges differ between the two panels.

spp. presence and the examined landscape factors (i.e., distance from the ocean, distance from the nearest river mouth, and distance from the nearest bank; Figure 4). The DIC-selected model using the average factor values suggested that the expected probabilities of presence were an order of magnitude larger in river mouth habitats relative to pool habitats (Figure 4).

River mouth interannual variation

Three to six estimates of density (larvae/m^2) were produced using *N*-mixture models for six of the river mouths with multiple site visits (Table 4). Estimated densities of larval lampreys varied among river mouths, within river mouths, among years, and among seasons (Table 4). Despite considerable variability, some patterns emerged. During the late-summer and early fall low-flow periods (August–September) of 2016 and 2018, estimated densities of all larval lampreys were higher for river mouths upstream of Bonneville Dam (Wind, Hood, and Klickitat rivers) than for those downstream of Bonneville Dam (Kalama, Washougal, and Sandy rivers), although density at the Hood River mouth was not substantially higher (i.e., 95% CIs overlapped; Table 4; Figure 5). For river mouths downstream of Bonneville Dam (Kalama, Washougal, and Sandy rivers), estimated densities in 2016 were similar to or slightly higher than those in 2018. In contrast, for the Wind and Klickitat River mouths (both upstream of Bonneville Dam), density estimates were lowest in 2013, intermediate in 2016, and highest in 2018, although 95% CIs overlapped among some estimates (Figure 5). The Hood River mouth showed a similar increase in density over the course of the study but was not surveyed in 2018 (Figure 5).

In contrast to results for all larvae, estimated densities of presumed age-0 larvae (i.e., larvae ≤30 mm TL) in river

TABLE 4 Median densities (larvae/m^2) and 95% credible intervals (95% CIs) estimated by *N*-mixture models for all lamprey larvae, 30-mm and smaller larvae, and larvae larger than 30 mm, summarized for repeat site visits to tributary river mouths. "Quadrats" are the number of quadrats that were sampled during each site visit and used to estimate density. Site visits conducted during low-flow conditions are italicized. Site visits conducted in 2016 are shaded in light gray, and site visits conducted in 2018 are shaded in dark gray.

			Total larvae		Larvae ≤30 mm		Larvae >30 mm	
River mouth	Month and year	Quadrats	Density (larvae/m^2)	95% CI	Density (larvae/m^2)	95% CI	Density (larvae/m^2)	95% CI
Kalama	*Sep 2016*	*34*	*0.76*	*0.39–1.29*	*0.05*	*0.00–0.23*	*0.76*	*0.39–1.29*
	Apr 2018	35	2.68	1.93–3.64	0.99	0.57–1.57	1.74	1.15–2.51
	Aug 2018	*34*	*0.24*	*0.07–0.56*	*0.05*	*0.00–0.24*	*0.24*	*0.07–0.56*
Washougal	*Aug 2016*	*34*	*0.43*	*0.18–0.83*	*0.24*	*0.07–0.57*	*0.24*	*0.07–0.57*
	Apr 2018	34	9.63	7.93–11.63	1.72	1.15–2.50	7.93	6.49–9.72
	Aug 2018	*35*	*0.41*	*0.18–0.83*	*0.23*	*0.07–0.55*	*0.23*	*0.07–0.56*
Sandy	*Sep 2016*	*32*	*0.80*	*0.43–1.38*	*0.67*	*0.33–1.18*	*0.18*	*0.04–0.51*
	Apr 2018	37	0.82	0.45–1.34	0.18	0.04–0.49	0.70	0.36–1.20
	Aug 2018	*32*	*0.25*	*0.08–0.60*	*0.19*	*0.04–0.51*	*0.12*	*0.02–0.40*
Wind	Apr 2011	31	2.66	1.90–3.70	0.05	0.00–0.26	2.67	1.87–3.65
	May 2012	34	2.30	1.62–3.20	0.36	0.14–0.74	1.99	1.35–2.83
	Aug 2013	*102*	*1.42*	*1.09–1.82*	*0.08*	*0.02–0.19*	*1.35*	*1.03–1.76*
	Aug 2016	*34*	*2.24*	*1.57–3.13*	*1.20*	*0.73–1.87*	*1.08*	*0.63–1.74*
	Apr 2018	34	7.73	6.29–9.49	2.50	1.77–3.44	5.28	4.13–6.67
	Sep 2018	*34*	*3.22*	*2.36–4.28*	*0.04*	*0.00–0.23*	*3.22*	*2.35–4.28*
Hood	Apr 2011	34	0.17	0.04–0.46	0.04	0.00–0.24	0.17	0.04–0.46
	Sep 2013	*35*	*0.42*	*0.18–0.83*	*0.11*	*0.02–0.34*	*0.36*	*0.14–0.76*
	Aug 2016	*32*	*1.07*	*0.62–1.71*	*1.07*	*0.62–1.71*	*0.05*	*0.00–0.26*
Klickitat	May 2011	34	0.04	0.00–0.24	0.04	0.00–0.24	0.04	0.00–0.24
	Jun 2012	34	0.36	0.14–0.74	0.05	0.00–0.23	0.36	0.14–0.74
	Aug 2013	*102*	*2.19*	*1.75–2.71*	*0.75*	*0.52–1.04*	*1.46*	*1.12–1.88*
	Aug 2016	*34*	*3.67*	*2.76–4.81*	*3.35*	*2.48–4.44*	*0.23*	*0.07–0.56*
	Apr 2018	46	2.71	2.04–3.56	0.03	0.00–0.18	2.71	2.04–3.56
	Sep 2018	*34*	*3.80*	*2.88–4.97*	*0.82*	*0.44–1.38*	*3.03*	*2.20–4.07*

