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Larval lamprey distribution and habitat use in small stream channels on the Oregon coast

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Larval lamprey distribution and habitat use in small stream channels on the Oregon coast

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Abstract

Potential fish passage barriers have been identified in over 4,100 small streams (i.e., <8 m wide) in coastal Oregon basins from the Nehalem River south to the Coos River and may be blocking Pacific lamprey access to spawning and rearing habitat. The impact of these barriers is unknown because of a lack of information on how Pacific lampreys use these small stream habitats. We conducted a pilot study using multi-state occupancy modeling to better understand distribution, habitat use, and sampling detection of larval Pacific lampreys in small streams to improve monitoring techniques and begin to evaluate the effect of barriers on lampreys in the Coastal Oregon Province. Electrofishing surveys were conducted by a two-person field crew from July through October, 2012. Sampling occurred in two small wilderness basins and streams in the Siuslaw, Umpqua, and Coos river basins. Streams channels ranged from 0.8 to 20 m wetted width and contained no known barriers to upstream migratory fish passage. Pacific lamprey larvae occupied all streams in the sample frame and overlapped substantially with Western brook lamprey in longitudinal distribution patterns. Detection probability of larvae in the low abundance state was high ($p^1=0.85$). Larvae in general were more likely to occupy pools than fast-water units and were rarely detected in high abundance in fast-water units. Pacific larvae were more abundant and occupied a greater proportion of the sample sites compared to Western brook larvae. Pacific lamprey larvae were detected in stream channels as small as 4 m wide. Larval occupancy and detection estimates obtained in this study are useful for designing future studies. Several improvements to the study design will lead to more precise estimates and greater scope of inference in continued research into larval distribution in small stream channels.

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Introduction

There is concern that Pacific lamprey (Entosphenus tridentata) populations have declined throughout much of their distribution in the United States (Close 2001, ODFW 2005, Luzier et al. 2009, Moyle et al. 2009, Swift and Howard 2009). However, in most areas there is little information about population status and the factors that may be limiting their distribution and abundance (CRITFC 2004, ODFW 2005). Despite this lack of information, it is generally accepted that the construction of barriers that block or provide inadequate passage for adults migrating upstream to spawn represents one of the key factors in the decline of Pacific lamprey where counts of migrating adults are kept (Swift and Howard 2009, Mesa and Copeland 2009, Luzier et al. 2011). Indeed, recent research in the Columbia River mainstem has highlighted the passage problems for adult lamprey at large hydroelectric dams (Moser et al. 2002, Moser et al. 2008, Keefer et al. 2009). Interestingly though, there has been little attention paid to the impact of smaller barriers (e.g., culverts) on lamprey distribution and abundance. A number of studies have demonstrated that these smaller barriers have substantially reduced habitat available to salmonids (e.g., Botkin et al. 1994, Mirati 1999). In coastal Oregon basins from the Nehalem River south to the Coos River, there are 4,177 known and potential fish passage barriers (Oregon Fish Passage Barrier Data Standard dataset, Figure 1). This dataset, referred to henceforth as the Oregon fish barrier dataset, does not represent a complete census of potential barriers in the region, but it is the most comprehensive dataset available. These barriers are typically culverts associated with road crossings and generally affect small streams (Figure 2). Given the large number of barriers, and their unknown influence on Pacific lamprey, this has been identified as a critical uncertainty in need of research (Mesa and Copeland 2009).

To evaluate how artificial barriers have affected Pacific lamprey populations, it is first important to understand the factors that influence lamprey occupancy and abundance in smaller streams within river networks where there are no known barriers to adult migration. Pacific lamprey spawning is typically associated with relatively low elevations and large stream sizes (Pirtle et al. 2002, Gunckel et al. 2009), and both Pacific and Western brook lamprey larvae can occupy the largest stream channels in a river network (Jolly et al. 2011, 2012). However, little is known about Pacific lamprey use of smaller streams and the relative importance of these habitats to lamprey populations. There is some evidence that Pacific lamprey do use smaller stream channels for spawning and larval rearing. For example, Torgersen and Close (2004) documented larval lamprey rearing in stream channels as small as 4 m wetted width in the Middle Fork John Day River, Columbia Basin, Oregon. In addition, the distribution of adults prior to, and during spawning in the Smith River basin, in the Coastal Oregon Province, suggests that Pacific lamprey adults use channels with wetted widths as small as 5 m (Gunckel et al. 2009, Starcevich et al. 2013). Thus, it is reasonable to assume that barriers that prevent access to smaller tributaries will adversely affect lamprey populations.

