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Spawning Distribution and Habitat Use of Adult Pacific and Western Brook Lampreys in Smith River, Oregon

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Abstract.—Pacific lampreys *Entosphenus tridentatus* (formerly *Lampetra tridentata*) and western brook lampreys *L. richardsoni* are observed in many coastal Oregon basins; however, few data are available to adequately describe their distribution and spawning habitat associations. To document landscape-scale distribution and habitat use of spawning adult lampreys, we conducted biweekly redd surveys at 62 randomly selected sites in Smith River (Umpqua basin, Oregon). Characteristics of lamprey habitat were measured at the redd, habitat unit, and reach scales to quantify available and occupied habitat. Pacific lampreys were found primarily in wider, low-elevation streams, whereas western brook lampreys were more widespread but concentrated in headwater and low-order streams. At the unit scale, unit type and dominant substrate were weakly correlated to presence of spawning lampreys. Both species spawned in gravel rich habitats, predominantly pool tail-outs and low gradient riffles. This study infers habitat associations and broad-scale distribution within a coastal basin to assist in the design of monitoring strategies and population assessments at a regional scale.

Introduction

Coastal Oregon populations of Pacific lamprey *Entosphenus tridentatus* (formerly *Lampetra tridentata*) and western brook lamprey *L. richardsoni* are considered depressed due to habitat loss and passage problems (Close et al. 2002; Nawa 2003; ODFW 2006). The Pacific lamprey was listed as an Oregon State sensitive species in 1993 and in 1996 was protected through restriction of harvest (ODFW 2006). The western brook lamprey is not protected and has no special state status. Abundance of Pacific lampreys throughout the coast and Columbia River has declined dramatically since the1960s. Dam counts at Winchester (Umpqua River), Bonneville (Columbia River), and Leaburg (McKenzie River) dams show a dramatic decrease from historical levels (Kostow 2002; Nawa 2003; ODFW 2006). In 2003, 11 environmental groups petitioned the U.S. Fish and Wildlife Service to list Pacific, western brook, and two other lamprey species as endangered in the Pacific Northwest and California (Nawa 2003). Even though the petition cited habitat losses due to reduced instream flows, water diversions, dredging, scour and channnelization issues, pollution, and degradation of riparian communities, the U.S. Fish and Wildlife Service determined that the petition did not contain adequate information to warrant a listing (USFWS 2004). The Oregon Department of Fish and Wildlife recently reviewed the status of western brook and Pacific lampreys and found populations to be "at risk" of extinction (ODFW 2006) due to habitat loss, passage barriers and pollution. However, data necessary to conduct a more thorough and detailed assessment are lacking.

Many of the lacking data are critical to the effective management and conservation of Oregon's coastal lamprey species. The Columbia River Basin Lamprey Technical Workgroup

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(CRBLTW 2005) and members of Columbia River Inter-Tribal Fish Commission (CRITFC 2004) have identified and prioritized critical data gaps for Pacific lamprey, many of which also apply to western brook lamprey. Among these are (1) methods to assess distribution and abundance of all life stages and appropriate techniques for monitoring population status; (2) population structure and delineation; (3) population dynamics; (4) basic biology, including interspecific and community level relationships; (5) limiting factors and threats, including passage issues, and (6) habitat needs and requirements.

In coastal basins, data describing distribution and abundance of lampreys are rare despite extensive and rigorous sampling since 1998 under the Oregon Plan for Salmon and Watersheds. Survey methods employed to determine status and trends in salmonid populations have not proved applicable for lampreys. Surveyors collecting information on adult steelhead *Oncorhynchus mykiss* during February through May observe adult Pacific and western brook lamprey individuals and redds, but the observations tend to be incidental rather than quantitative. Juvenile western brook and Pacific lampreys are not observed by snorkelers or collected by traditional electrofishing technology used for salmonids. Although out-migrating juvenile lampreys are collected in salmonid migrant traps operated by the Oregon Department of Fish and Wildlife, trap efficiency for lampreys is unknown (D. Jepsen, Oregon Department of Fish and Wildlife, personal communication). Furthermore, these traps are not placed in randomly selected watersheds such that findings at trap sites cannot be extrapolated to other drainages. Habitat surveys conducted under the Oregon plan may be applicable, but habitat specific models are not available. Finally, with the exception of Winchester Dam on the North Umpqua River, counts of adult lampreys that pass dams are largely unavailable because dams in Oregon coastal basins are positioned in the upper portions of drainages. Existing sampling indicates that lampreys are present in coastal basins, but monitoring strategies need to be modified in order to determine an appropriate sample frame and collect data in a quantitative fashion.

Our goal was to identify habitat variables associated with spawning Pacific and western brook lampreys in order to infer distribution throughout coastal Oregon. The objectives of this study were to (1) determine distribution of spawning Pacific and western brook lampreys in the Smith River basin, (2) describe redds of both species, and (3) describe associations of spawning adults in relation to habitat unit- and reach-scale habitat characteristics.

Methods

Study area

This study was conducted in the Smith River, a tributary of the Umpqua River (Figure 1). The study area consists of 463 km of main-stem and tributary streams upstream of Smith River Falls (river kilometer 48). The basin area above Smith River Falls is approximately 525 km^2. The riparian community is dominated by red alder *Alnus rubra* with an understory of sword fern *Polystichum munitum*, salal *Gaultheria shallon*, and vine maple *Acer circinatum*. Smith River above the falls is inhabited by Pacific and western brook lampreys, coho salmon *O. kisutch*, Chinook salmon *O. tshawytscha*, steelhead, coastal cutthroat trout *O. clarkii*, large-scale sucker *Catostomus macrocheilus*, redside shiner *Richardsonius balteatus*, longnose dace *Rhinichthys cataractae*, and Umpqua pikeminnow *Ptychocheilus umpquae*. Land is owned predominately by the U.S. Bureau of Land Management and private forest companies and managed for timber harvest.

