Spatial Distribution and Habitat Use of Pacific Lamprey (Lampetra tridentata) Ammocoetes in a Western Washington Stream

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Scott Barndt
US Forest Service

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Jen Stone
U.S. Fish and Wildlife Service
Columbia River Fisheries Program Office
1211 SE Cardinal Court, Suite 100
Vancouver, WA 98683 USA
jen_stone@fws.gov
and
Scott Barndt
U.S. Forest Service, Gallatin National Forest
P.O. Box 130, Bozeman, Montana 59771 USA
sbarndt@fs.fed.us

ABSTRACT

We investigated the spatial distribution and habitat associations of Pacific lamprey (*Lampetra tridentata*) ammocoetes in a southwest Washington stream. The ammocoetes exhibited a highly aggregated, non-random spatial distribution pattern. Conductivity, dissolved oxygen, and gradient influenced ammocoete distribution at the large scale (across 50 m reaches), whereas wetted width, percent fines, canopy density, and velocity influenced distribution at the small scale (1 m^2 quadrats). We observed optimum water depths of 70 cm and current velocities of 0 to 10 cm/sec. In general, ammocoetes preferred fine substrates though larger ammocoetes were found at low densities in large gravel substrates. Our findings illustrate the importance of slow water environments for the rearing stage of Pacific lamprey. Restoration activities should be designed to restore watershed function and process in a way that naturally allows systems to retain these critical habitats. Additionally, when considering ammocoete habitat use and distribution, it is important to take into account the scale of the observations.

INTRODUCTION

Pacific lamprey (*Lampetra tridentata*) abundance in the Columbia River basin has declined over the past 50 years, and the species was petitioned for listing as endangered or threatened under the Endangered Species Act in 2003. Adult Pacific lamprey counts at mainstem hydropower facilities have decreased by an order of magnitude since 1950 (Close 2001), and electrofishing surveys in Columbia River tributaries suggest that recruitment in recent years has been low (Close 1998). Actions are currently being considered for the recovery of Pacific lamprey populations in the Columbia River (Close et al. 1995).

Lamprey production and survival are partially dependent upon in-stream habitat availability (Applegate 1950). Pacific lamprey spend four to six years as ammocoetes burrowed in fine stream sediments consuming diatoms, algae, and detritus (Scott and Crossman 1990). They transform from ammocoetes to macropthalmia from July to October (Scott and Crossman 1990), and their habitat preference switches to coarser substrates that they can adhere to during their migration to the ocean.

Few studies have focused on the relationships among ammocoete abundance, distribution, and habitat (Malmqvist 1980, Potter et al. 1986, Beamish and Jebbink 1994, Beamish and Lowartz 1996, Torgersen and Close 2004). Even fewer have recognized the need for evaluating habitat relationships at different biologically meaningful scales (Torgersen and Close 2004). With Pacific lamprey conservation becoming an immediate issue in the Pacific Northwest (Close et al. 2003), a more complete understanding of habitat use by this species will allow us to design and implement appropriate conservation initiatives and better target habitats in need of restoration. As part of a larger project designed to explore the movement, abundance, and distribution of Pacific lampreys in a tributary downstream of major hydropower operations, we examined Pacific lamprey ammocoete distribution and habitat associations at two spatial scales- reach (50 m) and subreach (1 m^2).

METHODS

Cedar Creek is a tributary to the North Fork Lewis River within the Columbia River basin with summer discharges averaging around 0.42 m^3/s. Historically, the 89.3 km^2 drainage was heavily logged and timber was driven to downstream mills by splash damming. These actions removed large woody debris and scoured the stream channel, resulting in channelization in some instances and channel readjustment (lateral movements, head cutting, etc.) in others. The net result was degraded habitats, especially due to the decrease in sediment storage (Megahan 1982), which potentially reduced ammocoete rearing habitat. Land ownership on Cedar Creek is largely private and land-uses are primarily agriculture and silviculture.

