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Role of large- and fine-scale variables in predicting catch rates of larval Pacific lamprey in the Willamette Basin, Oregon

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Abstract – Pacific lamprey *Entosphenus tridentatus* is an anadromous fish native to the Pacific Northwest of the USA. That has declined substantially over the last 40 years. Effective conservation of this species will require an understanding of the habitat requirements for each life history stage. Because its life cycle contains extended freshwater rearing (3–8 years), the larval stage may be a critical factor limiting abundance of Pacific lamprey. The objective of our study was to estimate the influence of barriers and habitat characteristics on the catch-per-unit-effort (CPUE) of larval Pacific lamprey in the Willamette River Basin, Oregon, USA. We sampled lampreys at multiple locations in wadeable streams throughout the basin in 2011–13 and used an information theoretic approach to examine the relative influence of fine- and large-scale predictors of CPUE. Pacific lamprey was observed across the basin, but its relative abundance appeared to be limited by the presence of natural and artificial barriers in some sub-basins. Lower velocity habitats such as off-channel areas and pools contained higher densities of larval lamprey; mean Pacific lamprey CPUE in off-channel habitats was 4 and 32 times greater than in pools and riffles respectively. Restoration and conservation strategies that improve fish passage, enhance natural hydrologic and depositional processes and increase habitat heterogeneity will likely benefit larval Pacific lamprey.

Key words: Pacific lamprey; Willamette River (USA); native species; habitat associations; conservation

Introduction

Anadromous fishes are inextricably linked to environmental conditions in both freshwater and marine habitats (McDowall 1988), and conservation of these fishes requires an understanding of how factors interact within both environments (Parrish et al. 1998; Naiman & Latterell 2005). On the West Coast of North America, freshwater habitats provide the migration corridor to spawning locations for returning anadromous adults (e.g. Beamish & Levings 1991; Goniea et al. 2006; Clemens et al. 2012), rearing locations for juveniles (Bjornn & Reiser 1991; Reeves et al. 1995; Jolley et al. 2012) and migratory routes to the ocean for emigrating juveniles (e.g. Mueller et al. 2006; Petrosky & Schaller 2010). Although marine habitat and environmental conditions influence survival and growth of maturing fishes (e.g. Bisbal & McConnaha 1998; Levin et al. 2001; Murauskas et al. 2013), understanding the importance of environmental

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conditions in freshwater ecosystems is also critical to the management of anadromous stocks.

Pacific lamprey *Entosphenus tridentatus* is a native, anadromous fish in the Pacific Northwest with a historic distribution that ranged from Baja Mexico to the Bering Sea of Alaska (Scott & Crossman 1973). Its semelparous life cycle consists of 3–8 years in freshwater as filter-feeding larvae (ammocoetes), followed by a physiological and morphological transformation into outmigrants (macrophthalmia), and subsequent emigration to marine environments (Clemens et al. 2010). The parasitic marine stage lasts <3 and a half years (reviewed in Clemens et al. 2010), where individual lampreys can range as far north as the Northwest Pacific Ocean and Bering Sea (Sviridov et al. 2007; Orlov et al. 2008) before returning to freshwater to hold prior to spawning. The freshwater holding period can last from <1 month up to 2 years until making a final migration to their ultimate spawning areas (Clemens et al. 2010, 2012, 2013; Starcevich et al. 2013). Because freshwater rearing makes up a relatively large fraction of the life cycle of Pacific lamprey, this stage is generally viewed as critical for the viability of the species (e.g. CRITFC 2011).

Across its range in western North America, Pacific lamprey has declined considerably over the last half century (Luzier et al. 2011), including extirpation from multiple drainages (Ward et al. 2012). Returns to the first upstream dam on the Columbia River (Bonneville Dam) averaged >100,000 adults between 1939 and 1969, but have declined to an average of <40,000 between 1997 and 2010 (Murauskas et al. 2013). Similarly, annual returns at the only major dam on the North Umpqua River, Oregon (Winchester Dam) in 2013 were estimated to be 1044 adults (K. Crispen Coates, Cow Creek Band of Umpqua Tribe of Indian, personal communication), whereas historic returns (1965–1971) were estimated to be 14,532–46,785 adults (Goodman et al. 2005). Despite the many important ecological and cultural roles of Pacific lamprey (outlined in Close et al. 2002), conservation efforts have been hampered by a negative association with invasive sea lamprey *Petromyzon marinus* (Clemens et al. 2010), a perceived threat to commercial fisheries (e.g. Beamish & Levings 1991) and numerous knowledge gaps in its biology (Mesa & Copeland 2009; Clemens et al. 2010; Luzier et al. 2011; CRITFC 2011).

Larval Pacific lamprey abundance in streams is a function of rearing habitat quality, as well as accessibility for returning adults. Adult passage at hydroelectric facilities has received substantial research attention, and management actions have prioritised this potential limiting factor (e.g. Moser et al. 2002a; Keefer et al. 2010). However, the habitat requirements and ecology of the larval stage have been relatively understudied (Moser et al. 2007; CRITFC 2011) but see Torgersen & Close 2004; Jolley et al. 2012). Previous work has evaluated larval habitat requirements within individual streams (e.g. Torgersen & Close 2004); however, there is a pressing need for broader evaluations, which can weigh the relative importance of fine-scale habitat characteristics against spawning distribution-related variables, such as migration distance and the presence of smaller obstructions (e.g. culverts, diversions, cascades).

Across the range of Pacific lamprey, the Willamette River, Oregon (USA), has one of the largest adult returns and is one of the few remaining harvest locations for Pacific Northwest tribes (CRITFC 2011). Although the Willamette River Basin appears to contain a relatively robust Pacific lamprey population, the basin contains habitat perturbations that commonly impair stream habitats across the Pacific Northwest [e.g. loss of large woody structure, land use conversion, stream diversion and channelisation, point and nonpoint source pollution, and fish passage issues (Sedell et al. 1990; Naiman & Bilby 1998; Mulvey et al. 2009)]. Because Pacific lamprey have persisted in this mix of impaired and relatively intact habitat conditions, insights into the ecology of Willamette River Basin Pacific lamprey may be readily applied to other freshwater habitats across its range. Our objective was to estimate the effect of fine-scale habitat characteristics, landscape disturbance indices and putative barriers on the abundance of larval Pacific lamprey. Our multiyear study addressed critical knowledge gaps about the larval stage that have been identified in conservation planning, (e.g. Luzier et al. 2011) and can be used to make broader inferences about limiting factors for larval Pacific lamprey and other Western lampreys (e.g. Western brook lamprey *Lampetra richardsoni* and Pacific brook lamprey *L. pacifica*) in the Pacific Northwest.