Sample site selection

In each of 2004 and 2005, 50 sample sites of 1,000 m were selected from a frame representing the rearing distribution of coho salmon and steelhead above Smith River Falls. Given the lack of available information regarding Pacific and western brook lamprey distributions, the

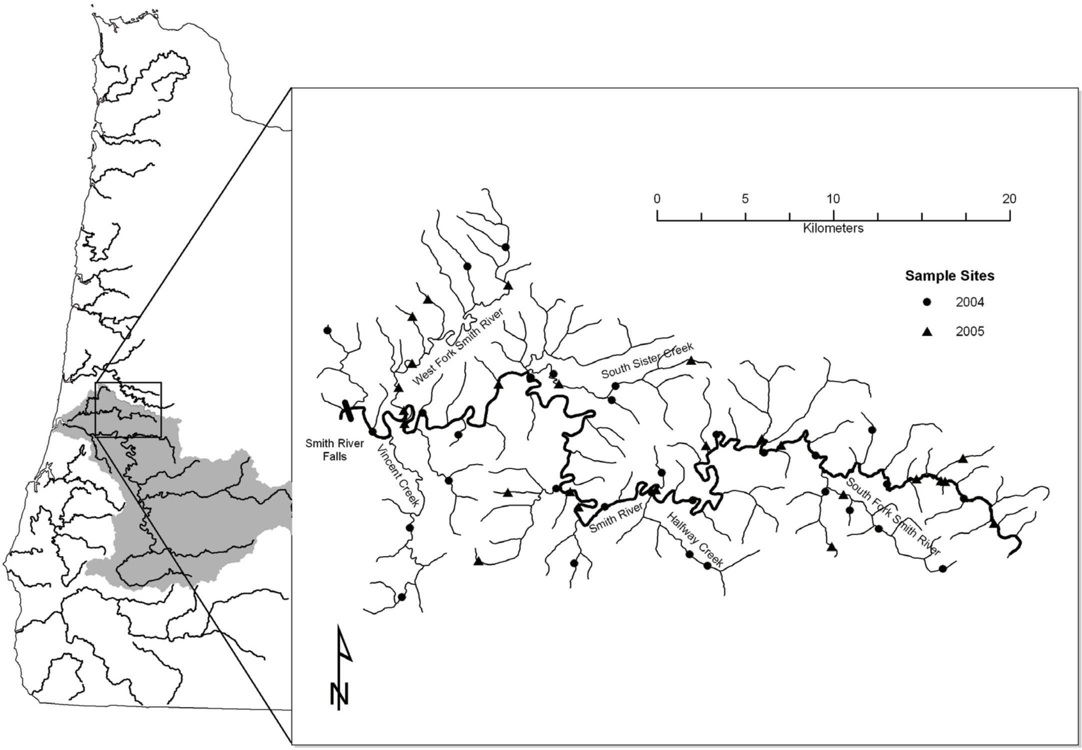

Figure 1. Smith River study area in Oregon and the Umpqua River basin.

salmon and steelhead rearing sample frame offered the best starting point to describe potential lamprey distribution in the basin. Sites were chosen in priority order using the variable probability. Stevens and Olsen (2004) generalized random tessellation stratified algorithm and were randomly selected and spatially balanced ensuring an unbiased and representative sample. Site locations were unique each year.

Geographic coordinates of each site were plotted on U.S. Geological Survey 1:24K topographic maps and uploaded into a handheld Global Positioning System (GPS) unit. Field crews located the precise position of each site, using a map, compass, and the GPS unit. The coordinates represented the downstream end of the sample site, which extended upstream a channel distance of 1,000 m.

We surveyed 31 sites in 2004 and in 2005. Of the original sample draw of 50 sites in 2004, 2 were dry, 2 were not surveyable, and 3 were surveyed by crews targeting steelhead trout where lamprey data were not consistently collected; 1 site was not surveyable in 2005. Field crews were unable to incorporate the remaining sites (12 in 2004 and 18 in 2005) into the biweekly survey rotation. These sites were low priority and eliminating them did not disrupt the spatial balance of the remaining 31 sample sites.

Spawning surveys

All sites were surveyed biweekly from between March 29 and June 24, 2004, and March 28 and June 30, 2005. Newly observed lamprey redds were measured, recorded, and flagged. For each redd, crews noted species; measured length, width, depth of the redd, depth of the water, water velocity, and distance to the nearest cover; and conducted a pebble count. Cover was defined as any structure under which an adult lamprey could hide. Velocity was measured at the midpoint of the lengthwise axis, on the thalweg side of the redd (Figure 2). Calipers were used to measure the maximum diameter of 15 neighboring (touching) pebbles along both a lateral and vertical transect originating at the top-thalwag corner of the redd (Figure 2) to represent pre-excavation substrate.

Habitat surveys

Habitat surveys were conducted at the end of the season after most spawning activity had ceased. Stream habitat was quantified according to methods described by Moore et al. (2007), with some modifications. The modifications included (1) omission of riparian surveys, (2) measurement of length and width for all habitat units, and (3) the addition of "pool tailout" as a unit separate from other pool units. A total of 54 reach-scale and 38 habitat-unit-scale variables were summarized for each site. In general, descriptions were recorded for channel dimensions, streambed composition, geomorphic reach characteristics, riparian cover, and shade. In order to associate each redd with habitat and reach-scale data, redds were noted within the habitat units in which they occurred.

Spawning survey analysis

Basic descriptive statistics were used to describe spawn timing, redd characteristics (median, minimum, maximum, and standard deviation), and abundance of redds at each site. Redd density at each site was calculated as the number of redds divided by channel area (redds/m^2). Distribution was inferred from maps of redd density at each site generated in a geographic information system. Redd counts at each site were extrapolated to provide estimates of total redd abundance, and associated measures of precision were calculated using a local-neighborhood variance estimator (Stevens 2002; Stevens and Olsen 2003).

Habitat association analysis

The reach-scale habitat data set was reduced by removing highly correlated variables as determined by correlation analysis. Of two or more highly correlated variables, we retained the variable with the more accurate or precise measurement. Appendix A.1 lists all variables included in the analysis at each scale. We evaluated similarity of reach-scale habitat characteristics between all sites. Similarity was calculated using a relative Sorenson's distance measure, and non-

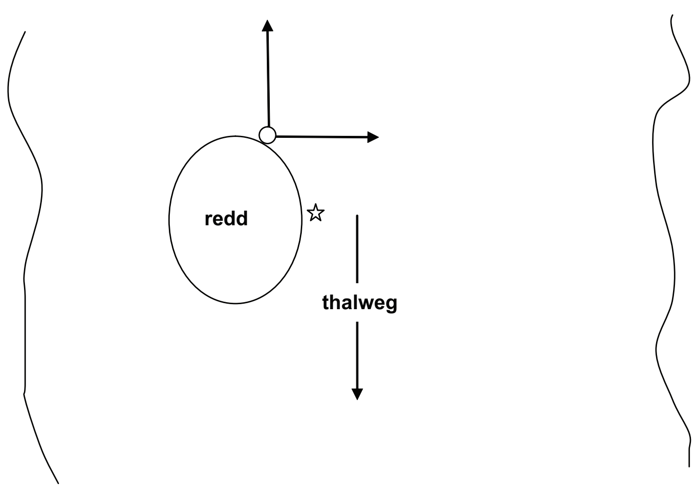

Figure 2. Location of water velocity measurement (☆) and origin of pebble counts (O) in relation to the lamprey redd and thalweg.

metric multidimensional scaling (NMS) ordinations were generated in PC-ORD software (Kruskal 1964; McCune and Mefford 1999). Three hundred iterations were used for each run to evaluate stability, and each analysis was conducted 10 times to ensure the lowest possible stress. The response variables, presence of lamprey redds and redd density, were overlaid on the ordination, and the ordinations were orthogonally rotated to load the maximum variation in lamprey presence on the first axis. Correlation coefficients of habitat variables to axis 1 were used to identify factors related to the presence and density of lamprey redds. Analyses of associations at the habitat unit scale were conducted in the same manner, except only those habitat units consisting of sites where lampreys were detected were included in the analysis.

