Spawning Patterns of Pacific Lamprey in Tributaries to the Willamette River, Oregon

Citation	Mayfield, M. P., Schultz, L. D., Wyss, L. A., Clemens, B. J., & Schreck, C. B. (2014). Spawning Patterns of Pacific Lamprey in Tributaries to the Willamette River, Oregon. Transactions of the American Fisheries Society, 143(6), 1544-1554. doi:10.1080/00028487.2014.949013
DOI	10.1080/00028487.2014.949013
Publisher	Taylor & Francis
Version	Version of Record
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Transactions of the American Fisheries Society 143:1544–1554, 2014

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2014.949013

ARTICLE

Spawning Patterns of Pacific Lamprey in Tributaries to the Willamette River, Oregon

M. P. Mayfield,[1] L. D. Schultz,* L. A. Wyss,[2] and B. J. Clemens[3]
Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331-3803, USA

C. B. Schreck
U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331-3803, USA

Abstract
Addressing the ongoing decline of Pacific Lamprey *Entosphenus tridentatus* across its range along the west coast of North America requires an understanding of all life history phases. Currently, spawning surveys (redd counts) are a common tool used to monitor returning adult salmonids, but the methods are in their infancy for Pacific Lamprey. To better understand the spawning phase, our objective was to assess temporal spawning trends, redd abundance, habitat use, and spatial patterns of spawning at multiple spatial scales for Pacific Lamprey in the Willamette River basin, Oregon. Although redd density varied considerably across surveyed reaches, the observed temporal patterns of spawning were related to physical habitat and hydrologic conditions. As has been documented in studies in other basins in the Pacific Northwest, we found that redds were often constructed in pool tailouts dominated by gravel, similar to habitat used by spawning salmonids. Across the entire Willamette Basin, Pacific Lampreys appeared to select reaches with alluvial geology, likely because this is where gravel suitable for spawning accumulated. At the tributary scale, spawning patterns were not as strong, and in reaches with nonalluvial geology redds were more spatially clumped than in reaches with alluvial geology. These results can be used to help identify and conserve Pacific Lamprey spawning habitat across the Pacific Northwest.

Monitoring the various life history phases of anadromous fishes is critical to understanding the ecology and population dynamics of target species (Johnson et al. 2007). Conducting redd counts to assess adult returns has been used to monitor salmonid populations for many years. Such assessments are popular because they are efficient and generally low in cost, and with relatively little effort large areas can be surveyed (Muhlfeld et al. 2006). Redd counts can also be used to detect temporal patterns in population abundance (e.g., Maxwell 1999; Al-Chokhachy et al. 2005) and understand how changes in environmental conditions or anthropogenic disturbances affect long-term trends in adult population returns and subsequent recruitment (Gallagher and Gallagher 2005). While redd count methods have been well developed for salmonids (e.g., see Dunham et al. 2001, 2009; Muhlfeld et al. 2006; Gallagher et al. 2007), the development of standardized spawning surveys for Pacific Lamprey *Entosphenus tridentatus* is in its infancy, and only a few known studies have focused on this species (e.g., Stone 2006; Brumo et al. 2009; Gunckel et al. 2009).

Pacific Lamprey is a native anadromous fish found throughout the coastal waters of western North America. Upon

*Corresponding author: luke.schultz@oregonstate.edu
[1]Present address: Rural Aquaculture Promotion, Peace Corps, Lusaka, Zambia.
[2]Present address: Calapooia Watershed Council, 136 Spaulding Avenue, Brownsville, Oregon 97327, USA.
[3]Present address: Oregon Department of Fish and Wildlife, 28655 Highway 34, Corvallis, Oregon 97333, USA.
Received May 16, 2014; accepted July 16, 2014

returning to freshwater, adult Pacific Lampreys have an extended freshwater holding period that may last from less than 1 month up to 2 years prior to making a final migration to their ultimate spawning areas (Clemens et al. 2010, 2013; Starcevich et al. 2013). Spawning can occur from March to July, and timing varies with water temperature and location (Pletcher 1963; Kan 1975; Gunckel et al. 2009), but it is generally initiated when the water temperature is 10–15°C (CRITFC 2011) and seasonal hydrographs are descending (Brumo et al. 2009). Adults construct redds in gravel and cobble substrates in a similar fashion to that of adult salmonids; however, both sexes participate in redd construction (Clemens et al. 2010) and individual lampreys typically build multiple redds. Pacific Lamprey is a gregarious spawner and researchers have observed up to 12 adults within an individual redd (Stone 2006).

The Pacific Lamprey has declined considerably across its range and has been extirpated from multiple drainages (Moser and Close 2003; Moyle et al. 2009; CRITFC 2011). Between 1939 and 1969, Pacific Lamprey returns at Bonneville Dam on the Columbia River averaged more than 100,000 adults, but have declined to an average of fewer than 40,000 between 1997 and 2010 (Murauskas et al. 2013). The Columbia River is not the only location that has experienced a decline of Pacific Lamprey runs; annual returns in 2009 and 2010 were estimated at fewer than 500 individuals at Winchester Dam on the North Umpqua River, while historical returns (1965–1971) were estimated to be between 14,532 and 46,785 (Goodman et al. 2005). Anadromous lampreys (including Pacific Lamprey) function as exchange vectors for nutrients between the streambed and water column as larvae (Shirakawa et al. 2013), provide an abundant and rich food source for predatory animals as larvae and outmigrants (e.g., Semakula and Larkin 1968), modify sediment conditions and invertebrate communities as a result of spawning activities (Hogg et al. 2014), and serve as a source of marine-derived nutrients to stream ecosystems following spawning (e.g., Guyette et al. 2013). Despite these important roles, conservation efforts have been hampered by many knowledge gaps in its biology (e.g., Clemens et al. 2010; CRITFC 2011; Luzier et al. 2011). Of the areas where the species has persisted, the Willamette River, Oregon, has one of the largest known adult returns (Kostow 2002), and Willamette Falls (approximately 42 km upstream from the Columbia River confluence) currently supports one of the few remaining traditional harvest locations for Pacific Lamprey for Native American tribes of the Pacific Northwest.