Methods

Larval lamprey and habitat sampling

We sampled wadeable locations in 14 tributary sub-basins of the Willamette River from July to October in 2011—2013 (Fig. 1). We sampled Clear, Crabtree, Deep, Marys and Thomas sub-basins in 2011; Abiqua, Butte, Clear, Crabtree, Deep, Marys, Mill, Thomas and Willamina sub-basins in 2012; and Calapooia, Clear, Luckiamute, Marys, McKenzie, Mohawk, Thomas and Tualatin sub-basins in 2013. In each of these sub-basins, we tried to sample three locations on the mainstem stream channel: one located near the downstream end of wadeable stream habitat, one near the Cascades Mountains or Coast Range ecotone with the

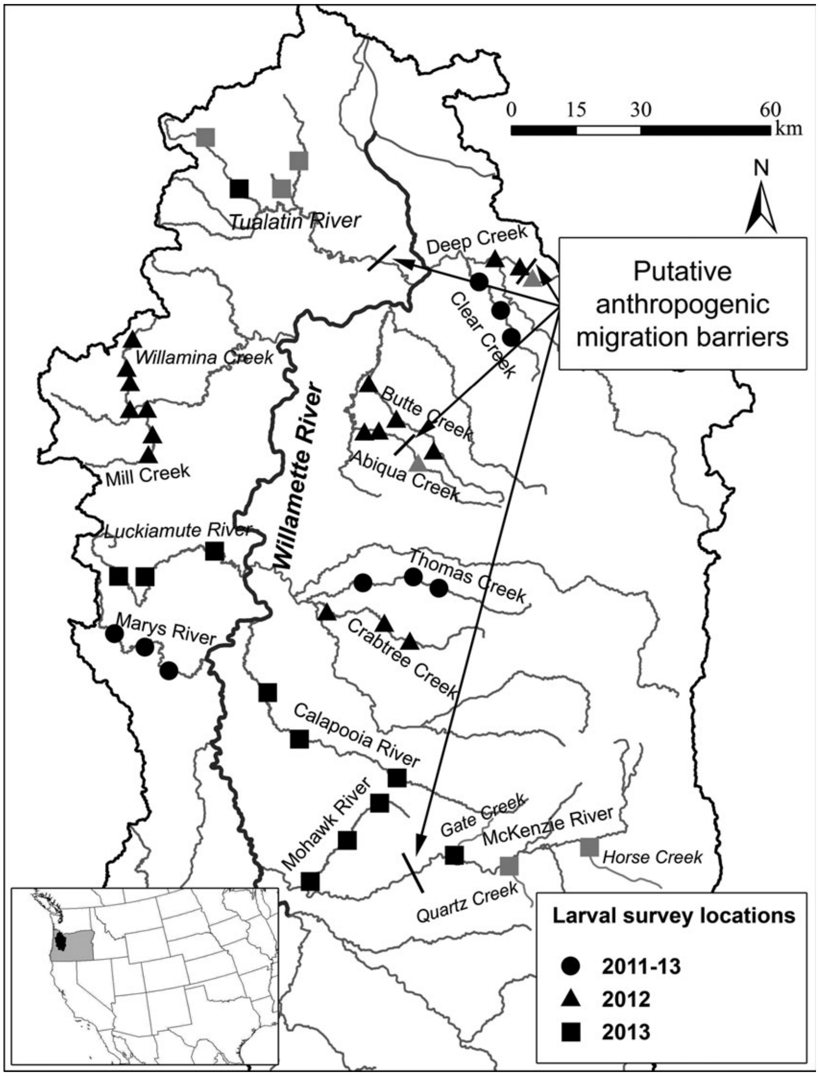

Fig. 1. Sampling locations for larval Pacific lamprey in the Willamette River Basin, Oregon (USA), 2011–2013. Closed symbols indicate reaches where Pacific lamprey were sampled, and open symbols indicate areas where Pacific lamprey were not detected. Each reach consisted of four habitat units and additional off-channel habitat units, if present (see Methods for more details).

Willamette Valley Ecotype (from Omernik 1987) and one roughly equidistant between these two locations. The exception was the Tualatin and McKenzie rivers, where the mainstem was mostly nonwadeable, so we sampled locations in wadable tributaries near the confluence with those larger rivers at similar positions within their respective watersheds. This approach was an attempt to capture a variety of habitat types and examine potential differences in relative abundance with landscape position and stream size longitudinally in these sub-basins.

At each of these locations, we sampled larval lampreys and quantified physical habitat characteristics in sample reaches. Each reach consisted of two pool and two riffle habitat units, with a nonsampled riffle/pool between to avoid recapture of the same individuals if sampling was completed over multiple days. If an off-channel habitat type (e.g. side channel, backwater, isolated pool) was present within a sample reach, it was sampled separately as an additional habitat unit. Although subjectivity is common in stream habitat classification, we selected habitat units that were representative of the surrounding stream habitat conditions within the vicinity of the sample reach (i.e. ~150 m up/downstream).

We used backpack electrofishing to sample larval lampreys from habitat units to estimate abundance. We moved upstream through each habitat unit using a single electrofishing pass to sample the entire unit with an AbP-2 backpack electrofisher (Engineering Technical Services, Madison, WI, USA). Netters followed the electrofisher and were equipped with 3/16-mesh dip nets, 500-μm D-frame invertebrate nets and fine mesh aquarium nets. The electrofisher applied a pulsed burst train (3 on: 1 off) with a 25% duty cycle to induce larval lamprey emergence from the substrate and a fast pulse at 30 pulses·sec^{-1} to temporarily immobilise individual larvae and facilitate capture. These electrofisher settings are commonly used in other lamprey research (e.g. Torgersen & Close 2004; Moser et al. 2007). Following electrofishing of each habitat unit, captured lamprey were anesthetised using

50 mg·l^{-1} tricaine methanesulfonate (MS-222) buffered with 125 mg·l^{-1} sodium bicarbonate ($NaHCO_3$), measured (total length, in mm), enumerated and allowed to recover before being returned to the stream near their capture location. We used caudal pigmentation characteristics as described in Goodman et al. (2009) and a regional dichotomous field key (S. Reid, Western Fishes, unpublished data) for identification. Identification of Pacific lamprey macrophthalmia was aided by the presence of large emergent/emerged eyes and silver body coloration. Only individuals >60 mm were identified to species because accurate keys for species identification have not yet been developed for lamprey <60 mm (Goodman et al. 2009). We did not attempt to identify brook lampreys to species because differentiating between these two species (i.e. Western brook lamprey and Pacific brook lamprey) requires an examination of trunk myomeres (Reid et al. 2011). To verify our identification of species, we submitted 272 samples from putative Pacific lamprey (size range 60—141 mm) for genetic analyses (Hess et al. 2014). Species identification was important for meeting our goal because differences in the relative catch rate of Pacific and brook lampreys provided insight into the influence of adult migration barriers. Pacific and brook lampreys are thought to have similar habitat associations and are commonly sympatric (Beamish & Lowartz 1996; Torgersen & Close 2004; Schultz et al. 2014); thus, areas that contain solely brook lamprey could suggest limited access for returning Pacific lamprey adults. Because the sampling area varied between different units, we measured the relative abundance of Pacific lamprey in each habitat unit using catch-per-unit-effort (CPUE), calculated as the number of fish sampled per square metre (fish m^2).