Results

Abundance

In 2004, field crews counted a total of 313 western brook lamprey redds between April 6 and June 7, with the maximum observed within a 2-week period occurring during the May 19 and June 1 survey cycle (Figure 3). In 2005, western brook lamprey spawning activity commenced 1 week later than in 2004. A total of 249 western brook lamprey redds were detected between April 25 and June 16. The maximum number of redds was counted during the May 24–June 6 survey cycle.

A total of 60 Pacific lamprey redds were counted between April 5 and May 5, 2004, with the peak count occurring during the April 7 and April 20 survey cycle (Figure 3). In 2005, Pacific lamprey redds were first detected 1 week later than in 2004; 69 Pacific lamprey redds were counted between April 14 and June 6. Two peak counts were noted in 2005. The first peak occurred between April 26 and May 9 and the second between May 24 and June 6. The later onset of Pacific lamprey spawning activity in 2005 was similar to that observed on the South Fork Coquille River (Brumo and Markle 2006) and may be related to higher stream flows and cooler water temperatures that spring.

We estimated a total of 4,692 (±76%, 95% confidence interval [CI]) western brook lamprey redds (11.25 redds/km) in 2004 and 4,265 (±91%, 95% CI) redds (10.22 redds/km) in 2005. Pacific lamprey redds were estimated to be 504 (±67%, 95% CI) (1.21 redds/km) in 2004 and 459 (±110%, 95% CI) redds (1.10 redds/km) in 2005.

Redd characteristics

Generally, lamprey redds were identified as round depressions in gravel or cobble substrates. Rocks moved by lampreys to dig the depression typically were piled on all sides of the depression rim and were lighter colored due to exposure of nonalgal-covered surfaces. A plume of finer substrate carried by the current was downstream of the depression as a result of spawning and egg burial; however, in places with low velocities, these finer substrates were not apparent. In many instances, few large rocks were left in the bottom of the depression (Figure 4). Pacific and western brook lamprey redds differed in size and substrate size. Redd characteristics for each species are summarized in Table 1.

Western brook lamprey redds were found in gravel rich and relatively shallow habitats, predominantly pool tailouts (46.3%), low-gradient (slope < 2%) riffles (22.2%), steps over cobble (16.1%), and lateral scour pools (13.1%). Redds were associated with a variety of cover types, most commonly rocky substrates (58.1%), wood (11.9%), and vegetation (8.9%). Because western brook lamprey redds are small, large cobble substrates serve as adequate cover under which spawning adults can hide. Fourteen percent of redds were not associated with any cover.

Pacific lamprey redds were most frequently observed in low-gradient riffles (50.4%), pool tailouts (36.8%), and lateral scour pools (11.2%). Only 43.2% of Pacific lamprey redds were associated with cover, predominately large substrates (26.4%), vegetation (8.0%) and wood (6.5%). The remaining 56.8% of the 125 redds