mouths upstream of Bonneville Dam (Wind, Hood, and Klickitat rivers) were higher during the low-flow time frame in 2016 compared with the 2013 and 2018 surveys, although some 95% CIs overlapped (Table 4; Figure 6). Additionally, density estimates during 2016 low-flow periods consisted of higher proportions of presumed age-0 larvae in the Wind, Hood, and Klickitat River mouths. In the Hood and Klickitat rivers, almost the entire expected density consisted of presumed age-0 larvae. In all years, the highest estimated densities of presumed age-0 larvae during low-flow conditions were observed for the Klickitat River mouth. Estimated densities of presumed age-0 larvae in the Kalama and Washougal rivers were consistently low during low-flow conditions in 2016 and 2018 (Table 4; Figure 6).

Multiple high-flow site visits (April–June) were conducted in the Wind and Klickitat River mouths during 2011, 2012, and 2018 (Table 4; Figure 7). As for the low-flow surveys, estimated larval densities in both river mouths were substantially higher during 2018 than during earlier sampling years (Figure 7). During high-flow periods, estimated densities of presumed age-0 larvae in the Klickitat River were very low (0.03–0.05 larvae/m^2; Figure 7). Estimated densities of presumed age-0 larvae in the Wind River mouth were more variable but showed the same pattern of substantially higher densities in 2018 than in 2011 and 2012 (Figure 7).

River mouth seasonal changes

In 2018, high- and low-flow sampling at five river mouths allowed for seasonal comparisons of expected larval density, size-class (i.e., proportions ≤30 and >30 mm), and occupancy (Table 4; Figures 8 and 9). During spring sampling,

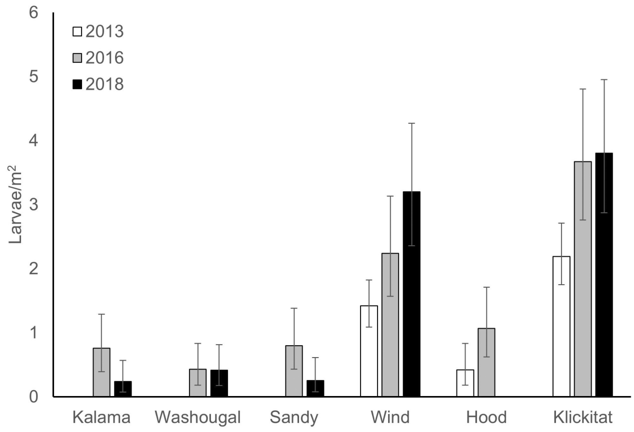

FIGURE 5 Densities (larvae/m^2) of larval lampreys during fall low-flow periods in river mouths of Columbia River tributaries as estimated by *N*-mixture models. Tributaries are ordered from downstream (left) to upstream (right). The Kalama, Washougal, and Sandy rivers are downstream of Bonneville Dam; the Wind, Hood, and Klickitat rivers are upstream of the dam. Error bars represent 95% credible intervals.