Although populations can be monitored with mark–recapture estimates at Willamette Falls (e.g., Baker and Graham 2012), little is known about Pacific Lamprey distribution and spawning characteristics within subbasins of the Willamette River system. This large basin (29,728 km^2) also contains a mix of highly urbanized land use, agriculture, and relatively intact headwaters (Mulvey et al. 2009). To understand how returning Pacific Lampreys use available habitat in river systems, it is important to develop methods for monitoring all life history phases, including the spawning phase. In general, redd counts for salmonids and Pacific Lamprey can be conducted using similar methods, but the associated assumptions specific to the species of interest must be examined and addressed (Dunham et al. 2009; Parsons and Skalski 2009). Spawning surveys for Pacific Lamprey have been problematic for several reasons, including confusion with salmonid redds (Stone 2006), false identification in low- and/or high-density areas (Brumo et al. 2009), questions about redd longevity and loss (Stone 2006), and the variable relationship between redd counts and abundance of spawning adults (Moser et al. 2007). Despite these potential sources of error, redd counts remain an efficient method to monitor populations and determine the presence of Pacific Lampreys, particularly with proper surveyor training (Mayfield et al. 2014). The objective of this study was to characterize Pacific Lamprey spawning activity in the Willamette River basin. Specifically, we aimed to evaluate habitat use and selection, temporal spawning trends, redd abundance, and distribution of redds at multiple spatial scales to better understand the spawning activity of Pacific Lamprey. We combined spawning surveys with existing streambed geology data and evaluated habitat selection patterns at multiple spatial scales across this large basin to gain insights into the freshwater ecology of Pacific Lamprey. Our results will inform management and conservation actions that will aid in the recovery of Pacific Lamprey.

METHODS

Spawning surveys and habitat characteristics.—We conducted spawning surveys of Pacific Lampreys in multiple tributaries of the Willamette River basin during 2012 and 2013 following initial exploratory surveys conducted during 2011. In 2011, we conducted short surveys to examine the logistics of performing future surveys and learn the field identification of Pacific Lamprey redds. Spawning surveys were established based on accessibility and logistical constraints in each stream and survey sections consisted of segments ranging from 1.3 to 11.6 km in length. Spawning surveys began in 2012 on Clear and Thomas creeks and the Marys River and comprised two survey segments in each stream (Table 1); the Marys River had contiguous survey segments and Clear and Thomas creeks had survey segments that were discrete spatially (Figure 1). We had previously conducted larval lamprey surveys in these tributaries, and adult migration studies documented adult lamprey movement into smaller tributary subbasins of the Willamette River (Clemens et al. 2012a, 2012b). In 2013, we continued spawning surveys in the Marys River and Clear and Thomas creeks and included a single survey segment on each of the Calapooia and Luckiamute rivers (Figure 1). In 2013, we also conducted surveys on the Santiam River and Ritner Creek (tributary to the Luckiamute River) to assess the occurrence of Pacific Lamprey spawning in large

TABLE 1. Survey length, number of visits, redd density, disturbance index, and proportion of underlying geology for Pacific Lamprey redd counts in tributaries of the Willamette River. Disturbance index is from Esselman et al. (2011) and is a measure of the cumulative amount of disturbance; the index ranges from 1.00 (high disturbance) to 4.00 (low disturbance). Underlying geology is from Walker and MacLeod (1991); geologic abbreviations are as follows: MG: mixed-grain alluvial; FG: fine-grain alluvial; MF: Missoula Flood alluvial; IR: intrusive rock; VR: volcanic rock; MS: marine sedimentary; TS: terrestrial sedimentary; alluvial underlying geology is shown in bold text.

						Percent of underlying geology						
Watercourse	Year	Survey length(km)	Visits	Redd density (redds/km)	Disturbance index	**MG**	**FG**	**MF**	IR	VR	MS	TS
Clear Creek, upper	2012	1.3	3	50.2	2.25							100
Clear Creek, lower	2012	2.4	3	165.0	2.25	100						
Luckiamute River	2013	5.6	4	47.2	1.25	80			15		5	
Thomas Creek, upper	2012	4.7	3	61.4	1.75	100						
	2013	4.7	3	116.2	1.75	100						
Thomas Creek, lower	2012	8.9	2	18.5	2.25	26	74					
	2013	7.0	3	137.0	2.25	26	74					
Marys River, upper	2012	8.5	3	14.1	1.50	70				30		
	2013	8.5	4	31.2	1.50	70				30		
Marys River, lower	2012	11.6	3	15.3	2.50	63				37		
	2013	11.6	3	21.3	2.50	63				37		
Calapooia River	2013	7.3	3	88.5	1.75	86		14				

and small stream systems, respectively. For both years, spawning was monitored from late April through mid-June, based on the timing of Pacific Lamprey spawning observed in other studies (Stone 2006; Brumo et al. 2009; Gunckel et al. 2009). Survey segments within each tributary were selected based on access and ability to safely float in personal watercraft (in floated survey segments) and to represent available habitat found in all underlying geologic types present.

Surveys on larger streams were conducted by two surveyors in individual inflatable pontoon boats. Each surveyor covered an area from stream bank to mid-channel to survey the entire channel. In the smaller streams (Clear and Ritner creeks), surveys were conducted on foot by observers walking upstream. We counted all Pacific Lamprey redds, live adults, and carcasses that were observed in each surveyed segment. Although subjectivity exists in redd surveys (e.g., Dunham et al. 2001; Al-Chokhachy et al. 2005; Muhlfeld et al. 2006), we defined redds as round depressions in the stream substrate that appeared to be actively excavated (Stone 2006). We used the presence of a relatively large piece of substrate at the upstream margin of the redd (Stone 2006), large rocks placed in the center of redds (Gunckel et al. 2009), upstream placement of excavated substrate, and the presence of adults on redds to help identify redds of Pacific Lampreys. Brook lampreys (including Western Brook Lamprey *Lampetra richardsoni* and Pacific Brook Lamprey *L. pacifica*; described in Reid et al. 2011) also spawn during the same time as the Pacific Lamprey, but their redds are generally much smaller. Median Pacific Lamprey redd size (measured as the excavated depression [redd pot], but excluding the downstream tailspill of disturbed substrate) is 0.124 m^2, whereas median Western Brook Lamprey redd size is between 0.01 m^2 and 0.03 m^2 (Stone 2006; Gunckel et al. 2009). If large areas of substrate appeared to be disturbed or redds appeared to overlap one another, as observed by Stone (2006) and Brumo et al. (2009), we counted each discrete depression as an individual redd.

To capture temporal variability in spawning activity, we surveyed each segment multiple times within the Pacific Lamprey spawning period, surveying each segment at least every 14 d as is recommended for salmonid surveys (Gallagher et al. 2007). Median and minimum Pacific Lamprey redd longevity was estimated by Stone (2006) as 40 and 10 d, respectively, so the sampling interval of 14 d should be appropriate to detect redds of various ages. Occasionally, hydrologic conditions precluded completion of surveys on schedule, and in these instances, surveys were completed as soon as stream hydrology and visibility permitted.

