The distribution and relative abundance of spawning and larval Pacific lamprey in the Willamette River Basin

Final Report to the Columbia Inter-Tribal Fish Commission for project years 2011-2014

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Executive Summary

Pacific lamprey is a jawless, anadromous fish, which was widespread in the Pacific Northwest; they are also an important cultural resource for many regional Native American tribes. The species declined substantially in the Columbia River in the last 50 years and has been lost from a substantial portion of its historic range. Until recently, the ecological requirements of Pacific lamprey have been largely ignored and there is a need to resolve many elements of its life history. The Willamette River appears to have one of the highest returns of any of the Columbia River tributaries, and also supports one of the only remaining traditional harvest locations in the Columbia River Basin. Despite high abundances in the basin, little is known about the distribution, habitat associations, and relative abundance of Pacific lamprey in the Willamette River Basin. In 2011-14, we investigated the freshwater components of the Pacific lamprey life cycle within the Willamette River Basin to provide insights into Pacific lamprey ecology that can be applied in Pacific lamprey recovery efforts in the Willamette and across the Pacific Northwest.

Pacific lamprey generally return to freshwater 8-12 months prior to spawning the following spring. Spawners deposit their eggs in depressions (redds) that they construct, similar to salmon. We conducted spawning ground surveys to enumerate Pacific lamprey redds and examine spawning habitat needs for the species. We found redds in all the stream segments we surveyed, indicating that the species is widely distributed throughout Basin, but the abundance of redds differed substantially in the different areas we surveyed. Pacific lamprey redds were more abundant in gravel substrates, similar to those used by salmonids, suggesting that ongoing habitat restoration will be mutually beneficial for these species of concern. We also used statistical techniques to analyze spawning survey data and provide recommendations for Pacific lamprey monitoring programs. In Chapter 2 and 3 of this report, we report these findings in greater detail.

After hatching, Pacific lamprey spend ~4-7 years rearing in freshwater as larvae prior to metamorphosing and migrating to the ocean. We conducted surveys throughout the Willamette Basin to assess habitat requirements and assess survival during this phase of their life cycle. We sampled throughout the Willamette Basin, and collected Pacific lamprey larvae in 45 of 53 sample locations. All locations where we failed to collect larvae were associated with anthropogenic migration barriers (often diversion dams). Larvae were found in areas composed of deep, fine sediment that provide suitable burrowing habitat, particularly off-channel habitats

(backwaters, alcoves, side channels). These findings suggest habitat restoration strategies that increase the complexity of stream channels will be beneficial to Pacific lamprey, and is also consistent with other ongoing restoration activities. Using size information, we estimated survival rates of larvae and found that survival was fairly high during the larval portion of the Pacific lamprey life cycle. We also used our data to provide sample size recommendations for implementing monitoring plans for larval populations. In chapters 4 and 5 of this report we provide greater detail on these findings and its implications. Chapter 6 provides a summary of all of these findings and provides numerous recommendations for management actions and developing monitoring plans, and outlines future research directions that have been identified from our work.

Chapter 1.

Introduction

The number of imperiled freshwater and diadromous fishes in North America has increased 92% since the late 1980s (Jelks et al. 2008), and the rate of extinction for freshwater fauna will likely increase into the future (Ricciardi and Rasmussen 1999). Causes for these declines include habitat loss, overexploitation, and hybridization and competition with introduced species. On the West Coast of North America, fish populations are further suppressed by artificial migration barriers that impede passage to spawning and rearing areas (Freeman et al. 2003). Negative ecological consequences of downward population trends are compounded by the loss of marine derived nutrients left by fish carcasses into recipient riverine ecosystems (Gende et al. 2002). These ecological losses are subsequently linked to cultural losses for native peoples that historically relied on anadromous fishes for their livelihood (Close et al. 2002). Conservation action is critical in the recovery of these species and an understanding of population trends is paramount to prioritizing management activities to address these declines (Williams 1991).

Pacific lamprey *Entosphenus tridentatus* is a cultural icon for many Native American tribes across the Pacific Northwest that has declined considerably across its range in western North America, including extirpation from multiple drainages (Moser and Close 2003, CRITFC 2011). Its semelparous life cycle consists of 3 – 8 years in freshwater as filter feeding larvae, followed by a physiological and morphological transformation into macrophthalmia, and subsequent outmigration to marine environments (Scott and Crossman 1973, Kan 1975, Clemens et al. 2010). The parasitic marine phase lasts less than 3.5 years (reviewed in Clemens et al. 2010), before to returning to freshwater to hold prior to spawning. The freshwater holding period can last from less than one month up to two years prior to making a final migration to their ultimate spawning areas (Clemens et al. 2010 and 2012, Starcevich et al. 2013). Throughout its life cycle, Pacific lamprey provide numerous ecosystem services by functioning as exchange vectors for nutrients between the streambed and water column as larvae (Shirakawa et al. 2013), providing an abundant and rich food source for predatory animals as larvae and outmigrants (e.g., Semakula and Larkin 1968), being a predation buffer for other fishes upon return to freshwater (e.g., Pacific salmonids *Oncorhynchus sp.*, Close et al. 1995), modifying sediment conditions and invertebrate communities as a result of spawning activities (Hogg et al. 2014), and as source of marine derived nutrients to stream ecosystems following spawning (e.g., Ward et al. 2012). Despite the 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 and Levings 1991), and numerous knowledge gaps in its biology (CRITFC 2011, Luzier et al. 2011).

Across the range of Pacific lamprey, the Willamette River, OR has one of the largest remaining adult returns (Figure 1-1; Kostow 2002). Willamette Falls also currently supports one of the few remaining harvest locations for Pacific lamprey. However, harvest data suggest that Willamette River populations of Pacific lamprey have mirrored those observed range-wide; estimated harvest in the Willamette River declined from ~250,000 pounds in 1943 to less than 12,000 since 2001 (Ward 2001). Recent population estimates at Willamette Falls ranged from 63,517 to 245,325 between 2010 and 2012, respectively (Baker and Graham 2012). Although the Willamette River appears to have mirrored the declining population trends in other river basins, it remains an important priority for conservation actions to maintain its current status. Furthermore, because populations in the Willamette Basin appear to be well relative to other systems, it provides an excellent system to gain insight into the ecology and management of Pacific lamprey that can be applied in other basins.

For these reasons, we conducted research in the Willamette River Basin to address critical knowledge gaps in the life history of Pacific lamprey (e.g., Mesa and Copeland 2009, CRITFC 2011, Luzier et al. 2011) and inform conservation actions to recover the species across its range. We built on previous work conducted in the Willamette River that assessed adult migration patterns (Clemens 2011), and evaluated spawning activity and larval abundance throughout the Willamette River Basin. Our work began in 2011 with spawning survey pilot studies and larval assessments conducted in five wadeable Willamette River tributaries (Wyss et al. 2012). In 2012, we conducted spawning surveys in three streams, and larval assessments on the same five streams as in 2011, and added four other tributaries (Wyss et al. 2013). Work from these two years was used to formulate hypotheses and additional data collection for this final report, with the specific objectives of:

1) Monitor adult spawning activities of Pacific lamprey by conducting quantitative surveys,

2) Identify rearing locations of ammocoetes/juveniles to estimate the relative abundance of lamprey and characterize associated habitats,

3) Collect data to assist other ongoing studies including a contaminant analysis study and a genetic study to better understand lamprey population biology.

Our findings can be used to make broader inferences about Pacific lamprey limiting factors in the Willamette River Basin and across its range, and may aid in the assessment and prioritization of management and conservation actions for the species. Furthermore, our findings have relevance to the conservation of other Western lampreys *Lampetra spp.*

This report contains multiple sections that address different facets of these objectives. In Chapter 2, we used data collected during spawning ground surveys to illustrate spawning habitat use patterns of Pacific lamprey across multiple spatial scales across the Willamette River Basin.

In Chapter 3, we used spatial resampling to assess necessary survey lengths to detect and estimate the density of redds and will be useful for the design of monitoring plans. In both of these chapters, we clearly illustrate the utility of conducting spawning surveys for Pacific lamprey, techniques that have previously been treated as problematic (e.g., Moser et al. 2007). We also highlight specific uncertainties that will need to be addressed to better utilize these techniques for monitoring of Pacific lamprey.

In Chapters 4 and 5, we examined the ecology of the larval life history stage. Chapter 4 contains an analysis of the habitat and co-occurring species associations of larvae in wadeable tributaries to the Willamette River, and Chapter 5 focused on insights gained from examining length frequency data from our field sampling. From these data we estimated mortality during the larval stage and used statistical resampling to evaluate sample sizes necessary to characterize larval length frequencies.

In Chapter 6, we describe projects in which we worked collaboratively to either collect field samples or used our data to address similar research objectives. The work presented herein will greatly advance efforts to conserve and recover Pacific lamprey populations in the Willamette River Basin, and across the Pacific Northwest.

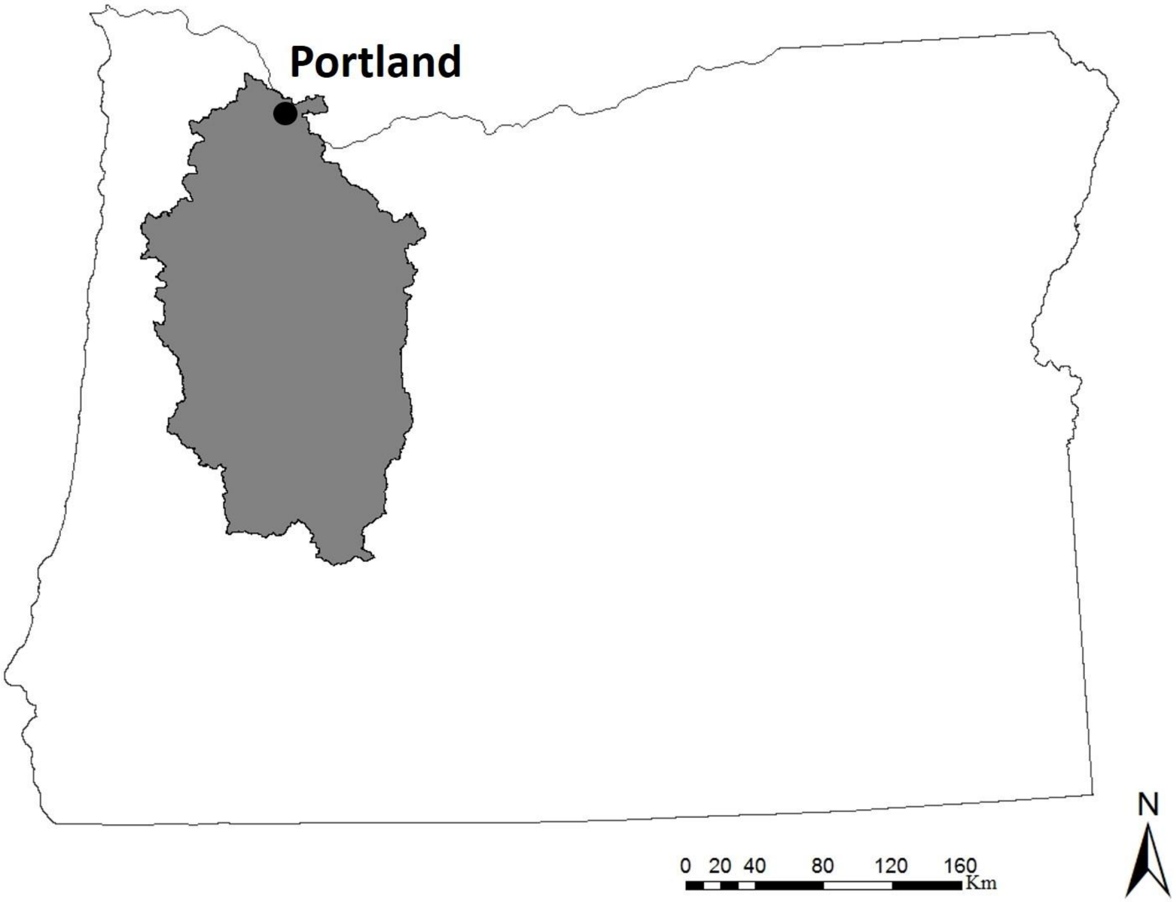

Figure 1-1.— The Willamette River Basin (grey) is the 19th largest river by discharge and the wettest (precipitation/land area) in the United States. It also supports one of the few remaining harvest locations for Pacific lamprey at Willamette Falls, near Portland, OR.

Chapter 2.

Spawning patterns of Pacific lamprey in tributaries to the Willamette River, Oregon, U.S.A.

ABSTRACT

Addressing the ongoing decline of Pacific lamprey across its range along the West Coast of North America will require an understanding of all life history phases. Currently, the use of spawning surveys (redd counts) is a common tool used for monitoring 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 activities at multiple spatial scales for Pacific lamprey in the Willamette River Basin, Oregon, U.S.A. Although redd density varied considerably across surveyed reaches, abiotic and hydrologic conditions were related to the observed temporal patterns of spawning. As has been documented in studies in other basins in the Pacific Northwest, redds were often constructed in pool tailouts dominated by gravel, similar to salmonid spawning requirements. Across the entire Willamette Basin, Pacific lampreys appeared to select reaches with alluvial geology, likely because this is where spawning gravel accumulated. At the tributary scale, spawning patterns were not as strong and reaches with non-alluvial geology redds were more spatially clumped than reaches with alluvial geology. These results describe spawning habitat use and can be used to identify and conserve Pacific lamprey spawning habitat across the Pacific Northwest.

INTRODUCTION

Monitoring of the various life 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 due to the efficiency, generally low cost, and the ability to survey large areas with relatively little effort (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 effects impact 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, Muhlfeld et al. 2006, Gallagher et al. 2007, Dunham et al. 2009), the development of methods for standardized spawning surveys for Pacific lamprey, *Entosphenus tridentatus*, is in its infancy, with only a few known studies focusing on the species (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009.

Pacific lamprey is a native anadromous fish that has declined considerably across its range in western North America, including extirpation 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 > 100,000 adults, but have declined to an average of < 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 < 500 individuals at Winchester Dam on the North Umpqua River, while historical returns (1965-1971) were estimated between 14,532 and 46,785 (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 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 of the Columbia River confluence) currently supports one of the few remaining traditional harvest locations for Pacific lamprey.

Upon returning to fresh water, adult Pacific lamprey have an extended freshwater holding period that can last from less than one month up to two years prior to making a final migration to their ultimate spawning areas (Clemens et al. 2010 and 2012, 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 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 similar to adult salmonids, however, it is believed that both sexes participate in redd construction (Clemens et al. 2010) and individual lamprey typically build multiple redds. Pacific lamprey is a gregarious spawner (Stone 2006) and researchers have observed up to 12 adults within an individual redd (Close 2006).

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, spawning characteristics, and population status within subbasins of the Willamette River system, a large (29,728 km^2) basin containing a mix of highly urbanized land use, agriculture, and intact headwaters (Mulvey et al. 2009). To understand how returning Pacific lamprey 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 to determine presence of Pacific lamprey, particularly with proper surveyor training (Wyss et al. 2013). 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 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 draw insights into the ecology of Pacific lamprey. Our results will inform management and conservation actions that will aid in the recovery of Pacific lamprey.

METHODS

Redd counts and habitat characteristics.— We conducted spawning surveys of Pacific lamprey in multiple tributaries of the Willamette River Basin during 2012 and 2013, following initial exploratory surveys conducted during 2011. Spawning surveys were established based on accessibility and logistical constraints in each stream and divided into segments ranging from 1.3 km to 11.6 km in length. Spawning surveys began in 2012 on Clear and Thomas creeks and the Marys River, with two survey segments in each stream (Table 2-1); the Marys River had contiguous survey segments and Clear and Thomas creeks had spatially discrete survey segments

(Figure 2-1). We had previously conducted larval lamprey surveys and adult migration studies documented adult lamprey movement into each of these tributaries (Clemens et al. 2012, Clemens et al. submitted). In 2013, we continued spawning surveys in the Marys River and Clear and Thomas creeks and added a single survey segment on the Calapooia and Luckiamute rivers each. 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 and small tributaries, 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). Our spawning survey methodology was based on those used in other adult Pacific lamprey studies (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009), and spawning surveys for anadromous salmonid species (Gallagher et al. 2007). 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, walking upstream. We enumerated 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 lamprey (Figure 2-2). Brook lampreys (including western brook *Lampetra richardsoni* and Pacific brook lamprey *L. pacifica*; described in Reid et al. 2011) also spawn during the timeframe of Pacific lamprey, but their redds are generally much smaller. Median Pacific lamprey redd size (measured as the redd pot, not including 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). Salmonid redds are generally more pear-shaped and larger than lamprey redds (e.g., steelhead *Oncorhynchus mykiss* redds), and were only occasionally encountered. 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 timeframe Pacific lamprey spawn, surveying each stream 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 days, respectively, so the sampling recurrence of 14 d should have been appropriate to detect redds of various ages. Occasionally, weather events and hydrologic conditions precluded completion of our surveys on schedule, and, in these instances, surveys were completed as soon afterwards as stream hydrology and visibility permitted.

We measured spawning habitat use of Pacific lamprey 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 in 2012 for comparison with available literature (e.g., Kan 1975, Stone 2006, Gunckel et al. 2009). Measurements included water depth at the upstream edge of the redd, width (perpendicular to flow), and length (parallel to flow) of the disturbed substrate within the redd pot, but not including the tailspill sediments. We used an analysis of variance (ANOVA) to assess differences in measured redd dimensions (response variable; redd length and width) across tributary subbasins. Additionally, we assessed pool/riffle scale habitat at Pacific lamprey spawning locations during 2012 surveys. We defined spawning locations as areas that contained one or more Pacific lamprey redds within the same general location, typically associated with a gradient break in the stream channel (e.g., pool tailout). At each location, we categorized the channel unit type (pool, pool tailout, riffle, or run) and substrate was characterized as the percentage of the spawning location consisting of the four most frequent substrate categories following Peck et al. (2006). We collected water temperature every 1hr from streams during the entire spawning period to relate abiotic and hydrologic factors to the timing of spawning using Maxim® iButton data loggers (Maxim Integrated, San Jose, CA).

We georeferenced all Pacific lamprey redds identified during surveys using a hand-held GPS unit 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 major river) of each redd location within a survey segment. We determined the underlying geologic types present in each survey segment using existing geologic maps (Oregon Department of Geology and Mineral Industries, no date) and calculated the proportion of alluvial (sediment deposits associated with moving water) underlying geology per survey. Alluvial geology was defined as reaches that were categorized as mixed-grain alluvial, fine-grain alluvial, or Missoula Flood alluvial underlying geology types from geologic maps. Land use practices might influence stream habitat conditions and subsequent spawning patterns for Pacific lamprey. For each survey segment, we obtained an index of cumulative stream disturbance, which accounts for land use, road density, population density, and stream barriers from Esselman et al. (2011). Although Pacific lamprey 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 counted for each survey segment) for analysis purposes, as is common in other spawning ground 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 (Wyss et al. 2013, unpublished data) in tributaries in which we have both of these data sources from the same year.

Temporal patterns.—We collected water temperature and stream discharge information from streams concurrently with spawning surveys to relate abiotic and hydrologic factors to the timing of spawning. We deployed temperature data loggers in each stream during the initial spawning survey (April/May) and continued recording data through September. Continuous water temperature data were recorded in one hour increments with Maxim® iButton data loggers (Maxim Integrated, San Jose, CA) for Thomas Creek and the Marys and Luckiamute rivers. We used U.S. Geological Survey (2013) stream discharge data from Thomas Creek, the Marys River, and the Luckiamute River at the city of Scio, Philomath, and Suver for each respective stream. In Clear Creek and the Calapooia River, we use the Clackamas River at Estacada and the Mohawk River near Springfield as proxy discharge measures, respectively. Specifically, we were interested in the relationship between discharge and temperature patterns and spawning intensity. As observed by Brumo et al. (2009) in the South Fork Coquille River, substantial flood events may result in bi-modal spawning pulses within the spawning season. To assess inter-annual trends of redd density, we evaluated the relationship between estimates of Pacific lamprey at Willamette Falls and our observed redd count data. Because Pacific lamprey enter freshwater in the summer and hold until the following spring prior to spawning (Clemens et al. 2012a), we compared Willamette Falls estimates from Baker and Graham (2012) in the previous year to redd counts in the two streams that we surveyed both years (i.e., the Marys River and Thomas Creek).

Spawning habitat selection.— We used Manly's selection ratio (Manly et al. 2002) to test if Pacific lamprey 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 if Pacific lamprey 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 indicate positive selection for a geologic type and ratio values less than 1.0 indicate a selection against that geologic type. We calculated 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 and detection conditions that might have occurred between years. We calculated the amount of habitat of each geologic type available as the proportion of each survey segment within each underlying geologic type. In Thomas Creek and the Marys River, we combined data from both survey surveys to increase sample sizes. To compute selection ratios for the entire Willamette River Basin, 2013 peak redd count data were combined from all survey segments and the proportion of survey segments located in each underlying geologic type was recalculated.

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 set range of values based on the survey length. For our study, t ranged from 0.1 km to half of the total survey length. For example, the total survey length for the Luckiamute River was 5.6 km, so t ranged from 0.1 - 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 to expected L values from a completely random spatial pattern of points to determine if redds were more clumped than the random distribution; L *v*alues less than 0.0 indicate underdispersion or clumping. Based on the L values for each search radius of t, we determined at which spatial scales 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 Core Development Team 2013).

RESULTS

Redd counts and habitat characteristics.— We surveyed a total of 37.5 km of stream habitat in 2012 and 43.3 km in 2013 (Table 2-1). We observed redds in each survey segment including single visits to 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 two 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 2-1). Redd density was related to the underlying geology; 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 comprised entirely of alluvial geology and had higher redd densities (Table 2-1). All spawning survey segments were ranked as having 'high' or 'very high' disturbance indices (ranging from 1.50 to 2.50, with 4.0 as the lowest level of disturbance) and no patterns were evident between disturbance indices and redd densities (Table 2-1). We observed Pacific lamprey redds and spawning adults in both Ritner Creek and the Santiam River, indicating that Pacific lamprey spawn in a variety of stream sizes.

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 existing literature (Kan 1975, Stone 2006, Gunckel et al. 2009), with mean redd width of 45.7 cm (range from 29 to 80 cm), mean redd length of 52.7 cm (range from 30 to 85 cm), and mean water depth of 60.1 cm (range from 24 to 99 cm). Using ANOVA, we found no significant difference in redd width ($P = 0.37$) or length ($P = 0.08$) measurements 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) comprised of gravel and cobble substrates.

Temporal trends.—We observed different temporal trends of spawning in the two years of our surveys, and the temporal patterns appeared to be related to hydrologic differences between years. In 2012, peak Pacific lamprey redd counts were observed in early June for the Marys River, late May for upper Thomas Creek, and was likely missed in lower Thomas Creek. All peak counts in 2012 occurred after an increased discharge event that precluded surveys (Figure 2-3a,b). In 2013, peak redd counts were observed from mid- to late May in all streams and occurred before the peak spring run-off discharge event, which occurred in late May (Figure 2-3a-e). We observed no apparent relationship between spawning activity and temperature (Figure 2-3a-e), but stream temperatures exceeded 10° C during all surveys. Across all surveys, redd counts were greater in 2013 than in 2012, but lower discharges in 2013 may have increased detection probability. However, our increased redd densities in 2013 also corresponded with Pacific lamprey population estimates at Willamette Falls; estimates at the falls increased from 107,289 to 245,325 between 2011 and 2012 (Baker and Graham 2012). For the three surveys that we were able to observe peak redd counts in both years (upper and lower Marys River, and upper Thomas Creek), we found a positive relationship between the previous year's Willamette Falls Pacific lamprey estimates and redd density (Figure 3a). Although we had limited data, we also found a positive relationship between peak redd counts and the number of radio tagged fish that entered each tributary from a previous study (Figure 2-4; data from Clemens et al. 2012a, 2012b). Although we only had two years of data, our data suggested a positive association between larval Pacific lamprey abundance and redd counts, however this relationship did not appear to be linear (Figure 2-5).

