
Julianne E. Harris,* Jeffrey C. Jolley, Gregory S. Silver, Henry Yuen, and Timothy A. Whitesel
U.S. Fish and Wildlife Service, Columbia River Fish and Wildlife Conservation Office, 1211 Southeast Cardinal Court, Suite 100, Vancouver, Washington 98683, USA

Abstract
Some lamprey species are in decline, and assessments of local abundance could benefit research and conservation. In wadeable streams, larval lampreys are collected by using specialized backpack electrofishing techniques, although catchability has not been sufficiently evaluated. We assessed removal models for estimating the local abundance of larval lampreys in experimental net-pen enclosures within a wadeable stream. Known numbers of larvae were seeded at densities of 4–130 larvae/m² into 1-m² enclosures that were lined with fine sand and placed into Cedar Creek, Washington (Columbia River basin). Depletion sampling in each enclosure (n = 69) was conducted by three to five electrofishing passes, and abundance was estimated by six removal models that assumed different catchability functions. Catchability averaged 0.28. For the standard removal model, which assumed that catchability varied independently by enclosure but not by pass, the 95% highest posterior density credible intervals (95% HPD-CIs) were very large relative to the abundance estimates. Models assuming that catchability was either equal or a random factor among all enclosures and passes generally produced accurate (mean bias = –0.04) estimates of abundance, and 95% HPD-CIs were much smaller. Based on our data set, the expected bias of abundance estimates for 80% of simulations was less than 20% if five passes were completed from at least four randomly selected quadrats and if catchability was assumed to be a random factor. Additional sampling may be needed at low lamprey densities (especially <4 larvae/m²). Our results suggest that local abundance of larval lampreys in wadeable streams can be effectively estimated by depletion sampling at multiple 1-m² quadrats and by use of a hierarchical removal model.

Some lamprey species (Petromyzontiformes) worldwide are experiencing declines in their native ranges (Renaud 1997; Close et al. 2002; IUCN 2013). One particular species of conservation concern is the ecologically and culturally important Pacific Lamprey Entosphenus tridentatus (Close et al. 2002; Wang and Schaller 2015). Accurate (i.e., close to the true value) and precise (i.e., low variability) estimates of local abundance for Pacific Lampreys and other lamprey species are generally lacking (Mesa and Copeland 2009; Mayfield et al. 2014) and could aid conservation by helping to assess and characterize areas of concentration, local status, habitat preferences, and the impacts of local threats (e.g., passage impediments).

The freshwater larval stage is often targeted for Pacific Lamprey research and assessment (Moser et al. 2007; Cowx et al. 2009). Larval Pacific Lampreys burrow in stream and river sediments and filter-feed before transforming into migratory juveniles (Scott and Crossman 1973; Dawson et al. 2015). In wadeable streams, larval lampreys are detectable by using the standard electrofisher settings that are typically employed in
salmonid surveys (Dunham et al. 2013). However, prolonged exposure to electrofishing can produce narcosis and prohibit the emergence of burrowed larvae; thus, specialized techniques are preferred for studies targeting larval lampreys (Bergstedt and Genovese 1994; Pajos and Weise 1994; Moser et al. 2007). Specifically, backpack electrofishing has been adapted to target these larvae through the delivery of electrical current in two stages (Weisser and Klar 1990). However, due to the burrowing behavior of larval lampreys, questions remain about the catchability of electrofishing techniques and the accuracy of local abundance estimates produced from removal models.

Removal models are commonly used to estimate the local abundance of fish, including larval lampreys, in rivers and wadeable streams (Cowx 1983; Pajos and Weise 1994; Stone and Barndt 2005). Removal models use depletion sampling; thus, usually only one site visit is required, and no marking of individuals is needed. These models typically assume that catch (Cj) from each removal pass j is a function of the estimated number of individuals available at the start of that pass (Nj) and catchability (q), which is the estimated proportion of individuals that are caught during each pass. Abundance is the estimated number of individuals that were present before any passes were completed (i.e., Nj), and q is estimated from the declining pattern of catches over all passes.

Although removal methods are used to estimate abundance (Meyer and High 2011; Saunders et al. 2011), results can be inaccurate if the model assumptions are not met. Removal models commonly assume a closed population, constant sampling effort across electrofishing passes, and an equal probability of capture (i.e., q) for each individual and each pass (Ruiz and Laplanche 2010; Meyer and High 2011). Although some assumptions can be reasonably met through appropriate sample design, q often differs among sites and among passes within a site. Catchability can vary as a function of fish size, density, or behavior as well as due to environmental conditions, such as turbidity, water velocity, and water temperature; when heterogeneity in q is ignored, estimates of abundance can be imprecise and often biased low (Hintz 1993; Pajos and Weise 1994; Rosenberger and Dunham 2005; Meyer and High 2011). Patterns in q vary depending on the species of interest and the electrofishing sampling technique used and have not been sufficiently examined for larval lampreys (Steves et al. 2003; Silva et al. 2014).