Western brook lamprey (*L. richardsoni*) occur in Cedar Creek's major tributary, Chelatchie Creek. At the ammocoete stage they are morphologically very similar to Pacific lamprey, making differentiating the two species difficult. To minimize potential miss-identifications of ammocoetes, we limited our study to mainstem Cedar Creek where we rarely observe adult western brook lamprey.

Surveys were conducted during the summers of 2000, 2001, and 2002, when a total of 31 reaches were sampled. There were no distinct floods or spates during or between sampling events that might have dramatically altered ammocoete distribution or habitat availability, and flow regimes were similar between years. Mean water temperatures observed during sampling differed by only 1°C.

We used a systematic sampling design with one random start to evaluate ammocoete abundance and distribution. Sample reaches occurred every 1000 m along the stream from the mouth to the upper extent of lamprey spawning habitat and were selected using a geographic information system. The start of the sample reach was identified using a Trimble® global positioning system. Each 50 m reach was divided into six cross-sectional transects spaced 10 m apart. Each transect contained two 1 m^2 sampling quadrats (consisting of a PVC frame) that were placed at water's edge (margin) on the odd-numbered transects and at 1/3 and 2/3 of the wetted width (inside) on even-numbered transects (Fig. 1).

Water quality parameters (temperature, pH, dissolved oxygen, and conductivity) were recorded at the downstream end of each reach and stream gradient was measured as surface slope for the entire reach. Wetted width and canopy density (measured by a spherical densiometer; Platts 1987) were recorded for each transect. We measured water depth, water velocity (at 60% depth), flow direction (denoted as positive for downstream, negative for eddy), and substrate type (modified Wentworth, Wentworth 1922) at each quadrat. Substrate data were categorized by size class (fines = <1 – 8 mm, small gravel = 9 – 16 mm, large gravel = 17 – 64 mm, cobble = 65 – 256 mm, boulder = 257 – 4096 mm, and bedrock = >4096 mm) and its frequency was evaluated as a percentage of the total. Dominant substrate types were identified as those that made up the majority of the sample.

We acquired spatial databases containing coarse land-use purposes at an intended use scale of 1:2,400 from a Clark County 2000 dataset. Land use purposes included: deforested, grain, forestry, residential, and other. Reaches adjacent to two types of land-use parcels were designated as a composite category (i.e., cleared/forestry).

Ammocoetes were removed from each quadrat by 70% depletion electrofishing. Actual numbers of ammocoetes captured from each quadrat were not expanded to population estimates because too few ammocoetes were captured from each pass. Therefore we report the sum of the captured ammocoetes per quadrat (Zippin 1958, Lockwood and Schneider 2000). Our results are based on the assumption of equal catchability across all habitat types and age classes and represent the minimum number of ammocoetes present (Pajos and Weise 1994) in each quadrat. This method is conservative but preserves biological trend (Pajos and Weise 1994). Ammocoetes less than 10 mm in length were difficult to capture and their presence was noted instead of enumerated. An AbP-2 backpack electrofisher (Engineering Technical Services,

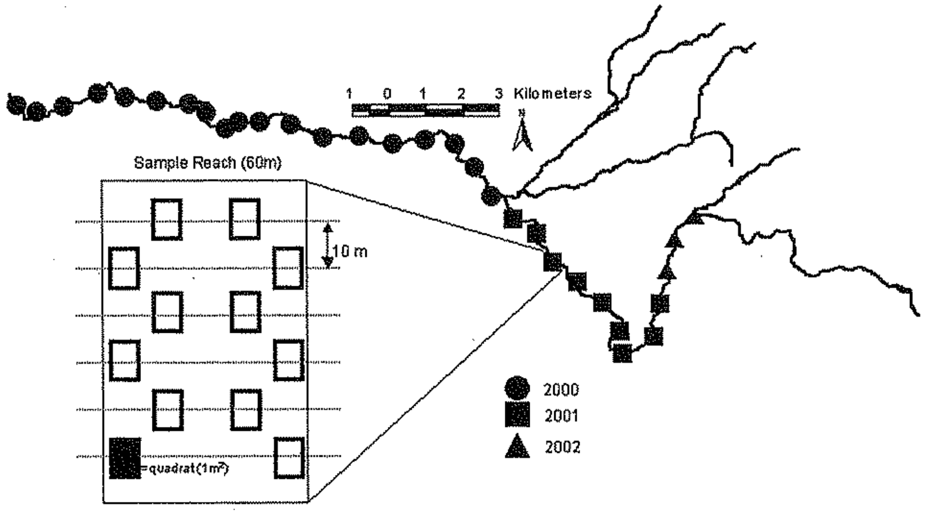

Figure 1. Location and arrangement of sample reaches on Cedar Creek, Washington.