We measured spawning habitat use by Pacific Lampreys at the microhabitat and pool–riffle scales (10^{-1} m and 10^{0} m, respectively, as defined in Frissell et al. 1986). We measured the microhabitat dimensions of a subset of putative Pacific Lamprey redds (i.e., the first ~15–20 redds in each stream surveyed) in 2012 for comparison with available literature (e.g., Kan 1975; Stone 2006; Gunckel et al. 2009). We also measured water depth at the upstream edge of the redd, and width (perpendicular to flow) and length (parallel to flow) of the disturbed substrate within the excavated redd pot, but excluding the tailspill sediments. We used an ANOVA to assess differences in measured redd dimensions (response variable: redd length and width) among streams. Additionally, we assessed

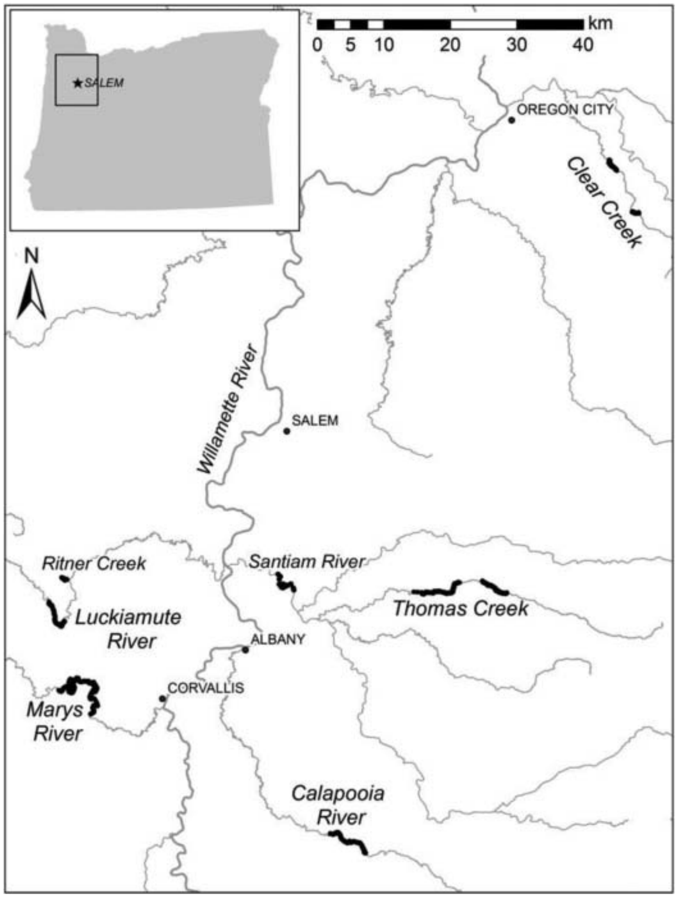

FIGURE 1. Locations of Pacific Lamprey spawning survey segments (designated by thick bold line) in the Willamette River basin, Oregon, 2012–2013. Surveys in Ritner Creek and the Santiam River were conducted once during the 2013 season to document the occurrence of Pacific Lamprey spawning in two streams of different size: small (Ritner Creek, 4–5 m wide) and large (Santiam River, 70–90 m wide).

pool–riffle scale habitat at Pacific Lamprey spawning locations during the 2012 surveys. We defined spawning locations as areas that contained one or more Pacific Lamprey redds within the same general vicinity, typically associated with a gradient break in the stream channel (e.g., an individual pool tailout or run habitat unit). At each spawning location, we categorized the channel unit type (pool, pool tailout, riffle, or run) and characterized substrate as the percentage of the spawning location consisting of the four most frequently occurring substrate categories following Peck et al. (2006). We collected water temperature data every 1 h from streams during the entire spawning period to relate hydrologic factors to the timing of spawning using Maxim iButton data loggers (Maxim Integrated, San Jose, California).

We georeferenced all Pacific Lamprey redds identified during surveys using a hand-held GPS unit (Delorme Earthmate PN-20; accuracy, <15 m) to assess larger scale habitat patterns. Using the linear referencing tools in ArcGIS version 10.1 (ESRI 2012), we determined the stream kilometer (as measured from the confluence of the tributary with a larger downstream river) of each redd location within a survey segment. We determined the underlying geologic types present in each survey segment using existing geologic maps (Walker and MacLeod 1991) and calculated the proportion of alluvial underlying geology per survey. Alluvial geology was defined as sediment deposits associated with moving water that were categorized as mixed-grain alluvial, fine-grain alluvial, or Missoula Flood alluvial types from geologic maps. Because sample sizes were limited ($n = 8$), we used a Pearson correlation coefficient to evaluate the relationship between underlying geology and observed redd abundance.

Land use practices can influence stream habitat conditions and subsequent spawning patterns for Pacific Lamprey. For each survey segment, we obtained an index of anthropogenic stream disturbance. Anthropogenic disturbance was described using a cumulative disturbance index obtained from data layers in the National Fish Habitat Partnership data system (Wang et al. 2011). These disturbance indices account for multiple types of anthropogenic disturbances, and combine disturbance scores from local catchment areas and all upstream catchments (Esselman et al. 2011). Although Pacific Lampreys likely pass through areas of higher disturbance during their upstream migration, we used the disturbance index measure for the stream segment at the survey segment to evaluate the effects of land use on spawning location selection. We used the observed peak redd density (i.e., the highest number of redds per kilometer for each survey segment) for analysis purposes, as is common in other redd count literature (Gallagher et al. 2007).

To assess potential relationships between adult and larval abundance, we compared peak redd densities to observed mean larval Pacific Lamprey densities from our associated sampling (Schultz et al. 2014) in tributaries for which we have both of these data sources from the same year. For this comparison, we did not perform any formal statistical tests because we had only five data points, and statistical tests likely would not provide much substantial evidence for the underlying biology. Instead, we visually examined bivariate plots of these data to infer patterns and generate subsequent hypotheses.

Spawning habitat selection.—We used Manly's selection ratio (Manly et al. 2002) to test whether Pacific Lampreys selected spawning areas based on underlying geologic structure at two spatial scales: within individual tributaries and across all tributaries surveyed in the Willamette River basin. While selection may imply a behavioral choice, we defined selection following Manly et al. (2002) as the amount of a resource used in proportion to that available. We used chi-square tests (Manly et al. 2002) to examine whether Pacific Lampreys constructed redds in proportion to the amount of habitat available (i.e., underlying geologic types) in each survey segment. Selection ratio values greater than 1.0 indicated positive selection for a geologic type and ratio values less than 1.0 indicated a selection against that geologic type. We calculated the standard error of the selection ratio estimates using the equation in Rogers and White (2007) and constructed 90% Bonferroni-adjusted confidence intervals around selection ratio estimates. For each survey segment, we used the peak redd counts from 2013 and enumerated the number of redds in each underlying geologic type using ArcGIS. For these analyses only data from 2013 were used to control for the variable hydrologic, detection, and observer conditions that might have differed between years. The amount of habitat of each geologic type available was defined as the proportion of each segment within each underlying geologic type. We combined data from the two contiguous survey segments in Thomas Creek and the Marys River to increase sample sizes for each of these two streams. To compute selection ratios for the entire Willamette River basin, peak redd count data for 2013 were combined from all survey segments and the proportion of survey segments located in each underlying geologic type was recalculated. We specified $\alpha = 0.10$ for all statistical analyses.