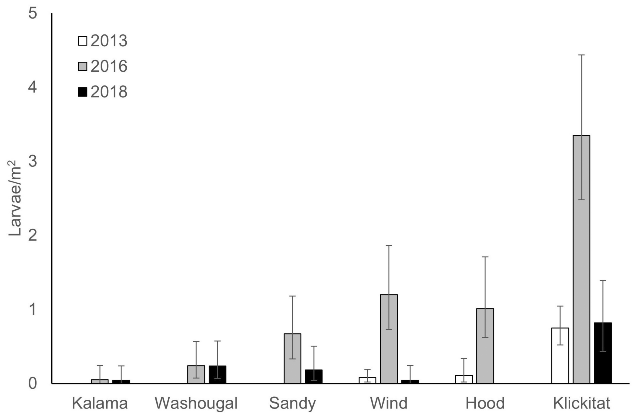

FIGURE 6 Densities (larvae/m^2) of presumed age-0 (≤30-mm) larval lampreys during fall low-flow periods in river mouths of Columbia River tributaries as estimated by *N*-mixture models. Tributaries are ordered from downstream (left) to upstream (right). The Kalama, Washougal, and Sandy rivers are downstream of Bonneville Dam; the Wind, Hood, and Klickitat rivers are upstream of the dam. Error bars represent 95% credible intervals.

the Washougal and Wind River mouths had the highest expected densities across all years and sites (Table 4). Results from the *N*-mixture models indicated that all quadrats were likely occupied (i.e., median abundance ≥1), suggesting that larvae were present throughout much of the sampled habitat in these river mouths during the spring. The Kalama, Washougal, and Wind River mouths exhibited substantial decreases in estimated densities as well as decreases in river mouth occupancy from spring to fall in 2018. In addition, at these three locations, the pattern of lower larval densities in the spring as compared to fall

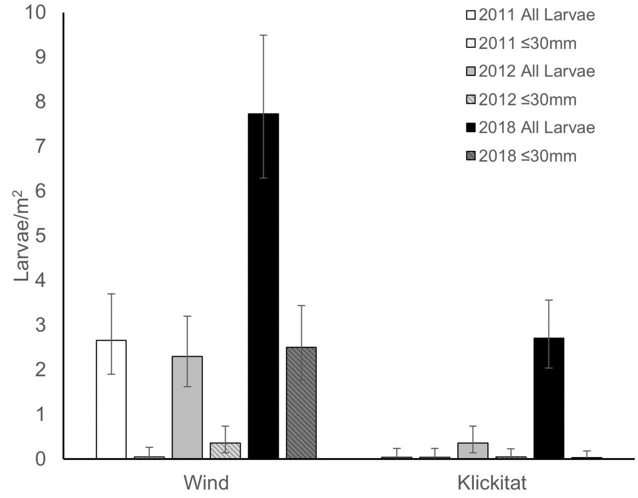

FIGURE 7 Densities (larvae/m^2) of all larval lampreys and presumed age-0 (≤30-mm) larval lampreys during spring high-flow periods in river mouths of Columbia River tributaries as estimated by *N*-mixture models. Both tributaries (Wind and Klickitat rivers) flow into the Columbia River above Bonneville Dam. Error bars represent 95% credible intervals.

existed both for larvae larger than 30 mm TL and for presumed age-0 larvae (i.e., ≤30 mm TL). The relationship was not as pronounced in the Wind River for larvae greater than 30 mm TL, as there was some overlap in the 95% CIs. The Sandy River mouth likewise had decreases in expected density and occupancy from high- to low-flow conditions, although overall densities were consistently low across seasons (Table 4). The Sandy River mouth had the lowest expected densities during high-flow conditions across all river mouths as well as the lowest expected occupancy for both seasons, dropping from 16.2% in high-flow conditions to 6.2% in low-flow conditions. Results for the Sandy River mouth are not displayed in the figures due to the overall low densities and occupancy and the minimal apparent seasonal changes in occupancy or density.