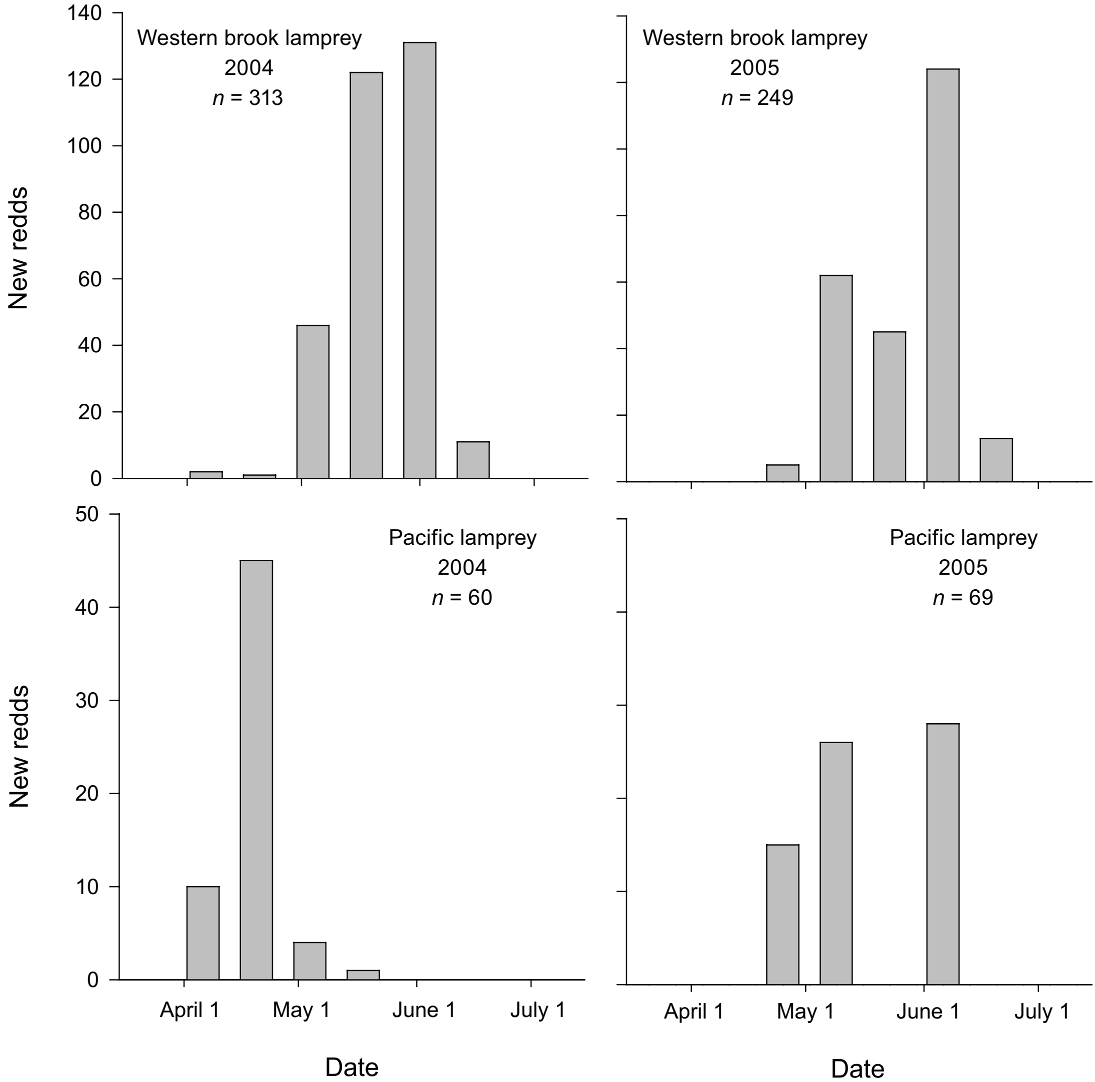

Figure 3. Spawn timing of western brook and Pacific lampreys in 2004 and 2005. Each bar represents a 2-week survey cycle. Surveys were conducted from March 29 through June 24 in 2004 and March 28 through June 30 in 2005.

were observed away from channel features that could serve as cover.

Site occupancy and distribution

Field crews detected western brook lamprey redds in 20 of 31 sites in 2004 and 16 of 31 sites in 2005 (Table 2). Pacific lamprey redds were identified in fewer sites, 8 in 2004 and 9 in 2005.

Generally, western brook lampreys were widespread in the smaller-order tributary streams (Figure 5), whereas Pacific lampreys only occupied large main-stem reaches of Smith River and West Fork Smith River (Figure 6).

Habitat associations

Habitat surveys were completed at 56 of the 62 sites where redd surveys were conducted. Physi-

Figure 4. Pacific lamprey redd (Photo by G. Susac, Oregon Department of Fish and Wildlife).

cal habitat variables were quantified at all sites where lampreys were detected; however, in 2005, habitat surveys at six sites where lampreys were absent were omitted due to time constraints. The data set was too small to describe associations between habitat characteristics and redd density at each site and habitat unit; therefore, our response variable was limited to lamprey presence.

Table 1. Summary of physical characteristics of western brook and Pacific lamprey redds. Redd depth is the distance from the bottom of the depression to the surface of the substrate; water depth is the distance from the substrate to the water surface; substrate is the average maximum diameter of 30 pebbles.

Variable	Median	Minimum	Maximum	SD
Western brook lamprey ($n = 539$)				
Length (cm)	12.0	4.0	115.8	7.8
Width (cm)	11.0	4.5	73.2	7.8
Redd Depth (cm)	3.0	−3.5	12.2	2.1
Water Depth (cm)	13.0	0.3	51.0	7.6
Velocity (m/s)	0.2	0.0	0.7	0.1
Substrate (mm)	24.0	7.8	65.2	9.0
Pacific lamprey ($n = 125$)				
Length (cm)	39.0	21.3	210.0	18.3
Width (cm)	36.6	20.0	270.0	23.9
Redd Depth (cm)	7.6	−12.0	18.3	3.8
Water Depth (cm)	44.0	16.0	105.0	23.2
Velocity (m/s)	0.6	0.2	1.0	0.2
Substrate (mm)	48.1	27.0	88.8	12.9

Table 2. Occupancy statistics for sites surveyed for lamprey redds in the Smith River basin, 2004 and 2005.

Year	Sites surveyed	Sites occupied	Minimum number at occupied site	Maximum number at occupied site
		Western brook lamprey redds		
2004	31	20	1	136
2005	31	16	1	114
		Pacific lamprey redds		
2004	31	8	1	15
2005	31	9	1	48

Reach-scale analysis

The reach-scale habitat data set was reduced from 54 to 19 variables (Appendix A.1) and was best described in a two-dimensional ordination that explained 93% of the total variation within the data set. When rotated to load variation associated with presence of western brook lamprey redds on the first axis, the ordination shows that western brook lamprey redds were predominantly detected at higher elevation sites with smaller active channel widths. Axis 1 explains 88% of the variation and is positively correlated with elevation (r^2 = 0.849) and negatively correlated with active channel width (r^2= 0.772) (Figure 7). However, this relationship is relatively weak given the detection of western brook lamprey redds at some low elevation sites. Figure 8 quantifies the median and range of elevation and active channel width for all sites and those at which western brook lamprey redds occur.

When orthogonally rotated to load variation associated with presence of Pacific lamprey redds on the first axis, the ordination of reach-scale variables shows that Pacific lamprey redds were present in sites at lower elevations and with wider active channels (Figure 9). Axis 1 explained 85% of the variation and was nega-

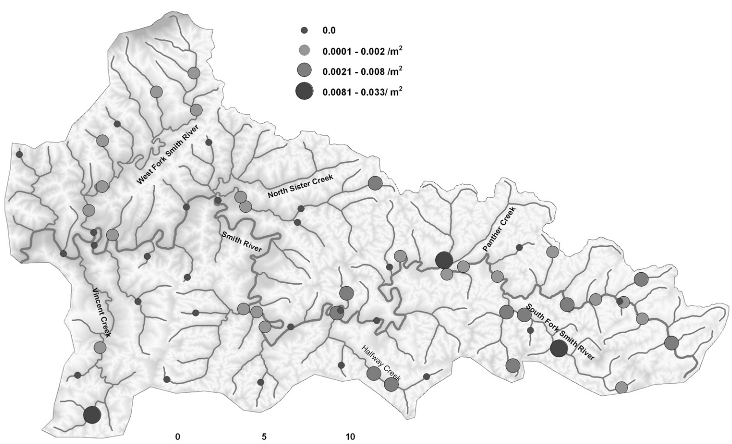

Figure 5. Site occupancy and redd density for western brook lampreys in the Smith River basin, 2004 and 2005.