Spatial patterns.—To evaluate the spatial patterns of Pacific Lamprey redds across the Willamette River basin, we used a one-dimensional modified Ripley's K-function (Ripley 1976; Kraft and Warren 2003; Fortin and Dale 2005) with an edge correction factor and the peak redd counts for each survey segment from the 2013 field season. This test is a variation of the nearest-neighbor spatial statistic, but instead of measuring the distance from one redd to the next closest redd, Ripley's K-function analyzes the number of redds within a stream segment of length t from each individual redd, where t is a value set according to the survey length. An edge correction factor is applied to account for the underestimation bias of points on the edge of our surveys; redds on the edge of the study segment that might actually be close to counted redds are systematically excluded from the data set. For our study, t ranged from 0.1 km to one-half of the total survey length because that would be the maximum distance upstream or downstream that another redd could be from the exact center of the survey segment. For example, the total survey length for the Luckiamute River was 5.6 km, so t ranged from 0.1 to 2.8 km for this survey. The one-dimensional modified Ripley's K-function allowed us to examine the degree of spatial "clumping" of redds in different geologic types. The resulting modified K-function value (L) for the differing values of t was compared with expected L values from a completely random spatial pattern of points to determine whether redds were more clumped than the random distribution; L values less than 0.0 indicate underdispersion or clumping. Based on the L values for each search radius of t, we determined the spatial scales at which redds were grouped. For Pacific Lamprey, we observed in the field that redds were often constructed in close proximity to one another in suitable spawning gravel, so we would expect significant evidence for clumping at very small values of t. Significant clumping at larger values of t would indicate that the distribution of redds may be driven by large-scale habitat factors, such as underlying geology, and not just localized factors (e.g., availability of spawning substrate). All analyses for the Ripley's K-function were conducted in Program R (R Development Core Team 2013).

RESULTS

Spawning Surveys and Habitat Characteristics

We surveyed a total of 37.5 km of stream habitat in 2012 and 43.3 km in 2013 (Table 1). We observed redds in all survey segments including single surveys conducted in the Santiam River and Ritner Creek. Spawning surveys began in late April and continued until mid-June to observe the initial, peak, and the descending limb of spawning activity, although this was not consistently achieved in all streams or years. Rain events prohibited effective surveying in several segments in both years, but at least three surveys were conducted on all but three segments across the 2 years. Peak redd densities varied between streams, ranging from 14.1 redds/km in the Marys River in 2012 to 165.0 redds/km in the lower segment of Clear Creek in 2012 (Table 1). Across all surveys and both years, spawning activity occurred when water temperatures exceeded 10°C and redd building appeared to be most intense between 10°C and 15°C. Redd density was related to underlying geology (Pearson's $r = 0.451$); streams with a lower proportion of alluvial underlying geologic types (e.g., the Marys and Luckiamute rivers) had lower observed redd densities, while the Calapooia River, lower Clear Creek, and Thomas Creek were

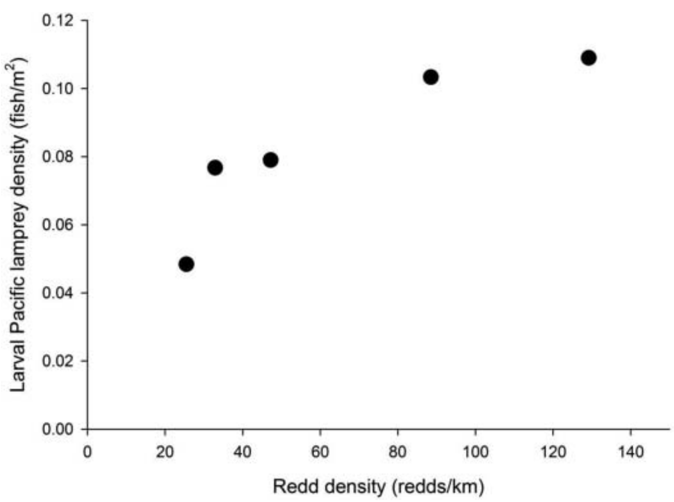

FIGURE 2. Relationship between adult Pacific Lamprey spawning (mean redd density; redds/km) and larval production (overall mean larval Pacific Lamprey density from the same year of sampling; individuals/m^2) in tributaries to the Willamette River. Larval data are from Schultz et al. (2014). This graph may also be interpreted as the relationship between larvae attracting adult spawners via pheromone responses (e.g., Yun et al. 2011).

composed entirely of alluvial underlying geology and had higher redd densities (Table 1). All spawning survey segments were ranked as having "high" or "very high" disturbance indices (ranging from 1.50 to 2.50, with 4.0 being the lowest level of disturbance), and no patterns were evident between disturbance indices and redd densities (Pearson's $r = 0.08$; Table 1). We observed Pacific Lamprey redds and spawning adults in both Ritner Creek and the Santiam River, indicating that Pacific Lampreys spawn in a variety of stream sizes. Our data suggested a positive association between larval Pacific Lamprey abundance and redd counts; however, this relationship did not appear to be linear (Figure 2).

Our field habitat measurements provided a meaningful quantitative description of Pacific Lamprey redds and spawning locations. Redd dimensions of 58 redds measured in 2012 were consistent with those in existing literature (Kan 1975; Stone 2006; Gunckel et al. 2009); mean redd width was 45.7 cm (range, 29–80 cm), mean redd length was 52.7 cm (range, 30–85 cm), and mean water depth was 60.1 cm (range, 24–99 cm). Using ANOVA, we found no significant difference in redd width ($P = 0.37$) or length ($P = 0.08$) between tributary subbasins. In 2012, we evaluated habitat characteristics for 133 spawning locations that included one or more Pacific Lamprey redds. Spawning locations were commonly associated with gradient breaks (e.g., pool tailouts and run habitats) with gravel and cobble substrates.

Habitat Selection

Pacific Lampreys did not select spawning habitats randomly. Rather, there was evidence that across the entire Willamette River basin Pacific Lampreys selected for reaches with gravel- and cobble-dominated alluvial geologic types (selection ratio = 1.87, 90% CI = 1.71–2.03) and selected against volcanic (selection ratio = 0.35, 90% CI = 0.27–0.43) and intrusive (selection ratio = 0.33, 90% CI = 0.12–0.54) rock underlying geologic types (Figure 3). Other alluvial geologic types (mixed-grain and Missoula Flood alluvial) did not show clear selection patterns. There was weak evidence for a selection pattern for marine sedimentary reaches (selection ratio = 0.76). At the tributary scale, Pacific Lampreys did not select for alluvial geology in all streams, but there was some preference for alluvial geology over other geologic types (Figure 3). Within tributary subbasins there was evidence ($P < 0.01$) that Pacific Lamprey redds were located in geologic types disproportionately to their availability (details below), with the exception of Thomas Creek ($\chi^2 = 0.27$, df = 1, $P = 0.60$). Thomas Creek contained both fine-grained and mixed-grain alluvial geology, but lampreys did not preferentially select between the two types. In the Luckiamute River, Pacific Lampreys selected for mixed-grain alluvial reaches (selection ratio = 1.12, 90% CI: 1.07–1.18) and against intrusive rock reaches (selection ratio = 0.42, 90% CI: 0.19–0.66), similar to patterns observed at the basin scale. In the Calapooia River, Pacific Lampreys selected for mixed-grain alluvial reaches (selection ratio = 1.05, 90% CI: 1.02–1.09) over Missoula Flood alluvial geologic reaches (selection ratio = 0.69, 90% CI: 0.51–0.87). In contrast with other surveys, Pacific Lampreys selected for volcanic rock reaches (selection ratio = 1.22, 90% CI: 1.04–1.40) and against mixed-grain alluvial reaches (selection ratio = 0.89, 90% CI: 0.80–0.98) in the Marys River.