Hierarchical removal models can produce accurate and precise abundance estimates when multiple sites are sampled or when auxiliary information on q is available (Wyatt 2002; Mäntyniemi et al. 2005). Specifically, when multiple sites are sampled and when estimates of q are generated from a common distribution, abundance estimates can be improved in comparison with separately estimated site-specific q (Rivot et al. 2008). When using a Bayesian approach with a prior distribution that appropriately informs the catchability parameter, abundance estimates can be more accurate and precise than those obtained when an uninformative prior is used (Hedger et al. 2013). Wyatt (2002) developed an early hierarchical removal model using Bayesian methods that resulted in more accurate and precise estimates for multiple-site studies than were produced by fixed-effects models. Mäntyniemi et al. (2005) further developed the Wyatt (2002) model to allow for declining q over successive passes rather than assuming equal q among passes. Ruiz and Laplanche (2010) found that declines in q over successive passes could be a result of differences in q among fish sizes. Often, larger fish have higher q than smaller fish; thus, a higher proportion of large fish is caught during early passes, leaving a higher proportion of smaller, less-catchable fish during later passes, which leads to a decline in q by pass. The use of removal models that appropriately account for patterns in catchability can result in improved abundance estimates.

We used an experimental approach in which known numbers of larval lampreys were sampled, allowing us to examine catchability via backpack electrofishing and to assess the accuracy and precision of abundance estimates generated by six removal models that each assumed a different catchability pattern. Specific objectives were to (1) evaluate q of larval lampreys at each electrofishing pass, (2) examine the possible effects of lamprey TL and density on q, (3) assess the accuracy and precision of lamprey abundance estimates generated by the six removal models, and (4) simulate the accuracy expected under different levels of sampling effort. Our results can be used to guide future research studies and monitoring programs for larval lampreys.

METHODS

Field methods.—We conducted depletion sampling in experimental net-pen enclosures (hereafter, “enclosures”) that were seeded with known numbers of larval lampreys. Depletion sampling was conducted in Cedar Creek, a third-order (1:100,000-scale) tributary to the Lewis River (Columbia River basin) in Clark County, southwest Washington. Sampling was conducted during four periods: August 2003 (14 enclosures; 24–130 larvae/enclosure), August–September 2004 (10 enclosures; 5–15 larvae/enclosure), September 2005 (27 enclosures; 4–16 larvae/enclosure), and September–October 2006 (18 enclosures; 4–8 larvae/enclosure). Enclosures were 1 m² (0.4-mm net mesh), as suggested by Torgersen and Close (2004) and Cowx et al. (2009). Enclosures were filled with about 15 cm of fine sand, as larval lampreys have been observed to burrow to 15 cm (or less) and appear to select fine substrates when available (Hardisty and Potter 1971; Smith et al. 2011; Liedtke et al. 2015). Sand was sourced from dewatered streambanks; thus, no larval lampreys could have been present in the sand before its placement into an enclosure. The enclosures were designed to prevent entrance or exit of any larval lampreys. Enclosures were placed in a 30-m-long × 5-m-wide glide, and water depth
inside each pen ranged from 21 to 62 cm. This glide was selected because it permitted habitat characteristics (visibility, depth, and velocity) to be generally similar within each enclosure. Enclosures were separated from each other by a minimum of 1 m, thereby preventing electrical output in one enclosure from affecting the adjacent enclosures (Luzier et al. 2006).