Habitat selection.— Pacific lamprey did not select spawning habitats randomly. Rather, there was strong evidence that across the entire Willamette River Basin Pacific lamprey selected for reaches with fine-grained, alluvial geologic types (selection ratio = 1.87; 90% CI: 1.71 – 2.03) and selected against volcanic and intrusive rock underlying geologic types (selection ratios = 0.35; 90% CI: 0.27 – 0.43 and 0.33; 90% CI: 0.12 – 0.54, respectively; Figure 2-6). Other alluvial geologic types (mixed-grain and Missoula floods alluvial) showed neutral selection. There was weak evidence for selection against marine sedimentary reaches (selection ratio = 0.76), although it was not statistically significant (90% CI: 0.16 – 1.35). At the tributary scale, Pacific lamprey did not select for alluvial geology in all streams, but there was some preference for alluvial geology over other geologic types (Figure 2-6). Within tributary subbasins there was strong evidence ($P < 0.01$) that Pacific lamprey redds were located in geologic types disproportionately to their availability, 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 lamprey did not preferentially select between the two types. In the Luckiamute River, Pacific lamprey 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 lamprey 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 lamprey 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.—Our use of 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 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 2-7). In the Luckiamute River, which had intrusive and sedimentary rock reaches, we observed significant spatial clumping when $t < 1.6$ km (Figure 5d). In the Marys River, a stream with volcanic rock intrusions, redds were spatially clumped for all tested values of *t* (Figure 7). Results from both the Luckiamute and Marys rivers indicated that in streams with less alluvial geology, redd distribution is driven by large-scale factors (underlying geology) rather than localized habitat characteristics (suitable substrate).

DISCUSSION

We conducted spawning surveys that targeted Pacific lamprey in multiple tributaries to the Willamette River Basin over the course of two years and analyzed habitat associations of redd density across multiple spatial scales. At microhabitat scales Pacific lamprey 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 lamprey were similar to those of anadromous salmonids (Geist and Dauble 1988); 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 lamprey exhibited less preference for different underlying geologic types, but the degree of spatial clumping was related to the geologic structure. Our work adds to the understanding of Pacific lamprey ecology and is directly applicable to conservation and monitoring efforts.

Our spawning surveys across the Willamette River Basin suggest that Pacific lamprey spawn in a variety of environmental conditions and physical habitats. In both years, the spawning season appeared to correspond with water temperature observed by other researchers (i.e., 10-15° C; reviewed in Clemens et al. 2010, 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 Pacific lamprey are likely generalist spawners 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 confirmed by our data. Spawning distribution is likely limited by anthropogenic passage issues; Pacific lamprey have different passage requirements than salmonids and even small diversion dams can completely block adult passage (Moser et al. 2002, Moser and Mesa 2009, Keefer et al. 2010). 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 lamprey using small patches (~10 m^2) of spawning gravels within a matrix of bedrock streambed in many of our survey segments.

Pacific lamprey evolved to be able to spawn in a wide range of habitats across a large geographic range (Clemens et al. 2013). These attributes are likely a result of its evolutionary history. Upon entry into fresh water, Pacific lamprey likely do not home in the strict sense (Spice et al. 2012). Instead, bile acid chemicals from larval lamprey (not-necessarily conspecific) act as attracting pheromones to adult Pacific lamprey (Robinson et al. 2009, Yun et al. 2011), and genetic evidence supports this migratory model (Hess et al. 2012). Within the Columbia River system migration timing is related to temperature and discharge (Keefer et al. 2009, Clemens et al. 2012, Clemens et al. submitted), and Pacific lamprey generally complete a two-stage migration, holding in larger river systems during the winter months prior to completing final movements into their ultimate spawning locations (Clemens et al. 2012, Clemens et al. submitted). Our results suggest that availability of spawning habitat within tributaries does not necessarily regulate the distribution of returning Pacific lamprey 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 lamprey is the presence of larvae in perspective spawning tributaries. We have limited data that indicate a positive association between larval Pacific lamprey abundance and redd counts; our initial data analysis suggests a positive association, but it does not appear to be a one-to-one relationship. For example, a doubling of redd density corresponded to only a 30% increase in larval density, which indicate that larval habitat may be more limiting than spawning habitat, although this is strictly speculative. Rather than interpreting this data in the context of a stock-recruitment relationship, an alternative hypothesis is that the relative abundances of larvae function to attract spawning adults, as has been observed with sea lamprey (Vrieze and Sorensen

2001). Future studies might elucidate the relationship between adult returns and larval production, and address knowledge gaps in Pacific lamprey migration ecology.

Although redd surveys are thought to be an imprecise measure of lamprey abundance (Moser et al. 2002; Moser et al. 2007), redd and spawning adult counts may facilitate trend assessments of lamprey status more accurately than traditional measures of adult abundance, such as counts at dams, which are often poor measures of escapement (Moser and Close 2003, Lampman 2011). 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), and our data suggest that spawning surveys reflect changes in escapement across years and tributaries. Redd surveys also have the utility of confirming access of adult Pacific lamprey to spawning areas, and can be utilized to assess distribution above putative barriers. Our use of 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 spatially random, 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 (Chapter 3). 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, 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 lamprey are widely distributed In the Willamette River Basin throughout accessible habitats (Clemens et al. 2012, Clemens et al. submitted), and we documented spawning activity in all reaches that we surveyed. Our results indicate that Pacific lamprey is a spawning generalist 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 by recovery efforts (Mesa and Copeland 2009, CRITFC 2011, Wyss et al. 2013) and our data suggest that if adult Pacific lamprey can access previously blocked stream reaches they should be able successfully colonize it (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 organisms 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 production potential for multiple fish species across riverscapes of the Pacific Northwest. Finally, continued research efforts that address knowledge gaps in the other life history phases of Pacific lamprey will be necessary to better understand its ecology and continue to proactively address declining trends.

Table 2-1. Survey length, 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; index ranges from 1.00 (high disturbance) to 4.00 (low disturbance). Underlying geology from Oregon Department of Geology and Mineral Industries (no date); alluvial underlying geologic types are shown in bold.

		Survey length	Redd density	Disturbance	Percent of underlying geology						
Survey segment	Year	(km)	(redds*km^{-1})	index	**MG**	**FG**	**MF**	IR	VR	MS	TS
Clear Ck., upper	2012	1.3	50.2	2.25	--	--	--	--	--	--	100
Clear Ck., lower	2012	2.4	165.0	2.25	100	--	--	--	--	--	--
Luckiamute R.	2013	5.6	47.2	1.25	80	--	--	15	--	5	--
Thomas Ck., upper	2012	4.7	61.4	1.75	100	--	--	--	--	--	--
	2013	4.7	116.2	1.75	100	--	--	--	--	--	--
Thomas Ck., lower	2012	8.9	18.5	2.25	26	74	--	--	--	--	--
	2013	7.0	137.0	2.25	26	74	--	--	--	--	--
Marys R., upper	2012	8.5	14.1	1.50	70	--	--	--	30	--	--
	2013	8.5	31.2	1.50	70	--	--	--	30	--	--
Marys R., lower	2012	11.6	15.3	2.50	63	--	--	--	37	--	--
	2013	11.6	21.3	2.50	63	--	--	--	37	--	--
Calapooia R.	2013	7.3	88.5	1.75	86	--	14	--	--	--	--

Geologic abbreviations are as follows: MG: mixed-grain alluvial; FG: fine-grain alluvial; MF: Missoula Floods alluvial; IR: intrusive rock; VR: volcanic rock; MS: marine sedimentary; and TS: terrestrial sedimentary; alluvial reaches are bolded.

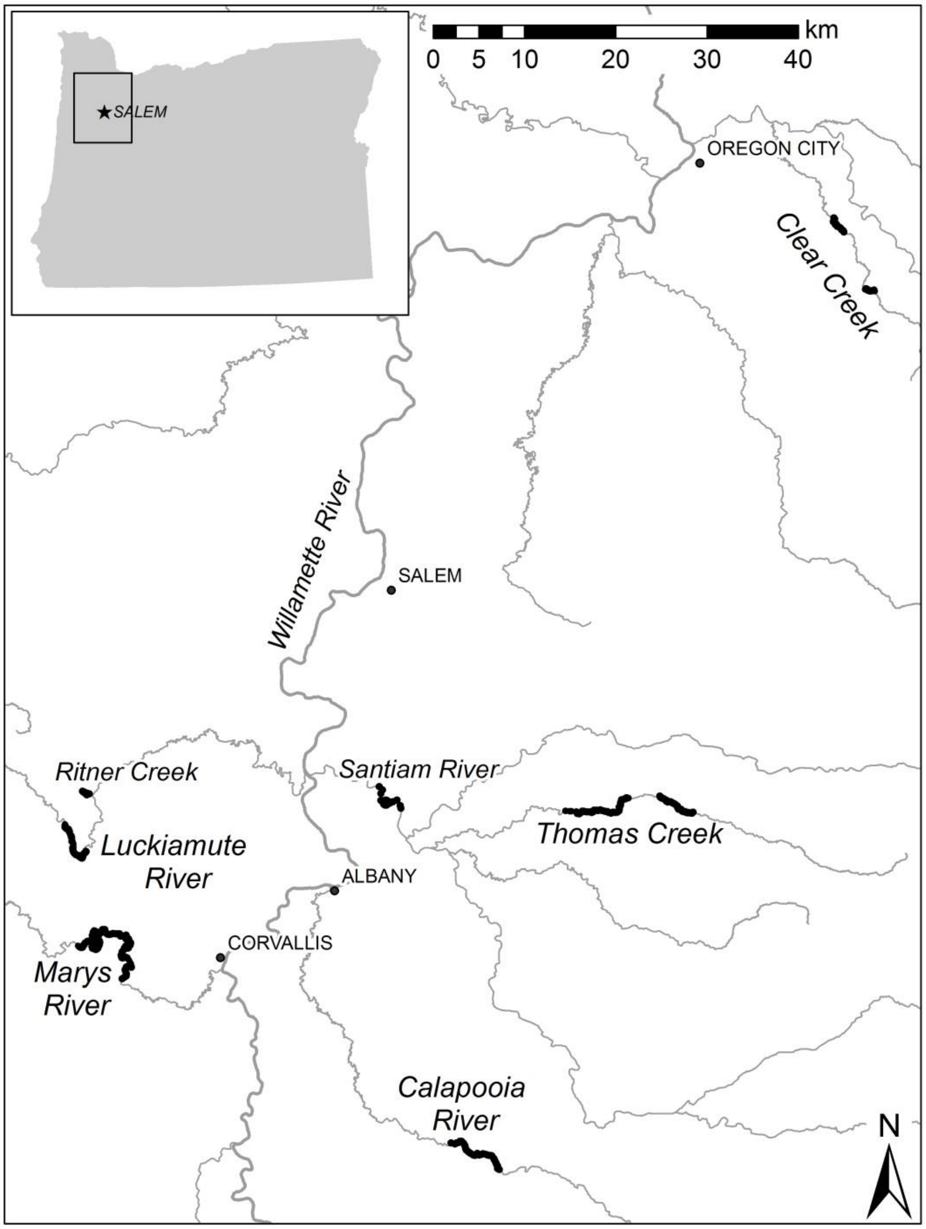

Figure 2-1.— Locations of Pacific lamprey spawning surveys (**bold**) in the Willamette River Basin, 2012-13. Surveys in Ritner Creek and the Santiam River were conducted once during the 2013 season to document the occurrence of Pacific lamprey spawning in two streams of different size: small (Ritner Creek, 4-5 m wide), and large (Santiam River, 70-90 m wide).

Figure 2-2.— Representative photos of Pacific lamprey redds from spawning surveys conducted in 2012-13. Top photo shows two adult lamprey constructing a redd in Thomas Creek, 2012. The bottom photo illustrates the relative size of redd from Thomas Creek, 2013.

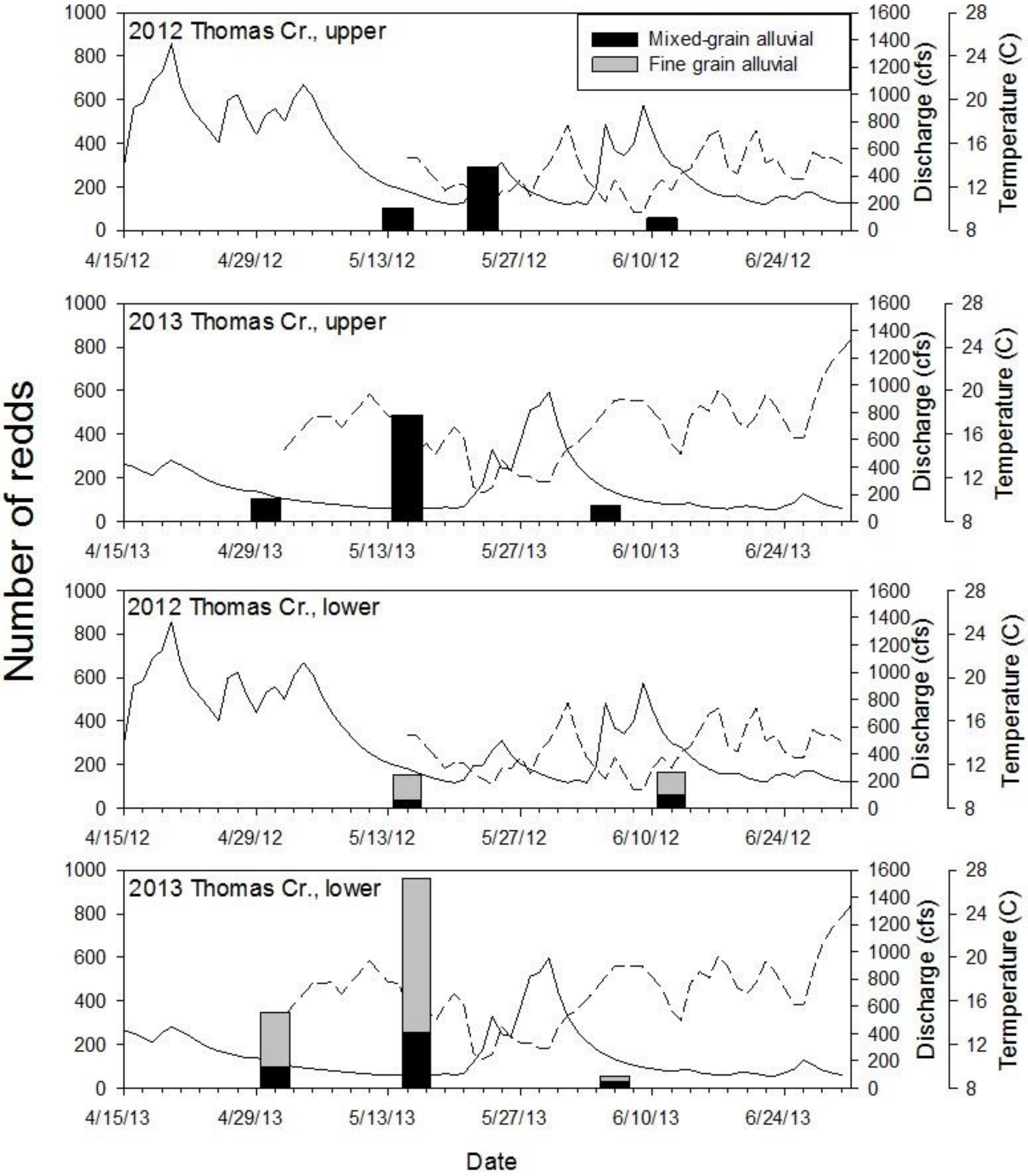

Figure 2-3a.— Pacific lamprey redd counts compartmentalized by underlying geology as stacked bars (Oregon Department of Geology and Mineral Industries, no date), discharge (solid line), and maximum daily temperature (dashed line) for two survey segments on Thomas Creek, Oregon 2012-2013. Discharge data is from Thomas Creek near the city of Scio, Oregon, U.S.A. (USGS 2013).

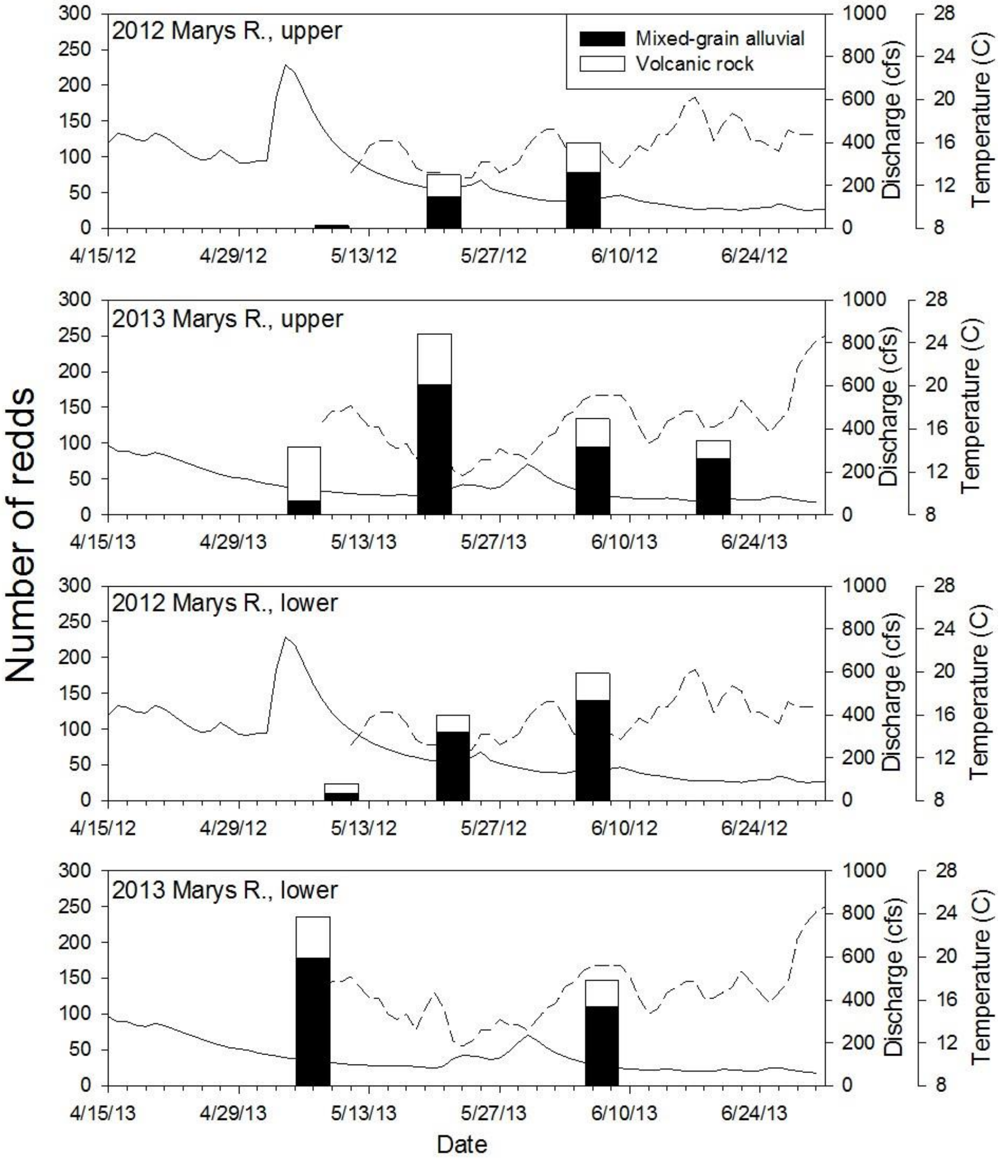

Figure 2-3b.— Pacific lamprey redd counts compartmentalized by underlying geology as stacked bars (Oregon Department of Geology and Mineral Industries, no date), discharge (solid line), and maximum daily temperature (dashed line) for two survey segments on the Marys River, Oregon 2012-2013. Discharge data is from the Marys River near the city of Philomath, Oregon, U.S.A. (USGS 2013).

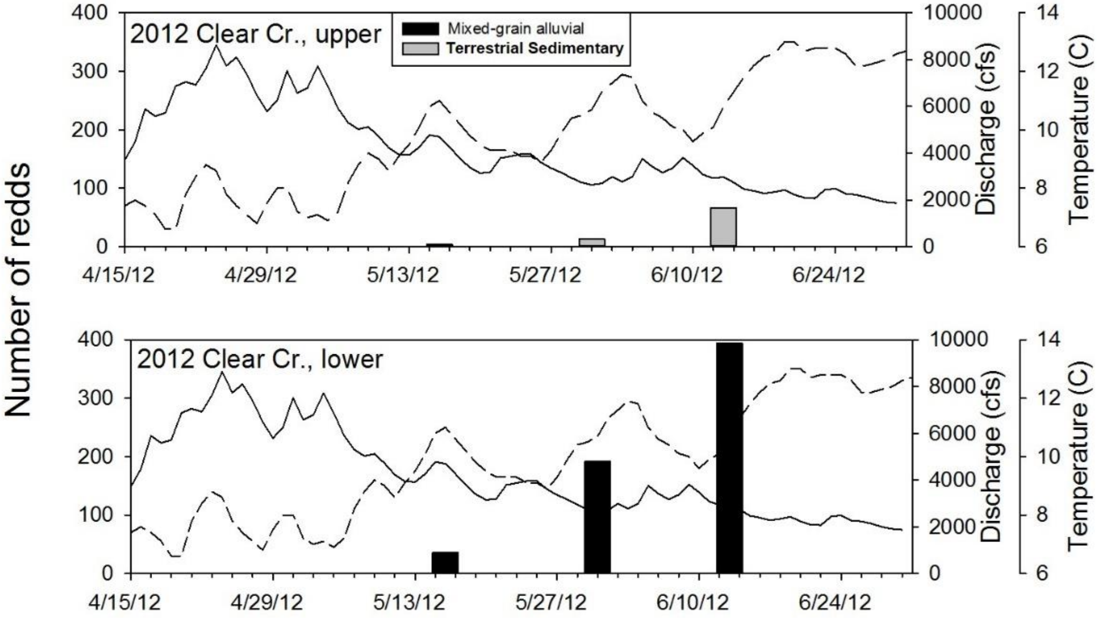

Figure 2-3c.— Pacific lamprey redd counts compartmentalized by underlying geology as stacked bars (Oregon Department of Geology and Mineral Industries, no date), discharge (solid line), and maximum daily temperature (dashed line) for two survey segments in Clear Creek, Oregon, 2012. Discharge and temperature data is from the Clackamas River near the city of Estacada, Oregon, U.S.A. (USGS 2013).

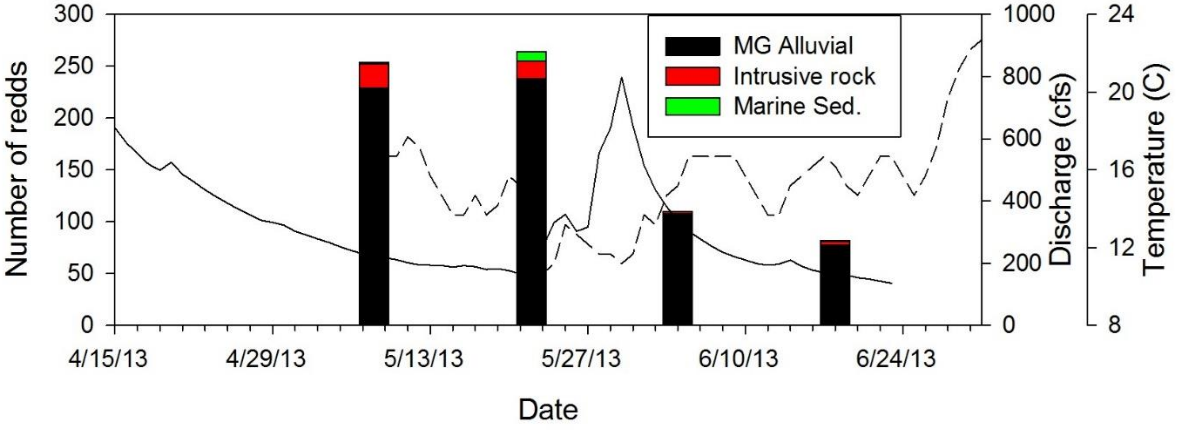

Figure 2-3d.— Pacific lamprey redd counts compartmentalized by underlying geology as stacked bars (Oregon Department of Geology and Mineral Industries, no date), discharge (solid line), and maximum daily temperature (dashed line) for a survey segment in the Luckiamute River, Oregon, 2013. Discharge data is from the Luckiamute River near the city of Suver, Oregon, U.S.A. (USGS 2013). Underlying geology included: mixed grain alluvial (MG Alluvial), intrusive rock, and marine sedimentary (Marine Sed.).