Studies of larval lamprey microhabitat use have shown that these benthic filter feeders are associated with fine sediment and patchily distributed depositional areas, such as eddies,

backwaters, side channels, and stream margins (Beamish and Lowartz 1996; Sugiyama and Goto 2002). However, the microhabitat focus in these studies does not allow for an evaluation of abundance and distribution patterns at larger spatial scales (Torgersen and Close 2004), which leaves a gap in our ability to manage lamprey populations.

To determine how fish passage barriers are affecting lampreys, there is a need for accurate and unbiased estimates of the distribution and relative abundance of Pacific lampreys in small streams. Traditional surveys to obtain these data have most commonly used mark-recapture or depletion methodology, which generally requires substantial resources and effort. Furthermore, the precision of these estimates is often relatively poor and can only be improved with much greater effort across the sample frame. Interestingly though, detection of a response to changes in habitat variables (e.g., access) do not require absolute estimates of abundance so managers are often better served by having a general understanding of how fish are distributed throughout a system and at what relative abundance (e.g., rare, common). Occupancy sampling designs place an emphasis on estimating distribution and relative abundance. Occupancy estimation often requires less effort and can provide managers with a surrogate to abundance from which to base judgments about a species status or management action. By this standard, the efficacy of future management actions can be evaluated within an existing monitoring framework. The reduction in resources and effort needed in implementing occupancy sampling design ensures that long-term monitoring can be maintained given limited funding. Occupancy sampling designs have been increasingly used in fisheries ecology and this approach was recently applied to larval fish ecology in small streams in the Great Plains, USA (Falke et al. 2010).

A primary source of error in sampling or monitoring programs is caused by non-detection of a species that is actually present at a site (MacKenzie et al. 2006). When this error is not accounted for, estimates of occupancy and relative abundance and the effects of a predictor variable can be biased (MacKenzie et al. 2006). Occupancy sampling designs allow one to estimate the probability of detection by re-visiting sample sites multiple times. This sampling design allows one to construct a capture history for a site, which, when combined with similar data at other sites in the sample frame, forms the basis for estimating the probability of detection.

Our objective was to determine the effect of barriers on small streams on lamprey distribution and relative abundance. We had three sub-objectives:

- 1) Evaluate the distribution and abundance of larval lamprey in small streams with no known barriers
- 2) Evaluate the relationship between habitat and larval lamprey distribution and abundance
- 3) Develop a survey design to optimize sampling efficiency and precision of estimates

To address these sub-objectives, we surveyed several small streams in mid-coastal Oregon using an occupancy design to estimate occupancy and detection probability in different habitats. Our data can be used to inform future monitoring designs and prioritize barrier removal.



Figure 1. Map of 4,177 known and potential fish passage barriers in Oregon coastal basins. Point data are from the Oregon Fish Passage Barrier Data Standard dataset, ODFW.



Figure 2. Frequency distribution of barrier width in the Coastal Oregon Province; 96% of which are culverts.

Study Area

The study was conducted in the mid-region of the Oregon Coast, USA. This region experiences a maritime climate of moderate temperatures with frequent rain storms and flashy flows October through June and low precipitation and baseflow conditions July through September. The sample streams were selected to provide longitudinal distribution information on larval lamprey rearing in streams without barriers. We first selected watersheds in which the main channels did not contain known or potential barriers to salmonids, based on the fish barrier dataset and local knowledge. We then filtered stream list to only include those that were either federally managed or had few private landowners to ensure adequate access. Last, we weighted basins based on their proximity to each other (closer = higher ranking) to reduce labor and travel costs. Given these criteria, we selected Wolf Creek (Siuslaw River basin), Smith River (Umpqua River basin), and West Fork Millicoma River (Coos River basin), which are three adjacent coastal basins with sedimentary geology (Figure 3). Exploratory surveys were also conducted in Rock Creek and Cummins Creek, two small wilderness basins with volcanic headland geology. The sample frame ranged from 56 to 416 m in elevation and 0.1 to 2.9% in reach slope (Table 1). The season was defined as the period of base flow conditions from July through mid-October.