Enclosures were seeded with larval lampreys that were collected from Cedar Creek by using an AbP-2 backpack electrofisher (ETS Electrofishing, Verona, Wisconsin). The AbP-2 electrofisher produces two distinct pulse frequencies (or outputs) that are activated by separate switches on the anode pole (Weisser and Klar 1990). The primary output is pulsed DC in a 3:1 pulse pattern (i.e., every fourth pulse deleted), which appears to effectively stimulate the emergence of lamprey larvae from their burrows without inducing muscle tetany and immobilizing them in the substrate (Weisser and Klar 1990; Moser et al. 2007). The secondary output is a higher-frequency standard-DC pulse (30 Hz) that is activated to induce muscle tetany and to aid the dipnetting capture of emergent larvae in the water column (Weisser and Klar 1990; Hintz 1993; Bowen et al. 2003). The AbP-2 backpack electrofisher was specifically designed to target larval Sea Lampreys Petromyzon marinus (Weisser and Klar 1990), but it is now widely used to target the larvae of other lamprey species, including the Pacific Lamprey (Torgersen and Close 2004; Stone and Barns 2005; Jolley et al. 2012; Reid and Goodman 2015). Collected lampreys were anesthetized in a solution of tricaine methanesulfonate (MS-222), measured for TL (mm), and placed in a recovery bucket of fresh river water. Individuals at least 60 mm TL were identified as Pacific Lampreys according to their caudal pigmentation (Goodman et al. 2009); others were recorded as an unknown lamprey species since individuals smaller than 60 mm TL could be Pacific Lampreys or Lampeutra spp. lampreys. Enclosures were then seeded with known numbers of larval lampreys at varying densities. High densities of lampreys were seeded in enclosures during 2003 (24–130 larvae/m²), but densities in successive years were reduced to reflect those that are more likely to occur in nature (<16 larvae/m²; Silva et al. 2014; reviewed by Dawson et al. 2015). Larval lampreys ranged from 20 to 125 mm TL. In 2003 and 2004, lampreys of multiple sizes were seeded into each enclosure. In 2005 and 2006, the experimental approach was adapted to allow for comparison of q as a function of the lengths and densities represented in the wild. Enclosures were seeded at densities of 4, 8, or 16 larvae/m² (4, 8, or 16 individuals/enclosure) by using larvae from only one length-group: 20–40 mm (extra small), 50–70 mm (small), 80–100 mm (medium), or 110–125 mm (large).

Larvae were allowed to acclimate in the enclosures for a minimum of 24 h. Each enclosure (n = 69) was sampled with three to five backpack electrofishing passes by a two- or three-person crew. The duration of each pass was 90 s, with a 15-min break between passes. After each pass, collected lampreys were removed from the enclosure, counted, and released into the stream.

Estimating catchability and abundance.—All models were evaluated with Bayesian methods using OpenBUGs software (Spiegelhalter et al. 2010). Each model was run with two initial chains, an appropriate burn-in period to achieve convergence, and enough iterations to produce stable parameters as assessed by examining history and density plots (Kéry 2010; Spiegelhalter et al. 2010). For each estimated parameter (abundance, q, etc.), the median of the posterior distribution was used as a measure of central tendency (estimate), and the smallest interval that included 95% of the posterior distribution (highest posterior density credible interval [95% HPD-CI]) was used to illustrate precision. The 95% HPD-CIs are appropriate for posterior distributions that are unimodal, but they do not assume a particular distribution; they can be especially useful when a posterior distribution is asymmetrical (Ono et al. 2012; Holbrook et al. 2014), as was common for the abundance estimates we generated from removal sampling.

Our first objective was to evaluate q by electrofishing pass. To produce a general estimate of q (population-level estimate of q), we included all enclosures and all passes as samples. To evaluate patterns in q by electrofishing pass, we first included all enclosures as samples and then we included only enclosures in which at least one individual remained at the start of the fifth pass as samples. Catchability (qij) for each experimental enclosure i and each removal pass j was estimated from a binomial distribution with catch (Cij) and the actual number of individuals in the enclosure at the start of that pass (Nij). Overdispersion (variability greater than expected based on the binomial model) is common in biological studies. Any variability in qij exceeding the expected variability was assumed to be random and was estimated using a normal distribution on the logit scale (i.e., we estimated the logit of catchability, Lqij ~ Normal[LUq, σ]); thus, all qij were between 0 and 1 on the real scale (Kéry et al. 2009; Kéry and Schaub 2012; Servany et al. 2014). Estimates of LUq and σ were from uninformative priors (Normal[0, 100] and Uniform[0, 10]) as in Kéry and Schaub (2012).

Our second objective was to estimate q as a function of lamprey length-group (extra small, small, medium, and large) and density (4, 8, and 16 larvae/m²). We used logistic regression to predict the total proportion of larvae caught during the first pass, with density and length-group included as independent class variables, by using the methods and uninformative priors described by Kéry (2010).

Our third objective was to evaluate the accuracy and precision of abundance estimates produced by six removal models, each assuming a different function of q: standard q, equal q, declining q, quadratic, q, gamma q, beta q, and informed q. The standard q model is the most commonly used removal model; q was assumed equal for all passes but was estimated for each enclosure separately. The equal q model integrated information from all enclosures and passes to produce one estimate of q. For the declining q model (Mäntyniemi et al. 2005), we assumed equal q for all enclosures,
but we allowed \( q \) to decline with each pass according to the following pattern:

\[
q_j = \mu \frac{\eta}{\eta + j + 1},
\]

where \( \mu \) is catchability for the first pass, and \( \eta \) defines the decline pattern with each successive pass. As modeled by Mäntyniemi et al. (2005), \( \eta \) is nonnegative; as \( \eta \) increases, the pattern will approach that of equal \( q \). To allow for a more flexible pattern in \( q \) by pass (not just a linear decline), we evaluated the gamma \( q_j \) model, which assumed equal \( q \) for all enclosures but allowed \( q \) to vary among passes according to a gamma distribution, which can take on many shapes. Catchability in the gamma \( q_j \) model was estimated using a logit model so that \( q \) was between 0 and 1,

\[
q_{ij} = 1/(1 + \exp[-Lq_{ij}]),
\]

where \( Lq_{ij} = \mu \times \text{Gamma}(\alpha, \beta) \).