Spatial Patterns

The one-dimensional modified Ripley's K-function allowed us to examine spatial patterns in Pacific Lamprey spawning habitat selection. In survey streams composed entirely of alluvial underlying geology (i.e., the Calapooia River and both Thomas Creek surveys), redds were clumped at small scales ($t < \sim 0.5$ km), but there was no strong evidence for clumping at larger scales (Figure 4). In the Luckiamute River, which had intrusive and sedimentary rock geologic types, we observed significant spatial clumping when $t < 1.6$ km (Figure 4). In the Marys River, a stream with volcanic rock intrusions, redds were clumped spatially for all tested values of t (Figure 4). Results from both the Luckiamute and Marys rivers indicate that in streams with less alluvial geology, redd distribution is driven by large-scale factors (underlying geology), which set the template for localized habitat characteristics (suitable substrate).

DISCUSSION

We conducted spawning surveys that targeted Pacific Lampreys in multiple tributaries to the Willamette River and analyzed habitat associations of redd density across multiple spatial scales to provide insights into the species' ecology and conservation. At microhabitat scales, Pacific Lampreys constructed redds in habitats similar to those observed by other researchers (Stone 2006; Brumo et al. 2009; Gunckel et al. 2009). At the pool–riffle scale, spawning habitat locations for Pacific Lampreys were similar to those of anadromous salmonids (Geist and Dauble 1998); gravel-dominated habitats at gradient breaks constituted the majority of our observed spawning locations. At coarser spatial scales, our analyses added to work by Gunckel et al. (2009) and described patterns of Pacific Lamprey spawning habitat use across the Willamette River basin related to large scale habitat features and underlying geology. Across the entire Willamette River basin, spawning adults showed a preference for streams with alluvial geology. However within tributary subbasins, Pacific Lampreys exhibited less preference for different underlying geologic types, but the degree of spatial clumping was related to the geologic structure.

Our spawning surveys across the Willamette River basin suggest that Pacific Lampreys spawn in a variety of environmental conditions and physical habitats (Schultz et al.

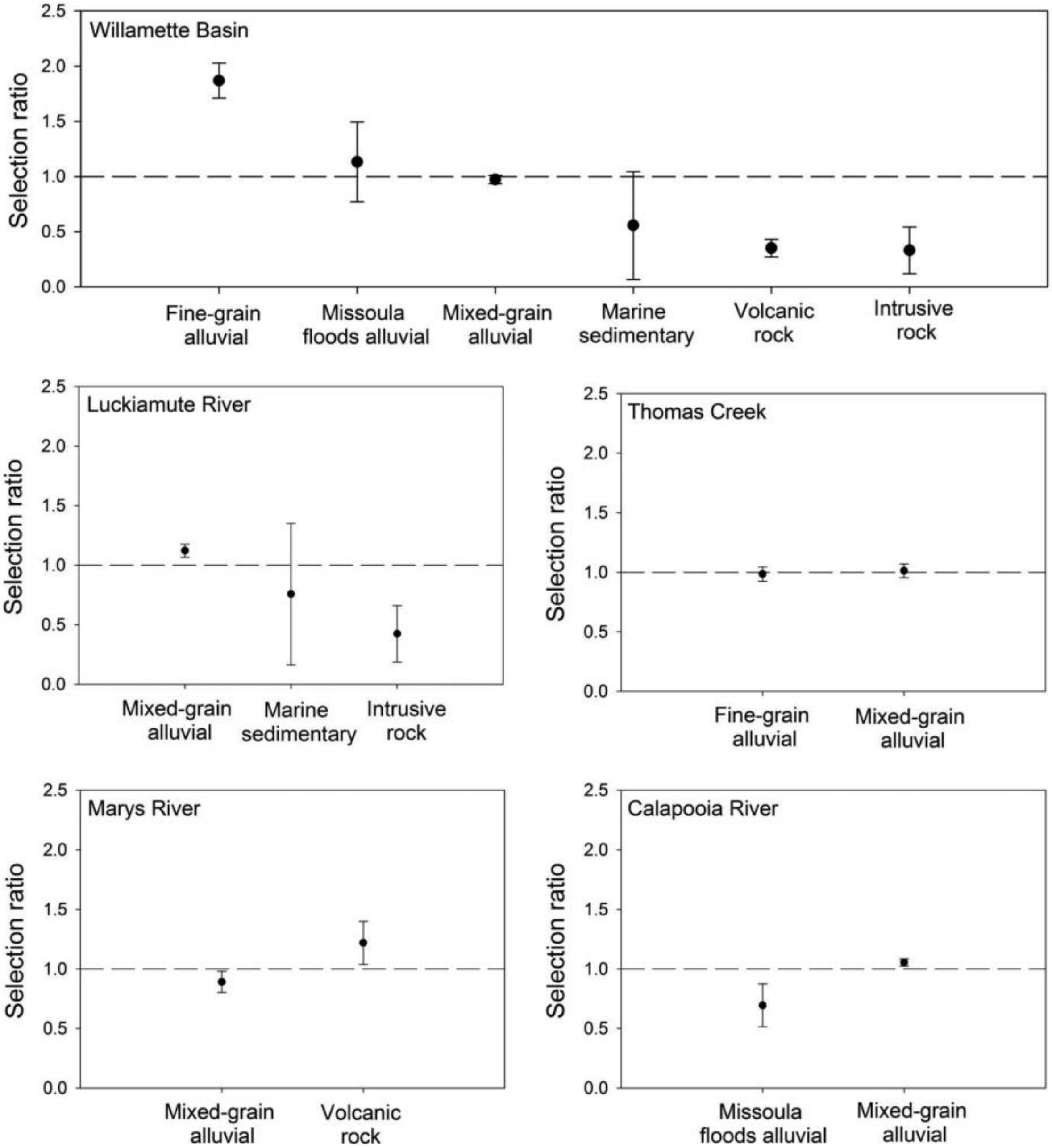

FIGURE 3. Manly's selection ratios for Pacific Lamprey habitat use during spawning for surveys in the entire Willamette River basin and four tributary subbasins. Error bars indicate 90% Bonferroni-adjusted confidence intervals. Selection was estimated using underlying geology data from the Oregon Department of Geology and Mineral Industries for all available geologic reaches.