Methods

Sample site selection

Because we were interested in the distribution of larval lamprey in smaller streams, the lower limit of sampling in each basin was at the point where the wetted width of the main channel was >15 m during base flow. To detect longitudinal changes in occupancy and abundance, each watershed was divided into a series of potential sample reaches using tributary junctions. We

then selected a starting reach at random from the first two reaches in each stream, and sampled every other reach in an upriver direction. Within each sample reach, we established three start locations systematically spaced at 10%, 50%, and 90% of the reach length (coordinates were identified using GIS). Sampling sites at each start location consisted of a pool and fastwater channel unit. Any off-channel habitat units (e.g., backwaters, isolated pools, secondary channels) adjacent to the sample site were also surveyed for larvae. Surveyors located a site using a global positioning system [GPS] and sampled the channel unit nearest to the site point. After conducting a fish survey at that channel unit, the crew moved upstream past at least two channel units to sample the alternate channel unit type. The spatial separation between sampled channel units was incorporated to reduce dependence between samples. To estimate detection probability, we used a double sampling design in which a subset of the channel units were surveyed a second time (MacKenzie et al. 2006). For channel units in which no Pacific lamprey larvae were detected, every other unit was re-sampled. For channels units in which larvae were captured, every third unit was re-sampled. To satisfy the assumption of a closed population (MacKenzie et al. 2006), this second visit occurred within a week of the first, and sampling in general occurred during a season in which little larval movement was expected (Hardisty and Potter 1971).

Fish sampling

Fish were captured by electrofishing using an AbP-2 electrofisher (ETS Electrofishing, LLC). The 2-person crew conducted a slow, single-pass in each channel unit beginning at the downstream end of the unit and moving upstream. The primary electrofishing channel delivered 3 pulses/s (125 VDC) at a 25% duty cycle, with a 3:1 burst pulse train to draw larvae from the substratum (Weisser and Klar 1990). The second electrofishing channel, which was rarely needed, was set to 30 pulses/s (125 VDC) to facilitate capture of larvae in the water column. Larval lamprey were netted and placed in a bucket with aeration on the stream side. After completing an individual channel unit, the lamprey were anesthetized using ~50 mg/L of MS-222 and sodium bicarbonate solutions and the length and species of all larvae >60 mm total length [TL] was documented. The genera of larvae (>60 mm TL) was identified by examination of caudal fin and ridge characters and ventral pigmentation (Goodman et al. 2009). Surveyors received field training in the use of these characteristics prior to the start of sampling and used a field identification key for lampreys of western Oregon developed by Stewart Reid (Western Fishes) to identify Western brook and Pacific lamprey larvae. After processing, larvae were allowed to recover prior to release. Surveyors also visually estimated (without capture) the number of larvae that were too small (<60 mm TL) to be visually identified to species level.

Habitat surveys

We completed a habitat inventory (modified from Moore et al. 2005) for each channel unit at the completion of the first visit to a site. Three transects were spaced at 25%, 50%, and 75% of the unit length. Along these transects, measurement were taken of wetted channel width, active channel width, and the depth at 25%, 50%, and 75% of the wetted width. Sediment was

categorized as Type 1 (i.e., organic matter, silt, some sand), Type 2 (i.e., sand and small gravel), or Type 3 (i.e., gravel and larger sediment sizes) after Slade et al. (2003), which corresponded respectively to ideal, adequate, and inadequate larval lamprey rearing habitat. In each unit, we estimated the percentage of area covered by each sediment type. In addition, we measured the average length, average width, and maximum depth for each patch of type 1 sediment. Maximum depth was measured by pushing (by hand) a 6.5 mm diameter piece of graduated rebar into the sediment patch in several locations within the patch and recording the deepest measurement. Counts of large wood pieces were categorized as in-stream or overhanging, and short (<2 m long) or long (>2 m long). Other characteristics recorded included channel length, maximum depth and pool tail crest (pools only), riparian canopy cover, channel slope (in fastwater units), channel form, valley width index, riparian vegetation class, and land use type. Off-channel habitats were measured separately from the main channel unit for length, width, and depth; sediment area was estimated for each category type; and Type 1 sediment patches were measured for length, width, and depth.