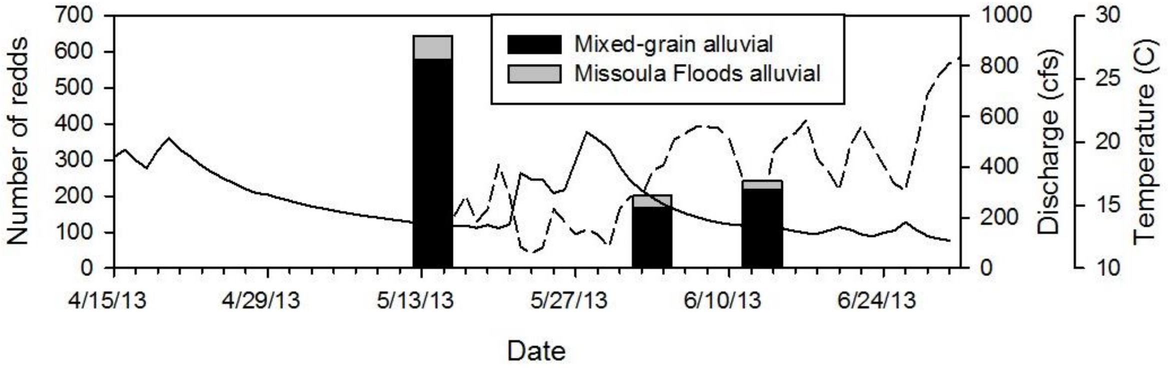

Figure 2-3e.— Pacific lamprey redd counts compartmentalized by underlying geology as stacked bars (Oregon Department of Geology and Mineral Industries, no date), discharge (solid line), and maximum daily temperature (dashed line) for a survey segment in the Calapooia River, Oregon, 2013. Discharge data is from the Mohawk River near the city of Springfield, Oregon, U.S.A., a stream with similar flow regimes and headwater location (USGS 2013).

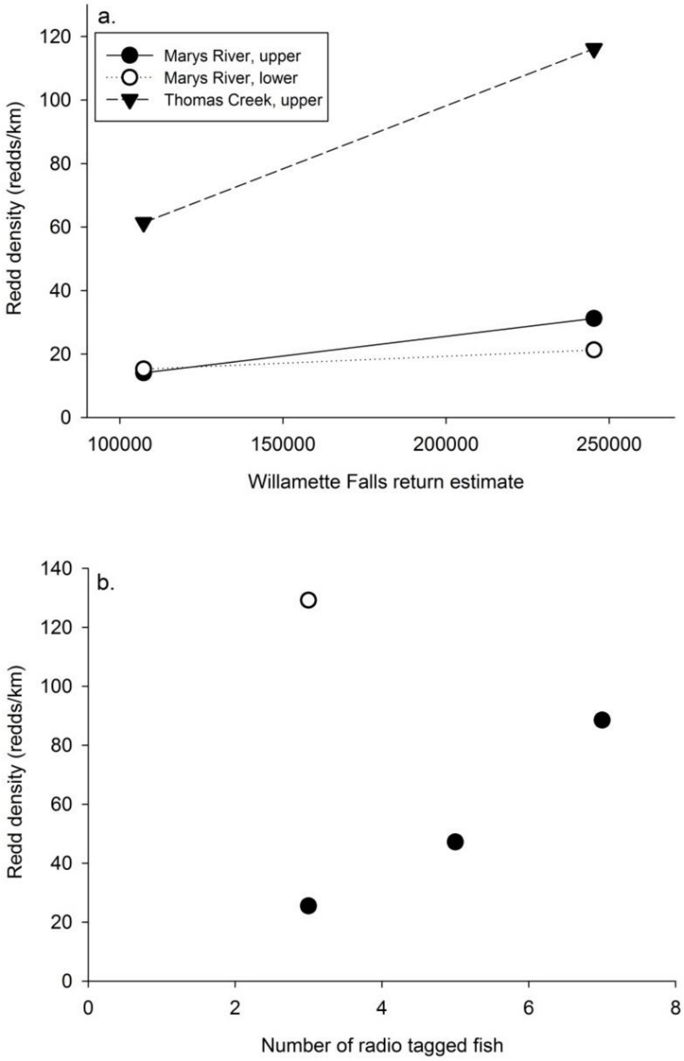

Figure 2-4.— Relationships between Pacific lamprey population estimates at Willamette Falls (Baker and Graham 2012) and observed redd densities in the following year in the Marys River and Thomas Creek (a.), and radio tagged adults found in the stream in 2009-10 (Clemens et al. 2012a, 2012b) and peak redd densities in 2013 (b.). In panel b., In Thomas Creek (open circle) the number of radio tagged fish was estimated by multiplying the total number of fish that entered the Santiam River (N=52) by the percentage of discharge contributed by Thomas Creek (USGS 2013).

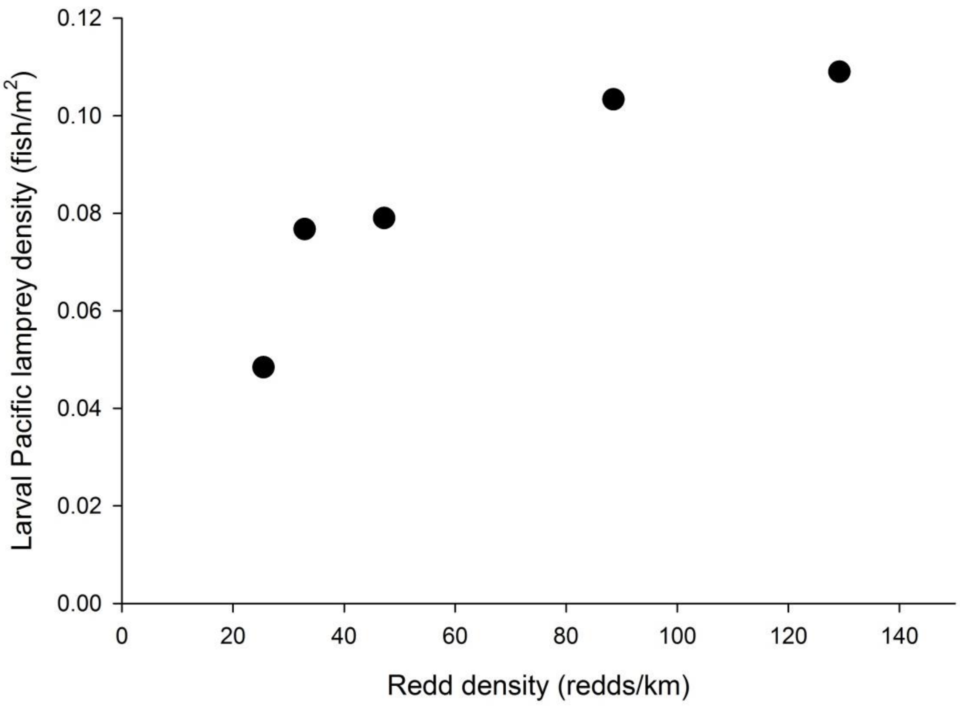

Figure 2-5.— Relationship between adult Pacific lamprey spawning (mean redd density; redds/km) and larval production (overall mean larval Pacific lamprey density; individuals/m^2) in tributaries to the Willamette River.

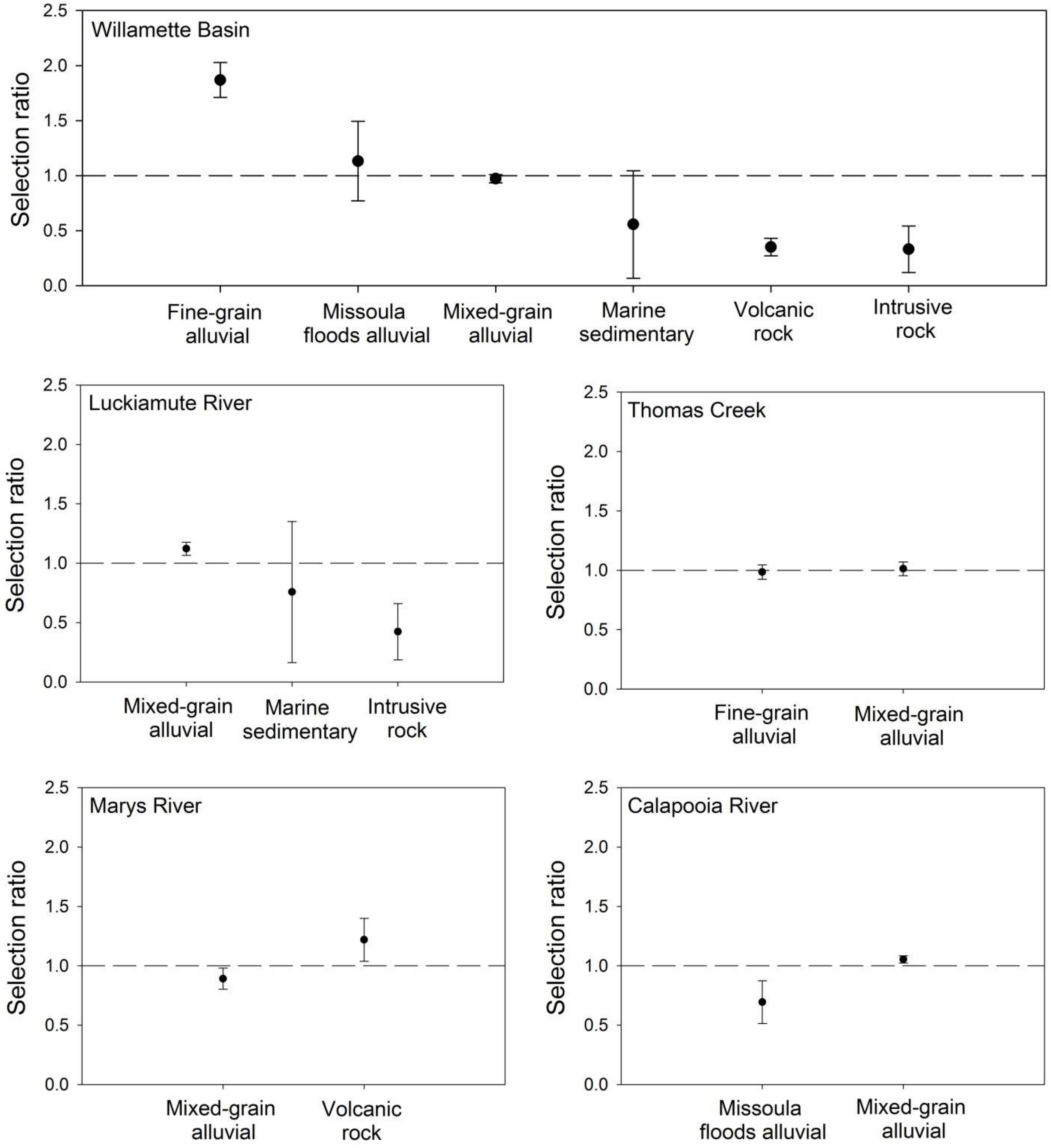

Figure 2-6.— Selection ratios for Pacific lamprey habitat use during spawning for surveys in the entire Willamette River Basin and four tributary subbasins. Error bars indicate 90% Bonferroni adjusted confidence intervals. Selection was estimated using underlying geology data from Oregon Department of Geology and Mineral Industries for all available geologic reaches.

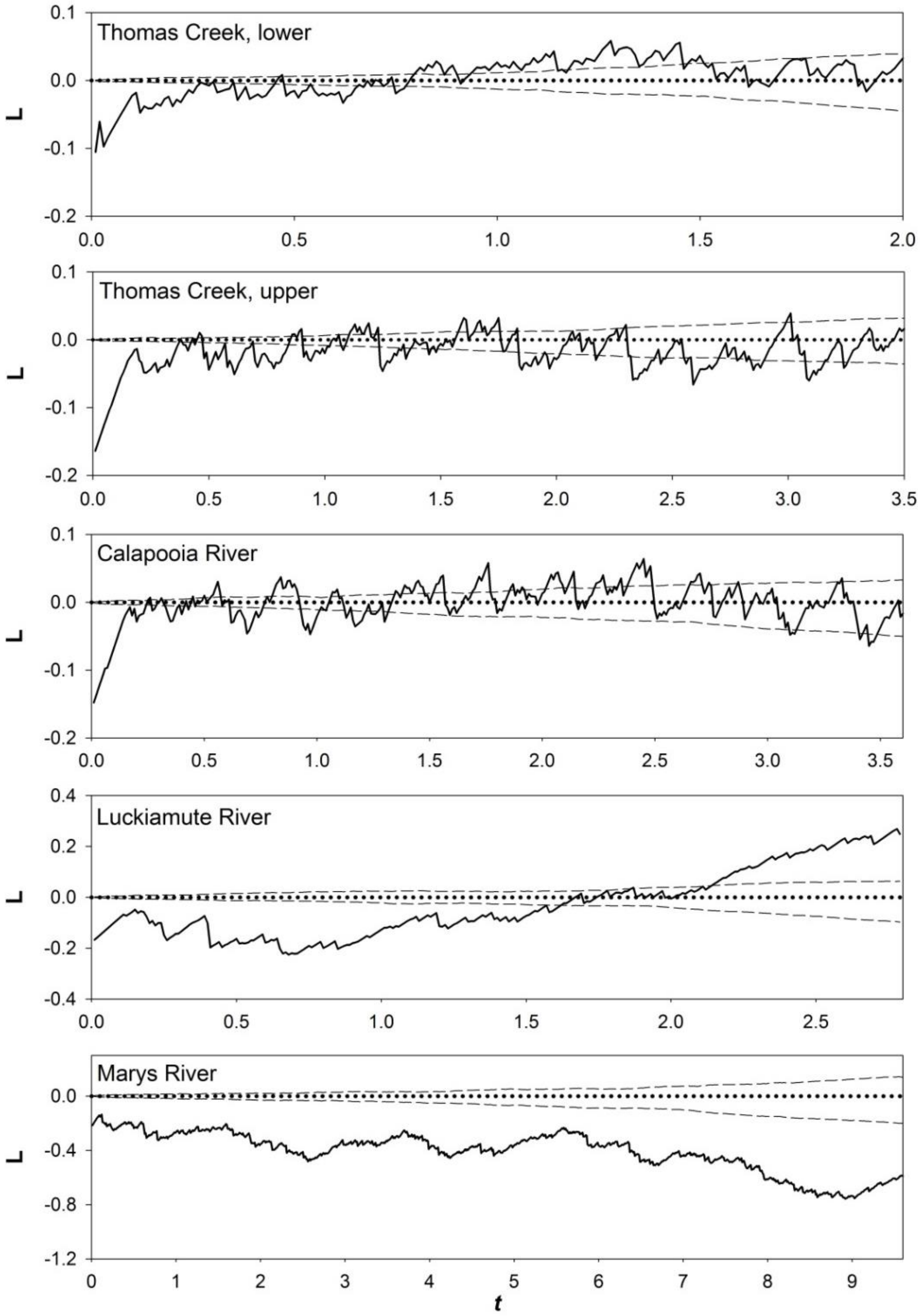

Figure 2-7.— Results from the modified Ripley's K function (*L*; solid line) by survey distance (t), and the zero line (dotted line) for Pacific lamprey spawning activity for five segments of spawning surveys in the Willamette River Basin, Oregon, U.S.A. 2013. Dashed lines are confidence intervals around zero based on simulations run assuming a completely random spatial pattern, *L* values < 0.0 (dotted line) indicate underdispersion or 'clumping'.

Chapter 3.

Using spatial resampling to assess redd count survey length requirements for Pacific lamprey

ABSTRACT

Pacific lamprey has declined across its range along the West Coast of North America and an understanding of all life history phases is needed to address population recovery. Spawning surveys (redd counts) are common tools currently used to monitor returning adult salmonids, but the methodologies are in their infancy for Pacific lamprey. Our objective was to assess the minimum spawning survey distance required to detect the presence of Pacific lamprey redds and obtain precise redd density estimates from these data. To do this, we statistically resampled existing spawning locations of Pacific lamprey collected during spawning surveys in four streams of the Willamette River Basin, Oregon during the spring of 2013. We found that the minimum survey length for Pacific lamprey redd detection was inversely related to the observed redd density and was always less than 1.2 km. Survey length requirements to obtain precise redd counts (± 20% of observed redd densities) were also inversely related to redd density and habitat availability and varied between 1.3 km and 13.7 km. Our results suggest that spawning surveys are a potential tool for monitoring adult Pacific lamprey abundance, but the specific objectives of monitoring programs and acknowledgement of unknowns must be considered prior to implementation into recovery plans.

INTRODUCTION

Pacific lamprey is considered a cultural and ecological icon for native peoples of the Pacific Northwest (CRITFC 2011). The species has declined considerably across its range in western North America, and complete extirpation has occurred in multiple drainages (Moser and Close 2003, CRITFC 2011). Between 1939 and 1969, Pacific lamprey counts at Bonneville Dam on the Columbia River averaged over 100,000 adults, but declined to an average of less than 40,000 between 1997 and 2010 (Murauskas et al. 2012). The Columbia River is not the only location that has experienced a decline of Pacific lamprey runs; annual abundance in 2009 and 2010 were estimated at less than 500 individuals at the Winchester Dam on the North Umpqua River, while historical adult abundance (1965-1971) was estimated between 14,532 and 46,785

(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 numerous knowledge gaps in its biology (CRITFC 2011, Luzier et al. 2011). Of the areas where the species has persisted, the Willamette River, Oregon, has one of the highest remaining adult abundances (Kostow 2002) and Willamette Falls (approximately 42 km upstream of the Columbia River confluence) currently supports one of the few remaining harvest locations for Pacific lamprey. Although migrating adult populations can be monitored at natural and man-made barriers, little is known about the species spawning distribution, characteristics (e.g., abundance, timing, habitat use), or populations within tributaries (CRITFC 2011).

To understand how Pacific lamprey use available habitat in a large river system, it is important to develop methods for monitoring all life history stages, including the spawning stage. Redd surveys have been used to monitor both anadromous and non-anadromous salmonid populations for many years due to their nonintrusive nature, relatively low cost, and ability to survey large areas with little effort (Gallagher et al. 2007, Dunham et al. 2009). While redd count methods have been routinely implemented for salmonids, the development of standardized spawning surveys for Pacific lamprey is in its infancy (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009). In general, salmonid and Pacific lamprey redds can be counted using similar methods, but the assumptions related to redd counts, specifically redd detection rates, must also be examined and addressed for Pacific lamprey (Dunham et al. 2009).

Spawning surveys for Pacific lamprey have traditionally been problematic for several reasons including confusion of Pacific lamprey redds 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 relationship between redd counts and spawning adult numbers (Moser et al. 2007). Despite the potential sources of error, redd counts remain an efficient method to monitor populations and to assess Pacific lamprey distribution, particularly with proper surveyor training (Wyss et al. 2013). To use redd counts as an effective monitoring tool, it will be important to ensure that surveys are conducted in a manner that both reduces bias and increases efficiency. Our objectives were to evaluate the required length (i.e., distance) of redd surveys for spawning Pacific lamprey to allow for redd detection and to estimate redd density within an acceptable level of precision. To address this objective, we spatially resampled georeferenced spawning locations of Pacific lamprey. By determining the suitable length of

Pacific lamprey redd surveys, our analyses will increase surveying efficiency, allow sampling of larger spatial areas, and help address pertinent management questions.

METHODS

Redd counts.— We monitored Pacific lamprey spawning activity from late April through mid-June 2013 in four tributaries to the Willamette River Basin: Calapooia River, Luckiamute River, Marys River, and Thomas Creek (Figure 3-1). Our spawning survey methodologies were based on those used by other adult Pacific lamprey studies (Stone 2006; Brumo et al. 2009; Gunckel et al. 2009), and included insights from preliminary spawning surveys conducted in the Willamette River Basin during 2011 (Clemens et al. 2012) and redd counts for anadromous salmonid species (Gallagher et al. 2007). Survey locations were selected based on stream access, our ability to safely float in personal watercraft, and on streams where larval Pacific lamprey sampling was also conducted (Wyss et al. 2012, 2013). We selected survey segments to represent available habitat in each tributary; survey segments included all underlying geologic types present in each tributary.

We conducted spawning surveys in multiple tributaries to the Willamette River to capture the spatial variability of spawning activity. Redd count surveys were initiated during 2012 to evaluate and refine survey methodology. These included two survey segments on both the Marys River and Thomas Creek; the Marys River had contiguous survey segments and Thomas Creek had spatially discrete survey segments (Figure 3-1). In 2013, redd count surveys continued in those streams and we added single survey segments on the Calapooia and Luckiamute rivers (Figure 3-1). We had no *a priori* knowledge of the current distribution of Pacific lamprey in these latter two rivers, except for indications that adults had entered to these streams based on radiotelemetry data (Clemens et al. 2012). We used only 2013 data for the analysis presented. In that year we surveyed these four streams with different habitats and peak redd densities, and all surveys were conducted with the same personnel that were trained to classify Pacific lamprey redds. Additionally, relatively low water discharge and increased water clarity in 2013 increased our confidence in redd observation and counts.

All surveys were conducted by two surveyors in individual inflatable pontoon boats with each covering an area from stream bank to mid-channel to observe the entire channel. We enumerated all Pacific lamprey redds, live adults, and carcasses that were observed in each surveyed segment. Although subjectivity exists in redd surveys (Dunham et al. 2001), we defined redds as round depressions in the stream substrate that appeared to be actively excavated (Stone 2006). Larger rocks are frequently moved by Pacific lamprey to the edge of redd depressions (Gunckel et al. 2009), and we used this additional characteristic to differentiate Pacific Lamprey redds from those of other fishes. Additionally, the presence of actively spawning adult Pacific lamprey in redds helped confirm our redd identification. Brook lamprey (*Lampetra richardsoni* or *L. pacifica*) also spawn during the timeframe of Pacific lamprey. However, median brook lamprey redd size (0.03 m^2) is much smaller than median Pacific lamprey redd size (0.124 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.

Each segment was visited multiple times from April through June to capture temporal variability in spawning activity and to observe peak redd counts (i.e., the highest number of redds observed in all visits). Because no information related to the frequency of surveys needed for monitoring Pacific lamprey redds is currently available, we attempted to visit each survey segment every 10-14 days, as is recommended in the salmonid literature (Gallagher et al. 2007). We considered our sampling recurrence appropriate to detect redds of various ages because median longevity of Pacific lamprey redds has been observed at 40 days with a minimum longevity of 10 days (Stone 2006). Occasionally, weather events and hydrologic conditions precluded completion of our surveys on schedule, and surveys were completed as soon as stream conditions permitted surveying.

We georeferenced all Pacific lamprey redds identified during surveys using a hand-held GPS unit to generate redd distribution maps for each survey (Figure 3-2). We used linear referencing tools in ArcGIS Version 10.1 (ESRI 2012) to determine the stream kilometer (as measured from the confluence of the tributary with a major river) of each redd location within a survey. We used existing geologic maps (Oregon Department of Geology and Mineral Industries, no date) to calculate the percent of the stream survey distance with alluvial underlying geology in each survey segment. Alluvial geology was defined as underlying sediments that were deposited by moving water, and included fine-grain alluvial, medium-grain alluvial, and Missoula Flood alluvial geologic types from geologic maps. In our related work (Chapter 2), we found that Pacific lamprey selected for reaches with alluvial geology across the Willamette River

Basin, and the resulting spatial distribution of redds (i.e., “clumpiness”) was strongly related to these underlying geologic patterns. Our surveys encompassed a wide range of stream types and habitats on both the west and east sides of the Willamette Basin, with headwaters located in the Coast Range and Cascade Mountains, respectively (Table 3-1). We conducted several surveys in each segment at different times during the spawning season, but the peak redd density observed for each survey segment was used for analysis purposes, as is commonly done with redd count data analyses (Gallagher et al. 2007).