2014). In both years, the spawning season appeared to correspond with water temperature observed by other researchers in other basins (i.e., 10–15°C: CRITFC 2011; Starcevich et al. 2013). We documented spawning activity in small streams (i.e., Ritner Creek, mean width = 4–5 m) and large tributaries (i.e., Santiam River, mean width = 70–90 m), which indicates that the Pacific Lamprey is likely a generalist spawner in regards to stream size. Pacific Lamprey has previously been categorized as "periodic strategists" that capitalize on infrequent opportunities for reproduction in highly variable environments (Clemens et al. 2013), a classification that is corroborated by our data. Spawning distribution is likely limited by passage barriers; Pacific Lampreys have passage requirements that are different from salmonids and even small diversion dams can completely block adult passage (Moser et al. 2002; Moser and Mesa 2009; Keefer et al. 2010). In surveys associated with this work (Schultz et al. 2014), the

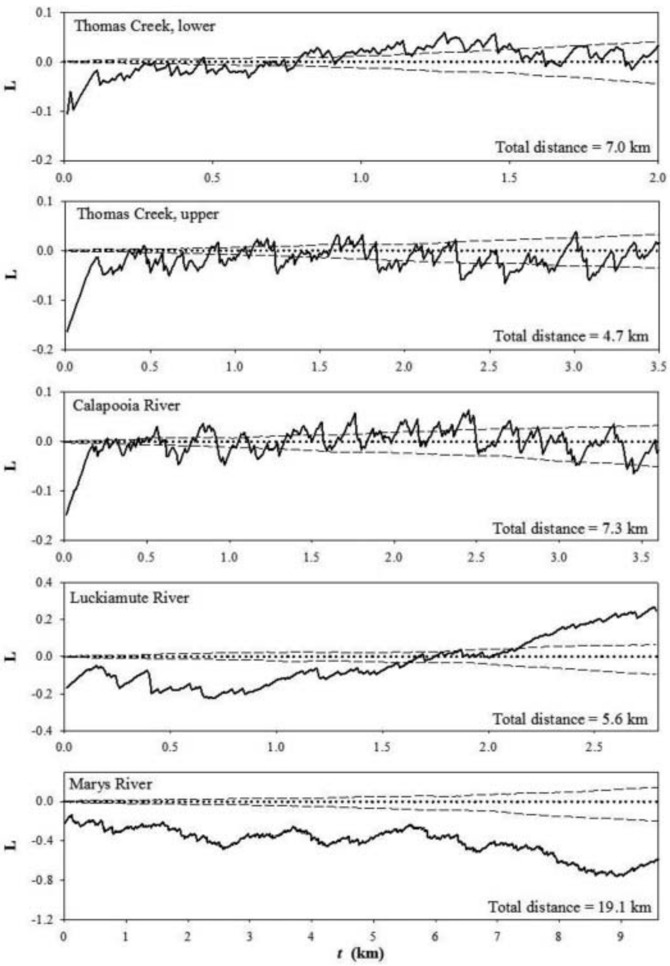

FIGURE 4. Results from the modified Ripley's K-function (L; solid line; Fortin and Dale 2005) by survey distance (t), total distance surveyed, and the zero line (dotted line) for Pacific Lamprey spawning surveys in streams of the Willamette River basin, Oregon, in 2013. Dashed lines are 95% confidence intervals around zero based on simulations run assuming a completely random spatial pattern; L values $<$ 0.0 (dotted line) indicate underdispersion or "clumping."

only locations sampled where larval Pacific Lampreys were not collected were associated with these types of migration barriers.

Pacific Lamprey evolved to be able to spawn over a large geographic range, and the ability to spawn in a wide range of habitats and in highly variable environments (Clemens et al. 2013) is likely a result of this evolutionary history. Upon entry into freshwater, Pacific Lampreys likely do not home in the strict sense (Spice et al. 2012). Instead, bile acid chemicals from larval lampreys (not necessarily conspecific) act as attracting pheromones to adult Pacific Lampreys (Robinson et al. 2009; Yun et al. 2011). Within the Columbia River system, migration timing is related to temperature and discharge (Keefer et al. 2009; Clemens et al. 2010, 2012a), and Pacific Lampreys generally complete a two-stage migration, holding during the winter months prior to completing final movements into their ultimate spawning locations (Clemens et al. 2012a, 2012b; Starcevich et al. 2013). Our results suggest that availability of spawning habitat within tributaries does not solely regulate the distribution of returning Pacific Lampreys to these ultimate spawning locations. Rather, hydrologic conditions at spawning locations likely operate in concert with downstream environmental conditions to trigger final migration and spawning initiation (e.g., water temperature the previous year: sensu Clemens et al. 2009).

Another factor that might be involved in the selection of spawning locations for adult Pacific Lampreys is the presence of larvae in prospective spawning tributaries. We have limited data that indicate a positive association between larval Pacific Lamprey abundance and redd counts. However, it does not appear to be a one-to-one relationship, which suggests that larval habitat may be more limiting than spawning habitat, although this is strictly speculative. Evidence from Sea Lamprey *Petromyzon marinus* in the Great Lakes also suggests they have similar habitat limitations (e.g., Morman et al. 1980). An alternative hypothesis to this stock–recruitment relationship is that the relative abundances of larvae function to attract spawning adults (i.e., larval abundance dictates adult return abundance), which has also been observed with the Sea Lamprey (Vrieze and Sorensen 2001; Wagner et al. 2009; Neeson et al. 2011). However, future studies are needed to elucidate the relationship between adult returns and larval production for the Pacific Lamprey, but these data provide a starting point for more comprehensive analyses of this nature.

Our use of the modified Ripley's K-function allowed us to examine the spatial clumping of redds and infer both the distribution of habitat use and the interspecific spawning behavior of Pacific Lampreys. Across the Willamette River basin, spawning fish selected tributaries with alluvial geology that consisted of gravel-dominated streambeds, yet redds were widely distributed across all locations surveyed and spawning patches (i.e., the physical area of spawning locations) were highly variable in size. In survey segments with less alluvial geology, we observed more clumping of redds within a relatively small proximity. For example, we observed Pacific Lampreys using small patches (~10 m^2) of spawning gravels within a matrix of bedrock streambed in many of our survey segments. This analysis may also be an indication of the gregarious nature of adult lampreys during spawning. Prior to spawning, adult male Sea Lampreys release pheromones that induce search behavior in ovulating females (Li et al. 2003), and Pacific Lampreys probably have similar physiology (Robinson et al. 2009). These conspecific cues are probably most influential in the clumping of redds when adult abundances are relatively low (Greene and Stamps 2001).