Data analysis

We used a single-season, multi-state occupancy model (MacKenzie et al. 2006) to estimate occupancy and detection probability for Pacific and Western brook lamprey larvae and to evaluate the influence of habitat on occupancy and relative abundance. Larval counts were categorized into three states: non-detection, low abundance, and high abundance. Criteria for the states are found in the results section below. Using larval counts obtained from double sampling, we estimated the probability that larvae occupied a channel unit in low abundance (ψ^1), the probability that larvae occupied a channel unit in high abundance (ψ^2), and the probability of detecting each species given that the channel unit was occupied in low abundance (ρ^1) or high abundance (ρ^2). Probabilities are reported as figures between 0 (i.e., no probability of species occupancy) and 1 (i.e., 100% probability of occurrence).

We constructed several models using larval abundance state as the response variable and channel unit type, species, unit width, unit area, channel unit sediment area, and off-channel unit sediment area as explanatory variables. We used Akaike information criterion model selection procedures with a correction factor for low sample size [AIC_c] to select the models of best fit. To model detection, the low abundance state (ρ^1) was set as the reference and we evaluated single-factor and single-covariate models of the high abundance state (ρ^2). We used the best fitting detection model as the baseline for modeling occupancy. To estimate occupancy, we modeled the above covariates individually and as part of additive and interaction models. Models were ranked by AIC_c values and evaluated using the Δ AIC (i.e., the difference in AIC_c values between a given model and the highest ranked model) and Akaike weight (w_i), which is a relative measure of the weight of evidence for a model given the data (Burnham and Anderson 2002). The best fitting model had the lowest AIC_c and the highest w_i. Because of model uncertainty, we drew inferences from models with w_i > 0.05 (Falke et al. 2010). We conducted the analysis using WinBUGS.



Figure 3. Map of study area and sample sites (yellow dots) in the mid-coastal region of Oregon.

		Subbasin area	Elevation F (m)		Reach slope (%)		Reach	Unit	Pacific	Western brook
Basin	Subbasin	(km²)	Mean	SE	Mean	SE	(N)	(N)	(N)	(N)
Coastal trib	Cummins Cr.	57	82	25	1.5	0.5	2	12	3	1
Coastal trib	Rock Cr.	33	60	0	1.3	0.0	1	6	3	0
Siuslaw R.	Upper Wolf Cr.	79	247	13	0.8	0.2	4	16	38	37
Umpqua R.	Upper Smith R.	200	226	16	0.8	0.3	8	48	257	73
Coos R.	WF Millicoma R.	141	261	37	1.2	0.3	7	40	507	5

Table 1. Study area characteristics and counts of reaches and channel units sampled and larval lamprey (>60 mm TL) captured for each study subbasin.

Fish passage barriers

To better understand the size of streams affected by barriers in the Oregon Coastal Province, data on the width of known or potential fish passage barriers were summarized for Oregon coastal basins (Nehalem River south to the Coos River). These data were queried from the Oregon fish barrier dataset (https://nrimp.dfw.state.or.us/nrimp/default.aspx?pn=fishbarrierdata). This dataset was compiled between 2008 and 2012, using data from over 300 published and unpublished references dating from 1962-2002, and from several agencies, counties, and watershed councils. The database contains state-wide information on over 30,000 natural and artificial fish passage barriers. It is not a complete census, but the dataset provides the best available information on known and potential barriers in Oregon.

Certain types of artificial barriers were queried out of the dataset (i.e., culverts, dams, and bridges) with fish passage status described as blocked, partially blocked, or unknown (N=4,036). As lamprey adults are not known for their leaping ability, culverts categorized as "passable" were included when the reported "drop" between the downstream end of the culvert and the stream surface was greater than 0.6 m (N=141). The subset of known or potential barriers used in this summary was 4,177; 96% were culverts and 78% provided data on barrier width (Figure 2).