Spatial resampling analysis.— We used spatial resampling of the georeferenced redd locations of each survey segment to evaluate suitable survey lengths (i.e., distance) in future sampling. A sequence of simulated subsample lengths was developed, beginning with 0.1 km and continuing every 0.1 km until a final subsample length of 1.0 km less than the total survey segment length (e.g., the Calapooia River survey was 7.3 km, therefore we used subsample lengths varying from 0.1 - 6.3 km at 0.1 km intervals). For each subsample length, a continuous segment of that length was randomly selected from within our spatial dataset of redd locations and the density of redds in that segment was calculated. This procedure was repeated (with replacement) 10,000 times for each subsample length. Subsamples were restricted to be fully within the actual surveyed stream segment to ensure that no edge correction was needed. From each simulated subsample length, we determined the mean, maximum, and minimum redd density values from the 10,000 resamples. All resampling simulations were completed in Program R (R Core Team 2013).

We used the mean, maximum, and minimum redd density values for each subsample to determine the minimum survey distance necessary to detect Pacific lamprey redds, and the distance required to obtain precise redd density estimates. The minimum distance to detect redds was determined by identifying the survey length in which all simulations had a redd density greater than 0.0 redds/km. We considered redd density estimates to be precise if both the minimum and maximum redd counts for each simulated segment length were within ± 20% of the observed redd density for the entire survey segment. We included this measure of error to account for the differences in surveyor redd detection rates. Our experience with Pacific lamprey redd surveys provide evidence that our redd counts were minimally biased, but it is likely that we and others may misidentify or omit redds during surveys. Although there is much variation in redd detection rates in the literature, we chose 20% error based on the estimated detection rates of 0.83 from bull trout redd surveys (Muhlfeld et al. 2006), and made it slightly more conservative by rounding to an estimated detection rate of 0.80. This estimate is conservative based on other salmonid redd counts which estimated individual detection rates ranging from 0.28 to 2.54 (Dunham et al. 2001, Gallagher and Gallagher 2005).

RESULTS

Redd count surveys.— During the 2013 spawning season, we surveyed 43.3 km of stream habitat in locations throughout the Willamette River Basin, with individual survey lengths varying from 4.2 km in upper Thomas Creek to 19.2 km of total continuous survey distance in Marys River (Table 3-1). Peak redd densities differed among streams, varying from 22.9 redds/km in the Marys River to 137.0 redds/km in the lower segment of Thomas Creek (Table 3-1). Although our sample size and range of observed percentage of alluvial underlying geology was limited, variation in redd densities appeared to be related to the percentage of alluvial underlying geology; streams with lower observed redd densities (i.e., the Marys and Luckiamute rivers) had a lower proportion of alluvial geology, while the Calapooia River and Thomas Creek were composed entirely of alluvial geology and had much higher redd densities (Table 3-1). In the two streams with multiple years of survey data (i.e., the Marys River and Thomas Creek), the redd densities from 2013 were similar to those observed in previous years.

Spatial resampling simulations.— We observed an inverse relationship between the minimum survey distance needed to detect Pacific lamprey redds and observed redd density with our spatial resampling simulations. In the Marys River, the survey with the lowest redd density, a survey distance of 1.2 km was needed to detect redds (Table 3-1 and Figure 3-3). In contrast, in both sections of Thomas Creek, which had our highest observed redd densities, only 0.3 km was needed to detect redds (Table 3-1 and Figure 3-4). For the Luckiamute and Calapooia rivers, two streams with moderate redd densities, the survey length needed for detection was 0.7 km and 0.5 km, respectively (Table 3-1 and Figures 3-3, 3-4).

The survey length needed to obtain simulated redd densities within ± 20% of observed redd densities generally decreased as observed redd density and the percentage of alluvial geology increased (Table 3-1). Because the minimum and maximum simulated redd density values were not symmetrical around the mean, the required survey lengths for each stream were different for the lower error level (80% of observed redd density) and the upper error level

(120% of observed redd density) and we used the longer survey length in our assessments. The three surveys with the highest redd densities (upper and lower Thomas Creek and the Calapooia River) required minimum survey lengths of 2.4 km, 3.2 km, and 3.0 km, respectively, to obtain a subsample within ± 20% of the observed redd density (Table 3-1 and Figure 3-4). In the streams with lower redd densities, a longer survey length was needed to obtain precise redd density estimates. For the Luckiamute River, a survey length of 4.9 km was needed to obtain precise redd density estimates, whereas the Marys River required a survey length of 13.7 km.

DISCUSSION

Our spawning survey efforts have incorporated methods and findings from previous Pacific lamprey spawning surveys in the Pacific Northwest (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009) to learn more about monitoring the spawning phase of the Pacific lamprey life cycle. Our findings suggest survey length requirements for detecting and evaluating the abundance of spawning adult Pacific lamprey, and can be used in the development of monitoring programs. Furthermore, these data may be used to assess the relative precision of spawning surveys that have already been completed and adapt survey methodology and biological interpretations accordingly. Our spatial resampling approach may also be applied to existing datasets from spawning surveys for other fishes to optimize fieldwork efficiency. Although redd surveys are generally considered an imprecise measure of Pacific lamprey abundance (Moser et al. 2007), redd counts may facilitate trend assessments of status more accurately than traditional measures of adult abundance such as counts at dams, which are often poor reflections of escapement (Moser and Close 2003, Lampman 2011). However, addressing several key uncertainties might allow using redd counts to compute population metrics for Pacific lamprey.

Although we only used one year of survey data with relatively good spawning survey conditions, the stream segments we surveyed had a range of redd densities and geologic composition, and our results indicate how survey length relates to these factors. With the exception of the Luckiamute River, our resampled mean redd density showed very little bias relative to what we observed in our spawning surveys. In the Luckiamute survey, one of the spawning locations located near the end of the survey segment contained a high density of redds, so these redds were probably often missed in resamples. Our use of the minimum and maximum observed values (of 10,000 observations) rather than other statistics of variance (e.g., 95%

confidence intervals) from our resampling techniques provided the most conservative survey length recommendations possible from our data. Because of our approach, our results can be applied to inform survey methods in other basins with a mix of hydrologic conditions, alluvial and intrusive geology, stream flow regimes, and anthropogenic impacts. However, in other basins similar techniques should be used to validate spawning surveys lengths and refine monitoring methodologies.

Implementation of spawning surveys for Pacific lamprey can be informed by our analyses, but clearly outlining the objectives of a monitoring plan for Pacific lamprey spawning activity will dictate the logistics of conducting surveys. Surveys should be conducted during the spring when water temperature is 10-15°C (see further details in Chapter 6). If detection of Pacific lamprey is the study goal, our spatial resampling analysis suggest that completing short spawning surveys (of at least 1.2 km) over a large spatial scale may be the most effective way to detect redds if adults are present in the segments. If the monitoring objective is to obtain reliable redd density estimates, temporal trends, and other spawning characteristics, our results indicate that available spawning habitat and underlying geologic structure are important to consider to obtain relatively precise redd density estimates. Although our survey segments contained a relatively narrow range of percent alluvial underlying geology, some of our related work suggests that Pacific lamprey select for areas with these underlying sediments (Chapter 2). Stream segments with alluvial underlying geology, in addition to providing a source of suitable spawning gravel, are also more likely to retain these sediments than areas with bedrock streambeds (May and Gresswell 2003), particularly in streams that have experienced historic habitat degradation (e.g., splash dams; Miller 2010) and loss of large wood (Sedell and Froggatt 1984). In other areas, particularly river basins with little alluvial geology, examining the relationship between underlying geology and redd density will be important for developing and refining spawning survey methodology.

An additional consideration prior to implementing monitoring programs is the site-specific statistical power of redd counts for population monitoring. By acknowledging a potential error rate of ± 20% in redd counts the statistical ability to detect small temporal changes in populations based on spawning activity is greatly reduced and may not even be possible (Maxwell 1999, Wagner et al. 2013). If greater statistical power is desired to detect changes in spawning populations, it will be necessary to increase survey length to capture a larger sample of spawning activity and increase precision of redd counts. The spatial pattern of Pacific lamprey redds is often “clumped” and can deviate significantly from a completely random spatial pattern (Chapter 2), which leads to reaches that consist of short segments with many redds tightly packed in gravel of suitable size for spawning, and long segments with no redds. Even in stream segments with relatively high redd densities, longer surveys may be need to account for this habitat patchiness. Because redds are often clumped and the relationship between redd density and adult abundance is uncertain (Chapter 2), it may be more effective to use approaches that account for detection probability and abundance (e.g., a multistate occupancy model; Nichols et al. 2007) to evaluate trends in adult populations.

Using redd counts to monitor temporal trends in populations with any amount of statistical power requires the reduction of bias, particularly bias associated with redd detection (Maxwell 1999, Wagner et al. 2013). Proper training of personnel conducting spawning surveys is essential to ensure the most accurate redd counts possible (Dunham et al. 2009). Our spawning surveys were conducted by two personnel; one person had extensive salmonid spawning survey experience and the other had one year of Pacific lamprey spawning experience. While Pacific lamprey redds are often located in similar habitat types (i.e., pool tailouts, riffles) as salmonids, they generally tend to be much smaller than anadromous salmonids (Stone 2006, Gunckel et al. 2009, Clemens et al. 2012, Wyss et al. 2013) and Pacific lamprey typically place excavated substrate pieces at the upstream end of redds (Stone 2006). Redd superimposition is an additional issue that we and other researchers (e.g., Al-Chokhachy et al. 2005, Brumo et al. 2009, Gunckel et al. 2009) have observed during redd surveys that might lead to an underestimation of redd counts. False identification of redds may also be more likely to occur in areas with low redd densities (Muhlfeld et al. 2006). Clearly specifying *a priori* what characteristics constitute a counted redd will greatly increase the precision of redd counts between observers and time conditions (Wyss et al. 2013). Environmental conditions can also affect the ability to accurately detect redds; in wet years, it is more likely that redds will be washed out between surveys (Jones 2012) or that visibility levels reduce redd detection probability.

Pacific lamprey population metrics and trend assessments derived from spawning surveys should also be interpreted with caution (*sensu* Maxwell 1999). For spawning surveys to provide cost-effective measures of redd density across stream segments, the relationship between redds counts and adult abundance, factors that influence variability between surveyors, and male-to-female sex ratios must be examined (Dunham et al. 2001, Dunham et al. 2009, Parsons and Skalski 2009). While some assumptions of redd identification error can be obtained from salmonid studies, there are many factors that are unknown for Pacific lamprey, including how many redds are constructed per adult and the proportion of test redds constructed. Stone (2006) observed one female build multiple redds with several males and Close (2006) observed twelve individuals on one redd, characteristics that we frequently observed during our surveys. These types of spawning characteristics must be further investigated before Pacific lamprey redd counts can be used for monitoring with more statistical power.

Despite the unknowns in Pacific lamprey spawning behavior, redd counts remain useful as a means of understanding the distribution of this anadromous fish across its range and can easily be integrated with existing spring spawning surveys. Pacific lamprey redds are often encountered during steelhead surveys but the surveys usually end before peak Pacific lamprey spawning has occurred (E. Brown, Oregon Department of Fish and Wildlife, Oregon Adult Salmonid Inventory and Sampling Project, personal communication). Extending these Steelhead surveys through June would likely capture the majority of the Pacific lamprey spawning season. Logistical constraints would dictate the feasibility of walking or floating surveys, but we have documented spawning activities in rivers as small as 3-5 m wide (baseflow) to rivers as large as 100-150 m wide (Chapter 2). However, the ability to accurately observe all available spawning habitat in wide stream segments (>25m wide) is greatly compromised relative to smaller habitats. Redd counts also have considerable potential value as a coarse measure of adult Pacific lamprey abundance. Our results provide a starting point for developing a monitoring design using redd counts for Pacific lamprey populations. These monitoring plans will provide an informative tool for monitoring the response of the spawning life history stage to management actions and help address the ongoing decline of Pacific lamprey.

Table 3-1. Observed peak redd density, percent alluvial geologic composition, and survey length requirements of three spawning activity metrics for survey segments in the Willamette River Basin. Survey length requirements were calculated from spatial resampling simulations to determine length needed to detect Pacific lamprey spawning presence (> 0.0 redds/km) and redd densities within acceptable error range (lower error level = 80% of observed and upper error level = 120% of observed). Mean stream width was measured during summer baseflow conditions.

					Survey length requirements (km)		
Survey	Length (km)	Observed peak (redds/km)	Mean stream width (m)	% alluvial	Detection	80% of observed	120% of observed
Marys River	19.2	22.9	17.3	67	1.2	10.4	13.7
Luckiamute River	5.6	47.2	16.8	80	0.7	4.9	2.4
Calapooia River	7.3	88.5	15.7	100	0.5	2.8	3.0
Thomas Creek, upper	4.2	116.2	19.6	100	0.3	2.4	1.3
Thomas Creek, lower	7.0	137.0	19.7	100	0.3	2.4	3.2

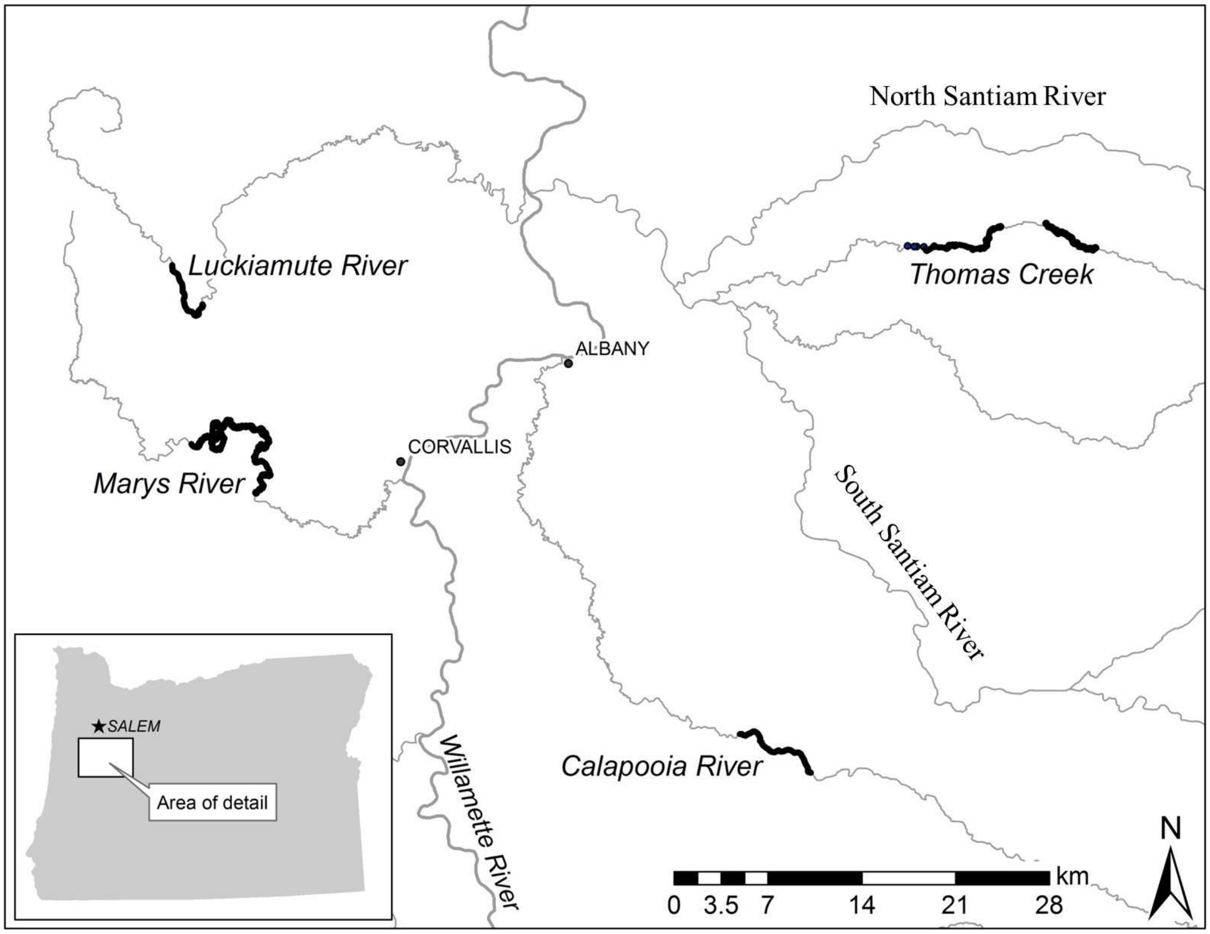

Figure 3-1.— Pacific lamprey spawning survey locations in four tributaries of the Willamette River, 2013. Segments of streams surveyed are in bold. Figure 2 provides additional detail on the distribution of redds within survey segments.

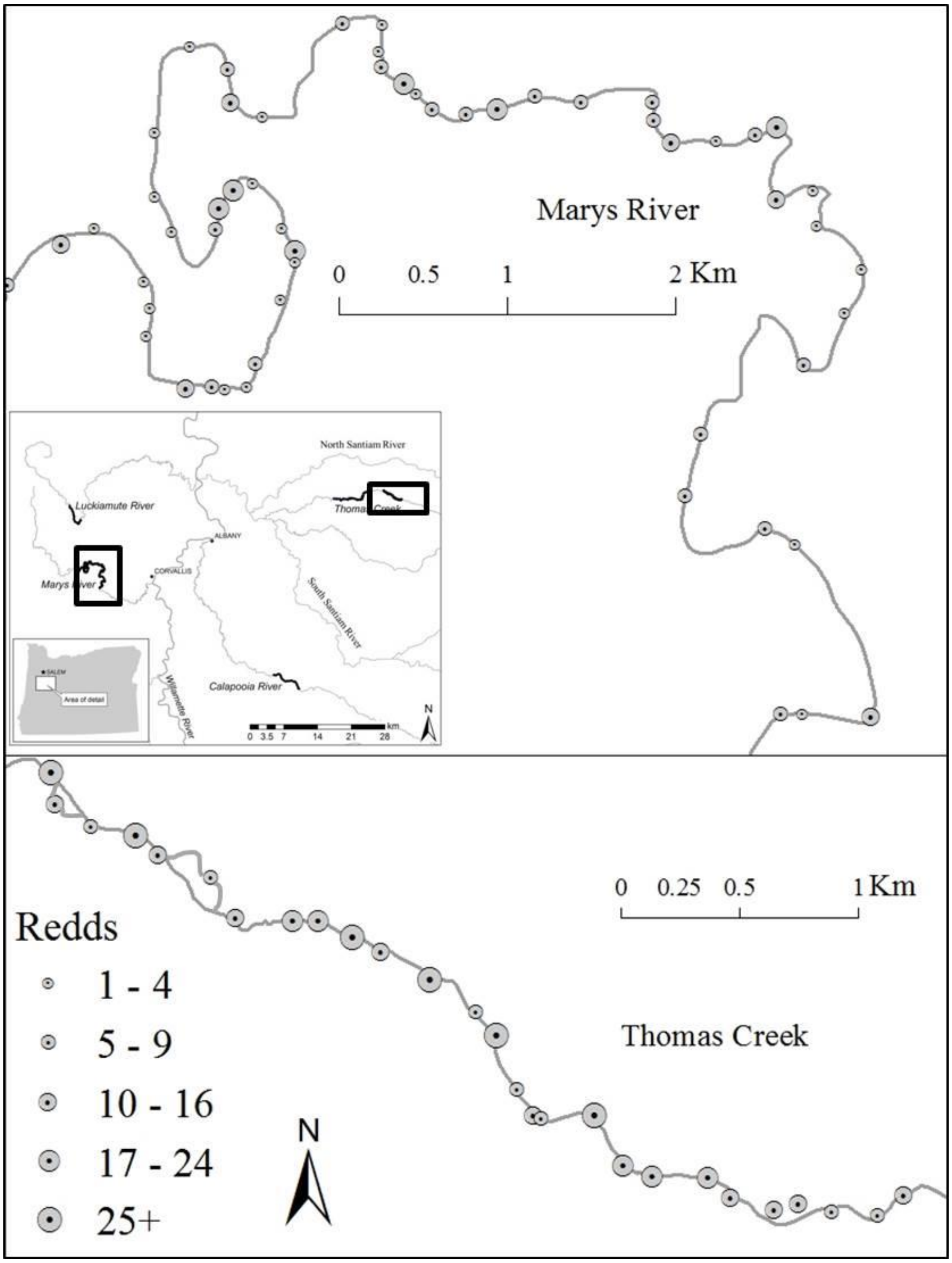

Figure 3-2.— Distribution of Pacific lamprey redds in the upper survey segment of Thomas Creek and the Marys River, Oregon. For each location that redds were observed, the number of redds at that location is indicated by the size of the symbol, and the map indicates the degree of clumpiness of Pacific lamprey redds for relatively high and low redd densities, respectively. We spatially resampled from this observed distribution to assess minimum survey distance to detect redds and obtain redd densities within 20% of observed. Note: inset is Figure 3-1.

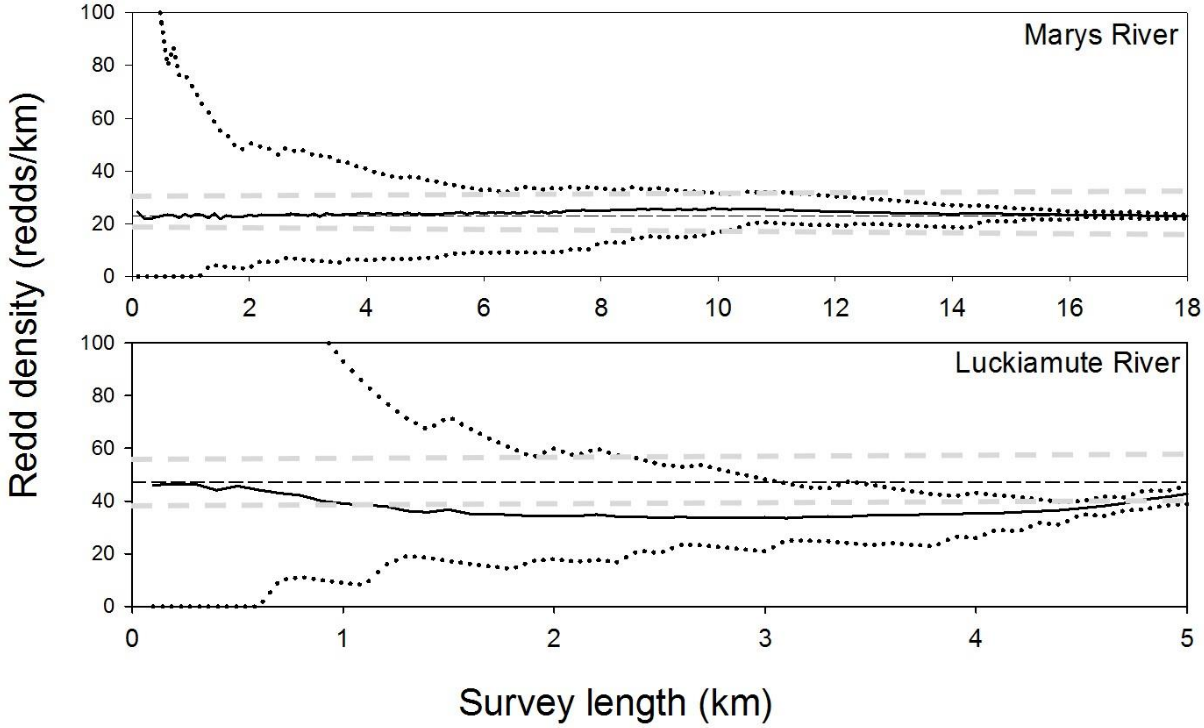

Figure 3-3.— Spatial resampling simulation results of mean redd density (solid line), minimum and maximum values (dotted lines), and the observed mean redd density (dashed line) for study surveys in the Luckiamute and Marys Rivers, two streams with a mix of alluvial and non-alluvial underlying geology. Dashed gray lines are ± 20% of the observed redd density, and where minimum and maximum values both lie within the dashed lines indicate survey length requirements to obtain a relatively precise redd density measurement. Note: differences in scale of y-axes between panels.