We measured geomorphic characteristics of each habitat unit by establishing five evenly spaced transects perpendicular to the stream channel along the length of each habitat unit. At each transect, we measured wetted stream width and dominant substrate at five evenly spaced points along the transect starting at the wetted stream margin. The percentage of fine substrate area was computed by dividing the number of points on transects with sand or finer substrate by the total number of points measured within a habitat unit.

For each reach, we also summarised large-scale variables to evaluate the potential effects of anthropogenic disturbance, migration distance and barriers on larval Pacific lamprey abundance. Anthropogenic disturbance was quantified using a cumulative disturbance index obtained from data layers in the National Fish Habitat Partnership data system (Wang et al. 2011). These disturbance indices provide a composite index for a stream reach that accounts for multiple types of anthropogenic disturbances and combine disturbance scores from local catchment areas and all upstream catchments (Esselman et al. 2011). Disturbance scores range from one to four, with one being highly disturbed and four being undisturbed. We computed the distance from each sampling location to the Columbia River to assess the influence of adult migration distance on the abundance of larval Pacific lamprey. Finally, we evaluated the effect of barriers by determining whether or not individual habitat units were upstream of natural or anthropogenic obstructions. Barriers were identified using the Oregon Fish Passage Barrier Data Standard data set (OFPRBS; Oregon Department of Fish and Wildlife 2012). The OFPRBS contained a georeferenced list of 30,000 statewide natural and anthropogenic obstructions in streams (e.g. bridges, cascades, culverts, dams). Of these, the Willamette River Basin contained ~7000 barriers, most of which were on first or second order tributaries in the headwaters of forested stream networks, so only four barriers were present interspersed amid our sample reaches (described in detail in Schultz et al. 2014). Although obstructions were given standardised passability ratings which include complete, partial and unknown, we classified reaches as barrier-influenced if obstructions of any kind, and with any passability rating, existed downstream. We included all barriers because passability is often judged based on teleost swimming abilities and because lamprey passage requirements differ from other fishes (Moser & Mesa 2009; Keefer et al. 2010). Although some of these barriers may provide partial passage, we were interested in how any degree of impaired passability influenced larval populations above these potential barriers.

We used an information theoretic approach to examine the relative influence of habitat characteristics, measured at different spatial scales, on the CPUE of larval Pacific lamprey (Burnham & Anderson 2002). Candidate models represented nested and competing hypotheses regarding predictors of larval lamprey CPUE. We ranked models using Akaike's information criterion, adjusted for small sample sizes (AIC_c), and Akaike weights w_r. All models contained a random effect for 'sub-basin', which was used to account for the lack of spatial independence among sub-basins (see Schultz et al. 2014). A fixed effect for 'year' was also included in all candidate models. Although interannual CPUE was not of great interest to our study, 'year' was included as a fixed effect because a random intercept could not be reliably estimated with the 3 years of sampling in this data set. The candidate set consisted of a global model with large-scale (i.e. disturbance, migration distance, barrier presence) and fine-scale habitat variables (i.e. habitat unit type, mean sediment depth, percentage of fine substrate; Table 1). Models with only the suite of large-scale or fine-scale variables were included along

Table 1. Candidate models, number of parameters (K), log-likelihood, AIC_c, ΔAIC_c and w_i values for negative binomial mixed-effects models used to predict catch-per-unit-effort (CPUE) of Pacific lamprey in wadeable streams within the Willamette River Basin, Oregon (USA) between 2011 and 2013.

Candidate model	K	LogL	AIC_c	ΔAIC_c	w_i
Global	11	−985.6	1994.1	0	0.999
Fine-scale	8	−1016.4	2049.2	55.1	<0.001
Habitat unit	7	−1036.3	2086.9	92.8	<0.001
% area fines	6	−1047.6	2107.5	113.4	<0.001
Disturbance	6	−1059.9	2132	137.9	<0.001
Large-scale	8	−1058.1	2132.7	138.5	<0.001
Barriers	6	−1070.3	2152.8	158.7	<0.001
Migration distance	6	−1076.3	2164.9	170.7	<0.001
Null	5	−1078.7	2167.7	173.5	<0.001

The global model contained a linear combination of all large-scale (anthropogenic disturbance [Esselman et al. 2011], migration distance, barrier presence) and fine-scale predictors (habitat unit, sediment volume).
Reduced models included suites of fine-scale and large-scale predictors, and single-predictor models.
The null model consisted of a random effect for sub-basin and a fixed effect for sampling year.

with models that contained individual predictors. A null model was also included to assess goodness of fit (i.e. the support of candidate models versus a model of annual mean CPUE). The null model contained a ‘sub-basin’ random effect and a ‘year’ fixed effect.

A generalised linear mixed modelling approach was used to describe the influence of habitat variables on Pacific lamprey CPUE (Venables & Dichmont 2004; Bolker et al. 2009). We fitted negative binomial mixed-effects models using larval lamprey catch within each habitat unit as the response variable and area sampled (m^2) as an offset (Irwin et al. 2013). Negative binomial regression is one of several preferred methods for modelling overdispersed count responses and for handling a high number of zero counts (Ver Hoef & Boveng 2007; Zuur et al. 2009). All continuous predictors were standardised by subtracting the sample mean and dividing by the standard deviation, which allowed effect sizes of continuous variables to be compared on the same scale. Fit of top models was assessed by examining Anscombe residuals (Hilbe 2008; Irwin et al. 2013). We interpreted parameters of top ranking models by calculating the exponential function of parameters, which describes the multiplicative effect of a single standard deviation increase of a continuous predictor or a different level of a categorical predictor on the expected CPUE of larval lampreys (McCullagh & Nelder 1989).

Results

We captured a total of 11,153 larval lamprey between 2011 and 2013, 7574 Pacific lamprey (67.9%), 1128 brook lampreys (10.1%) and 2451 unidentified lamprey (<60 mm; 22.0%). Genetic analysis in

Table 2. Mean, standard deviation (SD) and range of stream habitat features, lamprey density and total catch in habitat units in the Willamette River Basin, Oregon (USA) between June and October, 2011–2013. ‘Disturbance’ is a measure of anthropogenic development (following Esselman et al. 2011).