University of Wisconsin, Madison, Wisconsin) was used. The electrofishing unit delivered 3 pulses/second (125 volts DC) at 25% duty cycle, with a 3:1 burst pulse train (three pulses on, one pulse off) to remove ammocoetes from the substrate (Weisser and Klar 1990). Once ammocoetes emerged, 30 pulses/second was applied to stun the ammocoetes. Each quadrat was sampled for 90 seconds per pass, with a minimum of two and a maximum of five passes. Captured ammocoetes were anesthetized with MS-222 (Summerfeldt and Smith 1990), identified to species (Richards et al. 1982), and measured for length. If ammocoetes were not captured from any of the 12 quadrats per reach, up to three additional 1 m^2 sites having potentially "ideal" habitat attributes (see Farlinger and Beamish 1984) were sampled to assess the occurrence of false-absences (i.e., the species was present but not detected during the survey (Peterson and Dunham 2003)). These additional quadrats were sampled according to the above procedure, though only presence/absence information was recorded.

Preference curves for water depth, water velocity, and dominant substrate type were calculated. We calculated the proportional use values (Gore et al. 1990) as:

$$Pi = \frac{ni/N}{vi/Vt} = \frac{Ni/\Sigma n}{Vi/\Sigma v}$$

where *ni* is the number of ammocoetes observed in the *i*th category of habitat variable *V*, *N* is the total number of ammocoetes observed, *vi* is the frequency of occurrence of the *i*th value of variable *V*, *Vt* is the total number of all measurements made of variable *V*. We then calculated the suitability index values by dividing all the *Pi* values by the maximum *Pi* value for each habitat variable. The results provide each habitat condition with a score between 0 and 1, with 0 representing unsuitable and 1 representing optimal (Bovee 1986).

We pooled the data across years for the statistical analysis because few fish were captured in the upper sections of Cedar Creek (2001 and 2002 sampling efforts) and there were no unusual events (i.e., spates, changes in spawner abundance) that would significantly alter habitat use, availability, or ammocoete distribution among years. Habitat variables were divided into those measured at the reach scale (water quality and gradient), and those measured at a subreach scale (transect and quadrat measurements). We used multiple linear and logistic regression analyses (for variable screening purposes, (Myers 1990)) to describe the correlations between habitat variables and ammocoete occurrence (binary response) or numbers of ammocoetes. These procedures are fully detailed by Sokal and Rohlf (1981) and were performed using SAS software (SAS Institute 1999). We assessed multicollinearity between habitat variables and excluded variables with a variation inflation factor exceeding 10 from the final models (Belsley et al. 1980). Both linear and logistic models were evaluated using non-transformed data. We calculated Nagelkerke's R^2 for logistic regression models (Nagelkerke 1991). An index of dispersal (*I*= variance:mean ratio, Elliot 1977) was calculated for reaches where at least one ammocoete was present in the sampled quadrats. We used a chi-square test of the dispersal indices to detect departures from the 95% confidence interval of a Poisson series. Departures above the interval would indicate an aggregated distribution (Elliot 1977). Non-parametric t-tests were performed using SAS software (SAS Institute 1999).

RESULTS

Habitat in Cedar Creek was heterogeneous. Dissolved oxygen, conductivity, and pH decreased by river kilometer and the percent of large gravel in the samples increased ($R^2 = 0.9045$, $P < 0.05$). Much of the sampled bedrock habitat was covered with a thin layer of silt.