Optimizing sample size and design

The detection and occupancy estimates obtained in this study can be used to determine how resources (such as field crew size and time) can be optimally allocated for similar research into larval distribution. Optimal allocation of resources entails sampling enough sites to obtain a desired level of certainty in the estimates but not so many that the sample size and design would exceed budget constraints (MacKenzie et al. 2006). Therefore, the following equation was used to estimate the minimum number of sites (s) required to obtain an occupancy estimate (ψ) with at a desired level of certainty (α) (MacKenzie et al. 2006):

$$s = \frac{Var(\psi)}{(\alpha)^2}$$

This estimates the minimum number of sample sites because it assumes that there is perfect detection (ρ =1) of larval lamprey. Occupancy and detection estimates from this study can also be used with the occupancy design simulation tables from MacKenzie and Royle (2005) to estimate optimal number of surveys per site and the percentage of sites that need to be surveyed once under the double sampling design.

Results

Fish sampling

We surveyed 22 reaches and 122 channel units (Figure 3), and re-sampled 38% of the channel units within a mean of 5 d after the first visit. We captured larval Pacific lamprey in all the watersheds (total N=808 larvae >60 mm TL) (Table 1). We captured Western brook lamprey larvae in all study watersheds except Rock Creek (total N=116). For lamprey larvae >60 mm TL, mean total length was 89 mm (SD=19 mm, max=193 mm) for Pacific larvae and 90 mm (SD=24 mm, max=170 mm) for Western brook larvae (Figure 4). We captured a maximum of 234 Pacific and 19 Western brook lamprey larvae in an individual channel unit (Figure 5). We defined abundance states using the length-frequency distribution of larval counts (Figure 5). Low abundance was defined as 1-20 larvae for Pacific lamprey and 1-10 larvae for Western brook lamprey. High abundance was defined as ≥ 21 larvae for Pacific lamprey and ≥ 11 larvae for Western brook lamprey. The pattern of longitudinal distribution varied among the study watersheds (Figure 6).

Modeling occupancy and detection

Assuming perfect detection of larvae and regardless of abundance state (i.e., $\Psi^1 + \Psi^2$), the "naïve" estimates of occupancy for Pacific lampreys were 0.60 for pools and 0.43 for fast water units (Table 2). Put another way, within our sample frame there is a 60% probability that Pacific lamprey larvae occupy a given pool and a 43% probability they occupy a given fast water unit within the sample frame. Probability of occupancy by Western brook lamprey larvae was 0.43 for pools and 0.12 for fast water units. In 93% of revisited sites (27 of 29 channel units), larvae were not detected in either visit. Similarly, in 83% of revisited sites (10 of 12 channel units), larvae were detected in both visits.

Detection probabilities were high for the larvae of both lamprey species (Table 2). The bestfitting model for detection of larval lamprey at high abundance included channel unit type as the only explanatory variable. This model was 19 times more likely than the next best-fitting model in which detection was explained by OC sediment area (Table 3). According the best fitting model, given they are present in a channel unit, the probability of detecting lamprey larvae in high abundance was 2.3 times (2.0-2.6 times, 95% confidence interval) greater in pools than in fast water units. Because species did not explain any of the variation in detection probability, and there was no difference in the mean body length of larvae among the species, we pooled data for both species and report a single detection probability (Table 2).



Figure 4. Length frequency histogram for all larval lampreys captured and measured during the study.



Figure 5. Frequency distribution of the number of larval lampreys (>60 mm TL) captured in an individual channel unit. The zero bars extend to 77 for Pacific lamprey larvae and 94 for Western brook larvae.



Figure 6. Pattern of larval lamprey distribution in the upper section of three coastal Oregon streams. The distribution is inferred based on simple capture at sample sites. Only larvae >60 mm total length (TL) were identified to species.