Hyperparameters \( \alpha \) and \( \beta \) were estimated from uninformative gamma priors (Gamma[0.01, 0.01]); the scaling term (\( \mu \)) was estimated from an uninformative normal distribution (Normal[0, 10^5]). The hierarchical beta \( q_{ij} \) model (developed by Wyatt 2002) assumed that all \( q_{ij} \) were estimated from a beta distribution, with hyperparameters \( \alpha \) and \( \beta \) again estimated from uninformative gamma priors. The beta \( q_{ij} \) model not only allowed for variability in \( q \) among enclosures and among removal passes but also facilitated calculation of the correlation \( \rho \) between catches, as was described by Hisakado et al. (2006) and used by Martin et al. (2011) to evaluate correlated behavior,

\[
\rho = \frac{1}{\alpha + \beta + 1}.
\]

For the informed \( q_{ij} \) model, we evaluated the use of an informative prior on \( q \). All \( q_{ij} \) were estimated from an overdispersed binomial model, with mean and SD values (LU/q and \( \sigma \)) estimated outside the model. Thus, information from the given population-level mean estimate of \( q \) along with catches from the specific unit and pass were used together to generate the estimate of \( q \) for that unit and pass along with the specific abundance estimate for that enclosure. The informed \( q_{ij} \) model illustrates the potential accuracy and precision that could result from the use of an informative prior, although this is an artificial situation conducted for evaluation only; usually, informative priors are based on the results of an independent or past study or are based on expert opinion (McCarthy and Masters 2005).

Each removal model assumed that catches \( C_{ij} \) from enclosure \( i \) and pass \( j \) were from a binomial distribution with \( EN_{ij} \) equal to the estimated number of individuals in the enclosure at the start of the pass and \( q_i \) equal to the specified catchability function. Unless otherwise noted (and similar to Mäntyniemi et al. 2005), prior distributions for estimated abundances (the estimated number of larvae in each enclosure before the first pass was completed, \( EN_{ij} \)) were from exponentiated uniform distributions (Uniform[0, 7], assuming abundance from 1 to 1,097), and prior distributions for \( q \) were from vague beta distributions (Beta[1.1, 1.1]). To compare estimated larval abundances to true numbers that were seeded into the enclosures, we estimated bias for each enclosure in accordance with Martin et al. (2011),

\[
\text{Bias} = \frac{EN_{i1} - Ni}{Ni},
\]

where \( N_i \) is equal to the actual number of seeded individual lampreys in enclosure \( i \). A positive value for bias suggests that larval abundance was overestimated, and a negative value suggests that abundance was underestimated. The mean bias and SD of bias were calculated for each model. We also used linear regression of \( EN_{i1} \) against the actual number seeded into the enclosure \( (N_i) \) to evaluate any impacts of larval density on abundance estimates over the total range of densities examined. Precision was evaluated visually by examining the 95% HPD-CIs for the abundance estimates. Variability was also examined by calculating the coefficient of variation (CV = [SD/median estimate] \times 100).

Our fourth objective was to evaluate the expected accuracy of abundance estimates produced at different levels of sampling effort. The accuracy of abundance estimates generated by removal models could potentially be improved by increasing both the number of 1-m² quadrats sampled in a target area (i.e., a stream or basin) and the number of passes completed in each sampled quadrat. We estimated the expected mean bias in abundance estimates when three to five electrofishing passes are conducted at 2–20 (in increments of 2) 1-m² quadrats in a target area. To examine mean bias in relation to the number of passes completed, we ran three removal models (standard \( q_i \), beta \( q_{ij} \), and informed \( q_{ij} \)) including data from three, four, or five passes to produce estimates of \( q \) as well as mean and SD values for bias. Since estimated distributions for abundance were asymmetrical and since most appeared similar to lognormal distributions, estimates of bias (mean and SD) were simulated as lognormal. To simulate expected accuracy relative to the number of quadrats sampled, we generated 1,000 random deviates of expected mean bias resulting from sampling 2–20 (by 2) 1-m² quadrats. Estimates of individual bias were drawn from a lognormal distribution with the mean and SD from the appropriate removal model. Simulations were performed by using R software (R Core Team 2013). We report when mean bias was less than 20% for at least 80% of the simulations; we consider this a threshold level of sampling effort to produce acceptably accurate abundance estimates (i.e., what we deem as acceptable) for the target area.
RESULTS