In contrast, the seasonal change observed during 2018 in the Klickitat River mouth was different from that observed for the other examined river mouths (Figures 8 and 9). Estimated density and occupancy increased from spring to fall, in part driven by an increase in presumed age-0 larval densities during the low-flow season (Table 4). Unlike 2016 densities, the 2018 overall densities at both the Wind and Klickitat River mouths were driven primarily by higher densities of larvae exceeding 30 mm TL.

DISCUSSION

Our study illustrates annual, seasonal, and spatial patterns in the distribution and density of larval lampreys

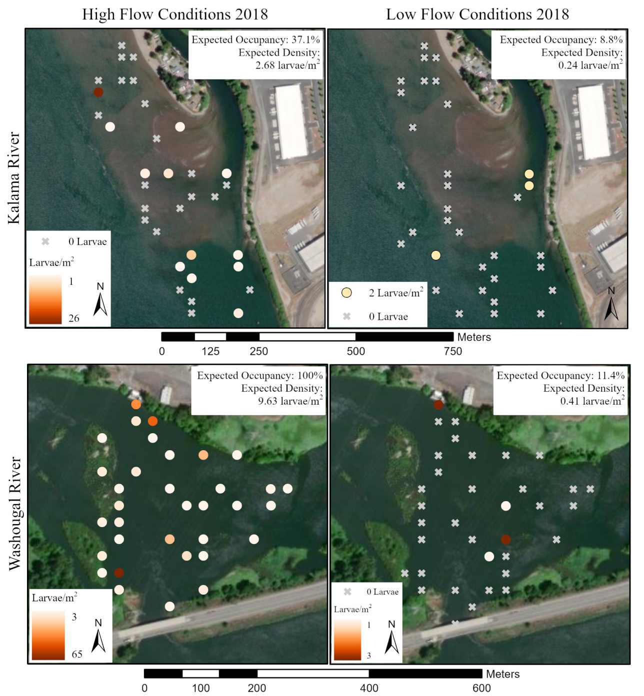

FIGURE 8 Expected percent occupancy, expected mean site density, and expected quadrat density of larval lampreys as estimated using *N*-mixture models for two tributaries (Kalama and Washougal rivers) to the Columbia River downstream of Bonneville Dam during high- and low-flow conditions in 2018. If estimated abundance at the quadrat was less than 1 larval lamprey, an "×" is displayed at the quadrat location, which was considered unoccupied; otherwise, a colored circle represents the estimated mean density at the quadrat (larvae/m^2). Density color scale varies by river mouth site and by site visit. Note that this imagery does not reflect water conditions at the time of the survey. The Sandy River is not displayed due to overall low densities, low occupancy, and minimal seasonal changes in occupancy.

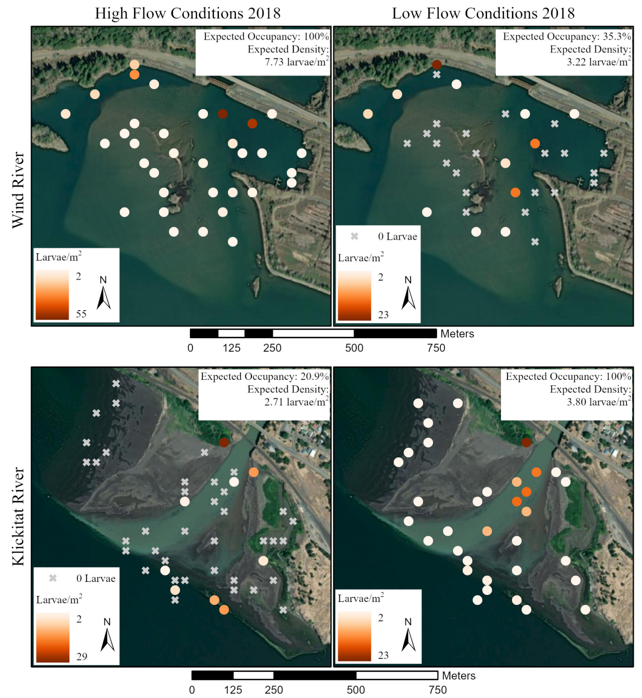

FIGURE 9 Expected percent occupancy, expected mean site density, and expected quadrat density of larval lampreys as estimated using *N*-mixture models for two tributaries (Wind and Klickitat rivers) to the Columbia River upstream of Bonneville Dam during high- and low-flow conditions in 2018. If estimated abundance at the quadrat was less than 1 larval lamprey, an "×" is displayed at the quadrat location, which was considered unoccupied; otherwise, a colored circle represents the estimated mean density at the quadrat (larvae/m^2). Density color scale varies by river mouth site and by site visit. Note that this imagery does not reflect water conditions at the time of the survey.