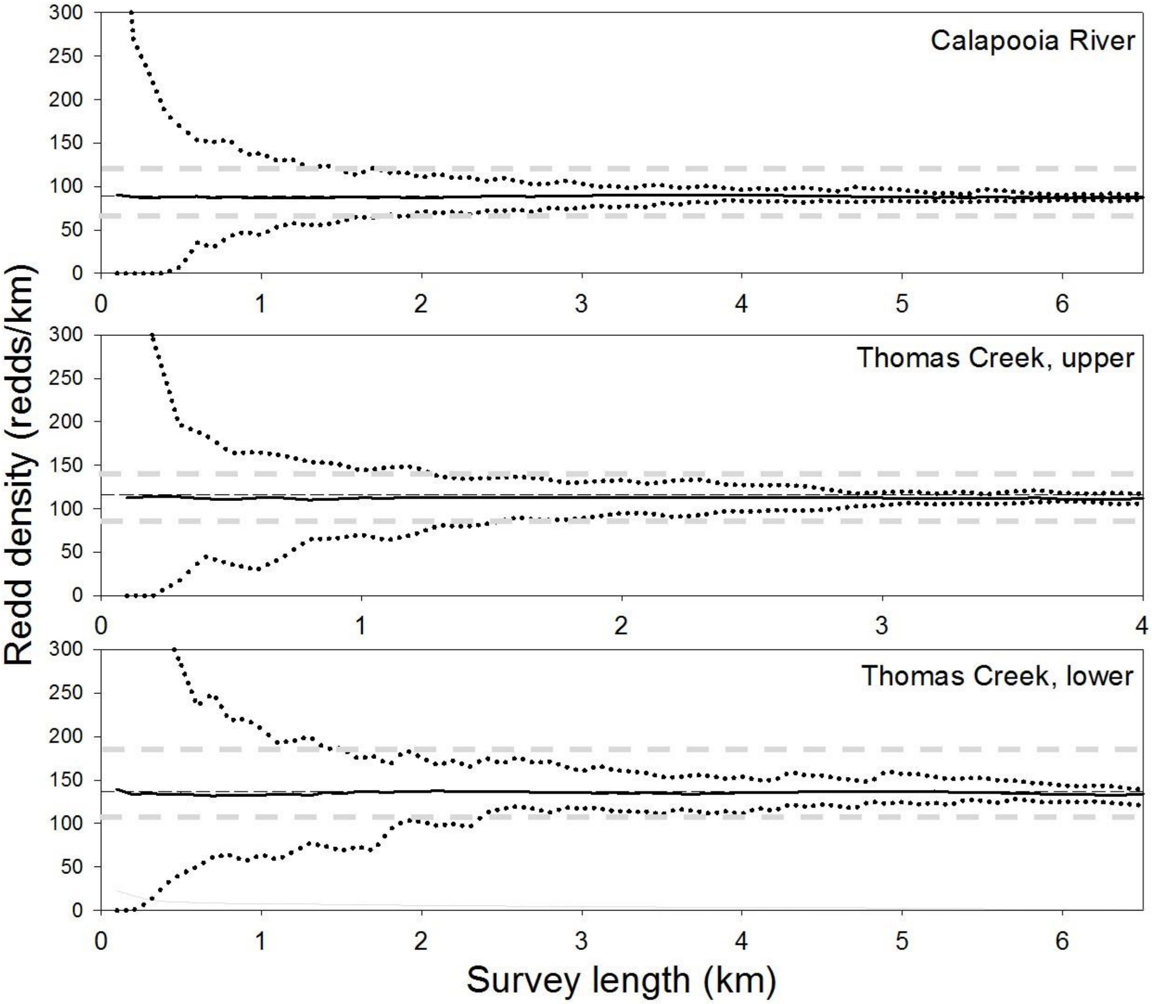

Figure 3-4.— Spatial resampling simulation results of mean redd density (solid line), minimum and maximum values (dotted lines), and the observed mean redd density (dashed line) for study surveys in the Calapooia River and Thomas Creek, two streams consisting of entirely alluvial underlying geology. Dashed gray lines are ± 20% of the observed redd density, and where minimum and maximum values both lie within the dashed lines indicate survey length requirements to obtain a relatively precise redd density measurement. Note: differences in scale of y-axes between panels.

Chapter 4.

Habitat associations of larval Pacific lamprey in wadeable tributaries to the Willamette River

ABSTRACT

Pacific lamprey is an anadromous fish native to the Pacific Northwest of North America that has declined significantly over the last 40 years. Effective conservation will require an understanding of the habitat requirements for each life history stage. Because its life cycle contains extended freshwater rearing (three to eight years), stream conditions during the larval stage may be a critical factor limiting abundance of Pacific lamprey. The objective of our study was to evaluate habitat associations of larval Pacific lamprey in the Willamette River Basin, Oregon, U.S.A. We sampled lampreys and quantified stream habitat at multiple locations in wadeable streams throughout the basin. Pacific lamprey was observed across the basin, but its distribution appeared to be limited by the ability of adults to access spawning habitats. All locations where Pacific lamprey was not collected were associated with migration barriers. Larval Pacific lamprey were most abundant in low velocity habitats with fine sediments (< 2.0 mm grain diameter), similar to other lamprey species. Mean Pacific lamprey density in off-channel habitats was 10 times greater than in main-channel habitats. Using hierarchical linear models to describe habitat associations, we found that larval Pacific lamprey were positively associated with deep sediments, yet the effect of this association varied considerably among subbasins. Our results can be used to proactively address the ongoing decline of Pacific lamprey by prioritizing conservation actions. Restoration and conservation strategies that increase habitat heterogeneity, enhance natural hydrologic and depositional processes, and improve fish passage will likely benefit larval stage Pacific lamprey.

INTRODUCTION

Anadromous fishes are inextricably linked to environmental conditions in both freshwater and marine habitats (McDowall 1988), and effective conservation must consider how factors interact within freshwater and marine environments to regulate populations of anadromous species (Parrish et al. 1998, Naiman and Latterell 2005). Freshwater habitats provide the migration corridor and spawning locations for returning adults of anadromous fishes (e.g., Beamish and Levings 1991, Goniea et al. 2006, Clemens et al. 2011), the rearing location of juveniles (Bjornn and Reiser 1991, Reeves et al. 1995, Jolley et al. 2012), and the juvenile migratory route to the ocean (e.g., van de Wetering 1998, Keefer et al. 2009, Petrosky and Schaller 2010). Although marine habitat and environmental conditions influence survival and growth of juvenile and maturing fishes (e.g., Bisbal and McConnaha 1998, Levin et al. 2001, Murauskas et al. 2013), understanding the importance of environmental conditions in freshwater ecosystems is critical to the management of anadromous stocks.

Pacific lamprey 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 and Crossman 1973). Its semelparous life cycle consists of 3 – 8 years in freshwater as filter feeding larvae, followed by a physiological and morphological transformation into macrophthalmia, and subsequent outmigration to marine environments (Scott and Crossman 1973, Kan 1975, Clemens et al. 2010). The parasitic marine stage lasts less than 3.5 years (reviewed in Clemens et al. 2010), where individual lampreys can range as far north as the Norwest Pacific Ocean and Bering Sea (Sviridov et al. 2007, Orlov et al. 2008) before to returning to freshwater to hold prior to spawning. The freshwater holding period can last from less than one month up to two years prior to making a final migration to their ultimate spawning areas (Clemens et al. 2010 and 2012; Starcevich et al. 2013). Because freshwater rearing consists of a relatively high fraction of the life cycle of the 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 (Moser and Close 2003, Ward et al. 2012). Lamprey returns to the first upstream dam on the Columbia River (Bonneville Dam) averaged greater than 100,000 adults between 1939 and 1969, but have declined to an average of less than 40,000 between 1997 and 2010 (Murauskas et al. 2013). Annual returns at the only major dam on the North Umpqua River, Oregon (Winchester Dam) between 2009 and 2010 were estimated at less than 1,000 adults, whereas historical 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 (Clemens et al. 2010), a perceived threat to commercial fisheries (e.g., Beamish and Levings

1991), and numerous knowledge gaps in its biology (Mesa and Copeland 2009, Clemens et al. 2010, Luzier et al. 2011, CRITFC 2011). Adult passage at hydroelectric facilities has received substantial research attention and management actions have prioritized this potential limiting factor (e.g., Moser et al. 2002a, Keefer et al. 2010). However, the habitat requirements and ecology of the larval stage has been relatively understudied (Moser et al. 2007, CRITFC 2011, but see Torgersen and Close 2004, Jolley et al. 2012).

Across the range of Pacific lamprey, the Willamette River, Oregon (U.S.A.) has one of the largest adult returns and is one of the few remaining harvest locations for Pacific Northwest tribes (Kostow 2002). Although the Willamette River Basin appears to contain a relatively healthy population, freshwater habitat perturbations that commonly impair stream habitats across the Pacific Northwest also frequently act as limiting factors in streams of the basin (e.g., loss of large woody structure, land use conversion, stream diversion and channelization, point and non-point source pollution, and fish passage issues; Mulvey et al. 2009). Because Pacific lamprey have persisted in this mix of impaired and relatively intact habitat conditions, insights into the ecology of Pacific lamprey drawn from the Willamette River system can be readily applied to other freshwater habitats across its range. Our objective was to first identify larval Pacific lamprey rearing locations in wadeable streams of the Willamette River Basin and then to assess habitat features associated with these locations. Results from our multi-year study will fill critical knowledge gaps about the larval stage that have been identified (e.g., Luzier et al. 2011). Furthermore, our findings can be used to make broader inferences about limiting factors for Pacific lamprey and other western lampreys (i.e., western brook lamprey *Lampetra richardsoni* and Pacific brook lamprey *L. pacifica*) in the Pacific Northwest, and may aid in the assessment and prioritization of management actions and conservation areas for these species.

METHODS

Larval lamprey and habitat sampling.—We sampled wadeable locations in 14 tributary subbasins of the Willamette River from July to October in 2012 and 2013 (Figure 4-1). At each of these locations, we collected larval lampreys and quantified physical habitat characteristics in sample reaches. Each reach consisted of two pool and two riffle habitat units, with a non-sampled riffle/pool between. 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 reach classification, we selected habitat units that were representative of the surrounding stream habitat conditions.

We used backpack electrofishing to collect larval lampreys from sample reaches to estimate abundance. We moved upstream through each entire habitat unit using a single electrofishing pass with an AbP-2 backpack electrofisher unit (Engineering Technical Services, Madison, Wisconsin). 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 to temporarily immobilize individual larvae and facilitate capture. These electrofisher settings are commonly used in other lamprey research (e.g., Torgersen and Close 2004, Moser et al. 2007, Dunham et al. 2013), and our work from 2011 suggested that detection probability was high for this approach (Wyss et al. 2012). Following electrofishing of each habitat unit, captured lamprey were anesthetized using 50 mg/L tricaine methanesulfonate (MS-222) buffered with 125 mg/L sodium bicarbonate ($NaHCO_3$), identified as Pacific lamprey or brook lamprey (*Lampetra* spp.), 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. Based on Goodman et al. (2009), only individuals > 60 mm were identified to species because accurate keys for species identification have not yet been developed for lamprey < 60 mm. 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 273 samples from putative Pacific lamprey (size range 54-141 mm) for genetic analyses. The genetic results confirmed that 99.6% of the lamprey tissue samples were correctly identified to species (J. Hess, Columbia River Inter-Tribal Fish Commission, personal communication).

We measured morphological characteristics of the streams in each habitat unit within sample reaches following the methods of Peck et al. (2006) to evaluate relationships between larval lamprey abundance and physical habitat. We measured five evenly-spaced transects perpendicular to the stream channel along the length of each habitat unit. At each transect, we measured bankfull, bar, and wetted stream width across the stream channel; and water depth, dominant substrate, and sediment depth at five evenly-spaced points along the transect starting at the wetted stream margin. Sediment depth was defined as the depth that a 10 mm diameter steel bar could be pressed into the substrate following Sugiyama and Goto (2002). In 2012, we also measured stream discharge and canopy cover, but preliminary results indicated that these metrics were independent of larval densities (Wyss et al. 2013) and they were discontinued in 2013.

For each reach we also summarized landscape-scale variables to evaluate the potential effects of riparian habitat and position within the riverscape on larval Pacific lamprey. Stream disturbance indices developed by Esselman et al. (2011), which account for multiple categories of anthropogenic disturbances, were used to obtain disturbance scores in the local catchment area (LDIST), disturbance in the all upstream catchments (NDIST), and cumulative disturbance scores (CUMDIST) from existing layers in ArcGIS Version 10.1 (ESRI 2012). We computed two metrics to account for survey position within the riverscape: 1) distance to the Columbia River and, 2) distance to the Willamette River, each which addressed separate spatial responses. The distance from the sampling location to the Columbia River examined the total distance that adult lamprey would have had to migrate upstream to seed larval habitat, and the distance to the Willamette River tested both the influence of habitat conditions that may change longitudinally within tributary subbasins, and the potential influence of adult migration distance within Willamette River tributaries.

Data analysis.—Our analytical approach of assessing habitat associations for larval Pacific lamprey contained two steps. In the first step, we examined the relationships between larval abundance and individual habitat characteristics to identify relevant characteristics. In the second step, we used those relevant characteristics in hierarchical linear models to better explain habitat associations of larval Pacific lamprey across the Willamette River Basin and account for spatial autocorrelation. Within habitat units, we summarized total catch and catch-per-unit-effort (CPUE; fish·m^{-2}) for each species (Pacific, brook, unidentified) and habitat characteristics to assess habitat associations of larval Pacific lamprey. To examine differences in total Pacific lamprey catch-per-unit-effort (CPUE) among tributary subbasins we used a one-way analysis of variance (ANOVA). Off-channel habitats (i.e., side channel, backwater, or isolated pool) were removed from these summaries because they were not encountered in every reach. However, we compared the density of larval Pacific lamprey in all off-channel units to the density in all main channel habitat units using a two-sample t-test. Summarized habitat characteristics for each unit included: maximum and mean water depth; mean wetted stream width; dominant substrate type; percentage fine substrate (i.e., < 2.0 mm grain diameter); area of fine substrate; total area sampled; mean sediment depth; and sediment volume (Table 4-1). The percentage of fine substrate 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. We computed the area of fine substrate by multiplying the percentage of fine substrate by the total area of habitat sampled. Similarly, sediment volume was calculated as the mean sediment depth (all substrates) multiplied by the area sampled.

As a first step to assess relationships between habitat characteristics and CPUE of larvae in habitat units, we performed simple linear regression with total lamprey or Pacific lamprey density as the response variable and different habitat characteristics as predictors across all habitat units. For the habitat characteristics sediment volume and area of fine substrate we used total catch as the independent variable. For all others, density was the dependent variable. We also examined the relationship between Pacific and brook lamprey CPUE using linear regression to assess whether habitat associations were similar between these species. With these regressions, we identified potentially biologically relevant habitat characteristics as those with statistically significant relationships ($\alpha < 0.05$) and relatively high associations ($r^2 > 0.20$) with Pacific lamprey CPUE.

Hierarchical modeling.—In the second step of our analysis, we used hierarchical linear models to evaluate the habitat associations of larval Pacific lamprey within different tributary subbasins. Hierarchical linear modeling can account for spatial autocorrelation within stream reaches by allowing regression parameters to vary and/or be fixed within nested scales (Snijders and Bosker 1999). Within this context, a random effect would estimate the degree that the relationship between the dependent and habitat unit-level independent variables varied between basins. A fixed effect would estimate the average effect of a given statistical variable averaged across all basins. For our modeling, we were primarily interested in the relationship between larval Pacific lamprey CPUE and the relevant variables identified from our initial simple linear regressions. We identified sediment depth as being strongly associated with Pacific lamprey CPUE (see Results) and also included distance to the Columbia River to test the effect of migration distance for adults on larval lamprey CPUE. A global linear model lacking hierarchical structure was fit to predict Pacific lamprey density with these two variables. We used an ANOVA of the residuals of the global model to test for spatial autocorrelation within the model. From this initial global model, we hypothesized a set of reduced models containing different combinations of the two variables, their interactions, and random or fixed slope and intercept effects. We evaluated the relative support of each model using Akaike's information criterion adjusted for small sample size bias (AIC_c) and Akaike weights (w_i) to evaluate the relative support of competing models as recommended by Burnham and Anderson (2002). We examined regression parameters from the best overall model to examine the influence of each of the variables on larval lamprey CPUE.

RESULTS

In 2012 and 2013, we captured 8,573 larval lamprey across the 14 tributary subbasins we sampled, composed of 5,662 Pacific lamprey (66%), 1,090 brook lampreys (12.7%), and 1,821 unidentified lamprey (<60 mm; 21.2%). Of these, 214 were metamorphosed Pacific lamprey macrophthalmia (2.5%), all captured after mid-August in each year. Mean total length for all lampreys was 80.5 mm (range: 10 – 163 mm); for Pacific lamprey, 88.9 mm (60 – 156 mm); and for brook lampreys, 94.6 mm (60 – 163 mm). We sampled 207 main channel habitat units and 13 off-channel habitat units. Pacific and/or brook lamprey were collected from all sample reaches, but not all habitat units. Pacific lamprey was present in all tributary subbasins sampled and in 45 of 53 sample reaches, excluding reaches in Abiqua, Dairy, Deep, Gales, Horse, McKay, and Quartz creeks (Figure 4-1). Sample reaches where we did not collect Pacific lamprey were associated with partial or complete anthropogenic migration barriers to upstream passage (Table 4-2, Figure 4-1). Brook lamprey was present in 49 of 53 sample reaches, but absent from three reaches where Pacific lamprey was collected. The abundance of Pacific lamprey was relatively consistent across our sample reaches; CPUE among tributary subbasins was not significantly different ($F_{2,\,13} = 1.52$, $P = 0.112$). Lampreys were collected from all off-channel units, and, when Pacific lamprey was present, the mean density in off-channel habitat units was more than 10 times greater than the mean density in main-channel units ($P = 0.032$; Figure 4-2).

Physical habitat sampling captured the variability of tributary subbasins across the Willamette River Basin (Table 4-1) and Pacific lamprey CPUE varied with habitat conditions. In general, reaches located further upstream in tributary subbasins were narrower, shallower, and characterized by coarser substrates than reaches lower in subbasins (Appendix 1). Within habitat units, the density of Pacific lamprey was significantly related to multiple stream habitat variables, but was most strongly related to sediment depth ($P < 0.001$, $r^2 = 0.22$; Table 4-3). Total catch of Pacific lamprey was also significantly related to both area of fine sediment and sediment volume ($P < 0.001$, $r^2 = 0.21$ and $P < 0.001$, $r^2 = 0.24$, respectively), but these two variables were significantly correlated with sediment depth and were therefore omitted from the hierarchical models. Pacific lamprey density was positively related to brook lamprey density ($P = 0.008$), suggesting that the two species have similar habitat associations.

Hierarchical modeling.—An ANOVA of the residuals of the fitted global model (i.e., sediment depth, distance to the Columbia River, and their interactions) indicated significant spatial autocorrelation across tributary subbasins ($F_{13,\,193} = 3.52$; $P < 0.001$). To account for this spatial autocorrelation, habitat units were nested within tributary subbasins to perform our hierarchical modeling. From our candidate model set, a model containing sediment depth with random intercept and slope parameters was the top overall model (by ΔAIC_c and w_i), and had almost twice as much model support (w_i) as the second ranked model of sediment depth with a random slope parameter and a fixed intercept parameter (Table 4-4). The top overall model also accounted for spatial autocorrelation across tributary subbasins; the ANOVA of model residuals by tributary subbasin was not significant ($F_{13,\,193} = 0.322$; $P = 0.988$). From the models we investigated, those containing the variable distance to the Columbia River were less supported than models that only contained sediment depth.

The influence of sediment depth on Pacific lamprey CPUE was positive across 13 of the 14 tributary subbasins that we considered (Figure 4-3), but the response was highly variable across streams. The inclusion of a random effect of sediment depth in the top overall model suggested that the influence of sediment depth varied by over 90% among tributary subbasins (random effect/fixed effect: $\sqrt{0.000286}/0.0187$; Table 4-5). However, across all tributary subbasins except the Tualatin River, Pacific lamprey density increased with sediment depth, and the model predicted Pacific lamprey densities to be near zero when sediment depth was less than 2.0 cm (Figure 4-3).

DISCUSSION

The distribution of larval Pacific lamprey in the Willamette River Basin was determined by the accessibility of stream habitats to migrating adult lamprey and availability of fine sediments to provide larval rearing habitats, although the degree of this relationship varied by tributary subbasin. These habitat associations were similar to brook and other lampreys (e.g., Potter et al. 1986, Torgersen and Close 2004). Although stream habitats are highly diverse and numerous habitat disturbances are present, the relatively similar abundance of Pacific Lamprey across the Willamette Basin provides opportunities to understand habitat needs for the species. The larval life history stage of Pacific lamprey can comprise three to eight years of its roughly eight to thirteen year life cycle (Clemens et al. 2010), and management actions directed at this stage will be critical to the recovery of the species. Our data provide insights into the ecology of larvae of Western lampreys, and can be used to evaluate potential threats to their persistence, assess and prioritize rearing habitat areas for conservation, develop monitoring plans, and address the decline of Pacific lamprey.

The occurrence of larval Pacific lamprey in the Willamette River Basin was primarily driven by the accessibility of upstream spawning habitats to returning adults. We found Pacific lamprey in 45 of 53 sampled reaches, and all reaches where it was not detected were located above partial or putative barriers to fish passage. Adult Pacific lamprey migrants often encounter passage issues from anthropogenic barriers and their passage requirements differ from salmonids (Moser et al. 2002b, Keefer et al. 2010, Jackson and Moser 2012). Partial fish passage barriers, including seasonal barriers, also influence larval lamprey abundances via limiting adult returns. In the Tualatin and McKenzie river subbasins, larval Pacific lamprey were collected in several reaches above putative barriers, suggesting that partial passage may occur in these locations, however, Pacific lamprey comprised < 10% of the total lamprey catch from these subbasins. In tributary subbasins with no known passage issues, Pacific lamprey catches comprised more than 82% of the identifiable lamprey catch. Improving passage efficiency for Pacific lamprey has been prioritized 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 and Moser 2012).

Although physical barriers are widely recognized as conservation challenges for Pacific Lamprey, chemical barriers may also present passage issues. Upon entry into freshwater, Pacific lamprey do not home in the strict sense (Hatch and Whitaker 2009, Spice et al. 2012). Instead, bile acid chemicals from larval lamprey function as attracting pheromones to adult Pacific lamprey (Robinson et al. 2009, Yun et al. 2011). Environmental pollutants can disrupt physiology and behavior of other fishes (e.g., Scott and Sloman 2004, Hughes et al. 2014), but the extent to which specific chemicals effect migration of Pacific lamprey is unknown. The Tualatin River subbasin contained relatively few larval Pacific lamprey, but brook lamprey catches were consistent with other basins that we sampled. Although the Tualatin River contained a putative physical barrier near its confluence with the Willamette River, 27% of the subbasin's watershed is urbanized and it contains the greatest stream length with impaired water quality of all the 12 Willamette River subbasins (Mulvey et al. 2009). These land use practices might contribute to water quality conditions that deter adult Pacific Lamprey from migrating into this subbasin. To restore Pacific lamprey to areas where it has 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.

Stream habitat conditions were the second major factor related to the abundance of larval Pacific lamprey across the Willamette River Basin. Our hierarchical modeling indicated substantial variability in slope parameter estimates between Pacific lamprey density and sediment depth, with random and fixed effect parameter estimates varying by more than 90% among tributary subbasins. Hierarchical interactions between site-level and stream-level variables are common in fisheries research (Dunham and Vinyard 1997), and partitioning variance from each of these sources is the goal of hierarchical linear modeling (Conroy and Peterson 2013). To better account for the observed variability across basins, we considered an additional variable (i.e., distance to the Columbia River) in our models. Although we were unable to better statistically explain these relationships, the biological mechanisms were clear from our results: with the exception of reaches in the Tualatin River subbasin, Pacific lamprey density increased with mean sediment depth. These results indicate that the availability of suitable burrowing habitat is critical to the larval life history stage of Pacific lamprey. To better understand mechanisms behind the variability of larval Pacific lamprey abundance across subbasins, similar assessments of habitat features may be necessary at finer spatial scales (i.e., within habitat units).

Pacific lamprey had a wide distribution across streams and reaches sampled in the Willamette River Basin, but CPUE varied considerably among habitat units and stream systems. Similar patterns (high site occupancy, with high variability in CPUE at finer scales) have also been observed by other researchers outside of the Willamette River Basin (e.g., Torgersen and Close 2004, Stone and Barndt 2005). We documented higher CPUE of lamprey rearing in slower habitat types, and off-channel habitats were particularly favorable larval rearing habitat. Previous work has reported larval Pacific lamprey associated with this habitat heterogeneity (Torgersen and Close 2004), and other lamprey species (including brook lamprey from this study) are associated with deep, fine sand or mud substrates with organic matter (e.g., Potter et al. 1986, Sugiyama and Goto 2002). Clearly, habitats that accumulate fine sediments are important burrowing habitats for larval lampreys and habitat restoration that promotes channel complexity would be beneficial to numerous aquatic organisms in addition to larval lampreys (Fausch et al. 2002).