We sampled at 69 enclosures to evaluate patterns in the $q$ of larval lampreys via backpack electrofishing. Of those 69 enclosures, 55 were sampled by four passes, 8 were sampled by four passes, and 6 were sampled by three passes. Among the 55 enclosures in which five passes were completed, 42 had at least one individual remaining at the start of the fifth pass; in the other 13 enclosures (unknown to the samplers), all individuals were caught before the start of the fifth pass. After five passes, a mean of 22% (range = 0–62%) of individuals remained in each enclosure. The population-level estimate of $q$ for larval lampreys at each backpack electrofishing pass was 0.28 ($LUq = -0.95, \sigma = 0.48$). There was substantial variability among experimental enclosures, and $q$ was not equal among all five passes (Table 1; Figure 1). On average, $q$ exhibited a dome-shaped pattern in relation to pass number (1–5), with the highest $q$ occurring for the second pass and the lowest $q$ observed for the fifth pass (Figure 1). When data from all enclosures ($n = 69$) were considered, the 95% HPD-CIs overlapped for passes 1–4, but the 95% HPD-CI from the final pass did not overlap those for passes 1–3. The 95% HPD-CI of the SD did not approach zero, illustrating overdispersion. No obvious pattern was observed for variability in $q$ in relation to pass (there was no indication that variability in $q$ increased or decreased with successive passes).

Proportions of larvae collected during the first electrofishing pass ranged from 0.20 (95% HPD-CI = 0.12–0.29) for large individuals (80–125 mm TL) at high densities (16 larvae/m$^2$) to 0.37 (95% HPD-CI = 0.20–0.55) for extra-small individuals (20–40 mm TL) at low densities (4 larvae/m$^2$; Figure 2).

The catchability function in the model affected the accuracy and precision of larval lamprey abundance estimates (Table 2; Figures 3, 4). For the standard $q_j$ model, 95% HPD-CIs on all but one enclosure included the true number of larvae that were seeded into the enclosure; however, 95% HPD-CIs were large and posterior distributions were highly asymmetrical for most enclosures, indicating low precision when $q$ was estimated for each enclosure separately (Figure 3). Although some estimates were either positively or negatively biased, abundance estimates from the equal $q$ and beta $q_j$ models were generally accurate, and 95% HPD-CIs were considerably smaller than those from the standard $q_j$ model (Table 2; Figure 3). The beta $q_j$ model assumed variability in $q$ among passes and among enclosures, which resulted in slightly larger 95% HPD-CIs than were observed for the equal $q$ model, although the correlation between catches was negligible (Table 2). The declining $q_j$ and gamma $q_j$ models both underestimated $q_j$ for each pass and generally overestimated abundance (Table 2; Figure 3).

![Figure 1](image)

**Figure 1.** Model estimates of larval lamprey catchability (±95% highest posterior density credible intervals) based on all enclosures ($n = 69$) or a subset of enclosures ($n = 42$) that were sampled by five passes and contained at least one larval lamprey at the start of the fifth pass.

<table>
<thead>
<tr>
<th>Pass</th>
<th>$n$</th>
<th>$Uq$</th>
<th>$LUq$</th>
<th>$\sigma$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All enclosures</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>69</td>
<td>0.30 (0.26, 0.34)</td>
<td>-0.84 (-1.03, -0.65)</td>
<td>0.50 (0.31, 0.73)</td>
</tr>
<tr>
<td>2</td>
<td>69</td>
<td>0.33 (0.29, 0.36)</td>
<td>-0.72 (-0.91, -0.55)</td>
<td>0.34 (0.03, 0.56)</td>
</tr>
<tr>
<td>3</td>
<td>65</td>
<td>0.28 (0.23, 0.33)</td>
<td>-0.94 (-1.17, -0.69)</td>
<td>0.47 (0.23, 0.74)</td>
</tr>
<tr>
<td>4</td>
<td>53</td>
<td>0.22 (0.16, 0.28)</td>
<td>-1.24 (-1.54, -0.71)</td>
<td>0.58 (0.20, 1.06)</td>
</tr>
<tr>
<td>5</td>
<td>42</td>
<td>0.14 (0.08, 0.19)</td>
<td>-1.85 (-2.26, -0.94)</td>
<td>0.46 (0.03, 1.24)</td>
</tr>
<tr>
<td>Subset of enclosures</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>42</td>
<td>0.22 (0.19, 0.26)</td>
<td>-1.26 (-1.46, -1.04)</td>
<td>0.20 (0.01, 0.49)</td>
</tr>
<tr>
<td>2</td>
<td>42</td>
<td>0.28 (0.22, 0.32)</td>
<td>-0.95 (-1.21, -0.75)</td>
<td>0.20 (0.01, 0.56)</td>
</tr>
<tr>
<td>3</td>
<td>42</td>
<td>0.24 (0.17, 0.31)</td>
<td>-1.17 (-1.54, -0.81)</td>
<td>0.55 (0.24, 0.95)</td>
</tr>
<tr>
<td>4</td>
<td>42</td>
<td>0.21 (0.14, 0.26)</td>
<td>-1.35 (-1.80, -1.01)</td>
<td>0.36 (0.02, 0.87)</td>
</tr>
<tr>
<td>5</td>
<td>42</td>
<td>0.14 (0.08, 0.19)</td>
<td>-1.85 (-2.26, -0.94)</td>
<td>0.46 (0.03, 1.24)</td>
</tr>
</tbody>
</table>
Those two models resulted in lower precision for estimates relative to the equal \( q \) and beta \( q_{ij} \) models. Like the declining \( q_i \) model, the gamma \( q_i \) model detected a reduction in \( q \) with successive passes, which resulted in positively biased estimates of abundance; this model was not able to detect the dome-shaped pattern in \( q \) that was apparent when we examined the pattern in catches over all enclosures (Figure 1). The informed \( q_{ij} \) model (the model that used an informative prior) produced generally accurate and precise abundance estimates (Figure 3). The CVs were much higher for the standard \( q_i \) model than for any other model (Figure 4). We observed a general decline in CV (although not in a linear pattern) as the actual number of larvae in the enclosure increased, suggesting comparatively lower precision of abundance estimates for enclosures that were seeded with lower numbers of larval lampreys (Figure 4).