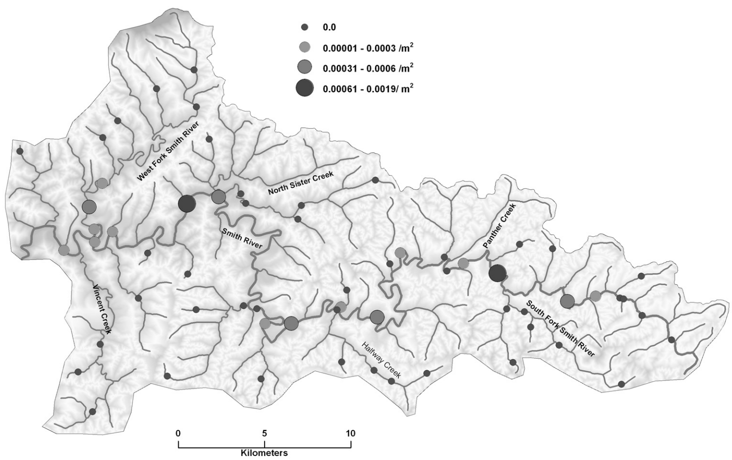

Figure 6. Site occupancy and redd density for Pacific lampreys in the Smith River basin, 2004 and 2005. Figure 6. Site occupancy and redd density for Pacific lampreys in the Smith River basin, 2004 and 2005.

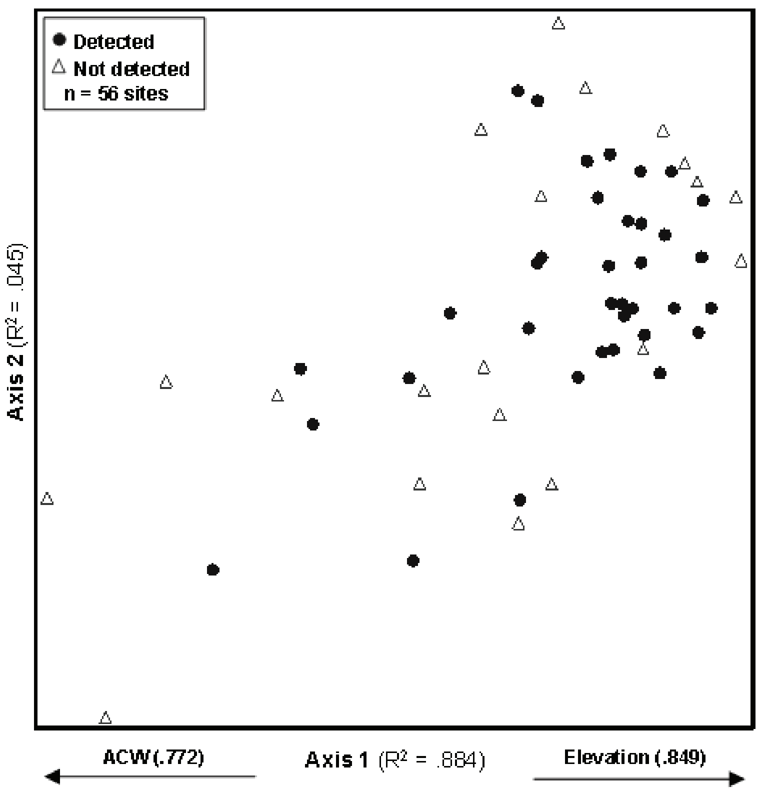

Figure 7. Nonmetric multidimensional scaling ordination of sites as described using reach sale habitat variables. Sites characterized by presence or absence of western brook lamprey redds. Arrows represent direction of correlation. Values in parentheses are correlation coefficients of habitat variables to axis 1. Only variables highly correlated with axis 1 are shown.

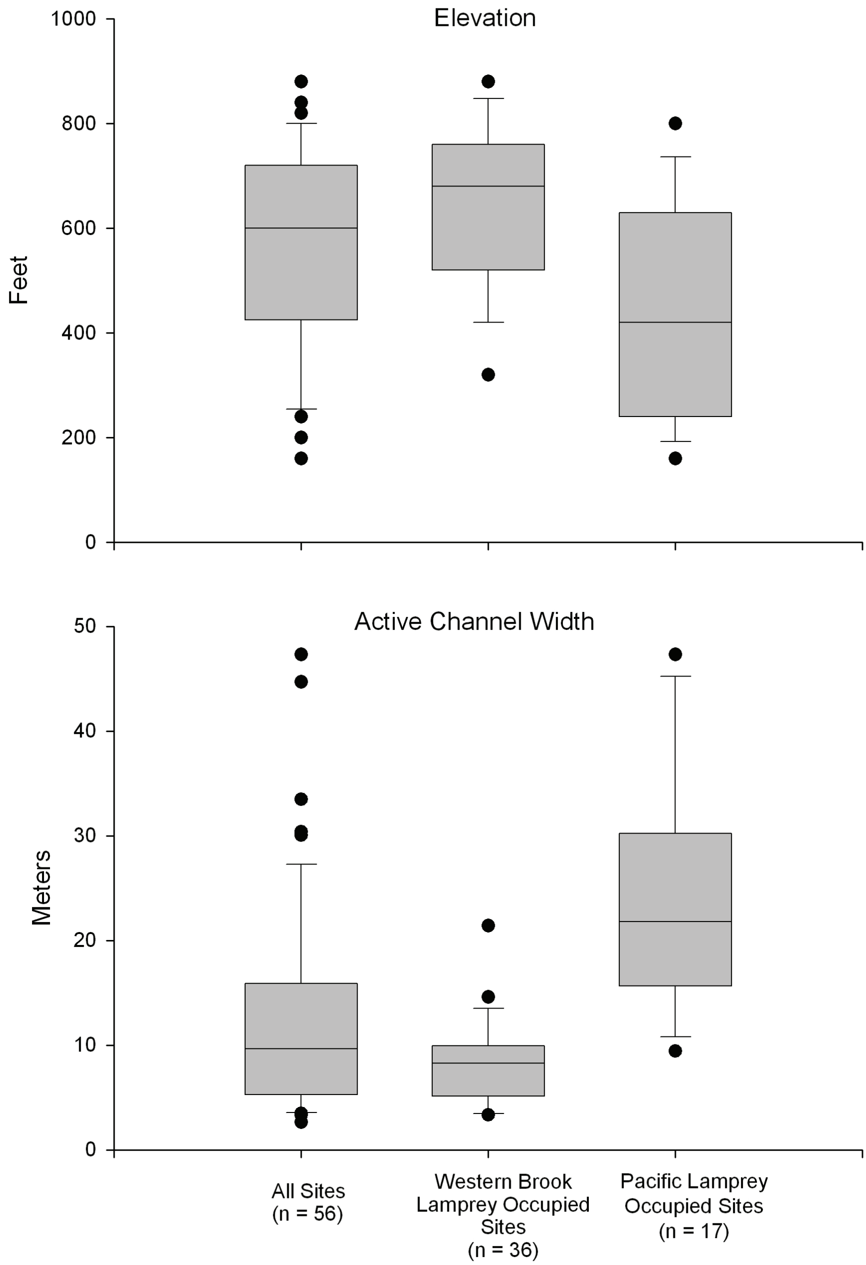

Figure 8. Box and whisker plots of reach variables associated with sites where the presence of western brook and Pacific lamprey redds were detected.

tively associated with elevation (r^2 = 0.656) and positively associated with active channel width (r^2= 0.851). The remaining reach-scale variables were weakly correlated with either axis. Figure 8 describes the median and range of these explanatory variables for all sites and those at which Pacific lamprey redds occur.