Our collection of larval lamprey coupled with habitat sampling may be used with other studies to develop monitoring plans for Pacific lamprey. In other lamprey monitoring programs, sampling is conducted by stratifying habitats into broad categories and effort is partitioned among categories to account for the patchy distribution of ammocoetes (Moser et al. 2007). In Great Lakes sea lamprey management, stream habitat is classified into one of three types and sampling effort is divided among types until 100 individuals are captured. Abundance for an entire stream system is derived from a combination of habitat survey and larval catch data (Hansen et al. 2003; Slade et al. 2003). In other larval lamprey assessments, a specified habitat area (e.g., 1, 7.5, or 15 m^2) is sampled at multiple locations throughout a stream network to assess abundance (e.g. Torgersen and Close 2004, Stone and Brandt 2005; Ward et al. 2012). Our data suggest that these approaches should allow for targeting lampreys in habitat patches most likely contain them. However, these habitat patches often make up very little of the available stream habitat. Sampling the entire stream channel allows for an assessment of lamprey numbers across all available habitats and can account for differential habitat use between size classes (e.g., Sugiyama and Goto 2002). A standardized larval Pacific lamprey sampling assessment methodology might optimize fieldwork efficiency and facilitate data sharing and comparisons across regions (Bonar et al. 2009). However, tailoring monitoring programs to address management objectives will be necessary to evaluate specific conservation actions and research questions (Moser et al. 2007).

Immediate management action is needed to address the decline of Pacific lamprey and our findings suggest that improving stream accessibility and habitat complexity will help halt the ongoing decline of Pacific lamprey, an immediate goal of recovery planning (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), and currently limit the availability of larval rearing habitat for Pacific lamprey. In the Willamette River Basin and other drainages, symptoms of these land use practices include high water temperature, degraded riparian condition, loss of large woody debris, lack of connectivity with the floodplain, and sedimentation (Kaufmann and Hughes 2006). Conservation strategies that improve watershed conditions and restore riparian communities will set the physical template for habitat restoration (Naiman and Latterell 2005). Instream projects that stabilize 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 passage will help increase the distribution and abundance of larval Pacific lamprey across its range. Finally, continued monitoring of the occurrence and relative abundance of larval Pacific lamprey will document changes in its distribution, increase the understanding of its ecology, and help explain its population dynamics (King 1995).

Table 4-1. Mean, standard error (SE), and range values of stream habitat features and lamprey density and total catch in habitat units in the Willamette River Basin, Oregon (U.S.A.), 2012-13. The habitat features LDIST, NDIST, and CUMDISTIND are measures of riparian disturbance derived from Esselman et al. (2011) and are described in more detail in the Methods.

Variable	Mean	SE	Range
Habitat features			
Mean water depth (cm)	23.8	0.84	4.9-53.2
Mean maximum water depth (cm)	79.4	3.07	15.9-250.0
Mean wetted width (m)	13.4	0.34	2.9-30.2
Total area sampled (m^2)	414	19.8	53-1962
Area with sand or finer substrate (m^2)	75.9	7.52	0-848
% of area with sand or finer substrate	20.1	1.71	0-100
Sediment depth (cm)	4.9	0.47	0.4-43.5
Sediment volume (m^3)	16.7	1.62	0.4-226.3
LDIST	2.7	0.08	1-4.0
NDIST	3.1	0.05	1.25-4.0
CUMDISTIND	2.4	0.06	1.0-4.0
Distance to Willamette (km)	59.9	1.95	18.2-124.5
Distance to Columbia	196.7	5.76	62.7-389.5
Lamprey			
Density of Pacific lamprey (fish $\cdot m^{-2}$)	0.062	0.0088	0-0.836
Density of all lamprey (fish $\cdot m^{-2}$)	0.101	0.013	0-1.22
Catch of all lampreys (#)	32.5	3.36	0-288
Catch of Pacific lamprey (#)	21.0	2.37	0-184
Density of brook lamprey (fish $\cdot m^{-2}$)	0.016	0.0043	0-0.788

Table 4-2. Putative migration barriers, height, and ownership associated with sample reaches using barrier data from the Oregon Fish Passage Barrier dataset (ODFW 2012). In every surveyed reach of river where juvenile Pacific lamprey were not found, migration barriers to adult lamprey were present downstream, although Pacific lamprey were found in several reaches upstream of potential barriers. River km is the distance upstream from a confluence with a larger river. Passage refers to Pacific lamprey and has not been explicitly evaluated in most cases, but is inferred from our data; in streams with partial passage, Pacific lamprey were found upstream of migration barriers but in much lower densities. Acronyms include: Oregon Department of Fish and Wildlife (ODFW) and Eugene Water and Electric Board (EWEB).

Putative barrier	Stream	River km	Height (m)	Owner	Passage
Oswego dam	Tualatin River	5.7	2	ODFW/ Lake Corp	Partial
Leaburg Dam	McKenzie River	54.6	5	EWEB	Partial
Silverton water supply dam	Abiqua Creek	17.7	4	City of Silverton	Unknown
Private diversion dam	Deep Creek	11.8	6	Private citizen	Unknown

Table 4-3. Results of simple linear regressions by independent habitat and lamprey assemblage variables of Pacific lamprey catch-per-unit-effort across sampled reaches within 14 tributary subbasins of the Willamette River, 2011-13. Significant relationships ($P < 0.05$) are shown in *italics*, and significant relationships with high relative correlations ($r^2 > 0.20$) are shown in bold. Effects can be positive (+) or negative (-) regression parameters, no effects are indicated by long dashes. The habitat features LDIST, NDIST, and CUMDISTIND are measures of riparian disturbance derived from Esselman et al. (2011) and are described in more detail in the Methods.

Independent	Dependent	P	r^2	Effect
Max depth	density	*0.003*	0.042	(+)
Mean depth	density	*<0.001*	0.096	(+)
Wetted width	density	0.054	0.018	–
Sediment depth	density	**<0.001**	**0.222**	(+)
%Fine substrate	density	*<0.001*	0.069	(+)
Area fine substrate	density	*0.026*	0.0239	(+)
Area fine substrate	total catch	**<0.001**	**0.213**	(+)
Sediment volume	density	*<0.001*	0.0585	(+)
Sediment volume	total catch	**<0.001**	**0.237**	(+)
Brook density	density	*0.008*	0.034	(+)
LDIST	density	*<0.001*	0.095	(-)
NDIST	density	*0.003*	0.041	(-)
CUMDISTIND	density	*<0.001*	0.081	(-)
Willamette	density	*<0.001*	0.057	(-)
Columbia	density	0.050	0.019	–

Table 4-4. Predictive models, number of parameters (k), log-liklihood, AIC$_c$, ΔAIC$_c$, and w_i values for hierarchical linear models used to predict abundance of Pacific lamprey in the Willamette River Basin, Oregon. Candidate models had both random intercepts and slopes (r), fixed slopes (fs) or fixed intercepts (fi), or both fixed slopes and intercepts (fs/fi), with mean sediment depth (Sed dep) and distance to the Columbia River (Columbia) as independent variables.

Candidate Model	k	LogL	AIC$_c$	ΔAIC$_c$	w_i
Sed dep (r)	5	206.07	-399.72	0	0.646
Sed dep (fi)	4	203.25	-398.31	1.41	0.320
Sed dep (r), Columbia (r), Sed dep*Columbia	7	208.61	-393.86	5.86	0.035
Sed dep, Columbia (fs/fi)	4	206.24	-391.35	8.36	0.010
Sed dep (fs)	4	167.08	-325.96	73.75	0.00
Columbia (r)	4	144.59	-276.76	122.96	0.00
Columbia (fs)	4	140.95	-273.71	126.01	0.00
Columbia (fi)	4	137.61	-267.02	132.69	0.00

Table 4-5. Parameter estimates and standard errors of fixed and random effects from the top overall model from a set of hierarchical linear models to predict Pacific lamprey abundance in tributary subbasins to the Willamette River, Oregon (U.S.A.).

Parameter estimate	Estimate	SE
Fixed effect		
Intercept	-0.0062	0.018
Sediment depth	0.019	5.33E-03
Random effect		
Intercept	5.96E-04	1.70E-03
Sediment Depth	2.86E-04	1.18E-03
Residual	6.84E-03	5.75E-03

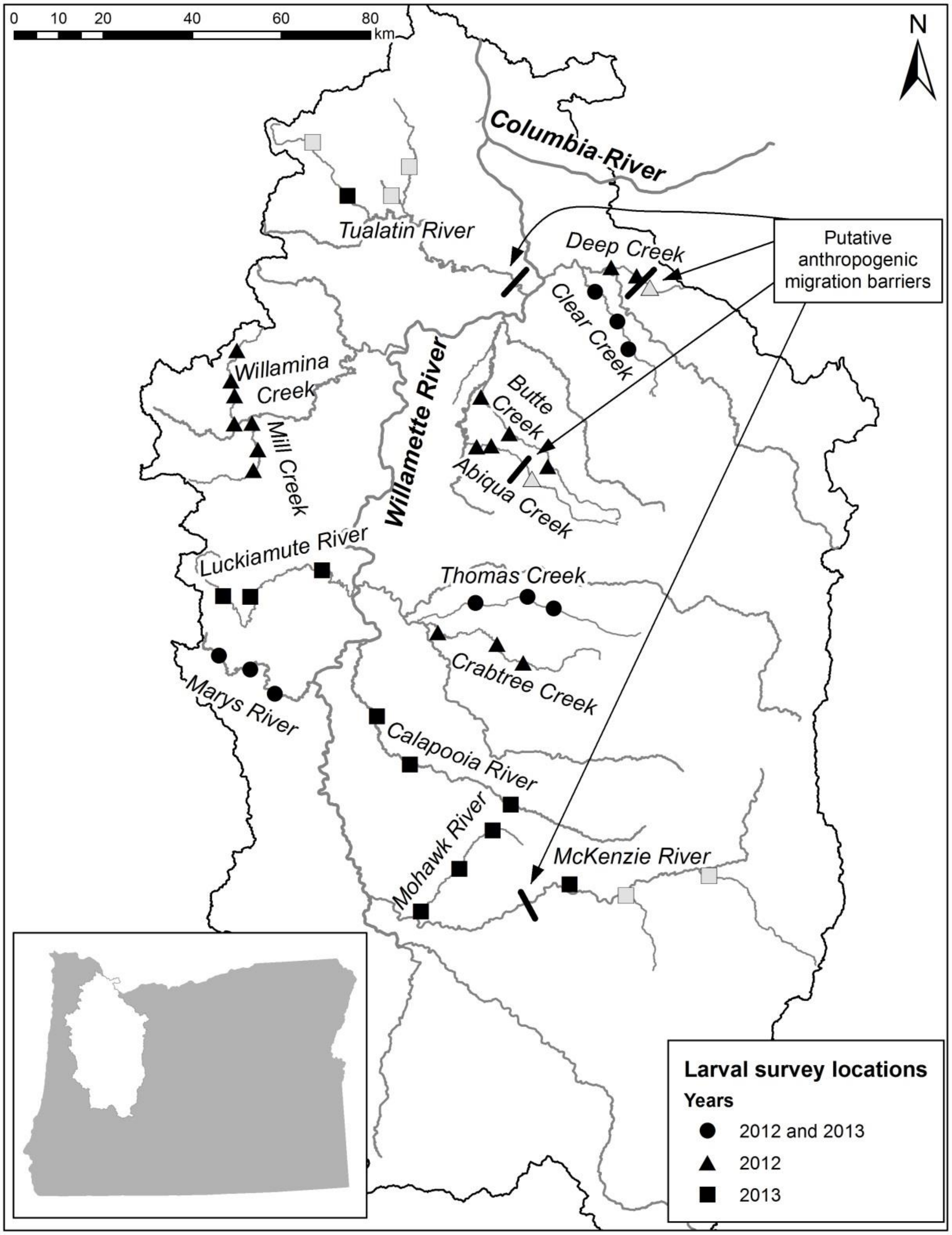

Figure 4-1.— Sampling locations for larval Pacific lamprey in the Willamette River Basin, 2012-13. Closed symbols indicate reaches where Pacific lamprey was collected and open symbols represent areas where Pacific lamprey was not collected. The putative anthropogenic migration barriers are inferred from our data, although they may be only partial barriers.

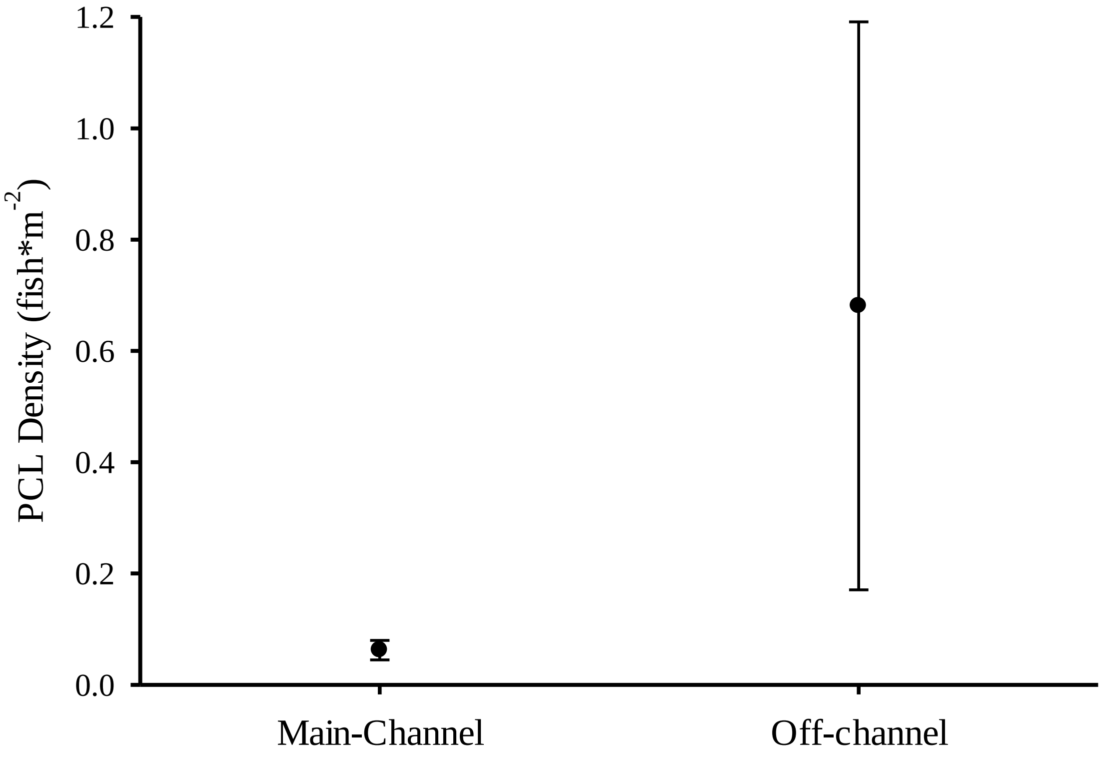

Figure 4-2.— Mean density of Pacific lamprey (PCL) collected from two habitat types in 14 streams of the Willamette River Basin, 2012-13. Error bars show 95% confidence intervals around the mean.

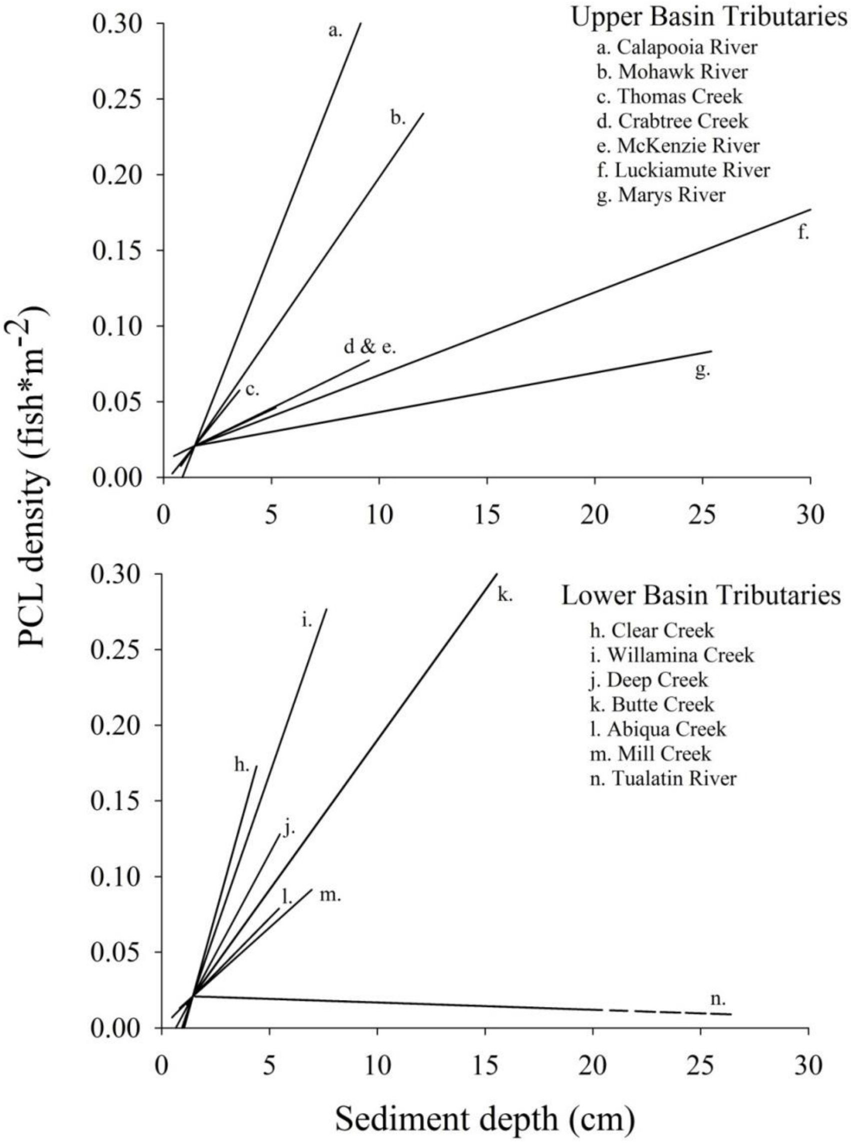

Figure 4-3.— Relationships between Pacific lamprey (PCL) catch-per-unit effort, where effort is the area sampled (m^2) and sediment depth across 14 tributary subbasins of the Willamette River Basin, OR 2012-13. All lines represent individual tributary subbasin models from a hierarchical linear model, and the figure is broken into upper (top) and lower (bottom) Willamette River Basin tributaries. Solid lines are regression parameters from tributary subbasins with positive slope coefficients; the dashed line is the regression parameter from the single tributary subbasin with a negative slope coefficient (i.e., Tualatin River). Tributary subbasin relationships are only plotted for the sampled range of sediment depths.

Chapter 5.

Mortality estimates and sample size requirements for characterizing larval Pacific lamprey populations

ABSTRACT

An understanding of the dynamics of a fish population is critical to assessing its status and prioritizing potential management actions. The population dynamics for larval Pacific lamprey *Entosphenus tridentatus* are not well understood, although the information would be valuable to inform life history models for the species. Furthermore, the efficiency of monitoring efforts for the species could be improved by evaluating samples sizes needed to adequately characterize length frequency distributions. Our study objectives were to first estimate mortality during the larval life history phase and, secondly, assess sample size requirements for monitoring larval Pacific lamprey. We estimated the likelihood of different levels of natural mortality using a random effects model that incorporated data from repeated measures of length-at-age for individual lamprey and length frequency from our surveys. We estimated annual mortality within individual age classes (20-61%) and across the entire larval phase (19-26%), indicating relatively high survival through this life history stage. Secondly, we used statistical resampling analyses to provide optimum sample sizes to describe length frequencies of larvae. We found that 100-200 individuals were needed to accurately characterize length frequency of larvae, but our data may also be used to estimate the relative precision of different observed sample sizes. Our findings suggest conservation actions to address population declines of Pacific lamprey and provide methods that can be used to monitor Pacific lamprey.

INTRODUCTION

The dynamics of a fish population is regulated by the interactions between its recruitment, growth and mortality patterns (King 1995), and understanding how these mechanisms operate is critical to understanding the status of a fishery (Schaefer 1957). Knowledge of these three dynamic rate functions (i.e., recruitment, growth, and mortality) can provide fisheries managers with insight into a species' ecology and evaluate the response of populations to environmental stressors (Adams et al. 1992) or conservation actions (Quist et al.

2007). This knowledge may be of particular interest for elucidating life history patterns of endangered or threatened species (e.g., Scoppettone and Vinyard 1991).

Pacific lamprey is a native anadromous fish that has declined considerably across its range in western North America, including extirpation from multiple drainages (Luzier et al. 2011). 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 (Clemens et al. 2010), a perceived threat to commercial fisheries (e.g., Beamish and Levings 1991), and numerous knowledge gaps in its biology (Luzier et al. 2011, CRITFC 2011). The semelparous life cycle of Pacific lamprey consists of a 3-8 year freshwater larval stage, followed by a transformation period and outmigration to marine environments (Kan 1975). Ocean residency generally lasts one or two years prior to returning to freshwater (Scott and Crossman 1973), where they hold for up to two years prior to making final migration to spawning areas (Clemens et al. 2010). Because a relatively high fraction of its total life cycle occurs in freshwater, research efforts have targeted uncertainties related to this life stage (Mesa and Copeland 2009).

Dynamic rate functions for fish populations are generally derived from length and age information from sampled populations (Isely and Grabowski 2007, Miranda and Bettoli 2007). Obtaining traditional growth and mortality estimates for Pacific lamprey is difficult because age data are sparse and reliable aging structures have not been identified for larvae (Meeuwig and Bayer 2005). However, body length is generally measured during field sampling of Pacific lamprey (e.g., Torgersen and Close 2004, Jolley et al. 2012, Dunham et al. 2013). In the absence of other options, mortality estimates can be generated from length frequency information using several assumptions (Miranda and Bettoli 2007). When cohorts are not clearly distinguishable in catch length distributions (e.g., lampreys), length frequency statistics can be used to approximate von Bertalanffy growth parameters (e.g., Chen and Watanabe 1989, Jensen 1996) from which mortality estimates can be generated (e.g., Wetherall et al. 1987). Additionally, length frequency information can provide insight into fish population dynamics by identifying inconsistent year classes or high mortality (Neumann and Allen 2007). In the absence of age information, length frequency analyses may provide ecological insights into the life history of Pacific lamprey and can be used to evaluate population responses to management.

Accurately describing the size structure of a population requires capturing an adequate sample size of individuals to reliably characterize its length-frequency distribution (Vokoun et al. 2001). Because researchers and managers are interested in maximizing efficiency of data collection, collecting too many individuals is also not cost efficient (Hansen and Jones 2008). Furthermore, if an adequate sample size cannot be obtained, understanding the relative precision of metrics derived from these smaller datasets would be of interest to management. Vokoun et al. (2001) and Miranda (2007) used statistical resampling of simulated and empirical datasets to assess sample size requirements for several North American sport fishes. Vokoun et al. (2001) suggested sample sizes of 300-400 individuals were suitable to describe population length frequencies; however, Miranda (2007) suggested that length frequency distributions of smaller species can be obtained with smaller samples sizes. A similar assessment of Pacific lamprey length frequency data would be useful in the development of monitoring plans for this species, and might have further utility for assessments of other lampreys (e.g., sea lamprey).

Conservation of Pacific lamprey across its range will require an ecological understanding of its larval life history stage (CRITFC 2011), and a development of monitoring efforts that effectively characterize the status of individual populations (Luzier et al. 2011). Our objectives were to: 1) describe patterns in larval Pacific lamprey size structure and estimate mortality across the Willamette River Basin, and 2) assess sample size requirements to characterize length frequency distributions for future larval Pacific lamprey monitoring plans. These mortality patterns provide insights into the ecology of the larval life history stage of this imperiled fish, and will aid in its conservation rangewide. In particular, the mortality estimates may inform life cycle modeling to prioritize conservation efforts. Furthermore, we used resampling of empirical larval Pacific lamprey length distribution datasets, which will help inform future monitoring efforts and optimize sampling efficiency.