As the number of electrofishing passes increased, estimates of mean bias became more negative and estimates of the SD in bias became smaller. Mean estimates of bias were negligible when all five passes were completed and when data were evaluated with either the beta \( q_{ij} \) model or the informed \( q_{ij} \) model; mean bias was 10% when data from at least four passes were evaluated using the beta \( q_i \) model or when data from at least three passes were evaluated using the informed \( q_{ij} \) model (Table 3; Figure 5). When the standard \( q_i \) model was used, average bias was not less than 20% for 80% of the simulations, even when simulations were produced under an assumption that twenty 1-m² quadrats were sampled by five passes. However, for the beta \( q_{ij} \) model, less than 20% average bias occurred for 80% of the simulations when four passes were completed from at least 14 quadrats or when five passes were completed from at least four quadrats. For the informed \( q_{ij} \) model, less than 20% average bias was found for 80% of simulated samples when four passes were made from at least 12 quadrats or when five passes were completed from at least four quadrats.

TABLE 2. Catchability (\( q \)) estimates (with 95% highest posterior density credible intervals [95% HPD-CI] in parentheses) produced from the six removal models for larval lampreys sampled by backpack electrofishing (\( i \) = experimental enclosure; \( j \) = electrofishing pass; \( LUq \) = logit of catchability; \( \sigma \) = SD of \( LUq \); \( \eta \) = defines the decline pattern with each successive pass; \( \alpha \) and \( \beta \) = hyperparameters estimated from uninformative priors; \( \rho \) = correlation coefficient). The proportion (\( \text{Prop} \)) of enclosures for which the true number was within the rounded 95% HPD-CI (i.e., lower limit rounded down and upper limit rounded up to the nearest whole number) is presented. The asterisk indicates values that were used as initial values in the model rather than being estimated by the model.