Results of the multivariate analysis of reach-scale habitat data corresponds well to overall distribution (Figures 5 and 6). Pacific

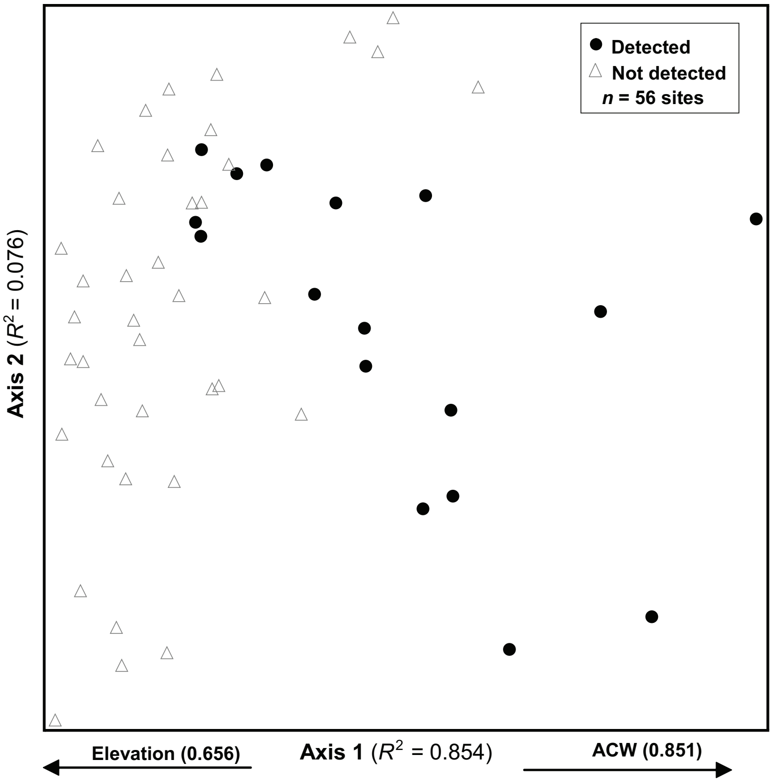

Figure 9. Nonmetric multidimensional scaling ordination of sites as described using reach-scale habitat variables. Sites characterized by presence or absence of Pacific lamprey redds. Arrows represent direction of correlation. Values in parentheses are correlation coefficients of habitat variables to axis 1. Only variables highly correlated with axis 1 are shown.

lampreys are found primarily in wider, high-order streams, whereas western brook lampreys are more widespread but concentrated in headwater and low order streams.

Habitat unit-scale analysis

The habitat unit-scale data set was reduced from 38 variables to 15 variables (Appendix A.1). A three-dimensional NMS ordination of all habitat units consisting of the 36 sites where western brook lamprey redds were detected explained 75.5% of the variation among units. When rotated to load variation associated with presence of western brook lamprey redds on the first axis, the ordination shows that the presence of redds was weakly correlated with a high percentage of gravel and low percentage of bedrock (Figure 10). Axis 1 explains 61% of the variation associated with all habitat units and was negatively associated with unit area (r^2 = 0.427), depth (r^2= 0.336), and percent bedrock (r^2 = 0.328) and positively associated with percent gravel (r^2 = 0.278), though associations were relatively weak. Table 3 describes significant values for these variables for sites with and without western brook lampreys.

To ensure that analysis of all habitat unit types combined did not mask trends within habitat types, we examined each habitat unit type separately and found similar results. For example, a NMS ordination of habitat unit-scale variables of only pool tailouts also suggests that western brook lamprey redds are weakly correlated with substrate. The presence of redds in pool tailouts is positively correlated with

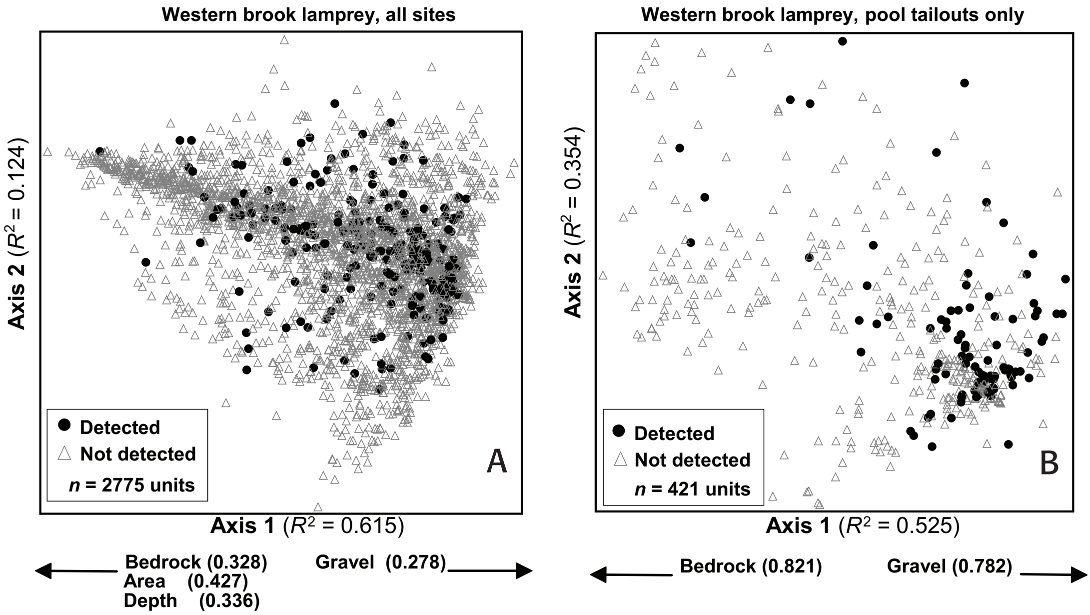

Figure 10. Nonmetric multidimensional scaling ordination of (A) all habitat units and (B) pool tailouts only consisting of sites where western brook lamprey redds were detected. Arrows represent direction of correlation. Values in parentheses are correlation coefficients of habitat variables to axis 1. Only variables correlated with axis 1 are shown.