Variable	Mean	SD	Range
Habitat features			
Water depth (cm)	23.1	11.8	4.88—53.24
Maximum water depth (cm)	76.5	41.4	15—250
Wetted width (m)	13.2	5.6	2.32—35.5
% of area with sand or finer substrate	22.2	23.8	0—100
Disturbance	2.4	0.9	1—4
Distance to Columbia (km)	194.3	82.9	62.7—389.5
Lamprey			
Density of Pacific lamprey (fish m^2)	0.088	0.293	0—3.802
Density of brook lamprey (fish m^2)	0.010	0.059	0—0.788
Density of all lamprey (fish m^2)[†]	0.148	0.385	0—4.832

[†]includes unidentified lampreys <60 mm.

2012–2013 indicated that >99% of Pacific lamprey were correctly identified, but most reaches contained both Pacific and brook lampreys. We captured a total of 214 Pacific lamprey macrophthalmia, representing 2.5% of the total catch; in all years, these individuals were captured after the middle of August. We sampled 267 main-channel units and 16 off-channel units accross a variety of habitats in sub-basins in the Willamette River Basin (Table 2). In general, reaches located further upstream in tributary sub-basins were narrower, shallower and characterised by coarser substrates than reaches lower in sub-basins. Reaches upstream of identified barriers generally appeared to contain physical habitat similar to reaches without barriers. Pacific lamprey were sampled from nearly all sample reaches (84.1%), but not all habitat units. Larval Pacific lamprey and brook lamprey were not detected at 29.5% of the sampled habitat units, primarily in Abiqua, Dairy, Deep, Gales, Horse, McKay and Quartz creeks, all of which contained downstream barriers (Fig. 1).

Model selection showed the greatest support for the global model, which contained all large-scale and fine-scale predictors (Table 1). Although all predictors were included in the top model, estimates of effect sizes varied considerably (Table 3). The variable with the greatest influence on larval CPUE was habitat unit type. Parameter estimates from the top model indicated that larval lamprey CPUE was higher in pools than in riffles, but highest in off-channel habitats (Fig. 2). Larval Pacific lamprey CPUE estimates were 4 [2.83, 5.78 (95% LCL, 95% UCL)] times higher in off-channel habitats than pool habitats and 32 (14.12, 71.01) times higher in off-channel habitats than riffle habitats.

The presence of downstream barriers appeared to influence larval Pacific lamprey CPUE; however, the directional effect of downstream barriers could not be

Table 3. Parameter estimates and standard errors (SE) of fixed and random effects from the global model of a set of negative binomial mixed models used to predict Pacific lamprey density in tributary sub-basins to the Willamette River, Oregon (USA), 2011—2013.

Parameter	Estimate	SE	$e^{(estimate)}$	LCL	UCL
Fixed effects					
α	0.665	0.068			
Intercept	−4.189	0.310	0.015	0.008	0.028
% area fine sediment	0.604	0.120	1.830	1.448	2.313
Habitat unit: off-channel	3.455	0.412	31.665	14.118	71.017
Habitat unit: pool	1.397	0.182	4.043	2.830	5.778
Barrier	−0.603	0.398	0.547	0.251	1.193
Disturbance	−0.787	0.248	0.455	0.280	0.740
Migration distance	−0.251	0.248	0.778	0.479	1.264
Random effect					
Sub-basin intercept		0.7076			

The exponential function of parameter estimates ($e^{(estimate)}$) indicates the multiplicative effect of a single standard deviation increase in a continuous predictor or a different level of a categorical predictor.
Lower and upper Wald 95% confidence limits (LCL, UCL) for these estimates were calculated as $e^{(estimate \pm 1.96*SE)}$.

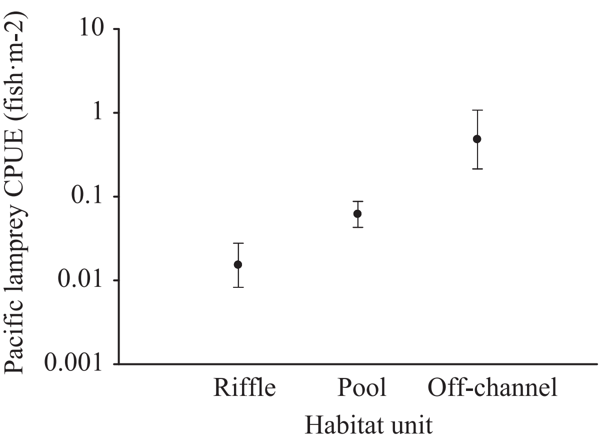

Fig. 2. Estimated mean catch-per-unit-effort (CPUE) from a negative binomial mixed model of Pacific lamprey catch rates in three habitat types in 14 streams of the Willamette River Basin from 2011 to 2013. Channel unit CPUEs are standardised using the mean of all other covariates in the model. Estimates are plotted on the $\log_{10}$ scale. Error bars denote 95% confidence intervals.

precisely identified because 95% Wald confidence intervals overlapped zero (Fig. 3). The point estimate for the effect of downstream barriers indicated that larval Pacific lamprey CPUE upstream of natural and anthropogenic barriers was 45.26% lower than in areas without downstream barriers (Fig. 3). The variable effect of downstream barriers was strongly influenced by a particular stream that was sampled in 2011 (i.e. Clear Creek). We sampled fewer reaches upstream of barriers in 2011 than in 2012 and 2013, and one of the three reaches above barriers that were sampled in 2011 contained high numbers of larval lamprey and substantially influenced the parameter estimate for barriers across all 3 years. In 2012 and 2013, we sampled twelve reaches upstream of barriers. If these years are analysed separately, the estimated reduction in larval Pacific lamprey CPUE upstream of barriers was substantial and more precise (64.69%; 95% confidence interval: 45.11, 77.3). All reaches where Pacific lamprey were not collected were upstream of barriers, although individuals <60 mm could not be identified to species and may have been Pacific lamprey. In several sub-basins (e.g. Tualatin River), brook lamprey CPUE was relatively high, but Pacific lamprey densities were substantially lower than other sub-basins.

Relatively minor predictors of larval CPUE were cumulative disturbance index, substrate characteristics and migration distance. Interestingly, higher larval densities were associated with greater anthropogenic disturbance (Fig. 3). Distance to the Columbia River had a slightly negative effect on larval Pacific lamprey CPUE, but was highly variable. Percentage fine sediment was positively related to larval Pacific lamprey CPUE. The 95% confidence interval for 'year' parameters overlapped zero considerably, indicating that Pacific lamprey CPUE did not differ substantially between years.