METHODS

Larval Lamprey Sampling.—We sampled larval lampreys from wadeable locations in 14 tributary subbasins of the Willamette River from July to October of 2011-13 (Figure 5-1). To capture fish from all available habitat, each of our study reaches consisted of two entire pool and riffle channel units. If an off-channel habitat (e.g., side channel, backwater, isolated pool) was present within a sample reach, it was sampled also sampled. We sampled three of these tributary subbasins (i.e., Clear and Thomas creeks and the Marys River) in all three years, and in two additional subbasins (i.e., Crabtree and Deep Creek) in 2011 and 2012. At each location, we used backpack electrofishing to characterize the abundance of larval lampreys. We moved upstream through each habitat unit using a single electrofishing pass with an AbP-2 backpack electrofisher unit (Engineering Technical Services, Madison, WI). The electrofisher applied a pulsed burst train (3 on: 1 off) with a 25% duty cycle to induce emergence from substrate, and a fast pulse at 30 pulses/sec to temporarily immobilize individual larvae and facilitate capture, settings that are commonly utilized in other lamprey research (e.g., Torgersen and Close 2004, Moser et al. 2007). Following completion of each habitat unit, individual captured lamprey were enumerated, measured (total length (mm)), and identified as Pacific lamprey or brook lamprey (*Lampetra spp.*). 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. Based on Goodman et al. (2009), only individuals > 60 mm were identified to species because accurate keys for species identification have not yet been developed for lamprey > 60 mm. We did not attempt to speciate brook lampreys because diffentiating between these two species requires an examination of trunk myomeres (Reid et al. 2011). We returned captured lamprey back to the stream near their capture location following processing.

Mortality estimation.—Because Pacific lamprey presents multiple challenges to computing traditional growth and mortality metrics, our analysis included several notable assumptions. First, we did not collect aging structures from any of the lamprey we collected in the field; instead we relied on published literature (i.e., Meeuwig and Bayer 2005) to construct von Bertalanffy growth curves and inform subsequent mortality estimates. Secondly, the fish used in Meeuwig and Bayer (2005) were collected from the Middle Fork John Day and South Fork Walla Walla rivers in Eastern Oregon. We assumed that growth between Pacific lamprey populations in the Willamette River Basin and those from farther up the Columbia River Basin exhibit similar growth patterns. Third, we included both Pacific lamprey and brook lamprey age data because these species displayed relatively similar growth patterns (Meeuwig and Bayer 2005), and we were able to increase our sample size for modeling growth curves. Finally, Pacific lamprey often display highly variable growth patterns within a year class. Often the largest individuals within a given age class may be over 100% longer than the smallest individuals within the same age class (Meeuwig and Bayer 2005, Jon Hess, CRITFC, unpublished). To account for this disparity, we included multiple age observations to fit the von Bertalanffy growth model and attempted to account for this high variability in the statistical approach we used. We also selected a mortality estimating model that included a single mortality rate for the entire larval life history phase (i.e., Jensen 1996) and one that provided estimates for each year-class within the larval phase (i.e., Chen and Watanabe 1989).

To estimate survival of larval Pacific lamprey, we compared two estimators of natural mortality by Chen and Watanabe (1989; Eq. 1) and Jensen (1996; Eq. 2) for all of the Pacific lamprey collected between 2011 and 2013. Each of these models has been used to estimate natural mortality in fishes based on von Bertalanffy growth parameters, such that

$$M(t) = \frac{K}{1-e^{-K(t-t_0)}}, \text{ and} \tag{1}$$

$$\frac{M}{K} = 1.5. \tag{2}$$

We used existing larval lamprey (both brook and Pacific lampreys) aging information collected by Meeuwig and Bayer (2005) to fit von Bertalanffy growth curves to length frequency data from Pacific lamprey collected in Willamette River tributaries. We believe that growth and mortality patterns in the life history of brook and Pacific lampreys are very similar, so we included aging data from both of these species to increase sample sizes for analyses (including brook lamprey increased sample size from 68 to 177). The aging data included multiple observations for each individual larval lamprey (Figure 5-2). Because age can be measured but is not known, we used a state-space model that treated age as a random Poisson process within our on Bertalanffy growth model. Within this model, the length of lamprey *j* is a function of the random variable λ_j that describes the expected age of an individual, and the parameters of the von Bertalanffy growth model (i.e., L_∞, K, t_0). We assumed that error w_j between the observed and expected values was log-normally distributed with a mean of zero and a standard deviation of σ such that

$$L_j = \mathrm{L}_\infty\left(1-\ e^{-K\left(\lambda_j-\ \mathrm{t0}\right)}\right)e^{w_j}, w_j \sim \mathcal{N}(0, \sigma). \tag{4}$$

The observed age for the *i*th observation from the *j*th lamprey ($t_{i,j}$) is based on a Poisson process where the expected age was λ_j

$$t_{i,j} \sim Poisson(\lambda_j). \tag{5}$$

The aging data contained several observed age estimates of zero (i.e., 54 of 972 age estimates). In addition to this not being biologically plausible, these age zeroes create issues for describing aging observations as a Poisson random variable. We used two approaches to account for this issue: we either excluded the zero observations from the dataset or set all age zero fish to 0.5. We used the random effects package in AD model builder (ADMB-RE; http://admb-project.org; Fournier et al. 2012) to estimate the parameters of the model (L_∞, K, t_0, w_j), as well as the random effects (λ_j). We have included the code for this procedure in Appendix 2. We then used the growth parameters from these model outputs to solve for M in the Chen and Watanabe (1989; Eq. 1) and Jensen (1996; Eq. 2) equations. We then converted our estimates of M (instantaneous natural mortality) to estimates of annual survival (S) for both equations and datasets with and without age-0 data points included.

Sample size estimation.—We used a resampling approach similar to Vokoun et al. (2001) to evaluate the appropriate sample size required to obtain a representative length-frequency distribution of a larval Pacific lamprey population. We included all sample reaches in which we collected >200 individual larval Pacific lamprey as individual samples for consideration within this analysis (total reaches = 13). We also included all Pacific lamprey captured across all sample reaches as an additional sample for this analysis, to account for any large scale variability that might have occurred across the entire Willamette Basin. From each of these samples, we used a bootstrap technique to randomly select, with replacement, a subsample of varying size from within each of the samples; subsample sizes ranged from 10 to 700 fish, at 10 fish intervals (i.e., 10, 20, 30, …700). We chose to use 700 as our upper subsample size because the most individual Pacific lamprey we captured at a single location in both years was 685 (Thomas Creek, 2013), which should represent the approximate upper limit on the number of larval lamprey that could be captured and processed at a single location.

To evaluate the relative precision of different sample sizes, we compared the length frequencies of these subsamples to the original samples using several measurements. For each subsample, we compared the percent of lengths in each length interval (S_l) to the percent observed in the original sample (T_l) and calculated the mean square difference (MSD) between the subsample and original sample as:

$$MSD = \sum_{l=1}^{n} (S_l - T_l)^2 \qquad (6)$$

where *l* is the length interval number. Because the width of individual length intervals (e.g., 2.5 mm, 5 mm, 10 mm length bins) can change the interpretation of length frequency distributions (e.g., Vokoun et al. 2001), we examined the effect of the width of length intervals with our resampling. For each subsample size, we performed 1000 resamples and computed the MSD for each of three length intervals: 2.5 mm, 5 mm, and 10 mm. The MSD values indicate the relation between the subsample and the original sample length-frequency distributions (Vokoun et al. 2001). From these resamples, we calculated the mean MSD and standard deviation values for each subsample size and the three different length intervals. Using visual assessment methodology (Vokoun et al. 2001, Gerritsen and McGrath 2007), we determined at what sample size the slope of the asymptotic MSD values began diminish. This was the point where increasing sample sizes led to diminishing returns in size structure precision (i.e., the slope of the curve began to level off).

For each subsample, we also compared the resulting length-frequency distribution to the original sample length-frequency distribution using a Kolmogorov-Smirnoff (K-S) test. This statistic is used to determine whether the distribution of a variable is different across groups, and is calculated as the largest absolute distance between the cumulative frequency distributions of the two samples (Zar 1996). We used K-S tests to evaluate differences in the length distributions between subsamples and the original sample. For each subsample size (from 10 to 700 fish), we calculated the percentage of the 1000 simulations that exceeded four pre-determined critical K-S distance values (i.e., 0.1, 0.15, 0.2, and 0.25). These critical distance values indicate the relative precision of the subsample compared to the original sample; in our analysis the K-S distance values of 0.1 was the most precise. From this process, we were able to estimate the relative precision of different sample sizes, and provide recommendations for future monitoring.

RESULTS

In 2011-13, we captured 7,583 larval Pacific lamprey (TL >60mm) across the 14 tributary subbasins we sampled. Mean total length for these fish was 89.1 mm (range: 60 – 156 mm). Locations where we captured > 200 individual Pacific lampreys included reaches on Thomas Creek (2 separate reaches in 2011, 2012 and 2013), Clear Creek (2012), Abiqua Creek, Crabtree Creek (2011), Willamina Creek, Butte Creek, the Luckiamute River, and the Calapooia River. However, for illustrative purposes we chose to present simulation results from three of these locations that showed contrast in length frequency distributions: Willamina Creek, the Calapooia River, and Thomas Creek (2013) (Figure 5-3). These three samples included a negative skewed sample, a relatively even distribution, and a positive skew, respectively. We also included all collected Pacific lampreys in aggregate for our final illustrative sample, which also showed a relatively even distribution (Figure 5-3).

Mortality estimation.—From the growth models with and without age zero data points, we estimated von Bertalanffy growth parameters of 171 mm and 214 mm for L_∞, 0.204 and 0.142 for K, and -0.36 and -0.19 for t_0, respectively (Figure 5-2). With these growth parameters, we successfully estimated mortality and survival metrics. Annual survival estimates ranged from 20-61% for different age classes with the Chen and Watanabe equation, and survival estimates tended to increase in older age classes. Survival estimates were 19-26% for entire larval life history phase (Jensen equation). For both equations, survival estimates varied between datasets with and without age-0 fish included (Table 5-1).

Sample size estimation.—From our resampling procedure, we observed an asymptotic decrease in MSD values with increasing sample size, regardless of the width of length intervals (Figure 5-2). However, larger length intervals generally had lower MSD values for a give sample size. Across all four locations, the largest gains in precision (i.e., MSD values declined with increasing sample size) occurred in sample sizes < 100. By visual inspection it appeared that the MSD slopes approached an asymptotic slope at sample sizes between 150-300 individuals. Samples sizes greater than 300 individuals had very similar MSD values, indicating very little increase in precision for these sample sizes.

Similarly, the probability of exceeding critical K-S distance values decreased with sample size for all critical distance values, and the patterns were consistent across all four sample locations (Table 5-1). For a given sample size, the probability of exceeding critical distance values was inversely related to the desired level of precision. There was a clear tradeoff between sample size and precision (i.e., critical distance); at relatively low precision (K-S distance value

0.25), only 100 samples were required for the probability to exceed the distance value in >50% of samples. At our most precise distance value (0.10), even with 500 samples the probability of exceeding the critical distance value was always <50%.

DISCUSSION

We used length frequency information from the Willamette River Basin, OR to estimate annual mortality and assess sample size requirements for the larval life history stage of Pacific lamprey. We combined length frequency data collected in the field with existing larval lamprey age data and estimated annual mortality for the entire larval life history phase (19-26% annual mortality) and for different age-classes within the larval phase (20-61% annual mortality depending on age class). With our statistical resampling we observed similar patterns between the MSD and K-S tests, suggesting that samples sizes of 100-200 individuals provided a representative length frequency distribution of larval Pacific lamprey populations. This information will be directly applicable to addressing the ongoing decline of Pacific lamprey across its range. In particular, efforts to construct life history models for the species and the development of monitoring plans for larval lampreys would be greatly aided by these findings.

The life history traits of Pacific lamprey have traditionally precluded an adequate assessment of its dynamic rate functions. In addition to not having reliable aging structures (Meeuwig and Bayer 2005), the inability to accurately identify Pacific lamprey until individuals have reached 60 mm (Goodman et al. 2009) and the morphological changes that occur as larvae undergo transformation (individual fish shrink in length; Youson 2003) into macrophthalmia has hindered these quantitative assessments. Statolith aging in macrophthalmia may be especially problematic as well (Barker et al. 1997). In the absence of these aging structures other researchers have used length frequency analyses to identify individual age classes from populations of larval lamprey (e.g., Kan 1975, Beamish and Medland 1988), but this technique has been questioned by recent genetic findings (J. Hess, CRITFC, unpublished data). We treated age as a random effect rather than a known quantity based on work by Cope and Punt (2007). Our approach provides a tool for the analysis of lamprey population dynamics and has considerable utility in other fisheries assessments. The approach did require several assumptions to be met, which suggests that these estimates should be applied cautiously. However, our approach does present a first attempt at completing an analysis of this type, and highlights research needs to improve upon these estimates in future work.

Our mortality estimates for Pacific lamprey (generally <30%) were very low relative to most other fish populations, especially for larval stages. During the larval life history phase, mortality routinely ranges over 80% and mortality events correlate with environmental factors (e.g., Farris 1960, Platt et al. 2003, Markle and Dunsmoor 2007). Our estimates roughly agree with those in Howe et al. (2012), who used a life cycle model to evaluate management actions to control sea lamprey, and included 5-19% mortality estimates for the larval age classes. Potter (1980) speculated that mortality in the larval phase for lampreys is low because their burrowing habitats do not expose them to high threats of predation. The possible exception is found in Hardisty (1961), who suggested that eel *Anguilla anguilla* were important predators to larval lampreys and estimated annual mortality of European sea lamprey to be ~40%. In contrast, our estimates for Pacific lamprey suggest that survival through the larval phase is likely one of the highest in its entire life cycle. Similar analyses from other locations throughout the range of Pacific lamprey would be beneficial to assess variability across its range and be incorporated into more refined life history models. In particular, length-based mortality estimates in areas with existing larval aging information (e.g., Middle Fork John Day) would be valuable to test some of the assumptions that we made to complete our analyses.

The resampling of our large larval Pacific lamprey dataset from across multiple locations throughout the Willamette River Basin provided strong quantitative information for the development of monitoring plans for the species. Our analyses suggested that 100-200 individuals would maximize fieldwork efficiency and adequately describe length frequency metrics for Pacific lamprey. However, if researchers are unable to obtain these sample sizes, our results provide estimates of the precision of a given sample size and the relative difference in precision from different sample sizes. For example, a sample size of 50 individuals is roughly 30% less precise than a sample size of 100 individuals. Generally, smaller length intervals require higher sample sizes to be precise in the analysis of length frequency distributions (Miranda 2007). In contrast, our analyses indicated that the precision of length frequency metrics derived from different length intervals was relatively similar. To determine the appropriate length interval for length frequency analyses, Anderson and Neumann (1996) recommended 10 mm length intervals for fish that reach 300 mm TL. Based on these suggestions and our findings (our largest observed individual was 156 mm), we recommend 5 mm length intervals for length frequency analyses of larval Pacific lamprey.

When compared to other species, sample size requirements of larval Pacific lamprey (~100-200) are generally much smaller. Although Anderson and Neumann (1996) suggested including at least 100 individuals to perform length frequency analyses, Gerritsen and McGrath (2007) recommended using 10 times the number of length intervals because precision deteriorates rapidly at smaller sample sizes. Miranda (2007) found that samples size of 225-1200 for largemouth bass *Micropterus salmoides*, 200-650 for white crappie *Pomoxis annularis*, and 150-425 for bluegill *Lepomis macrochirus* were necessary to describe length frequency of populations, and Vokoun et al. (2001) recommended sample sizes of 300-400 individuals for bluegill and channel catfish *Ictalurus punctatus*. In other lamprey studies, optimal habitats were sampled until 100 individuals were captured to assess Great Lakes sea lamprey (Slade et al. 2003). Our data suggest that this approach is probably appropriate, however different size classes are known to utilize different habitats (e.g., Young et al. 1990, Almeida and Qunitella 2002, Sugiyama and Goto 2002), which may influence the interpretation of length frequency analyses. Clearly a consideration of the goals and objectives of a monitoring program are necessary to best develop a sampling system (Moser et al. 2007). In the application of this work, river systems that tend to contain larger larval Pacific lampreys (e.g. Columbia River tributaries upstream of Bonneville Dam; R. Lampman, personal communication) should have similar quantitative assessments to refine monitoring programs.

We have provided information that will aid in evaluating and prioritizing conservation actions for Pacific lamprey, but actions to address its ongoing decline must be directed at multiple life history phases. To our knowledge, the mortality estimates presented herein are the first attempt to do so for larval Pacific lamprey, and can be used immediately to model the life cycle of the species. These models will help understand how each of the life history phases (e.g., freshwater rearing, outmigration, ocean parasitic phase) interact to regulate adult abundance of Pacific lamprey (*sensu* Howe et al. 2012). With sensitivity analyses, models may also be used to prioritize where research efforts should be directed to address critical uncertainties in different life history stages (e.g., Cortez 2002). Furthermore, evaluating the response of Pacific lamprey management actions with monitoring plans will be critical to refining life history models and restoring populations throughout the Pacific Northwest.

Table 5-1. Age-class-specific and cumulative instantaneous mortality and annual survival estimates from the Chen and Wantanabe and Jensen models with (left) and without (right) age-0 fish included for larval Pacific lamprey populations in wadeable tributaries to the Willamette River, 2011-13. Note: estimates from the Jensen equation are constant throughout the larval life history.

	Natural Mortality (M)				Annual Survival			
	Chen/Watanabe		Jensen		Chen/Watanabe		Jensen	
Age	Age-0	w/o age-0	Age-0	w/o age-0	Age-0	w/o age-0	Age-0	w/o age-0
1	0.95	0.81	0.31	0.21	0.39	0.45	0.74	0.81
2	0.57	0.50			0.57	0.61		
3	0.43	0.37			0.35	0.69		
4	0.36	0.31			0.70	0.74		
5	0.31	0.27			0.73	0.77		
6	0.28	0.24			0.75	0.79		
7	0.27	0.22			0.77	0.80		

Table 5-2. Probability of exceeding critical Kolmolgorov-Smirnov statistics values (K-S value) by sample size from four different samples of larval Pacific lamprey in wadeable tributaries to the Willamette River, OR. These results are obtained from 1000 resampling simulations of field data collected at these locations. The table can also be used to infer precision of a given sample size.

	Sample size							
K-S value	20	50	100	150	200	300	400	500
Willamina Creek (n = 201)								
0.10	1.00	1.00	1.00	0.97	0.95	0.85	0.66	0.58
0.15	1.00	1.00	0.93	0.81	0.64	0.39	0.23	0.16
0.20	1.00	0.94	0.69	0.51	0.29	0.12	0.05	0.02
0.25	1.00	0.81	0.44	0.26	0.12	0.03	0.01	0.00
Calapooia River (n = 365)								
0.10	1.00	1.00	1.00	0.98	0.95	0.81	0.68	0.55
0.15	1.00	1.00	0.91	0.75	0.63	0.39	0.23	0.15
0.20	1.00	0.94	0.67	0.41	0.30	0.11	0.05	0.02
0.25	1.00	0.80	0.42	0.21	0.11	0.03	0.01	0.00
Thomas Creek (n = 685)								
0.10	1.00	1.00	1.00	0.98	0.95	0.81	0.70	0.54
0.15	1.00	1.00	0.91	0.75	0.62	0.37	0.25	0.14
0.20	1.00	0.93	0.67	0.42	0.28	0.11	0.06	0.03
0.25	1.00	0.80	0.43	0.20	0.10	0.02	0.01	0.00
All sample locations combined (n = 7,583)								
0.10	1.00	1.00	1.00	0.99	0.97	0.82	0.72	0.58
0.15	1.00	1.00	0.94	0.81	0.63	0.39	0.27	0.16
0.20	1.00	0.94	0.73	0.49	0.29	0.12	0.06	0.02
0.25	1.00	0.80	0.46	0.25	0.10	0.02	0.01	0.00

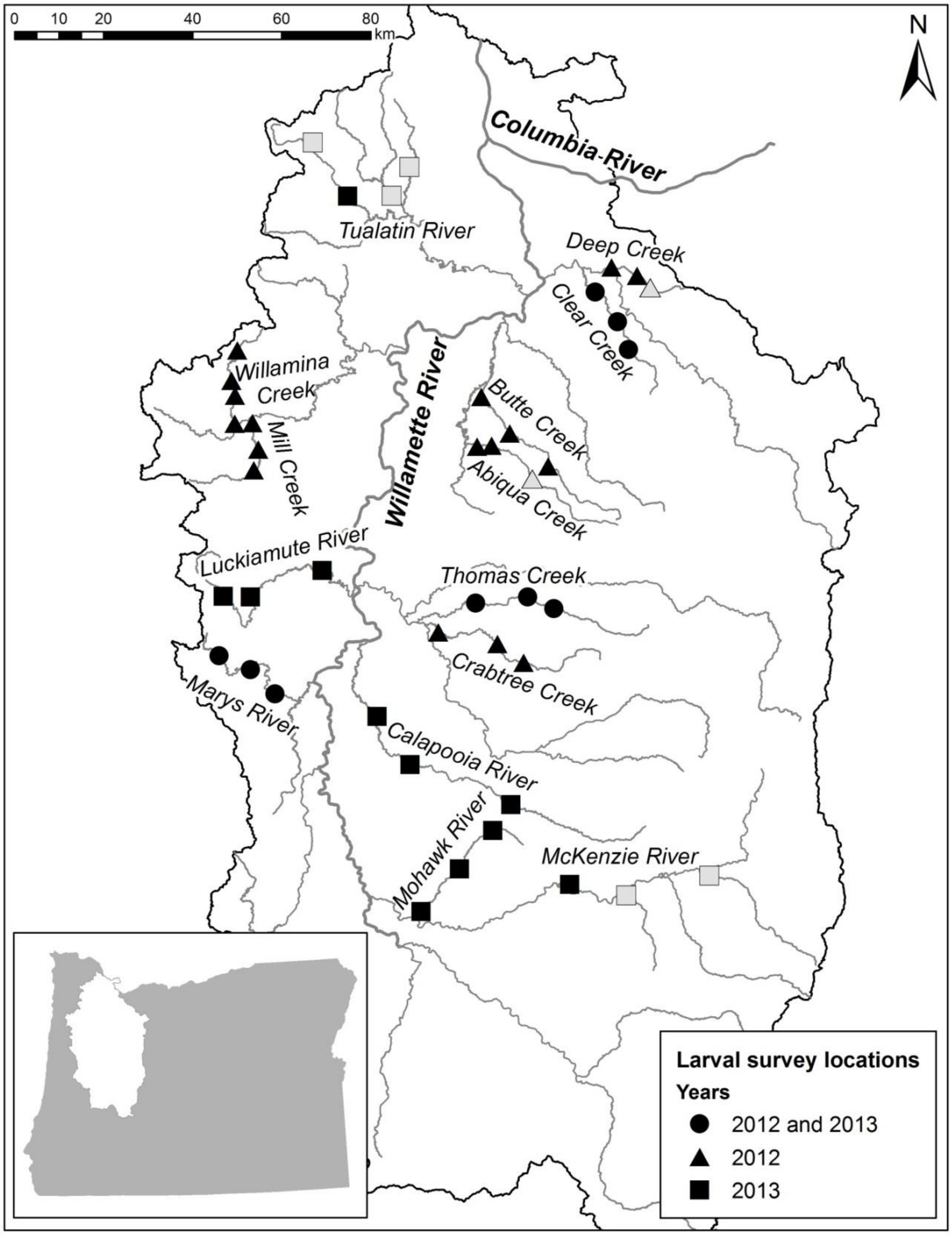

Figure 5-1.— Locations of larval Pacific lamprey sampling in the Willamette River basin, 2012-13. Pacific lamprey were collected from locations at black symbols, but not from grey symbols.