Table 3. Summary of habitat unit scale variables correlated with sites where presence of western brook lamprey redds was detected.

	Occupied units			Total units		
	Median	Min	Max	Median	Min	Max
			All unit types			
		$n = 251$			$n = 2775$	
% gravel	65	5	100	40	0	100
% bedrock	0	0	100	0	0	100
Unit area (m^2)	25.2	0.8	1,168.0	60.6	1.5	1,284.8
Unit depth (m)	0.15	0.03	1.4	0.15	0.01	0.60
			Pool tailouts only			
		$n = 94$			$n = 421$	
% gravel	80	5	100	50	0	100
% bedrock	0	0	90	0	0	100
Unit area (m^2)	9.6	0.8	325.6	7.6	0.2	325.6
Unit depth (m)	0.15	0.05	0.60	0.15	0.03	0.60

percent gravel (r^2 = 0.782) and negatively correlated with percent bedrock (r^2 = 0.821) (Figure 10). Axis 1 explains 53% of variation within variables.

Analysis of habitat unit characteristics consisting of the seven sites where Pacific lamprey redds were detected reveals results similar to those for western brook lampreys. The presence of Pacific lamprey redds was weakly correlated with high percentages of gravel and cobble and a low percentage of bedrock. A two-dimensional ordination of all units explained 75.5% of variation among units (Figure 11). When rotated to load the variation associated with presence of Pacific lamprey redds on the first axis, axis 1 explains 63% of the variation. Axis 1 was negatively correlated with percent bedrock (r^2 = 0.938) and positively correlated with percent gravel (r2 = 0.518) and cobble (r^2 = 0.446). The remaining habitat unit-scale variables were poorly correlated with either axis. Table 4 describes significant values for these variables at sites with and without Pacific lamprey redds.

Examination of unit-scale variables of pool tailouts only show similar results as those for analyses of all unit types combined and separately. A two-dimensional ordination of unit-scale variables describing all pool tailouts, orthogonally rotated to maximize variation associated with the presence of Pacific lamprey redds, shows that axis 1 is loosely correlated with percent gravel (r^2 = 0.332) and negatively correlated with percent bedrock (r^2 = 0.283) and shade (r^2 = 0.314); however, axis 1 explains just 25% of variation within the ordination (Figure 11).

Discussion

This study described habitat associations, distribution, and redds of Pacific and western brook lampreys while highlighting uncertainties inherent in estimating abundance of lampreys at a landscape scale. In general, we found that Pacific lampreys spawned in lower-elevation sites in the main-stem sections of Smith River, whereas western brook lampreys were more widespread

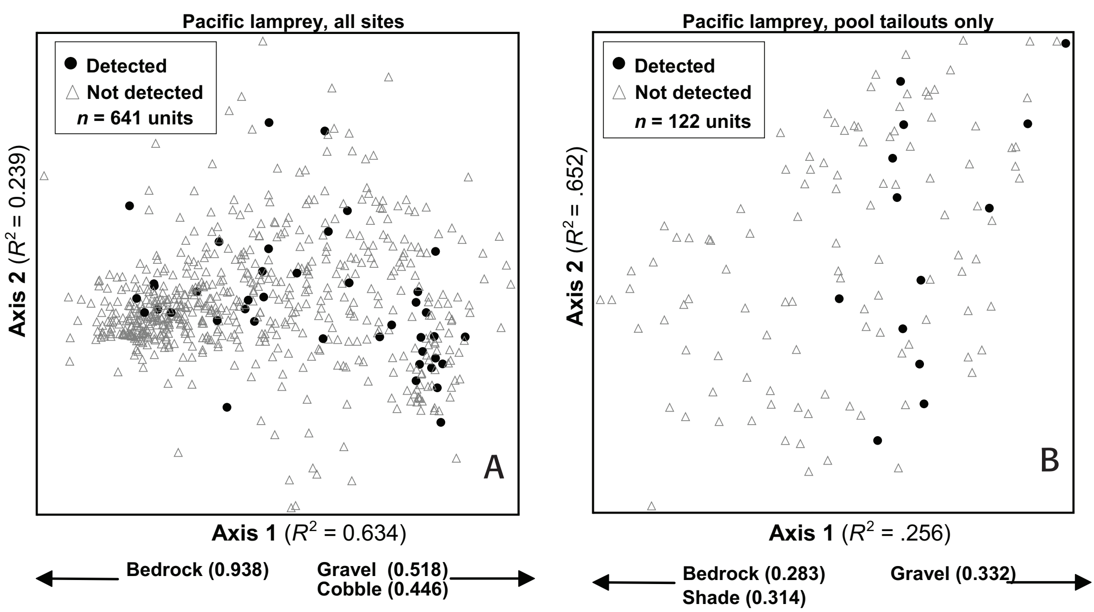

Figure 11. Nonmetric multidimensional scaling ordination of (A) all habitat units and (B) pool tailouts only consisting of sites where Pacific lamprey redds were detected. Arrows represent direction of correlation. Values in parentheses are correlation coefficients of habitat variables to axis 1. Only variables correlated with axis 1 are shown.

Table 4. Summary of habitat unit scale variables correlated with sites where presence of Pacific lamprey redds was detected.

	Occupied units			Total units		
	Median	Min	Max	Median	Min	Max
	All unit types					
	$n = 41$			$n = 641$		
% gravel	25	4.8	90	9.9	0	95
% bedrock	19.8	0	90	50	0	100
	Pool tailouts only					
	$n = 13$			$n = 122$		
% gravel	60	5	80	20	0	85
% bedrock	10	0	90	30	0	100

and distributed throughout the upper mainstem and tributary streams. This pattern of distribution is similar to that observed on Cedar Creek in the Lewis River system where Pacific lamprey spawning locations were in the lower sections of Cedar Creek and western brook lampreys were found in the upper tributaries (Pirtle et al. 2003).

Our a priori estimates of potential distribution (sample frame) and the identification of redds by species increased the amount of uncertainly in the redd abundance estimate. In addition, western brook lampreys may have extended upstream of our sample frame, which was based on the upper extent of steelhead. The precision of redd abundance estimates is less than desired. Our goal was to have a 95% confidence interval of less than 45%, though we preferred one of less than 35%. The large confidence intervals (67–110%) were likely due to the small sample size and high variance between sites. Even though the confidence intervals were wide, the actual estimates for each species and site occupancy remained virtually unchanged from 2004 to 2005. Tailoring the sample frame to the distribution of each species, increasing sample size, and refining the survey protocol may result in more precise estimates and should be considered if redd surveys using similar protocol are to be implemented as a long-term monitoring strategy.