Estimates of occupancy probability are provided for unit type and species because there was support ($w_i > 0.05$) in the models for both factors influencing larval occupancy (Table 2). The modeled occupancy estimates, regardless of abundance state (i.e., $\Psi^1 + \Psi^2$), were 0.64 for pools and 0.27 for fast water units for Pacific larvae and 0.44 for pools and 0.17 for fast water units for Western brook larvae. The best-fitting occupancy model included channel unit type as the explanatory variable (Table 3). This model had 1.9 times more weight of evidence than the next best model with species as a single explanatory factor. According to the best fitting model, the probability of lamprey larvae occupying pools in this study area was 1.7 times (1.1-2.5, 95% confidence interval) greater than the probability of occupying fast water units.

Larval distribution in relation to channel size

Pacific lamprey larvae were not detected in stream channels that were ≤ 4 m wide, which constituted a small percentage (15%) of pools sampled in this study, 31% between 4–8 m wide, 92% of pools >8 m in wetted width (Figure 7). Larval Western brook lampreys were not detected in pools <3 m wide, but they occupied 37% of pools between 3–8 m wide and 46% of pools >8 m wide.

Optimizing sample size and design

Our sample frame for this pilot study consisted of watersheds with sedimentary geology in the mid-coastal region of Oregon. The mean wetted width of stream channels in the sample frame ranged from 0.8 to 20 m. We used the following data to calculate minimum sample size: we sampled 60 sites (s), counting only pools; the occupancy probability (ψ) was 0.5, and the desired level of precision (α) for the occupancy estimate was 0.05. Assuming certain detection (ρ =1), the estimated minimum number of sites required to obtain an occupancy estimate with our desired level of certainty was 100 sites. Using the simulation tables provided by MacKenzie and Royle (2005) for the double sampling design, future studies would need 2 visits and the optimal fraction of total survey effort that should be devoted to sampling sites only once would be 44% to attain the desired level of precision in estimates.



Mean wetted width (m)

Figure 7. Frequency distribution by mean pool width of the percentage of the total number of pools sampled and occupied by Pacific and Western brook lamprey larvae.

Table 2. Naïve and model-based estimates of occupancy and detection of larval lamprey based on surveys of 104 channel units in three coastal Oregon streams. 95% confidence intervals are in parentheses. Naïve occupancy probabilities assume detection was perfect (i.e., p=1) and include the occupancy state of not-detected [ND].

Naïve occupancy						Detectability						
		Pools		Fast	water	units	Pools		Fast water units			
Species	Ψ^1	Ψ^2	ND	Ψ^1	Ψ^2	ND	Ψ^1	Ψ^2	Ψ^1	Ψ^2	p ¹	p ²
Pacific lamprey	0.35	0.25	0.40	0.25	0.02	0.73	0.38 (0.28-0.50)	0.26 (0.16-0.35)	0.22 (0.13-0.33)	0.05 (0.01-0.12)	0.85	0.64
Western brook lamprey	0.33	0.10	0.57	0.12	0.00	0.88	0.28 (0.18-0.40)	0.16 (0.07-0.24)	0.15 (0.08-0.24)	0.02 (0.00-0.07)	(0.72- 0.94)	(0.43- 0.83)

Table 3. Detection and occupancy modeling results for larval lamprey based on surveys of 104 channel units in three Oregon coastal streams. Only the abundant state (p^2) was modeled for detection. As channel unit type provided the best model for detection for p^2 , this factor was used for p^2 in all occupancy models. Channel unit type consisted of either pools or faster water units. Off-channel [OC] habitats included backwaters, isolated pools, and side channels. Sediment refers only to larval burrowing habitat (i.e., sediment types 1 and 2). Akaike weights (w_i) provide a measure of the relative weight of evidence for a model given the data.

Detection models (p ²)	Deviance	К	AIC _c	ΔAIC_{c}	Wi
Unit type	112.8	4	121.0	0.0	0.94
OC sediment area	118.5	4	126.7	5.7	0.05
Species	123.8	4	132.0	11.0	0.00
Unit width	131.8	4	140.0	19.0	0.00
Unit area	138.9	4	147.1	26.1	0.00
Unit sediment area	143.6	4	151.8	30.8	0.00

Occupancy models	Deviance	К	AIC _c	ΔAIC_{c}	Wi
Unit type	111.2	6	123.6	0.0	0.55
Species	112.5	6	124.9	1.3	0.29
Unit type + Species	109.4	8	126.1	2.5	0.16
Unit type x Species	110.1	10	131.2	7.6	0.01
Unit type + OC sediment	184.1	8	200.8	77.2	0.00
Unit type + unit sediment	213.9	8	230.6	107.0	0.00