Discussion

The relative abundance of larval Pacific lamprey in the Willamette River Basin was best explained by habitat unit type (i.e. pool, riffle, off-channel) and, to a lesser degree, reach-scale habitat features. At larger scales, the CPUE of larval Pacific lamprey in the Willamette River Basin was driven primarily by migration barriers to adults. Similar patterns of habitat use and distribution have been described for other lamprey species (e.g. Slade et al. 2003; Torgersen & Close 2004; Clemens et al. 2010; Jackson & Moser 2012). The findings from this study emphasise the importance of restoration activities that provide Pacific lamprey with increased access to streams with high habitat heterogeneity and channel complexity.

The density of Pacific lamprey was substantially higher in off-channel habitats; thus, streams with higher channel complexity (e.g. side channels, backwater pools) are likely to support greater abundances. Common mitigation measures for Pacific lamprey include barrier removal/modifications and translocation of adult fish above barriers (e.g. Close et al. 2009, Ward et al. 2012). Our study suggests that both of these approaches will be more valuable in streams with relatively high proportions of low-velocity habitats (i.e. pools and off-channel habitats), because these habitats can sustain higher densities of larvae. In fact, we estimate that 1 m^2 of low-velocity habitat is equivalent to roughly 11 m^2 of riffle habitat. Our research concurred with other work on Pacific

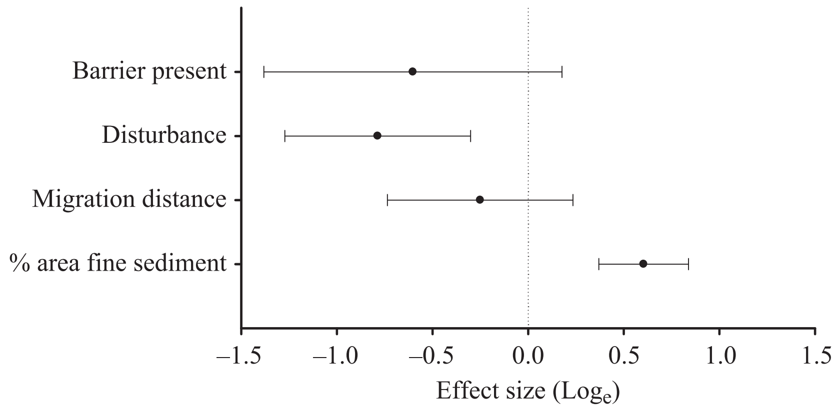

Fig. 3. Select parameter estimates and 95% confidence intervals from a negative binomial mixed-effects model describing the influence of habitat characteristics on Pacific lamprey catch-per-unit-effort (CPUE) in tributaries of the Willamette River, Oregon (USA) between 2011 and 2013. Effect sizes are shown on the natural log scale ($\log_e$). Confidence intervals that overlap with zero indicate that the direction of the effect could not be precisely determined. Habitat unit, a highly influential variable (Fig. 2), was omitted from this figure to better highlight the contrast between the effect sizes of these less influential variables. Note: lower disturbance scores indicate more disturbed habitats.

lamprey that suggests that the availability of fine sediment is an important habitat element for larvae (Torgersen & Close 2004; Stone & Barndt 2005). Future larval Pacific lamprey monitoring might consider additional habitat variables of interest such as substrate organic matter or chlorophyll *a*, which have been related to the distribution of other lampreys (e.g. *Geotria australis*; Potter et al. 1986).

Returning Pacific lamprey often encounter passage issues from anthropogenic barriers, and their passage requirements differ from salmonids (Moser et al. 2002b; Keefer et al. 2010; Jackson & Moser 2012). Improving passage efficiency for Pacific lamprey has been prioritised at large hydropower dams in the Columbia River system (e.g. Keefer et al. 2010; Mesa et al. 2010; Luzier et al. 2011), but the influence of smaller and more prevalent dams as potential migration barriers has received much less attention (CRITFC 2011 but see Jackson & Moser 2012). In the Tualatin and McKenzie river sub-basins, larval Pacific lamprey were sampled in several reaches above putative barriers, suggesting that some of the barriers that were identified in the study were not complete barriers to lamprey migration. Conversely, our evidence suggests that the Abiqua Creek sub-basin may contain a complete barrier to Pacific lamprey (Fig. 1). Opportunistic sampling above a ~5 m high municipal water supply diversion dam in 2014 failed to detect any larval Pacific lamprey (L. Schultz, unpublished data). The ability of an adult lamprey to pass a barrier is likely dependent upon hydraulic features and flow conditions within the obstacle (reviewed in Stillwater Sciences 2014), as well as attributes of individual spawners (Keefer et al. 2009). Future studies should incorporate barrier type into models of lamprey density and abundance to determine where barrier removals or modification would be most valuable for reconnecting lamprey habitat.

Although physical barriers are widely recognised as challenges to the conservation of Pacific lamprey (e.g. Moser & Mesa 2009; Clemens et al. 2010; Keefer et al. 2010), chemical barriers may also present passage issues. Upon entry into freshwater, Pacific lamprey do not home in the strict sense (Spice et al. 2012). Instead, adult Pacific lamprey are attracted to bile acid chemicals released by larval lamprey (Robinson et al. 2009; Yun et al. 2011). Environmental pollutants can disrupt physiology and behaviour of other fishes (e.g. Scott & Sloman 2004; Hughes et al. 2014), but the extent to which many chemicals effect migration of Pacific lamprey is unknown. The Tualatin River sub-basin contained relatively few larval Pacific lamprey, but brook lamprey catch rates were consistent with other sub-basins that we sampled. Although the Tualatin River contained a putative physical barrier near its confluence with the Willamette River, 27% of the sub-basin's watershed is also urbanised and it contains the greatest stream length with impaired water quality of all the 14 Willamette River sub-basins (Mulvey et al. 2009). Numerous stream segments within the watershed are listed on the 303d (impaired waterways) list of the United States Environmental Protection Agency (EPA 2014. For example, disturbances associated with land use practices that occur in the urbanised (downstream) reaches of the Tualatin River might contribute to water quality conditions that deter adult Pacific Lamprey from moving into this sub-basin or otherwise prohibit successful reproduction, despite habitat conditions being suitable for lampreys in the upstream reaches of the sub-basin. Although some chemicals have been identified that alter the behaviour of adult Pacific lamprey (e.g. atrazine, Smith 2012), it is possible that a combination of multiple chemicals work in concert to impede lamprey migratory cues. To restore Pacific lamprey to areas where they have been extirpated, anthropogenic physical and chemical migration barriers must be identified and management actions need to improve adult passage at these locations to seed suitable upstream habitats.