Pacific lamprey ammocoetes occurred in 30 of the 31 reaches. We observed two false-absences (ammocoetes detected outside of the quadrats) at the reach scale. The one reach that did not contain ammocoetes was a section of the creek that was recently and unnaturally diverted into an old channel and then into a holding pond for aesthetic purposes. This reach was a narrow riffle that contained uniform, unembedded cobble. Only 24% of the quadrats systematically sampled contained ammocoetes. The number of false-absences at the subreach scale is unknown, though on six occasions we detected ammocoetes on the second pass when the first pass yielded none.

Four hundred and seventy-two ammocoetes were captured from the systematically sampled area (372 m^2). The maximum number of ammocoetes observed in a quadrat was 44 and the average (excluding zeros) was five. Of the quadrats containing ammocoetes, 38% had only one, 37% had 2-6, and 22% had 7-17. Eleven ammocoetes had begun transforming.

Ammocoetes were distributed non-uniformly in the stream channel. In all but one reach, ammocoetes were present in fewer than 50% of the quadrats. The dispersal index (calculated for 28 of the 31 reaches) indicates that ammocoetes were distributed in a highly aggregated fashion (in 21 reaches) and significantly different from a random pattern (chi-square, $P < 0.01$). More ammocoetes were captured from margin quadrats (80%) than from inner quadrats (20%) (Nonparametric t-test, $P < 0.01$).

Lengths of Pacific lamprey ammocoetes captured ranged between 9 and 129 mm and averaged 53 mm (Fig. 2). Longer fish tended to be farther from the mouth of the stream ($R^2 = 0.0219$, $P < 0.01$). Ammocoetes captured in the inner quadrats were longer than those captured from the outer quadrats (Nonparametric t-test, $P = 0.04$). There was no relationship between the number of ammocoetes captured per quadrat and ammocoete length. Quadrats dominated by large gravel substrate contained ammocoetes that were significantly larger than those captured from fine and bedrock substrates (Nonparametric t-test, $P < 0.01$). Quadrats dominated by large gravel were more often found at 1/3 and 2/3 of the wetted width.

Preference curves were used to determine optimal ranges of water depth (Fig. 3), water velocity (Fig. 4), and dominant substrate (Fig. 5). The 70 cm depth was most heavily used relative to availability. Optimal ranges of -10 to 10 cm/sec velocities were observed, with the negative velocities indicating reversed flow in eddies. Overall, ammocoetes preferred fine-dominated substrate with near equal preference among the other types. Maximum densities (44 ammocoetes/m^2) were recorded in fine dominated substrates. We did not differentiate between the types of fine sediments when we characterized substrates and found ammocoetes in both sandy and silty substrates.

Using multiple regression analysis, we observed that conductivity was positively associated with ammocoete abundance ($R^2 = 0.2080$, $P = 0.02$) at the reach scale ($n=31$). The proportion of quadrats containing lamprey per reach was negatively associated with gradient and positively associated with dissolved oxygen ($R^2 = 0.3340$, $P < 0.05$). At the subreach scale ($n = 363$), wetted width, percent fines, and percent small gravel were positively associated with ammocoete presence, and velocity and canopy were both negatively associated with ammocoete presence ($R^2 = 0.34$, $P < 0.05$). At the subreach scale, percent fines were positively associated with ammocoete abundance ($R^2 = 0.2840$, $P < 0.01$). All other habitat variables were not significant.

Though the land-use designations were very coarse, patterns in ammocoete distribution emerged. Approximately 65% of the captured ammocoetes were from reaches designated either fully or in part as deforested property. All other land-use categories had similar ammocoete abundances, each accounting for approximately 8% of the total catch.