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimates of ( q )</th>
<th>Other parameters</th>
<th>Mean bias</th>
<th>SD of bias</th>
<th>Prop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard ( q_i )</td>
<td>Mean ( q = 0.35 \ (0.31, 0.38) )</td>
<td>( q_i = 0.11-0.80 )</td>
<td>0.38 (0.00, 1.47)</td>
<td>1.55 (0.28, 8.29)</td>
<td>0.96</td>
</tr>
<tr>
<td>Equal ( q )</td>
<td>( q = 0.32 \ (0.29, 0.36) )</td>
<td></td>
<td>-0.04 (-0.09, 0.01)</td>
<td>0.24 (0.20, 0.29)</td>
<td>0.83</td>
</tr>
<tr>
<td>Declining ( q_i )</td>
<td>( q_1 = 0.26 \ (0.17, 0.33) ) ( q_2 = 0.22 \ (0.11, 0.30) ) ( q_3 = 0.18 \ (0.08, 0.29) ) ( q_4 = 0.16 \ (0.06, 0.26) ) ( q_5 = 0.14 \ (0.05, 0.25) )</td>
<td>( \eta = 4.81 \ (1.70, 14.58) )</td>
<td>0.23 (-0.06, 0.81)</td>
<td>0.38 (0.23, 0.68)</td>
<td>0.96</td>
</tr>
<tr>
<td>Gamma ( q_{ij} )</td>
<td>( q_1 = 0.27 \ (0.16, 0.34) ) ( q_2 = 0.22 \ (0.10, 0.32) ) ( q_3 = 0.18 \ (0.08, 0.30) ) ( q_4 = 0.16 \ (0.05, 0.29) ) ( q_5 = 0.15 \ (0.04, 0.28) )</td>
<td>( \alpha = 1.40 \ (1.17, 1.56) ) ( \beta = 39.74 \ (12.39, 81.41) )</td>
<td>0.21 (-0.07, 0.94)</td>
<td>0.37 (0.21, 0.72)</td>
<td>0.96</td>
</tr>
<tr>
<td>Beta ( q_{ij} )</td>
<td>Mean ( q = 0.32 \ (0.28, 0.36) )</td>
<td>( q_{ij} = 0.25-0.41 )</td>
<td>-0.04 (-0.09, 0.03)</td>
<td>0.25 (0.20, 0.31)</td>
<td>0.86</td>
</tr>
<tr>
<td>Informed ( q_{ij} )</td>
<td>( Uq = 0.28 \ (LUq = -0.95, \sigma = 0.48) \star )</td>
<td>( q_{ij} = 0.18-0.46 )</td>
<td>0.01 (-0.03, 0.05)</td>
<td>0.28 (0.23, 0.34)</td>
<td>0.90</td>
</tr>
</tbody>
</table>
DISCUSSION

Our results suggest that depletion sampling by backpack electrofishing techniques can be used to effectively assess larval lamprey abundance in wadeable streams. We estimated the average probability of catching a larval lamprey during a 90-s electrofishing pass in a 1-m² enclosure to be 0.28. In our experimental setting, removal models produced accurate and precise estimates of larval lamprey abundance when information from multiple enclosures was used to inform the catchability parameter. Although we observed a dome-shaped pattern in q relative to pass number (1–5), models assuming equal q (equal q model) or that q was a random value from a distribution (beta qij model) produced the best estimates of abundance. Under the diverse environmental conditions expected in a natural system, the completion of five electrofishing passes from multiple 1-m² quadrats in the target area (i.e., stream or basin) and the modeling of q either as a random value (beta qij model) or as a function of habitat covariates expected to impact q would likely result in the most accurate and precise estimates of abundance for the target area as a whole. Quantification of larval lamprey abundance could benefit lamprey research and conservation substantially. Assessment of local abundance could be used to characterize larval habitat preferences or to monitor the effects of stream habitat restoration, alteration, or degradation on local status.

Hierarchical removal models in which q for all sites or passes is assumed to come from a common distribution appear useful for multiple species because such models draw on strength from multiple samples (i.e., sites and passes) but also allow for differences among sites and passes (i.e., due to environmental conditions, habitat, or density; Wyatt 2002; Rivot et al. 2008; Korman et al. 2016). Since larval lampreys exhibit patchy distributions even at a small scale (Ojutkangas et al. 1995; Torgersen and Close 2004; Lasne et al. 2010), the sampling of multiple 1-m² quadrats would potentially produce a more informed assessment for a target area (stream or basin) than the sampling of a single, larger site, such as a reach or habitat unit. Korman et al. (2016) used a hierarchical Bayesian model to estimate riverwide abundances for patchily distributed juvenile steelhead Oncorhynchus mykiss and found that increasing the number of sampled sites improved the estimates. For larval lampreys, estimating abundance at multiple 1-m² quadrats would provide added distribution information from the target area and would help in quantifying uncertainty,
which is crucial for extrapolating abundance to the entire target area (scaling up the estimates of abundance from 1-m² quadrats to the entire stream or basin). Our simulation results suggested that acceptable accuracy (<20% average bias for 80% of simulations) could be achieved by conducting five removal passes in four 1-m² quadrats; sampling more quadrats by using four

TABLE 3. Estimates of larval lamprey catchability ($q$) and bias relative to the number of electrofishing passes (3, 4, or 5) from three removal models with different assumptions regarding $q$ of larval lampreys (95% highest posterior density credible intervals are shown in parentheses). All models were run using only data from the 55 experimental enclosures in which all five passes were completed, but estimates for the number of passes = 3 or 4 were generated only with the data from the first three or four of the five passes.