Our top model suggested that larval Pacific lamprey density was higher in catchments with greater anthropogenic disturbance, which is contrary to what we predicted. However, the habitat requirements of larval lamprey are very different from the fish species the cumulative disturbance index is designed for (e.g. mostly teleost sport fishes; Esselman et al. 2011), which may explain the effect we observed. Another interpretation is that Pacific lamprey in the Willamette may not be negatively affected by riparian habitat degradation and could actually benefit from additional nutrients and sediments associated with disturbances from land use practices. However, this hypothesis conflicts with numerous studies that have identified a link between anthropogenic development and habitat degradation (e.g. Bjornn & Reiser 1991; Roni 2003; Naiman & Latterell 2005; Mulvey et al. 2009). More direct evaluations of disturbances from land use and additional investigations in other areas within the Pacific lamprey range will help to elucidate this relationship.

Our study also found that a consideration of habitat structure may be useful for improving the efficiency of sampling designs. Sampling programmes can produce more precise estimates if auxiliary variables that partition variability are included (Thompson 2012). All habitat units must be included in the survey if a study's goal is to make inferences about the entire population of lamprey, but more precise estimates can be obtained if more samples are gathered from habitat units with higher variability in the response. Variance in lamprey counts increases with the number of individuals sampled; thus, researchers can obtain more precise CPUE estimates with the same number of samples if a larger proportion of samples are allocated to low-velocity habitats (Slade et al. 2003; Moser et al. 2007). Several variables, including a few that we measured in this study (e.g. fine sediment percentage), could also be used to model variable detection probability among sites and improve estimates of effect sizes (Mackenzie et al. 2006; Royle & Dorazio 2008). Acknowledging imperfect detection of lampreys is important because field research often finds that animals have an affinity for habitats that are the most difficult for researchers to sample effectively. In the case of this study, it is conceivable that greater sediment volumes in a low-velocity area might increase the density of lamprey, but at the same time reduce electrofishing capture efficiency. We believe that future research should attempt to measure or account for habitat-specific detection probability, because this might help to better resolve the effects of fine-scale habitat variables. These methods would increase the realism of density models and allow for a continual refinement of the sampling process.

Immediate management action might address the decline of Pacific lamprey, and our findings suggest that improving stream accessibility and habitat complexity will help to restore the historic distribution of Pacific lamprey (CRITFC 2011). Freshwater habitats across the Pacific Northwest have been highly influenced by current and historic land use practices (Bisson et al. 1992; McIntosh et al. 2000) that limit the availability of larval rearing habitat for Pacific lamprey. Conservation strategies that improve watershed conditions and restore riparian communities will set the physical template for habitat restoration (Naiman & Latterell 2005). Instream projects that stabilise stream channels and retain fine substrates and woody structure might increase available rearing habitat for lamprey species (e.g. Roni 2003). Effective monitoring of the responses of physical habitat in these treatments will be necessary to inform subsequent management actions. Evaluating and addressing migration barriers followed by mitigation actions to improve adult passage will help increase the distribution and abundance of larval Pacific lamprey across its historic range. Finally, continued monitoring of the occurrence and relative abundance of larval Pacific lamprey will document changes in its distribution and increase the understanding of its ecology.

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References

Beamish, R.J. & Levings, C.D. 1991. Abundance and freshwater migrations of the anadromous parasitic lamprey, *Lampetra tridentata*, in a tributary of the Fraser River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 48: 1250–1263.

Beamish, F.W. & Lowartz, S. 1996. Larval habitat of American brook lamprey. Canadian Journal of Fisheries and Aquatic Sciences 53: 693–700.

Bisbal, G.A. & McConnaha, W.E. 1998. Consideration of ocean conditions in the management of salmon. Canadian Journal of Fisheries and Aquatic Sciences 55: 2178–2186.

Bisson, P.A., Quinn, T.P., Reeves, G.H. & Gregory, S.V. 1992. Best management practices, cumulative effects, and long-term trends in fish abundance in Pacific Northwest Systems. In: Naiman, R.J., ed. Watershed management: balancing sustainability and environmental change. New York, NY: Springer-Verlag, pp. 189–232.

Bjornn, T.C. & Reiser, D.W. 1991. Habitat requirements of salmonids in streams. In: Meehan, W.R. ed. Influences of forest and rangeland habitat on salmonid fishes and their habitats. Bethesda, MD: American Fisheries Society Symposium 19: 83–138.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24: 127–35.

Burnham, K.P. & Anderson, D.R. 2002. Model selection and inference: a practical information-theoretic approach. 2nd edn. New York: Springer-Verlag.

Clemens, B.J., Binder, T.R., Docker, M.F., Moser, M.L. & Sower, S.A. 2010. Similarities, differences, and unknowns in biology and management of three parasitic lampreys of North America. Fisheries 35: 580–594.

Clemens, B.J., Mesa, M.G., Magie, R.J., Young, D.A. & Schreck, C.B. 2012. Pre-spawning migration of adult Pacific lamprey, *Entosphenus tridentatus*, in the Willamette River, Oregon, U.S.A. Environmental Biology of Fishes 93: 245–254.

Clemens, B.J., van de Wetering, S., Sower, S.A. & Schreck, C.B. 2013. Maturation characteristics and life-history strategies of the Pacific lamprey, Entosphenus tridentatus. Canadian Journal of Zoology 91: 775–788.

Close, D.A., Fitzpatrick, M.S. & Li, H.W. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. Fisheries 27: 19–25.

Close, D. A., Currens, K. P., Jackson, A., Wildbill, A. J., Hansen, J., Bronson, P. & Aronsuu, K. 2009. Lessons from the reintroduction of a noncharismatic, migratory fish: Pacific lamprey in the upper Umatilla River, Oregon. In: Brown, L.R., Chase, S.D., Mesa, M.G., Beamish, R.J. & Moyle, P.B., eds. Biology, management, and conservation of lampreys in North America. Bethesda, MD: American Fisheries Society Symposium, 72: 233–253.

CRITFC (Columbia River Inter-Tribal Fish Commission). 2011. Tribal Pacific lamprey restoration plan for the Columbia River Basin. Accessed January 2012: http://www.critfc.org/lamprey/lamprey_plan.pdf.

Environmental Protection Agency (EPA). 2014. Clean Waters Act 303d List of impaired waters. Available: http://yosemite.epa.gov/R10/WATER.NSF/TMDLs/CWA+303d+List#Current%20Lists (accessed Aug 1, 2014).