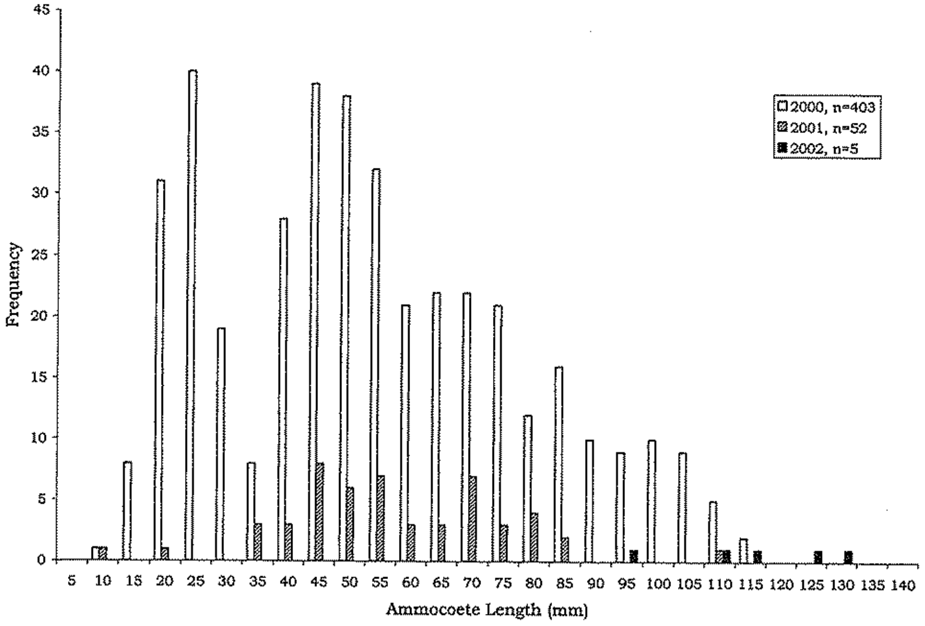

Figure 2. Length frequency diagram of ammocoetes in Cedar Creek, Washington.

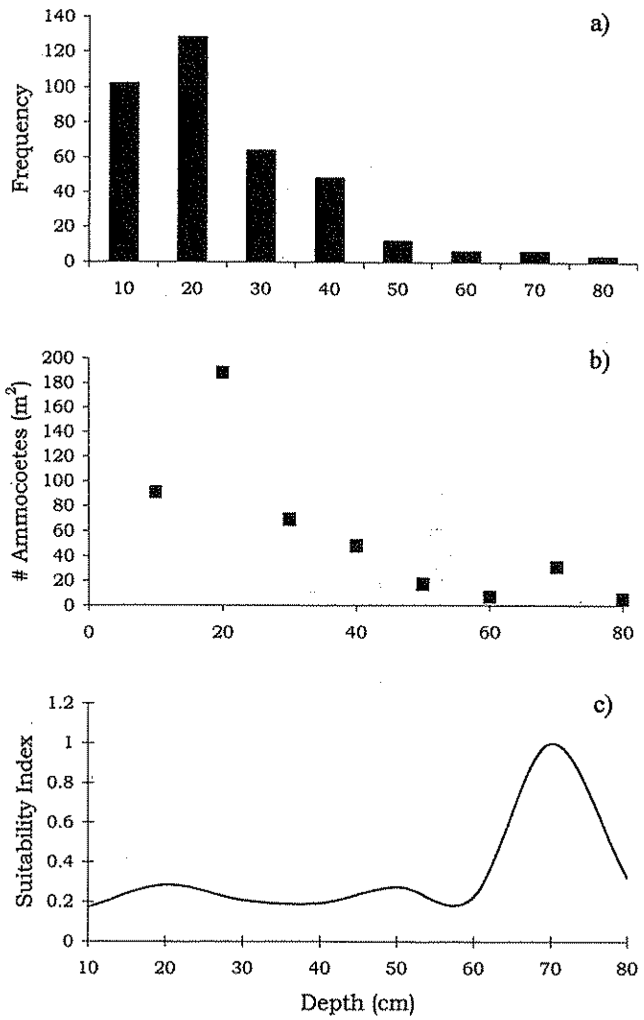

Figure 3. Overall availability (a), level of use (b), and preference (c) of ammocoetes for different water depths in Cedar Creek, Washington.

DISCUSSION

Slow water habitats structured the aggregated, non-uniform distribution of Pacific lamprey ammocoetes in Cedar Creek at both scales examined. The slow water velocities in these habitats result in the fine burrowing substrates preferred by lamprey ammocoetes (Farlinger and Beamish 1984). The calculated dispersal indices suggest larvae preferred the margins of the stream, and this is where 85% of the quadrats dominated by fine sediments were located. Almost 60% of the inner quadrats, where few ammocoetes were observed, were dominated by large gravel substrate. Further, significantly fewer ammocoetes were present in upstream reaches predominated by larger substrates.