Four factors complicated identification of redds. First, in 27 instances (23 western brook lampreys and 4 Pacific lampreys), redds were identified in large areas of cleaned and disturbed gravel, usually containing two to five depressions. These areas were two to three times the size of a typical redd. It was evident that substrate had been cleared due to lamprey spawning activity, but it was not obvious how many redds these areas represented. Each identifiable depression was counted as an individual red, but measurements were made with considerable uncertainty. These redds were not included in the summaries of physical redd characteristics described in Table 1.

Second, in a few instances field crews observed both western brook and Pacific lampreys filling in newly created redds. Lampreys moved small gravel and cobble from upstream into the depression until it was filled and flush with the substrate surface. In some cases, the depression was filled where it mounded above the surface of the substrate (depicted as negative values in minimum depth measurements in Table 1). This behavior, where common, may make the detection of redds difficult.

Third, in a few instances field crews observed western brook lampreys spawning in redds of Pacific lampreys. Field staff were diligent about revisiting old redds of both species to capture any superimposition by western brook lampreys. Studies in the South Fork Coquille River and Lewis River in Washington have also observed this behavior (Pirtle et al. 2003; Brumo and Markle 2006).

Last, crews were careful to properly identify western brook lamprey redds. In places where redds could be easily confused with large elk tracks, presence of a lamprey positively identified the redd. If a lamprey was not present, then the redd was not counted or measured. Similarly, Pacific lamprey redds could be confused with steelhead redds. Again, field crews made conservative redd calls and only identified redds certain to be created by lampreys.

These complications are likely sources of error for quantitative redd counts and should be taken into consideration if using redd surveys for population monitoring purposes. Similar to redd surveys for bull trout *Salvelinus confluentus* (Dunham et al. 2001) and other salmonids, crew experience is one method to minimize error associated with misidentification, superimposition, and lamprey spawning behavior. In addition, frequent surveys (no less than biweekly surveys) can ensure positive identification of redds and minimize error. In many instances, crews observed redds on one survey that were filled in, superimposed, or otherwise unidentifiable on the subsequent visit.

The multivariate analyses show many unoccupied habitat units that have very similar physical characteristics as those occupied by lampreys, even within the same reach. Thus, at fine scales, other ecological factors may have a stronger influence on spawning distribution than habitat structure. Presence of lampreys at a particular site may influence the behavior of other individuals. It is theorized that Pacific and western brook lampreys are attracted to streams and spawning sites by pheromones released by ammocoetes and mature adults as are sea lampreys *Petromyzon marinus* (Bjerselius et al. 2000; Vrieze and Sorensen 2001; Li et al. 2002). This phenomena may be evident at one particular site on Smith River where 48 Pacific lamprey redds were detected, a value much greater than the mean (Table 2). Habitat characteristics at this site were not significantly different from those of other sites and could not explain the unusually high density of redds. Lamprey pheromones may have a greater influence on distribution than habitat structure. In addition, even though this study quantified a myriad of habitat characteristics, it may not have measured the correct habitat unit-scale variables to fully explain habitat unit selection of spawning lampreys.

Connectivity and distribution of habitats may also have a significant influence on spawning site selection. For example, sites near high-quality rearing habitat for western brook lampreys or Pacific lamprey overwintering habitat may be more likely occupied than sites of similar character, but not near optimal habitats for other life stages. This study did not account for stream network distribution of other habitats important to western brook and Pacific lampreys.

This study found that reach-scale habitat variables correlated with stream size were the best descriptors of potential distribution of spawning lampreys of both species. Pacific lampreys spawned at lower elevation sites in larger stream sizes. Western brook lampreys were associated with higher elevation sites and smaller streams but were relatively widespread. At the habitat unit scale, unit type and dominant substrate were only weakly correlated with presence of spawning lampreys. Both species spawn predominantly in pool tailouts and low-gradient riffles, both gravel-rich habitat types. The association of reach- and unit-scale variables with distribution of adult lampreys helps refine the sample frame for monitoring adult populations and provides context for designing a sample strategy for juvenile lampreys.

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Table A.1. Redd and habitat variables included in the analyses. Habitat unit and reach variables were measured according to Moore et al. (2007).

Scale	Variable	Definition
Redd	Length	Length of redd (cm)
	Width	Width of redd (cm)
	Depth	Distance from the bottom of the depression to the surface of the substrate (cm)
	Water depth	Distance from the substrate to the water surface (cm)
	Velocity	Water velocity at the redd (m/s)
	Substrate	Average maximum diameter of 30 pebbles (mm)
	Cover	Cover type
Habitat unit	Unit type	Unit type designation
	Unit area	Length times width (m^2)
	Slope	Unit slope, measured with clinometer (%)
	Percent shade	Percent of 180° that topography or vegetation occludes the sky, measured with clinometer
	Depth	Maximum depth of pools, modal depth of fast water units (m)
	Percent silt/organic	Percent of wetted substrate surface area
	Percent sand	Percent of wetted substrate surface area
	Percent gravel	Percent of wetted substrate surface area
	Percent cobble	Percent of wetted substrate surface area
	Percent bedrock	Percent of wetted substrate surface area
	Large boulders	Number of boulders > 0.5 m above water surface, roughness index
	Percent undercut	Percent of right and left bank
	Large wood	Number of large wood pieces
	Large wood volume	Large wood volume (m^3)
	No. of key wood pieces	Wood $\geq 12 \times 0.6$ m
Reach	Elevation	Feet above sea level at downstream end of site
	Gradient	Gradient measured with clinometer
	Channel form	Channel morphology and constraint
	Land use	Dominant land use
	VWI	Valley width divided by active channel width
	Active channel width	Width of active channel (m)
	Percent silt	Percent of wetted substrate surface area
	Percent sand	Percent of wetted substrate surface area
	Percent gravel	Percent of wetted substrate surface area
	Percent cobble	Percent of wetted substrate surface area
	Percent bedrock	Percent of wetted substrate surface area
	Large boulders	Number of boulders > 0. 5 m above water surface, roughness index
	Percent undercut	Percent distance of left and right bank
	Large wood	Volume of large wood
	Width:depth	Mean width divided by mean depth
	Percent pool area	Percent of wetted area
	No. pools/100 m	Number of pools per 100 m
	Mean pool depth	Average pool depth
	No. of complex pools	Number of pools associated with wood