Esselman, P.C., Infante, D.M., Wang, L., Wu, D., Coper, A.R. & Taylor, W.W. 2011. An index of cumulative disturbance to river fish habitats of the coterminous United States from landscape anthropogenic activities. Ecological Restoration 29: 133–151.

Goniea, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H. & Stuehrenberg, L.C. 2006. Behavioral thermoregulation and slow migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135: 408–419.

Goodman, K., Ackerman, N., Gunckel, S., Beamesderfer, R., Krentz, L., Sheerer, P., Kern, C., Ward, D. & Ackerman, C. 2005. Oregon native fish status report. Salem, OR: Oregon Department of Fish and Wildlife, Fish Division.

Goodman, D., Kinzinger, A.P., Reid, S.B. & Docker, M.F. 2009. Morphological diagnosis of *Entosphenus* and *Lampetra* ammocoetes (Petromyzontidae) in Washington, Oregon, and California. In: Brown, L.R., Chase, S.D., Mesa, M.G., Beamish, R.J. & Moyle, P.B., eds. Biology, management, and conservation of lampreys in North America. Bethesda, MD: American Fisheries Society Symposium, 72: 223–232.

Hess, J.E., Campbell, N.R., Docker, M.F., Baker, C., Jackson, A., Lampman, R., McIlraith, R.B., Moser, M.L., Statler, D.P., Young, W.P., Wildbill, A.J. & Narum, S.R. 2014. Use of genotyping by sequencing data to develop a high-throughput and multifunctional SNP panel for conservation applications in Pacific lamprey. Molecular Ecology Resources. doi: 10.1111/1755-0998.12283

Hilbe, J.M. 2008. Negative binomial regression, 2nd printing. Cambridge, UK: Cambridge University Press.

Hughes, R.M., Dunham, S., Maas-Hebner, K.G., Yeakley, J.A., Schreck, C., Harte, M., Molina, N., Shock, C.C., Kaczynski, V.W. & Schaeffer, J. 2014. A review of urban water body challenges and approaches: (1) rehabilitation and remediation. Fisheries 39: 18–29.

Irwin, B.J., Wagner, T., Bence, J.R., Kepler, M.V., Liu, W. & Hayes, D.B. 2013. Estimating spatial and temporal components of variation for fisheries count data using negative binomial mixed models. Transactions of the American Fisheries Society 142: 171–183.

Jackson, A. & Moser, M. 2012. Low-elevation dams are impediments to adult Pacific Lamprey spawning migration in the Umatilla River, Oregon. North American Journal of Fisheries Management 32: 548–556.

Jolley, J.C., Silver, G.S. & Whitesel, T.A. 2012. Occupancy and detection of larval Pacific lampreys and *Lampetra spp.* in a large river: the Lower Willamette River. Transactions of the American Fisheries Society 141: 305–312.

Keefer, M.L., Moser, M.L., Boggs, C.T., Daigle, W.R. & Peery, C.A. 2009. Variability in migration timing of adult Pacific lamprey (*Lampetra tridentata*) in the Columbia River, U.S.A. Environmental Biology of Fishes 85: 253–264.

Keefer, M.L., Daigle, W.R., Peery, C.A., Pennington, H.T., Lee, S.R. & Moser, M.L. 2010. Testing adult Pacific lamprey performance at structural challenges in fishways. North American Journal of Fisheries Management 30: 376–385.

Levin, P.S., Zabel, R.W. & Williams, J.G. 2001. The road to extinction is paved with good intensions: negative association of fish hatcheries with threatened salmon. Proceedings of the Royal Society of London 268: 1153–1158.

Luzier, C.W., Schaller, H.A., Bostrom, J.K., Cook-Tabor, C., Goodman, D.H., Nelle, R.D., Ostrand, K. & Strief, B. 2011.

Pacific lamprey (*Entosphenus tridentatus*) assessment and template for conservation measures. Portland, OR: U.S. Fish and Wildlife Service

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. 2006. Occupancy estiamation and modeling: inferring patterna dn dynamics of species occurrence. Burlington, MA: Academic Press.

McCullagh, P. & Nelder, J.A. 1989. Generalized Linear Models. 2nd edn. London: Chapman & Hall.

McDowall, R.M. 1988. Diadromy in fishes: migrations between freshwater and marine environments. London, U.K.: Croom Helm.

McIntosh, B.A., Sedell, J.R., Thurow, R.F., Clarke, S.E. & Chandler, G.L. 2000. Historical changes in pool habitats of the Columbia River Basin. Ecological Applications 10: 1478–1496.

Mesa, M.G. & Copeland, E.S. 2009. Critical uncertainties and research needs for the restoration and conservation of native lampreys in North America. In: Brown, L.R., Chase, S.D., Mesa, M.G., Beamish, R.J. & Moyle, P.B., eds. Biology, management, and conservation of lampreys in North America. Bethesda, MD: American Fisheries Society, Symposium 72: 311–321.

Mesa, M.G., Magie, R.J. & Copeland, E.S. 2010. Passage and behavior of radio-tagged adult Pacific lampreys (Entosphenus tridentatus) at the Willamette Falls Project, Oregon. Northwest Science 84: 233–242.

Moser, M. L. & Mesa, M.G. 2009. Passage considerations for lamprey. In: Brown, L.R., Chase, S. D., Mesa, M. G., Beamish, R. J. & Moyle, P. B., eds. Biology, management and conservation of lampreys in North America. Bethesda, MD: American Fisheries Society, Symposium 72: 115–124.

Moser, M.L., Ocker, P.A., Stuehrenberg, L.C. & Bjornn, T.C. 2002a. Passage efficiency of adult Pacific lampreys at hydropower dams on the lower Columbia River, USA. Transactions of the American Fisheries Society 131: 956–965.

Moser, M.L., Matter, A.L., Stuehrenberg, L.C. & Bjornn, T.C. 2002b. Use of an extensive radio receiver network to document Pacific lamprey (*Lampetra tridentata*) entrance efficiency at fishways in the lower Columbia River, USA. Hydrobiologia 483: 45–53.

Moser, M.L., Butzerin, J.M. & Dey, D.B. 2007. Capture and collection of lampreys: the state of the science. Reviews in Fish Biology and Fisheries 17: 45–56.

Mueller, R.P., Moursund, R.A. & Bleich, M.D. 2006. Tagging juvenile Pacific lamprey with passive integrated transponders: methodology, short-term mortality and influence on swimming performance. North American Journal of Fisheries Management 26: 361–366.

Mulvey, M., Leferink, R. & Borisenko, A. 2009. Willamette Basin rivers and streams assessment. Hillsboro, OR: Oregon Department of Environmental Quality.