in the lower and middle Columbia River, a large river system that provides extensive rearing habitat for multiple species of native lampreys. The probability of larval presence decreased for both Pacific Lamprey and *Lampetra* spp. with increasing distance from the ocean, although comparatively high densities were observed in some river mouths in Bonneville Reservoir (e.g., Wind and Klickitat rivers). A decrease in larval presence with distance from the ocean may be caused in part by the main-stem dams acting as upstream migration barriers for the anadromous lampreys (i.e., Pacific and Western River lampreys), thus causing a declining percentage of adults to migrate and spawn past subsequent upstream dams (Moser et al. 2002; Keefer et al. 2009). Our results also suggest that the probability of larval presence for both Pacific Lamprey and *Lampetra* spp. declined with distance from the nearest tributary river mouth and with distance from the nearest bank. Our model therefore predicts that within the Columbia River, the probability of larval lamprey presence is lowest near the center of the river and when most distant from any upstream river mouth junction. Therefore, the probability of larval presence appears to be an order of magnitude higher in river mouth habitats than in reservoir pool habitats. This higher probability may reflect proximity to spawning locations in the tributary rivers, larval lamprey downstream movements, and the quality of river mouth delta habitats.

Although variable, estimated larval densities in the river mouths we examined (Table 4) were generally lower than those in smaller rivers across Oregon and Washington (Moser and Close 2003; Torgersen and Close 2004; Stone and Barndt 2005). We speculate that lower densities in the main-stem Columbia River may be related to redistribution (i.e., Zvezdin et al. 2022). Downstream dispersal of larvae can be motivated by many factors, including temperature (Bracken and Lucas 2013), high flows (Hardisty and Potter 1971; Potter 1980; Beamish and Levings 1991; Zvezdin et al. 2022), and receding flows (Hardisty and Potter 1971; Kelly and King 2001). Redistributions into the lower density environments may be advantageous since lower densities could potentially provide access to limited resources and reduce localized impacts of habitat fluctuations and predation on the lamprey populations. Although estimated densities were lower than those in small rivers, given the sheer size of the Columbia River, it is evident that the main stem serves as rearing habitat for native lampreys and that river mouth habitats are important within the main-stem system.

Analyzing data collected from repeated sampling at river mouths allowed us to identify patterns in larval density and occupancy across time. The most prolonged and consistent data in this study were from the Wind and Klickitat River mouths. Patterns showed increased larval densities from the earliest sampling (2011, 2012, and 2013) to the most recent site visits (2016 and 2018). Increased larval densities were evident in high- and low-flow conditions and may be related to increases in passage of adult Pacific Lamprey at Bonneville Dam. Facility modifications to improve passage success are ongoing (U.S. Army Corps of Engineers 2014); starting in 2004, three lamprey passage structures were added, which in more recent years have provided passage for 30–47% of migrating adult lampreys (Cates et al. 2020). However, overall escapement past the dam remains low and is estimated at around 50% (Moser et al. 2002, 2005; Keefer et al. 2019). Similarly high levels of attrition are observed at upstream dams, leading to declining percentages of adults migrating past subsequent dams (Keefer et al. 2009); this supports the negative relationship we observed between distance from the ocean and the probability of Pacific Lamprey larval presence. However, overall adult lamprey counts at Bonneville Dam have increased significantly over the course of the study (Cates et al. 2020; Fish Passage Center (unpublished data, www.fpc.org)), potentially driven by host fish abundance and ocean conditions (Murauskas et al. 2013; Clemens et al. 2019). The increased number of adult spawners at Bonneville Dam may have contributed to increases in larval lamprey density in river mouth habitats upstream of Bonneville Dam during this study.