Discussion

Pacific lamprey larvae were detected throughout the mid-coastal Oregon study area and were well distributed longitudinally in streams, including in channel units as small as 4 m wetted width. This study adds further evidence that larval rearing of Pacific lamprey can occur in small streams with no fish passage barriers. An evaluation of the Oregon fish barrier dataset suggests that potentially hundreds of passage barriers in this region may be blocking Pacific lampreys from accessing these habitats. These findings suggest that a closer examination of the impact of barriers on Pacific lampreys is merited and that Pacific lamprey passage should be considered when prioritizing barrier removal and replacing culverts.

Regional distribution

Pacific lamprey larvae occupied every stream in this study area. The study area included some diversity in watersheds: tributaries in much larger actively-managed basins as well as small wilderness watersheds that flow directly into the ocean, and watersheds with sedimentary geology as well as those with volcanic headland geology. Western brook lampreys were detected in all study streams, except Rock Creek. The lack of detection in Rock Creek may be related to the relatively small sampling effort conducted in this stream.

Longitudinal distribution

We evaluated the longitudinal distribution of larval lampreys in three watersheds with sedimentary geology. In the upper section of these watersheds, there was substantial overlap in the distribution of larvae of the two species, though there were some noteworthy differences. Larval distributions in the upper Smith River were consistent with the distribution of spawning adults reported for the two species (Pirtle et al. 2003; Gunckel et al. 2009) in which Pacific lampreys occupied the lower-elevation mainstem reaches and Western brook lampreys occupied the upper tributaries of the river network, with some overlap in the middle. Larvae of both species were distributed throughout the survey area in Wolf Creek, which ranged from 3-7 m wetted width. However, the sampling season ended prior to completing surveys on Wolf Creek so larval occupancy in the uppermost section of this stream (<3 m wetted width) is unknown. In the West Fork Millicoma River, Pacific larvae were distributed more extensively and farther upstream into smaller stream channels than Western brook larvae. In these smaller streams, extensive overlap in larval rearing between the species was not surprising as there was little difference in size between the species (among larvae >60 mm long) and there is considerable overlap in their feeding ecology and microhabitat use – thus larvae of both species are capable of rearing in the same habitat. Spawning adults of the two species, however, differ greatly in size and fecundity (Wydoski and Whitney 2003). Thus, the differences we observed in larval distribution patterns may be more a function of spawning habitat availability in a particular stream, differential spawning success by species or location, or some factor other than the availability of larval burrowing habitat.

This overlap of larval rearing between the two species may be important to conservation and restoration of Pacific lampreys in two ways. First, if this overlapping distribution pattern holds in small streams throughout the Coastal Oregon Province, then presence of larval Western brook lamprey may indicate suitable rearing habitat for Pacific lamprey. Furthermore, the sole presence of the non-anadromous Western brook lamprey above a culvert may be used as one indicator of a passage barrier of the anadromous Pacific lamprey. Second, although the factors influencing the migration of maturing Pacific lampreys to holding and spawning locations are not well understood (Keefer et al. 2013), pheromones released in the bile acids of rearing larvae are known to attract adults to spawning areas for Pacific lamprey (Robinson et al. 2009). Larval pheromones are consistent throughout petromyzontid lampreys and both sea lamprey (Petromyzon marinus) and silver lamprey (Ichthyomyzon unicuspis) are attracted to hetero- and conspecific larval pheromones (Fine et al. 2004). This suggests that larval Western brook lamprey presence may be another factor that attracts Pacific lampreys to smaller streams as well as an important catalyst to rapid natural recolonization of streams from which Pacific lampreys have been extirpated. Our study suggests that extensive overlap between these species in small streams may be common throughout this region and the interaction of the two species needs to be better understood.

Detection, occupancy, and habitat use

Detection probability of the low abundance state (≤ 20 for Pacific and ≤ 10 Western brook larvae) was high in this study and similar to the results of Dunham et al. (2013). Lower detection probability of the high abundance state was not because we detected high abundance on one visit and zero on another; this did not happen. Rather, it was lower because larval counts were often near the somewhat arbitrary threshold between the two states and the counts occasionally changed from one state to the other upon on the second visit.