Murauskas, J.G., Orlov, A.M. & Siwicke, K.A. 2013. Relationships between the abundance of Pacific lamprey in the Columbia River and their common hosts in the marine environment. Transactions of the American Fisheries Society 142: 143–155.

Naiman, R.J. & Bilby, R.E. 1998. River ecology and management: lessons from the Pacific coastal ecoregion. New York: Springer-Verlag.

Naiman, N.J. & Latterell, J.J. 2005. Principles for linking fish habitat to fisheries management and conservation. Journal of Fish Biology 67 (Supplement B): 167–185.

Omernik, J.M. 1987. Ecoregions of the coterminous United States. Map (scale 1:7,500,000). Annals of the Association of American Geographers 77: 118–125.

Oregon Department of Fish and Wildlife. 2012. Oregon Fish Passage Barrier Dataset. Available at: https://nrimp.dfw.state.or.us/nrimp/default.aspx?pn=fishbarrierdata. (June 2012).

Orlov, A.M., Savinyh, V.F. & Pelenev, D.V. 2008. Features of the spatial distribution and size structure of the Pacific Lamprey *Lampetra tridentata* in the North Pacific. Russian Journal of Marine Biology 34: 276–287.

Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. & Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Canadian Journal of Fisheries and Aquatic Sciences 55: 281–287.

Petrosky, C.E. & Schaller, H.A. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead. Ecology of Freshwater Fish 19: 520–536.

Potter, I.C., Hilliard, R.W., Bradley, J.S. & McKay, R.J. 1986. The influence of environmental variables on the density of larval lampreys in different seasons. Oecologia 70: 433–440.

Reeves, G.H., Benda, L.E., Burnett, K.M., Bisson, P.A. & Sedell, J.R. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. In: Neilsen, J.L., ed. Evolution and the aquatic ecosystem: defining unique units in population conservation. Bethesda, MD: American Fisheries Society, Symposium 17: 334–349.

Reid, S.B., Boguski, D.A., Goodman, D.H. & Docker, M.F. 2011. Validity of *Lampetra pacifica* (Petromyzontiformes: Petromyzontidae), a brook lamprey described from the lower Columbia River Basin. Zootaxa 3091: 42–50.

Robinson, C.T., Sorensen, P.W., Bayer, J.M. & Seelye, J.G. 2009. Olfactory sensitivity of Pacific lampreys to lamprey bile acids. Transactions of the American Fisheries Society 138: 144–152.

Roni, P. 2003. Responses of benthic fishes and giant salamanders to placement of large woody debris in small Pacific Northwest streams. North American Journal of Fisheries Management 23: 1087–1097.

Royle, J.A. & Dorazio, R.M. 2008. Hierarchical modeling and inference in ecology. Amersterdam: Academic Press.

Schultz, L.D., Mayfield, M.P., Wyss, L.A., Sheoships, G.T., Clemens, B.J., Chasco, B. & Schreck, C.B. 2014. The distribution and relative abundance of spawning and larval Pacific lamprey in the Willamette River Basin. Final report to the Columbia River Inter-Tribal Fish Commission for project years 2011-2014. Portland, OR.

Scott, W.B. & Crossman, E.J. 1973. Freshwater fishes of Canada. Ottawa, Ontario: Fisheries Research Board of Canada Bulletin 184.

Scott, G.R. & Sloman, K.A. 2004. The effects of environmental pollutants on complex fish behaviour: integrating behavioural and physiological indicators of toxicity. Aquatic Toxicology 68: 369–392.

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A. & Hawkins, C.P. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14: 711–724.

Slade, J.W., Adams, J.V., Christie, G.C., Cuddy, D.W., Fodale, M.F., Heinrich, J.W., Quinlan, H.R., Weise, J.G., Weisser, J.W. & Young, R.J. 2003. Techniques and methods for estimating abundance of larval and metamorphosed sea lampreys in Great Lakes tributaries, 1995 to 2001. Journal of Great Lakes Research 29: 137–151.

Smith, A. 2012. Effects of Atrazine on olfactory-mediated behaviors in Pacific Lamprey (*Entoshenus tridentatus*). MS Thesis. Corvallis, OR: Oregon State University.

Spice, E.K., Goodman, D.H., Reid, S.B. & Docker, M.F. 2012. Neither philopatric nor panmictic: microsatellite and mtDNA evidence suggests lack of natal homing but limits to dispersal in Pacific lamprey. Molecular Ecology 21: 2916–2930.

Starcevich, S.J., Gunckel, S.L. & Jacobs, S.E. 2013. Movements, habitat use, and population characteristics of adult Pacific lamprey in a coastal river. Environmental Biology of Fishes 97: 939–953.

Stillwater Sciences. 2014. Evaluation of barriers to Pacific lamprey migration in the Eel River Basin. Final report prepared for the Wiyot Tribe. Arcata, California.

Stone, J. & Barndt, S. 2005. Spatial distribution and habitat use of Pacific lamprey (*Lampetra tridentata*) ammocoetes in a Western Washington stream. Journal of Freshwater Ecology 20: 171–185.

Sviridov, V.V., Glebov, I.I., Starovoytov, A.N., Sviridova, A.V., Zuev, M.A., Kulik, V.V. & Ocheretyanny, M.A. 2007. Wounding of Pacific salmon in relation to the spatio-temporal variation in distribution patterns of important predatory fishes in the Russian economic zone. North Pacific Anadromous Fish Commission Bulletin 4: 133–144.

Thompson, S.K. 2012. Sampling. 3rd edn. Hoboken: John Wiley & Sons.

Torgersen, C.E. & Close, D.A. 2004. Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. Freshwater Biology 49: 614–630.

Venables, W.N. & Dichmont, C.M. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70: 319–337.

Ver Hoef, J. & Boveng, P. 2007. Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? Ecology 88: 2766–2772.

Wang, L., Infante, D., Esselman, P., Cooper, A., Wu, D., Taylor, W., Beard, D., Whelan, G. & Ostroff, A. 2011. A Hierarchical spatial framework and database for the national river fish habitat condition assessment. Fisheries 36: 436–449.

Ward, D.L., Clemens, B.J., Clugston, D., Jackson, A.D., Moser, M.L., Peery, C. & Statler, D.P. 2012. Translocating adult Pacific lamprey with the Columbia River Basin: state of the science. Fisheries 37: 351–361.

Yun, S.-S., Wildbill, A.J., Siefkes, M.J., Moser, M.L., Dittman, A.H., Corbett, S.C., Li, W. & Close, D.A. 2011. Identification of putative migratory pheromones from Pacific lamprey (Lampetra tridentata). Canadian Journal of Fisheries and Aquatic Sciences 68: 2194–2203.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. New York: Springer-Verlag.