Analysis of presumed age-0 larvae allowed us to evaluate variation that may be attributed to a single age-class, a spawning event, or seasonal high-flow events. Detection of true age-0 larvae could yield information on spawn timing (Brumo et al. 2009) and location since the small-bodied, weak-swimming larvae are likely to have originated from the nearest tributary river. Compared to 2013 and 2018, estimated densities of presumed age-0 larvae in 2016 were substantially higher during the fall in three of the six river mouth sites and were almost the same or moderately higher in the other three river mouths (see Table 4 and Figure 6), potentially indicating either an earlier period of high spawning productivity or high survival of larvae. Spawning of Pacific Lamprey has been documented within all tributaries examined in this study (Oregon Adult Salmonid Inventory and Sampling Project 2023; Washington Department of Fish and Wildlife 2023; R. Lampman, Yakama Nation, personal communication); however, there are no consistent annual evaluations of nest counts or adults. Therefore, we currently have no way to directly link annual variability in presumed age-0 larval densities in any specific river mouth to the numbers of spawning adults in that river. However, throughout the broader region, Pacific Lamprey nest counts were consistently high in 2016, whereas the nest counts in 2013 and 2018 were more variable (Clemens et al. 2021; Oregon Adult Salmonid Inventory and Sampling Project 2023; Washington Department of Fish and Wildlife 2023). A more comprehensive accounting of spawning adult numbers and location within tributaries could be helpful in evaluating a connection to changing densities of small larval lampreys and identifying environmental factors (e.g., water temperature and discharge) that contribute to spawning and rearing success.

Differences in the presence and density of larval lampreys among river mouths could be a function of differences in the hydrologic characteristics of those rivers. Differences in discharge, velocity, and temperature have been linked to the timing of adult migration (Keefer et al. 2009a; Clemens et al. 2012, 2017; Starcevich et al. 2014; Clemens and Schreck 2021), spawning (Stone 2006; Brumo et al. 2009; Clemens et al. 2009), and larval development (Meeuwig and Bayer 2005), all of which ultimately influence larval movements and distribution. The Kalama and Washougal rivers are rain-dominated systems that drain lower elevation watersheds. Both rivers have low base flow conditions during summer. In both river mouths, we observed presumed age-0 larvae as early as April. By contrast, the Hood and Klickitat rivers are mixed rain–snow systems that drain higher elevation watersheds, with glacially supplemented summer flows that keep base flows relatively high in the summer. In these two rivers, presumed age-0 larvae were all but absent during all spring site visits. Potentially, patterns in discharge and water temperature over the year affect the seasonal timing of spawning or downstream movement. Future efforts to link hydrologic characteristics to presumed age-0 lamprey observations could improve our understanding of how habitats may shift with predicted stream temperature and runoff timing variations driven by climate change.

Natural and anthropogenic changes in water levels between spring and fall may cause dramatic seasonal changes in larval lamprey presence and density. In 2018, both high- and low-flow conditions were sampled at five river mouths. In four river mouths, larval densities during the spring high-flow period were significantly higher than larval densities during the low-flow period the following fall. In the fifth river mouth (Klickitat River), larval densities were consistent across the two seasons. The fate of lampreys between spring and fall was not evaluated; however, there were several potential outcomes. Larval lampreys may volitionally migrate out of river mouth habitat as it becomes dewatered (Hardisty and Potter 1971; Harris et al. 2020); alternatively, the dewatering of sediments could result in direct mortality of larvae that remain or predation mortality of larvae that emerge and attempt to move toward the receding water (Liedtke et al. 2015; Harris et al. 2020). Smaller larvae are more vulnerable during these events than are larger larvae (Liedtke et al. 2023, this special section), and we observed avian predation of larvae on dewatered sediments while sampling. Satellite imagery in Figures 8 and 9 does not represent the water conditions that occurred during surveys; however, it does clearly display the shallow-water delta depositional areas that form at the four river mouths. These shallow areas are at the greatest risk of dewatering with water level changes.