At the channel unit level, Pacific and Western brook larvae used both pools and fast water units but had a higher probability of occupying pools in both low and high abundance. Larvae were more likely to be detected in high abundance in pools because larvae were most abundant in pools and rarely found in high abundance in fast water units. Channel unit type was the only habitat variable that explained a significant amount of variation in occupancy. Slow water channel units accumulate sediment needed for burrowing habitat so it is reasonable to assume that pools will have higher larval occupancy. Interestingly, one would expect channel unit area of Type 1 and 2 sediment (i.e., larval burrowing habitat) to be a good predictor of larval occupancy. The fact that it was not a good predictor of occupancy suggests that the method used in this study of estimating the quantity of available burrowing sediment was flawed. Off-channel habitats also act as sediment depositional areas but were rarely encountered within the sample frame. The rarity of these habitats may explain why this covariate was not related to larval occupancy. In-stream large wood, which augments channel complexity and often creates sediment depositional zones, was so rare in this sample frame that it was not included in the analysis. Coastal Oregon watersheds, including those in this study (see Miller 2010), have experienced over a century of extensive land use activities (e.g., logging, splash-dams and log drives, systematic wood removal). These activities have led to a reduction in channel complexity (Sedell and Froggatt 1984; Sedell and Duvall 1985; Miller 2010), which likely has had an adverse effect on lamprey habitat availability and current larval distribution patterns. Sampling at sites where large wood has been restored to streams may shed light on the relationship between larval lamprey burrowing habitat and in-stream large wood.

Larval lampreys were detected in our study in stream channels between 3 and 20 m wide, but channel unit width was not a good predictor of larval occupancy. This may be in part because Pacific and Western brook lamprey larvae were distributed throughout most of the range of channel widths sampled. No larvae were detected in the smallest stream channels (<3 m wide), but this represented a small percentage of the sampled channel units and longitudinal distribution data were obtained from only three streams. Pacific lamprey larval rearing has been observed in these smallest streams (Dunham et al. 2013; 2.9 m mean wetted width) and reported anecdotally (Stewart Reid, Western Fishes, personal communication), but importance of these channels to this species is unknown. Future distribution studies should include channels <3 m wide in the sample frame.

Optimizing sample size and design

Our observations in this pilot study provide insights into the design of future monitoring and research designs. First, if one is interested in larval distribution alone and not habitat use in general, it would be more efficient to only sample pool habitat. Fast water units were less likely to contain lamprey larvae but were larger in surface area than pools, and therefore required a disproportionate amount of time to electrofish. Second, the minimum sample size estimate based on the occupancy probability observed in this study and assuming perfect detection suggests that doubling the number of pools in this study to at least 100 channel units would obtain occupancy estimates with the desired level of precision (i.e., $\alpha = 0.05$). Since detection was not perfect, this sample size is likely an underestimate. Third, the double sampling design used in this study was not adequate to attain the desired level of certainty and resulted in imprecise estimates. Increasing the proportion of channel units that are re-sampled from 40% in this study to 56% as suggested by simulation results would add time to sampling, but this cost would likely be offset by the time saved by not sampling fast water units. Last, our results suggest that larval Pacific lampreys are prevalent in channels >8 m wide and, according to the Oregon fish barrier dataset, barriers may be somewhat rare in larger channels in this region. Therefore, the sample frame should include stream channels <8 m wide. This will save time by reducing sampling time in large channel units. The time saved could be used to sample a greater number of sites in a wider diversity of streams, which would widen the scope of inference of this study and improve its relevance for evaluating the impact of barriers on Pacific lampreys in the Coastal Oregon Province. The sample frame for the longitudinal distribution section of this study was limited to three mid-coastal streams with sedimentary geology. The north coast of Oregon is largely volcanic geology so larval habitat availability may differ from that in the mid/south coast.

Conducting a similar study, with the sampling design and effort suggested here, in the northern coastal region would allow for inferences to lamprey populations across the entire coastal region.

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