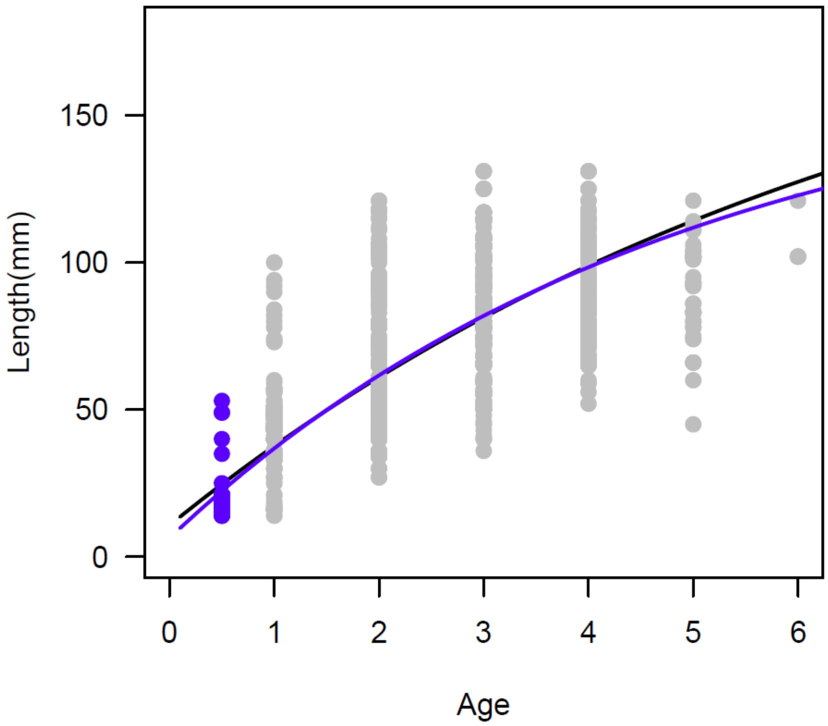

Figure 5-2.— von Bertalanffy model fits for datasets that include (solid purple) and exclude age-0 individuals (solid black line). Model fits are based on published age distribution dataset for larval lampreys collected from the Middle Fork John Day River and South Fork Walla Walla River (Meeuwig and Bayer 2005).

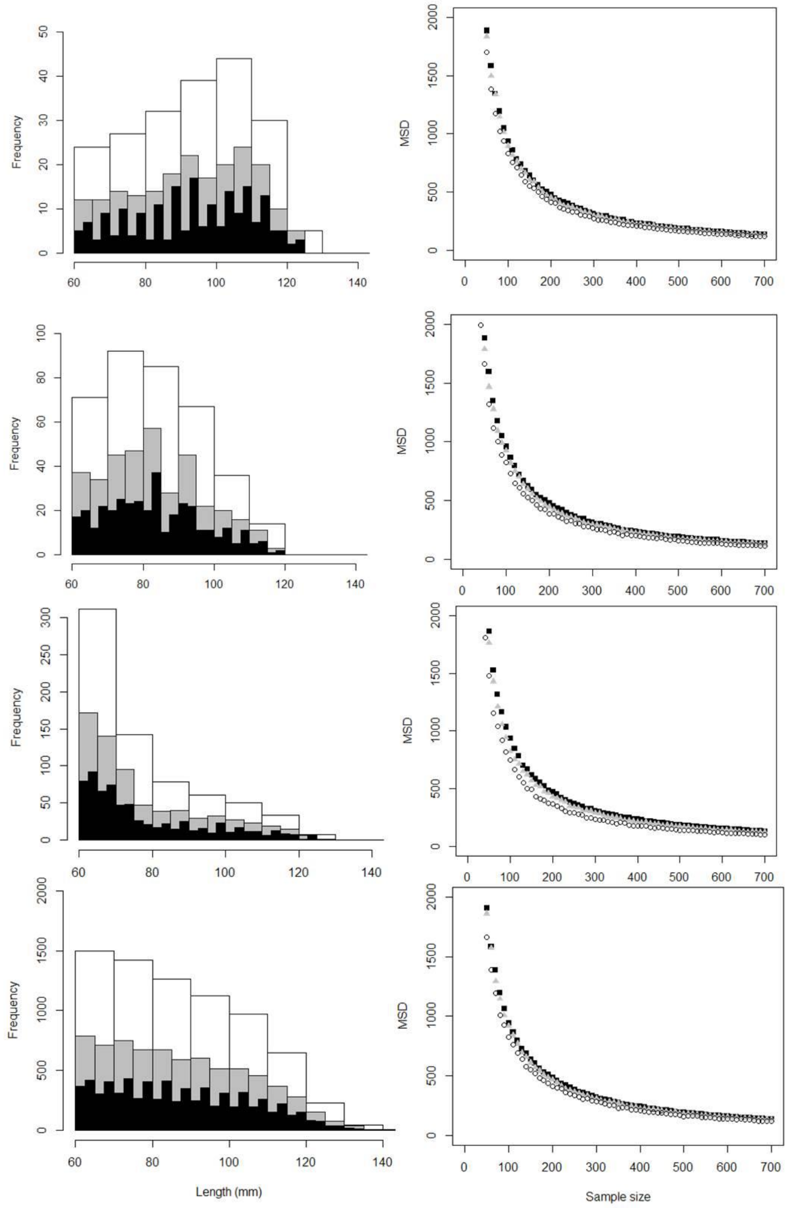

Figure 5-3.— Observed larval Pacific lamprey length frequency distributions (left) and mean square difference (MSD) between sub-samples and original samples of various subsample sizes (right). In all panels the color of points and bars indicates the length interval of the data: white – 10 mm, gray – 5 mm, and black – 2.5 mm. From top to bottom, the four locations include reaches on Willamina Creek, the Calapooia River, Thomas Creek (2013), and all sample locations combined. Sub-samples were obtained from 1000 resampling simulations of field data collected at these locations. Note: y-axis values vary in the length frequency distributions.

Chapter 6.

Summary, conclusions, and management implications

Our work expands the understanding of the freshwater life history phases of Pacific lamprey. Our data from our spawning surveys suggest that Pacific lamprey is a habitat generalist that has spawning habitat requirements relatively similar to salmonids. Upon entry into the Willamette River, we found that fish appeared to select tributaries with higher proportions of alluvial geology. However, within the individual tributaries, we found that redds were distributed in similar numbers regardless of underlying geology. We also used data from our spawning surveys to address survey length requirements in future monitoring efforts. Underlying geology again had a substantial and inverse effect on the survey length needed to detect and estimate abundance of redd density. In all simulations, less than 1.2 km was needed to detect the presence of Pacific lamprey redds, but the survey length required to estimate redd density varied between 3.2 km and 13.7 km.

We have demonstrated the utility of spawning surveys for monitoring Pacific lamprey. When initiating a monitoring program for the spawning phase of Pacific lamprey, there are several factors that should be considered in their development. The first is the historic/current presence of Pacific lamprey within the stream network of interest. This may be difficult to establish, but our work, traditional ecological knowledge, or anecdotal accounts might help establish this information. A second consideration is the availability of suitable spawning habitat. Our work indicates that Pacific lamprey are generally habitat generalists and can probably find suitable spawning habitat in most streams, however the underlying geology will likely affect the distribution of spawning habitats, and influence survey distance (Chapter 2, 3). Finally, the phenology of spawning activity for Pacific lamprey seemed to be predicable. Spawning appeared to be initiated when water temperatures were 10-15°C, which corresponds to about the end of the steelhead spawning season. Spawning in the Willamette River Basin seemed to remain relatively active until about the beginning of summer baseflow conditions in the streams we surveyed. However, spawning may extend into July in some basins (e.g., Brumo et al 2009). Based on redd longevity (Stone 2006), Pacific lamprey spawning activity should remain detectable for a month or longer. Considering these topics should provide a good framework for designing a monitoring plan.

Our larval lamprey sampling also advances the ecological understanding of this life history stage. In the Willamette River Basin adult migration barriers were the major factor related to the distribution of larvae, but stream channel disturbances are likely limiting larval lamprey habitat. We also found that Pacific and brook lampreys were associated with one another indicating that the conservation efforts should be mutually beneficial to both species. We used length frequency information to estimate mortality during the larval life history phase and found that morality was fairly low (i.e., <30%), especially for a larval fish population. This innovative approach is applicable to other lamprey populations and can be applied to fishes with similar life histories. Finally, we used length data from individual fish we collected in field sampling to evaluate sample size requirements for characterizing larval Pacific lamprey length distributions. We suggest that collecting 150-300 individuals will most efficiently describe size structure of lamprey populations. Furthermore, our analyses provide a course measure of the relative precision of a given sample size.

These data have addressed several knowledge gaps for the conservation of Pacific lamprey in the Willamette River Basin and across its range. Because much of the life cycle of Pacific lamprey occurs in freshwater (larval, freshwater holding, spawning) habitat conditions in these environments have the strong potential to greatly influence population dynamics for the species. Our work suggests conservation strategies that will address freshwater limiting factors including increasing connectivity across river networks, and an assessment of anthropogenic physical and chemical barriers that currently impede passage of adult Pacific lamprey. Stream restoration actions that increase channel complexity (side channels, backwaters, etc.) will provide abundance larval rearing locations, but also increase spawning habitats availability. Furthermore, these habitat manipulations will be mutually beneficial to other species that are currently of high conservation interest (e.g., salmonids), and other native aquatic and riparian fauna. We have also provided recommendations for monitoring both the spawning and larval life history phases of Pacific lamprey using a statistically robust framework. Implementing both management efforts to restore degraded stream habitats and monitoring to evaluate responses of Pacific lamprey to these manipulations will greatly advance the goal of Pacific lamprey recovery.

During the course of our work, we have identified several areas where research could be conducted to answer management-relevant questions and aid the conservation of Pacific lamprey within the Willamette River Basin and across its range.

Research Needs

1) Currently, spawning ground surveys for Pacific lamprey are valuable for providing information on the distribution of migrating adults and potentially providing indices of adult return abundance. However, for spawning grounds surveys to be implemented to effectively estimate adult abundance, several metrics need to be investigated. In particular, the number of redds constructed per adult and covariates (e.g., reach scale habitat variables) that influence this metric are of interest to translate redd count data to abundance estimates. Additionally, evaluating the number of adults that spawn in individual redds and the viability of these redds will aid in the interpretation of redd count data, elucidate ecological insights of the species and help inform translocation programs for Pacific lamprey.
2) Our work illustrates that the distribution of Pacific lamprey in the Willamette River Basin was strongly related to physical and possibly chemical (e.g., Tualatin River subbasin) migration barriers. However, these barriers were inferred from observed distribution data; we did not conduct a formal barrier assessment. Recent work has proposed approaches to assessing these barriers (e.g, Stillwater Sciences 2014), but continued work is needed to better understand characteristics that influence adult passage at anthropogenic and natural stream obstacles. These assessments will help delineate the historic distribution of Pacific lamprey and allow managers to evaluate and prioritize restoration actions at anthropogenic migration barriers.
3) This work has advanced the understanding of the larval life history of Pacific lamprey. Previous work from our group (e.g., Clemens et al. 2012b) and related work from the Columbia River (e.g., Moser et al. 2002a, Keefer et al. 2009, 2010) and coastal river basins (e.g., Lampman 2011, Starcevich et al. 2013) has described habitat use and migration characteristics of returning adult Pacific lamprey. However, the outmigrant and marine life history phases are relatively poorly understood. In particular, outmigrating Pacific lamprey are thought to experience relatively high

predation risk due to introduced predators (smallmouth bass *Micropterus dolomieui* and walleye *Sander vitreus*, Zimmerman 1999, Close et al. 2002, Fritts and Pearson 2004). Ongoing work in the Umpqua River Basin, OR indicates that smallmouth bass may consume substantial amounts of larval and metamorphosed lamprey (J. Dunham personal communication). Further assessments of this nature are needed to quantify survival/mortality during this phase and evaluate management actions to address limiting factors.

4) Within the context of the life cycle of Pacific lamprey, survival/mortality patterns from each life history phase can be incorporated into models to predict population responses to various management actions (e.g., Howe et al. 2012). These models may also be used to evaluate the sensitivity of survival estimates from each of these life history phases to direct research efforts. Although current research has documented a relationship between Pacific lamprey returns at Bonneville Dam and common marine hosts (Murauskas et al. 2013), additional research on the ecology of Pacific lamprey in estuarine and marine environments will address knowledge gaps during these portions of the life cycle.
5) Our work and a great deal of literature focused on salmonids (e.g., Naiman and Latterel 2005) have identified several freshwater limiting factors for the recovery of anadromous fish populations related to habitat degradation as a result of historic and current land use practices. Our work suggests that conservation actions that increase connectivity and complexity of river networks will be beneficial to addressing these limiting factors for larval Pacific lamprey. In addition to management actions that remedy habitat perturbations, a thorough evaluation of the physical and biological effects of habitat restoration activities are needed, across multiple spatial and temporal scales (*sensu* Roni 2003). These assessments can be incorporated into an adaptive management framework to optimize efficiency of restoration actions.

LITERATURE CITED

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Appendix 1 – Summary of stream habitat characteristics and Pacific and total lamprey catches for reaches sampled in the Willamette River Basin, 2012-2013.

Stream	Year	Reach	Mean width (m)	Mean sediment depth (cm)	Total sediment volume (m^3)	% fines	Pacific lamprey (fish/m2)	Total lamprey (fish/m2)
Abiqua	2012	Lower	11.84	4.45	98.23	0.17	0.102	0.122
		Middle	15.94	3.06	108.35	0.15	0.016	0.030
		Upper*	11.72	1.70	33.83	0.07	--	0.007
Butte	2012	Lower	6.93	29.46	138.08	0.96	0.634	0.892
		Middle	12.27	1.30	23.48	0.08	0.020	0.045
		Upper	12.28	2.39	39.57	0.13	0.001	0.001
Calapooia	2013	Lower	13.99	9.21	98.88	0.18	0.402	0.607
		Middle	15.65	4.38	79.17	0.09	0.020	0.054
		Upper	16.12	1.31	20.37	0.11	0.003	0.038
Clear	2012	Lower	15.07	2.24	55.37	0.14	0.118	0.159
		Middle	11.96	2.24	35.12	0.10	0.043	0.051
		Upper	12.53	1.95	41.29	0.12	0.026	0.035
Clear	2013	Lower	15.58	2.51	46.76	0.20	0.068	0.149
		Middle	11.44	2.66	35.21	0.11	0.064	0.095
		Upper	12.22	2.94	43.64	0.13	0.119	0.152
Crabtree	2012	Lower	24.95	7.56	313.61	0.33	0.042	0.057
		Middle	17.30	2.78	72.14	0.14	0.022	0.027
		Upper	19.92	0.57	10.64	0.02	0.002	0.006
Deep	2012	Lower	9.36	2.97	47.78	0.06	0.091	0.131
		Middle	5.64	1.77	8.52	0.12	0.006	0.053
		Upper	3.69	1.00	2.91	0.02	--	0.014
Luckiamute	2013	Lower	14.95	28.09	377.04	0.74	0.181	0.215
		Middle	17.98	2.02	38.66	0.14	0.024	0.031
		Upper*	15.43	4.17	58.79	0.26	0.069	0.100
Marys	2012	Lower	9.86	8.19	112.12	0.21	0.100	0.121
		Middle	17.21	2.29	63.26	0.22	0.044	0.054
		Upper	8.94	14.06	74.04	0.31	0.078	0.176
Marys	2013	Lower	10.87	6.28	99.13	0.88	0.084	0.110
		Middle	17.19	2.25	59.29	0.15	0.030	0.048

		Upper	9.31	20.85	156.09	0.88	0.041	0.084
Mill	2012	Lower	11.95	3.04	41.72	0.09	0.037	0.050
		Middle	11.65	2.80	62.68	0.13	0.026	0.039
		Upper	10.57	2.88	57.28	0.07	0.044	0.054
McKenzie	2013	Gate*	11.77	2.23	21.92	0.09	0.011	0.032
		Quartz*	10.03	1.98	20.12	0.08	--	0.002
		Horse*	10.63	4.64	36.62	0.28	--	0.086
Mohawk	2013	Lower	15.12	5.10	78.68	0.23	0.087	0.096
		Middle	20.00	5.01	80.28	0.28	0.109	0.152
		Upper	9.24	1.00	7.07	0.08	0.032	0.063
Thomas	2012	Lower*	15.16	3.15	97.62	0.17	0.095	0.106
		Middle*	14.87	2.60	58.52	0.23	0.102	0.132
		Upper	14.60	1.87	42.96	0.02	0.009	0.010
Thomas	2013	Lower*	15.59	2.77	88.49	0.13	0.197	0.251
		Middle*	13.72	2.96	67.56	0.26	0.059	0.087
		Upper	13.38	1.36	28.53	0.04	0.014	0.020
Tualatin	2013	McKay	6.96	15.28	34.59	0.80	--	0.222
		Dairy	9.46	24.42	88.16	0.82	--	0.142
		Gales, lower	11.21	8.01	113.20	0.41	0.028	0.093
		Gales, upper	10.56	3.32	28.66	0.10	--	0.330
Willamina	2012	Lower	12.42	2.44	37.69	0.10	0.007	0.011
		Middle	13.13	3.47	61.56	0.17	0.073	0.096
		Upper	7.70	2.63	14.22	0.18	0.140	0.166
		Falls Upper	8.13	1.84	17.60	0.09	0.157	0.266

*Reaches with off-channel habitat units (included in this summary but removed for regression models).

Appendix 2 – ADMB code that fits observed length frequency data to a von Bertalanffy growth model for Pacific lamprey based on available larval brook and Pacific lamprey age information (Meeuwig and Bayer 2005). ADMB software is freely available at http://www.admb-project.org/.

```
GLOBALS_SECTION
         #include <admodel.h>
         #define PI 3.141592654
         #include <iostream>
          ofstream mcmc("mcmc.out");

        DATA_SECTION

         init_int read;       //Number of Individuals
         init_int n;              //number of lamprey
          init_int UseZeroes;

         init_int Linf_phase    //Phase estimation of Linf
         init_int k_phase    //Phase estimation of K
         init_int t0_phase    //Phase estimation of t0
         init_int CV_Lt_phase   //Phase for sigma estimation
         init_int ageCV_phase   //Phase for sigma estimation
         init_int re_phase   //Phase for random effects

         init_matrix ag_data(1,n,1,read);

         init_vector len_data(1,n);

          init_int readCheck;
          !!if(readCheck!=123456789) exit(1);

          //counters
         int i;
         int r;

        PARAMETER_SECTION

        //VBGF parameters
         init_bounded_number log_Linf(3.0,5.5,Linf_phase)       //Linf
         init_bounded_number log_k(-9,0,k_phase)               //k
         init_bounded_number t0(-4,0,t0_phase)              //t0
         init_bounded_number log_CV_L(-10,5,CV_Lt_phase)          //observation error in lengths
         init_bounded_number log_age_CV(-10,5,ageCV_phase)          //observation error in lengths

          vector L(1,n); //expected lengths
```

```
    number reLike;
    number Linf;
    number k;

  random_effects_vector ln_age_re(1,n,re_phase)    //Random effects age vector

  objective_function_value obj_fun;

 LOCAL_CALCS
     //Change zeroes to 0.5
     //So you can use the poisson
     //distribution

     if(UseZeroes)
     {
        for (i=1;i<=n;i++) //for each lamprey
           for(r=1;r<=read;r++)
           {
               if(ag_data(i,r)==0)
                   ag_data(i,r) = 0.5;
           }
       }
 END_CALCS

PRELIMINARY_CALCS_SECTION

  log_Linf = 4;
  log_k = -5;
  t0 = 0;
  log_CV_L = -1;

PROCEDURE_SECTION
    Linf = mfexp(log_Linf);
    k = mfexp(log_k);

  obj_fun =0;
    dvariable trueAge;
    int age;

    for (i=1;i<=n;i++) //for each lamprey
    {
        trueAge = mfexp(ln_age_re(i));
         L(i) = Linf * (1-mfexp(-k * (trueAge - t0)));

        //likelihood of the VB parameters
        obj_fun += log_CV_L + 0.5*square((log(L(i) / len_data(i)))/mfexp(log_CV_L));

        //likelihood of the age parameters
         for(r=1;r<=read;r++)
```

```
         {
            if(ag_data(i,r)>0)
            {
             obj_fun += -1. * (ag_data(i,r)* log(trueAge) - trueAge - gammln(ag_data(i,r)+1));
            }
        }
    }

    if(mceval_phase())
    {
       mcmc<<k<<"\t"<<Linf<<"\t"<<t0<<endl;
    }
TOP_OF_MAIN_SECTION
  arrmblsize = 50000000;
  gradient_structure::set_GRADSTACK_BUFFER_SIZE(1000000);
  gradient_structure::set_CMPDIF_BUFFER_SIZE(1000000);
  gradient_structure::set_MAX_NVAR_OFFSET(2394763);
  gradient_structure::set_NUM_DEPENDENT_VARIABLES(5000);

REPORT_SECTION
  report<<"$n"<<endl;
  report<<n<<endl;
  report<<"$read"<<endl;
  report<<read<<endl;
  report<<"$Linf"<<endl;
  report<<Linf<<endl;
  report<<"$K"<<endl;
  report<<k<<endl;
  report<<"$t0"<<endl;
  report<<t0<<endl;
  report<<"$len"<<endl;
  report<<len_data<<endl;
  report<<"$age"<<endl;
  report<<ag_data<<endl;
```

Appendix 3 – Additional and incidental findings and a summary of collaborative work with other projects.

We collected tissue samples of Pacific lamprey in our study for continuing genetic research to better understand population biology (see Hess et al. 2012). A total of 274 genetic samples were collected from Pacific lamprey in 2012 across our study area and sent to CRITFC for genetic processing and analysis to be incorporated into an existing database (Table A-1). Samples were collected from 25 to 36 individuals in each basin, and an additional 11 individuals from the mainstem Willamette River. In November 2013, we also collected an additional 33 samples from the Mohawk, Calapooia, and Luckiamute Rivers. Samples were taken from all size classes of Pacific lamprey (TL > 60 mm).

As part of a cooperative project with CRITFC and the United States Geological Survey (USGS) to assess organic contaminants, we collected sediment and Pacific lamprey tissue from nine locations in 2012. Collections were completed based on instructions from USGS protocols and shipped for processing. We collected sediment and tissue samples from 9 locations in 2012 (Table A-2). Six of the locations were in the lower reaches from our larval sampling, and three additional locations in the mainstem Willamette River. Reaches in the Willamette were located: upstream of Willamette Falls at the confluence of the Tualatin River, between Willamette Falls and the Clackamas River confluence, and downstream of the confluence with the Clackamas River.

In 2013, we completed fieldwork to assess Pacific lamprey abundance relative to microhabitat features throughout the Willamette River Basin. At these locations, we electrofished 1 m^2 quadrats and collected sediment samples to quantify sediment grain sizes and chemical characteristics of these microhabitat patches. Lamprey abundance was positively associated with medium grain sand, but there was no clear relationship between abundance and percentage organic matter. To describe the cultural value of Pacific lamprey in the context of conservation planning, we also conducted interviews of tribal elders from the Siletz, Umatilla, and Grande Ronde tribes. These interviews tried to assess cultural knowledge of lamprey fishing, their role in cultural practices and how these activities have changed with the decline of lamprey. These two components of the project are currently being completed and will be detailed in the forthcoming master's thesis of Gabe Sheoships.

Table A3-1. Tissue samples were collected from Pacific lamprey in the Willamette River Basin, Oregon 2012 and sent to Jon Hess (CRITFC, Hagerman, ID) for genetic processing and analyses.

Creek	# samples	Year
Abiqua Creek	26	2012
Butte Creek	26	2012
Calapooia River	33	2013
Clear Creek	25	2012
Crabtree Creek	34	2012
Deep Creek	25	2012
Luckiamute River	33	2013
Marys River	36	2012
Mill Creek	25	2012
Mohawk River	33	2013
Thomas Creek	30	2012
Willamette River	12	2012
Willamina Creek	35	2012

Table A3-2. Locations of sediment and lamprey tissue samples collected for contaminant analyses in the Willamette River Basin, 2012, and submitted to E. Nilsen (USGS) for processing.

Stream	Date
Mill Creek	August 30
Marys River	July 31
Crabtree Creek	August 2
Clear Creek	August 27
Abiqua Creek	August 21
Butte Creek	August 23
Willamette River - West Linn*	September 17
Willamette River - Clackamette Park	September 17
Willamette River - Mary S Young Park	September 17

*No lamprey were detected from the Willamette River site at West Linn