Fluctuations in the main-stem water levels occur throughout the year, but during low-flow conditions in the fall, these fluctuations may result in larger extents of dewatering compared to the rest of the year. Tributary river mouths downstream of Bonneville Dam are subject to tidal influence, which in 2018 resulted in typical daily fluctuations of 0.6–1.2 m in gauge height at Vancouver, Washington (rkm 171; U.S. Geological Survey [USGS] gauge 14246900). Upstream of Bonneville Dam in 2018, daily changes of 0.3–0.6 m were typical and daily fluctuations as much as 1.2 m were not uncommon (rkm 243; USGS gauge 14128600). These daily operational fluctuations are consistent with water level changes that have been observed in previous years (Mueller et al. 2015). Twice-daily tidal fluctuations in the Columbia River result in short-term and routine dewatering cycles, while dam operations can result in rapid elevation changes that can persist for days. There is evidence that larval lampreys can tolerate short periods of dewatering (Liedtke et al. 2023) and potentially utilize the hyporheic zone for refuge (Rodríguez-Lozano et al. 2019); however, longer duration dewatering events likely have greater deleterious effects (Liedtke et al. 2023). The boat and deepwater sampling apparatus can sample sites as shallow as 0.2 m; depending on when sampling occurred relative to daily water fluctuations, quadrats that were regularly dewatered may have been sampled. This may be more likely in fall, when flows are generally lower and daily fluctuations, both natural and anthropogenic, are more likely to periodically expose shallow-water river mouth habitat. Reducing the rate, duration, and magnitudes of water level change in the regulated reservoir pools—particularly after seasonal high flows in the spring, when larvae often disperse—could assist larval lamprey movements into consistently wetted habitat and thus reduce the negative impacts of the operational fluctuations (Lamprey Technical Workgroup 2020; Liedtke et al. 2023).

A more spatially and temporally explicit understanding of larval lamprey occupancy patterns could inform best management guidance for lampreys in the Columbia River and other large main-stem rivers (Streif 2009; Lamprey Technical Workgroup 2020). Seasonal shifts in distribution and densities of larval lampreys could inform the planning process of proposed actions that could potentially harm lampreys, such as in-water construction (e.g., marina infrastructure, boat ramps, and utility lines) and dredging. For example, understanding seasonal changes could identify time frames during which these actions might be the least impactful. The present research has shown that a single sampling event is not likely to capture the scope and variability of larval lampreys' use of a river mouth, either annually or seasonally. In Washington and Oregon, time frames when in-water work activities will be least impactful on salmonid spawning, incubation, and migration have been determined. Depending on the waterway and the species present, in-water activities can occur over several months and vary among waterways. Preproject implementation surveys could identify time frames within the recommended salmonid in-water work period when larval lamprey densities are also lower, and thus in-water impacts could be reduced. For example, our surveys in 2018 documented declines in density and occupancy from spring to fall for most river mouths, suggesting that for 2018, fall in-water work might have had lower impacts on larval lampreys than work taking place earlier in the summer. More investigations are needed to evaluate whether larval densities are consistently higher in the spring compared to the fall across years and at additional river mouth locations. Evaluations are needed to determine (1) whether there are consistent patterns based on watershed characteristics; (2) whether seasonal/annual surveys are needed to inform location-specific management actions; and (3) how the identified patterns may shift with a changing climate. The timing of in-river work may be especially important for projects occurring near river mouths or other habitats where densities of larval lampreys may be high.

In conclusion, by compiling data from multiple studies, we were able to better understand large-scale influences on larval lamprey distribution, describe seasonal and annual trends in the lower and middle Columbia River, and document the importance of river mouths as rearing habitats. Synthesizing data collected for diverse purposes can have drawbacks—for example, if physical and habitat metrics are not collected consistently or if sampling designs change. However, the studies included herein used standardized deepwater sampling for larval lampreys and overlapped in geographical extent. Habitat characteristics (e.g., sediment; Torgersen and Close 2004; Dawson et al. 2015) likely influenced larval lamprey occupancy and density in our sampled quadrats, and future studies would benefit from consistent collection of fine-scale habitat data along with deepwater sampling for larval lampreys. Continued and expanded monitoring at river mouths in the Columbia River basin and elsewhere, along with expanded lamprey nest sampling, could inform biological connections and guide management actions (such as the timing of in-water work) to reduce negative impacts to lampreys in locations with high larval densities, areas that foster larval presence year-round, and locations that are seasonally important.

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CONFLICT OF INTEREST STATEMENT

All authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that supported the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This research was conducted in compliance with state scientific fish collection permits and in accordance with *Guidelines for the Use of Fishes in Research* (http://fisheries.org/docs/wp/guidelines-for-use-of-fishes.pdf).

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