Although redd surveys are thought to be an imprecise measure of lamprey abundance (Moser et al. 2002, 2007), counts of redds and spawning adults may facilitate trend assessments of Pacific Lamprey status more accurately than traditional measures of adult abundance (e.g., counts at dams). Despite the acknowledgment of potential sources of error, adult returns and redd counts were positively correlated in the South Fork Coquille River (Brumo et al. 2009). Redd surveys also have the utility of confirming access of adult Pacific Lampreys to spawning areas and can be used to assess distribution above putative barriers. The modified Ripley's K-function allowed us to quantitatively assess spatial patterns of Pacific Lamprey spawning habitat use that influence future monitoring considerations. In reaches with primarily alluvial geology, we observed spawning patterns that were approximately random spatially, but reaches with more intrusive bedrock geology showed significant spatial clumping across larger survey reach lengths. If the development of a large-scale Pacific Lamprey spawning monitoring program is desired, it will be important to account for this spatial variability to ensure that spawning surveys are not biased by the availability of suitable habitat. In areas with less alluvial underlying geology (e.g., the Marys River), longer survey segments would be needed to provide precise redd density estimates (Mayfield et al. 2014). Estimating spawner abundance reliably will require an assessment of several additional metrics related to the biology of Pacific Lamprey including the number of individual adults spawning in each redd, the viability of redds, the degree of "test redd" construction (i.e., depressions that appear to be redds but do not contain eggs), and the ratio of redds to adults.

Immediate management action is needed to address the decline of Pacific Lamprey and restore its cultural and ecological functions across the Pacific Northwest. Our findings suggest actions that increase accessibility and improve habitat conditions could contribute to halting the ongoing decline of Pacific Lamprey, an immediate goal of recovery planning (CRITFC 2011). Migrating Pacific Lampreys are widely distributed in the Willamette River basin throughout accessible habitats (Clemens et al. 2012a, 2012b), and we documented spawning activity in all reaches that we surveyed. Our results indicated that Pacific Lampreys are capable of spawning in a wide diversity of stream sizes and underlying geologic types, provided there are no barriers to upstream migration. Addressing passage barriers has been identified as a top priority for recovery (Mesa and Copeland 2009; CRITFC 2011; Wyss et al. 2013) and our data suggest that if adult Pacific Lampreys can access previously blocked stream reaches they should be able to successfully colonize them (e.g., Jones et al. 2003; Ward et al. 2012). Suitable spawning habitat is also consistent with spawning requirements for salmonids and conservation actions directed at either of these target fishes would be mutually beneficial. Across the Willamette River basin, despite habitat disturbance scores that indicated moderate to high disturbance indices for riparian conditions, we saw high densities of spawning activity relative to other documented surveys (e.g., Brumo et al. 2009; Gunckel et al. 2009). Nevertheless, habitat restoration projects that stabilize stream channels and maintain natural riparian areas and hydrologic processes could maximize benefits to stream habitats and increase the production potential for multiple fish species across riverscapes of the Pacific Northwest.

ACKNOWLEDGMENTS

Funding for this study was provided by the Columbia River Inter-Tribal Fish Commission through the Columbia Basin Fish Accords partnership with the Bonneville Power Administration under project 2008-524-00 (Brian McIlraith, project manager). We thank several landowners that provided survey access as well as logistical support for our project. Additional fieldwork assistance was generously provided by K. McDonnell and C. Christianson. M. Colvin, B. McIlraith, B. Heinith, J. Peterson, B. Gerth, G. Giannico, J. Jolley, G. Silver, and R. Wildman provided sampling and analyses advice as well as lending field equipment to our project. A critical review by A. Brumo, S. Whitlock, and three anonymous reviewers greatly improved the quality of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring Bull Trout populations. North American Journal of Fisheries Management 25:1505–1512.

Baker, C., and J. Graham. 2012. Willamette Falls escapement estimate. Confederated Tribe of the Warm Springs Indian Reservation, Annual Report to Bonneville Power Administration, Project 2008-308-00, Portland, Oregon.

Brumo, A. F., L. Grandmontagne, S. N. Namitz, and D. F. Markle. 2009. Approaches for monitoring Pacific Lamprey spawning populations in a coastal Oregon stream. Pages 203–222 *in* L. R. Brown, S. D. Chase, M. G. Mesa, R. J. Beamish, and P. B. Moyle, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

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

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

Clemens, B. J., S. Van de Wetering, J. Kaufman, R. A. Holt, and C. B. Schreck. 2009. Do summer temperatures trigger spring maturation in Pacific Lamprey, *Entosphenus tridentatus*? Ecology of Freshwater Fish 18:418–426.

Clemens, B. J., S. Van de Wetering, S. A. Sower, and C. B. Schreck. 2013. Migration characteristics and life history strategies of the Pacific Lamprey, *Entosphenus tridentatus* (Gairdner, 1836). Canadian Journal of Zoology 91:775–788.

Clemens, B. J., L. Wyss, R. McCoun, L. Schwabe, I. Courter, S. Duery, J. Vaughn, and C. B. Schreck. 2012b. Migration characteristics and habitat use of the imperiled adult Pacific Lamprey in the Willamette basin: prelude to estimating requirements for persistence. Final Report to the Columbia River Inter-Tribal Fish Commission, Portland, Oregon.

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

Dunham, J., B. Reiman, and K. Davis. 2001. Sources and magnitude of sampling error in redd counts for Bull Trout. North American Journal of Fisheries Management 21:343–352.

Dunham, J. B., A. E. Rosenberger, R. F. Thurow, C. A. Dollof, and P. J. Howell. 2009. Coldwater fish in wadeable streams. Pages 119–138 *in* S. A. Bonar, W. A. Hubert, and D. W. Willis, editors. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.

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

ESRI (Environmental Systems Research Institute). 2012. ArcGIS, version 10.0. ESRI, Redlands, California.

Fortin, M. J., and M. Dale. 2005. Spatial analysis: a guide for ecologist. Cambridge University Press, Cambridge, UK.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification. Environmental Management 10:199–214.

Gallagher, S. P., and C. M. Gallagher. 2005. Discrimination of Chinook Salmon, Coho Salmon, and steelhead redds and evaluation of the use of redd data for estimating escapement in several unregulated streams in northern California. North American Journal of Fisheries Management 25:284–300.

Gallagher, S. P., P. K. J. Hahn, and D. H. Johnson. 2007. Redd counts. Pages 197–234 *in* D. H. Johnson, B. M. Shrier, J. S. O'Neal, J. A. Knutszen, X. Augerot, T. A. O'Neil, and T. N. Pearsons, editors. Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. American Fisheries Society, Bethesda, Maryland.

Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall Chinook Salmon: the importance of geomorphic features in large rivers. Environmental Management 22:655–669.

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

Greene, C. M., and J. A. Stamps. 2001. Habitat selection at low population densities. Ecology 82:2091–2100.

Gunckel, S. L., K. K. Jones, and S. E. Jacobs. 2009. Spawning distribution and habitat use of adult Pacific and Western Brook lampreys in Smith River, Oregon. Pages 173–189 *in* L. R. Brown, S. D. Chase, M. G. Mesa, R. J. Beamish, and P. B. Moyle, editors, Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

Guyette, M. Q., C. S. Loftin, and J. Zydlewski. 2013. Carcass analog addition enhances juvenile Atlantic Salmon (*Salmo salar*) growth and condition. Transactions of the American Fisheries Society 70:860–870.