<table>
<thead>
<tr>
<th>Model</th>
<th>Number of passes</th>
<th>Catchability</th>
<th>Mean bias</th>
<th>SD of bias</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Standard $q_i$</td>
<td>0.33 (0.28, 0.38)</td>
<td>0.33 (0.28, 0.37)</td>
<td>0.34 (0.30, 0.38)</td>
<td></td>
</tr>
<tr>
<td>Beta $q_{ij}$</td>
<td>0.21 (0.13, 0.29)</td>
<td>0.26 (0.20, 0.32)</td>
<td>0.29 (0.25, 0.34)</td>
<td></td>
</tr>
<tr>
<td>Informed $q_{ij}$</td>
<td>0.29 (0.27, 0.30)</td>
<td>0.29 (0.27, 0.30)</td>
<td>0.29 (0.28, 0.30)</td>
<td></td>
</tr>
<tr>
<td>Standard $q_i$</td>
<td>0.89 (0.13, 2.72)</td>
<td>0.65 (0.08, 2.23)</td>
<td>0.43 (–0.01, 1.71)</td>
<td></td>
</tr>
<tr>
<td>Beta $q_{ij}$</td>
<td>0.38 (–0.01, 0.92)</td>
<td>0.10 (–0.05, 0.29)</td>
<td>–0.02 (–0.08, 0.07)</td>
<td></td>
</tr>
<tr>
<td>Informed $q_{ij}$</td>
<td>0.10 (0.01, 0.19)</td>
<td>0.04 (–0.02, 0.11)</td>
<td>–0.01 (–0.05, 0.05)</td>
<td></td>
</tr>
<tr>
<td>Standard $q_i$</td>
<td>2.71 (0.62, 12.52)</td>
<td>2.15 (0.38, 10.97)</td>
<td>1.63 (0.30, 8.90)</td>
<td></td>
</tr>
<tr>
<td>Beta $q_{ij}$</td>
<td>0.64 (0.37, 1.07)</td>
<td>0.38 (0.27, 0.53)</td>
<td>0.28 (0.22, 0.35)</td>
<td></td>
</tr>
<tr>
<td>Informed $q_{ij}$</td>
<td>0.48 (0.36, 0.62)</td>
<td>0.35 (0.27, 0.45)</td>
<td>0.28 (0.22, 0.36)</td>
<td></td>
</tr>
</tbody>
</table>
passes could also result in similar accuracy and could provide more detailed information on larval lamprey distribution. However, CVs showed that precision for the abundance estimates increased with the number of larvae that were seeded in the enclosure; thus, sampling a larger number of 1-m² quadrats would be required in target areas with low densities to obtain the same level of accuracy and precision. Furthermore, we did not sample from enclosures containing fewer than four individuals, but removal models estimate abundance from the pattern of declining catches, so they would be unlikely to perform as well when applied to target areas (or quadrats) with very low densities (<4 larvae/m²); in such cases, larger quadrats (a larger area that would contain more individuals) would be beneficial.

Unlike most fish that are sampled by electrofishing, larval lampreys burrow in fine substrates and must be stimulated to emerge into the water column for capture. Differences in burrow depth and distance from the electric field may affect a larval lamprey’s response to electrofishing: some individuals may immediately respond as predicted, others may require multiple passes to enter the water column, and still others may experience immobilization while remaining burrowed (Pajos and Weise 1994; Bowen et al. 2003). Habitat characteristics specific to the target area and quadrat, especially sediment, may affect lamprey burrowing depth and \( q \). Further research evaluating \( q \) under a variety of habitat conditions is warranted. Differences in sampling procedures are also likely to affect the larval response. Therefore, estimating \( q \) directly within a study by completing five electrofishing passes in multiple quadrats would likely result in the most accurate estimates of abundance.

When estimating \( q \) by depletion sampling in multiple quadrats is not an option, the use of an informative prior for the catchability parameter could improve the precision of larval abundance estimates. Although prior information is often used to guide research needs, study design, and interpretation of results, it is rarely used to explicitly inform analysis and
Assessment of larval abundance is important for research and conservation in a stream or basin; however, it would require substantial effort to complete on a larger scale, thus increasing interest in occupancy sampling as a method to assess rangewide status, especially for Pacific Lampreys (Jolley et al. 2012; Dunham et al. 2013; Reid and Goodman 2015). However, abundance estimation on a small scale could guide occupancy sampling design at the large scale by increasing our understanding of detection probability. The probability of detecting whether a target area is occupied is a function of abundance and distribution in the target area as well as the efficiency of the sampling method. Thus, information on $q$ and expected density in different habitats could help to identify the probability of detecting lampreys and, as such, could inform study design for occupancy sampling. Results from our study suggest that analysis of catch depletion data with a hierarchical removal model could facilitate the examination of expected $q$ and expected density under different environmental conditions as long as multiple 1-$m^2$ quadrats can be sampled.

**ACKNOWLEDGMENTS**

We thank T. Collier, B. Lé, S. Lohr, J. Stone, and C. Wang (U.S. Fish and Wildlife Service) for field assistance. Previous drafts of this paper were improved by comments from anonymous reviewers. References to trade names do not imply endorsement by the U.S. Government. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

**REFERENCES**