Hogg, R. S., S. M. Coghlan, J. Zydlewski, and K. S. Simon. 2014. Anadromous Sea Lampreys are ecosystem engineers in a spawning tributary. Freshwater Biology 59:1294–1307.

Johnson, D. H., B. M. Shrier, J. S. O'Neil, J. A. Knutzen, X. Augerot, T. A. O'Neil, and T. N. Pearsons. 2007. Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. American Fisheries Society, Bethesda, Maryland.

Jones, M. L., R. A. Bergstedt, M. B. Twohey, M. F. Fodale, D. W. Cuddy, and J. W. Slade. 2003. Compensatory mechanisms in Great Lakes Sea Lamprey populations: implications for alternative control strategies. Journal of Great Lakes Research 29 (Supplement 1):113–129.

Kan, T. T. 1975. Systematics, variation, distribution and biology of lampreys of the genus *Lampetra* in Oregon. Doctoral dissertation. Oregon State University, Corvallis.

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

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

Kraft, C. E., and D. R. Warren. 2003. Development of spatial pattern in large woody debris and debris dams in streams. Geomorphology 51:127–139.

Kostow, K. 2002. Oregon lampreys: natural history status and problems analysis. Oregon Department of Fisheries and Wildlife, Salem.

Li, W., M. J. Siefkes, A. P. Scott, and J. H. Teeter. 2003. Sex pheromone communication in the Sea Lamprey: implications for integrated management. Journal of Great Lakes Research 29:85–94.

Luzier, C. W, H. A. Schaller, J. K. Bostrom, C. Cook-Tabor, D. H. Goodman, R. D. Nelle, K. Ostrand, B. Strief. 2011. Pacific Lamprey (*Entosphenus tridentatus*) assessment and template for conservation measures. U.S. Fish and Wildlife Service, Portland, Oregon.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals. Kluwer Academic Press, Dordrecht, The Netherlands.

Maxwell, B. A. 1999. A power analysis on the monitoring of Bull Trout stocks using redd counts. North American Journal of Fisheries Management 19:860–866.

Mayfield, M. P., L. D. Schultz, L. A. Wyss, M. E. Colvin, and C. B. Schreck. 2014. Using spatial resampling to assess redd count survey length requirements for Pacific Lamprey. North American Journal of Fisheries Management 34:923–931.

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

Morman, R. H., D. W. Cuddy, and P. C. Rugen. 1980. Factors influencing the distribution of Sea Lamprey (*Petromyzon marinus*) in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 37:1811–1826.

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

Moser, M. L., and D. A. Close. 2003. Assessing Pacific Lamprey status in the Columbia River basin. Northwest Science 77:116–125.

Moser, M. L., and M. G. Mesa. 2009. Passage considerations for anadromous lampreys. Pages 115–124 *in* L. R. Brown, S. D. Chase, M. G. Mesa, R. J. Beamish, and P. B. Moyle, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

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

Moyle, P. B., L. R. Brown, S. D. Chase, and R. M. Quiñones. 2009. Status and conservation of lampreys in California. Pages 279–292 *in* L. R. Brown, S. D. Chase, M. G. Mesa, R. J. Beamish, and P. B. Moyle, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

Muhlfeld C. C., M. L. Taper, D. F. Staples, and B. B. Shepard. 2006. Observer error structure in Bull Trout redd counts in Montana streams: implications for inference on true redd numbers. Transactions of the American Fisheries Society 135:643–654.

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

Murauskas, J. G., A. M. Orlov, and K. A. Siwicke. 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.

Neeson, T. M., M. J. Wiley, S. A. Adlerstein, and R. L. Riolo. 2011. River network structure shapes interannual feedbacks between adult Sea Lamprey migration and larval habitation. Ecological Modelling 222:3181–3192.

Parsons, A. L., and J. R. Skalski. 2009. A statistical critique of estimating salmon escapement in the Pacific Northwest. Pages 192–213 *in* J. R. Skalski, editor. The design and analysis of salmonid tagging studies in the Columbia Basin. Technical report to Bonneville Power Administration, Project 198910700, Portland, Oregon.

Peck, D. V., A. T. Herlihy, B. H. Hill, R. M. Hughes, P. R., Kaufmann, D. J. Klemm, J. M. Lazorchak, F. H. McCormick, S. A. Peterson, P. L. Ringold, T. Magee, and M. Cappaert 2006. Environmental monitoring and assessment program–surface waters western pilot study: field operations manual for wadeable streams. U.S. Environmental Protection Agency, EPA/620/R-06/003, Washington, D.C.

Pletcher, F. T. 1963. The life history and distribution of lampreys in the salmon and certain other rivers in British Columbia, Canada. Master's thesis. University of British Columbia, Vancouver.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: http://www.R-project.org./ (September 2014).

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

Ripley, B. D. 1976. The second-order analysis of stationary point processes. Journal of Applied Probability 13:255–266.

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

Rogers, K. B., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data. Pages 625–676 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Schultz, L. D., M. P. Mayfield, B. J. Clemens, L. A. Wyss, G. T. Sheoships, B. Chasco, and C. B. Schreck. 2014. 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, Portland, Oregon.

Semakula, S. N., and P. A. Larkin. 1968. Age, growth, food, and yield of White Sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. Journal of the Fisheries Research Board of Canada 25: 2589–2602.

Shirakawa, H, S. Yanai, and A. Goto. 2013. Lamprey larvae as ecosystem engineers: physical and geochemical impact on the streambed by their burrowing behavior. Hydrobiologia 701:313–322.

Spice, E. K., D. H. Goodman, S. B. Reid, and M. F. Docker. 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., S. L. Gunckel, and S. E. Jacobs. 2013. Movements, habitat use, and populations characteristics of adult Pacific Lamprey in a coastal river. Environmental Biology of Fishes 97:939–953.

Stone, J. 2006. Observation on nest characteristics, spawning habitat, and spawning behavior of Pacific and Western Brook lamprey in a Washington stream. Northwestern Naturalist 87:225–232.

Vrieze, L. A., and P. W. Sorensen. 2001. Laboratory assessment of the role of a larval pheromone and natural stream odor in spawning stream localization by migratory Sea Lamprey (*Pertromyzon marinus*). Canadian Journal of Fisheries and Aquatic Sciences 58:2374–2385.

Wagner, C. M., M. B. Twohey, and J. M. Fine. 2009. Conspecific cueing in the Sea Lamprey: do reproductive migrations consistently follow the most intense larval odour? Animal Behavior 78:593–599.

Walker, G. W., and N. S. MacLeod. 1991. Map of Oregon. U.S. Geological Survey, Reston, Virginia.

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

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

Wyss, L. A., L. Schultz, G. T. Sheoships, and C. B. Schreck. 2013. Monitoring Pacific Lamprey relative abundance and distribution in the Willamette River basin. Annual Report to the Columbia River Inter-Tribal Fish Commission, Portland, Oregon.

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