Ammocoete habitat in Cedar Creek was limited and influenced ammocoete densities. Only 16% of the quadrats sampled were dominated by fine substrates and it was in these substrates that we observed our maximum densities of ammocoetes. Conversely, 50% of the sampled quadrats were dominated by large gravel, and these substrates on average supported no more than one ammocoete. Because there was no significant negative length/abundance relationship, we do not assume biomass saturation or territoriality, though density has been negatively associated with length at larger scales (Roni 2002). However, ammocoetes recovered from large gravel-dominated habitats were significantly larger than those recovered from fine and bedrock dominated substrates. Only the larger ammocoetes make use of the

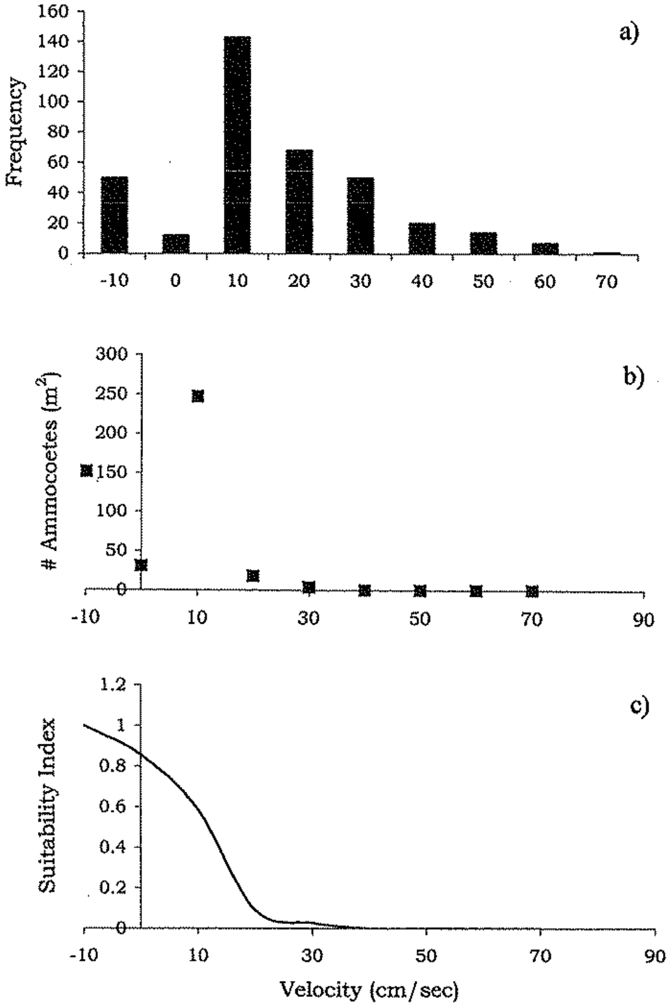

Figure 4. Overall availability (a), level of use (b), and preference (c) of ammocoetes for different water velocities in Cedar Creek, Washington. Negative velocities indicate reverse flow or eddy environments.

most abundant habitat type in Cedar Creek and are usually found in low abundances.

Velocity and substrate preferences of ammocoetes in Cedar Creek were similar to those reported by Close et al. (2003) on the Middle Fork of the John Day River and others (see Farlinger and Beamish 1984), with few exceptions. We observed that ammocoetes preferred eddies, whereas Close et al. (2003) did not report eddies. Additionally, they divided their ammocoetes into size classes and observed larger ammocoetes preferring faster water. They also divided fine substrate into categories of organic debris, silt, and sand, further specifying the ammocoete's preference of silty and sandy habitats over those of organic debris.

On average, ammocoetes were larger in the upper reaches of Cedar Creek. Torgersen and Close (2004) observed this relationship in the Middle Fork of the John Day River. One explanation for this is that the

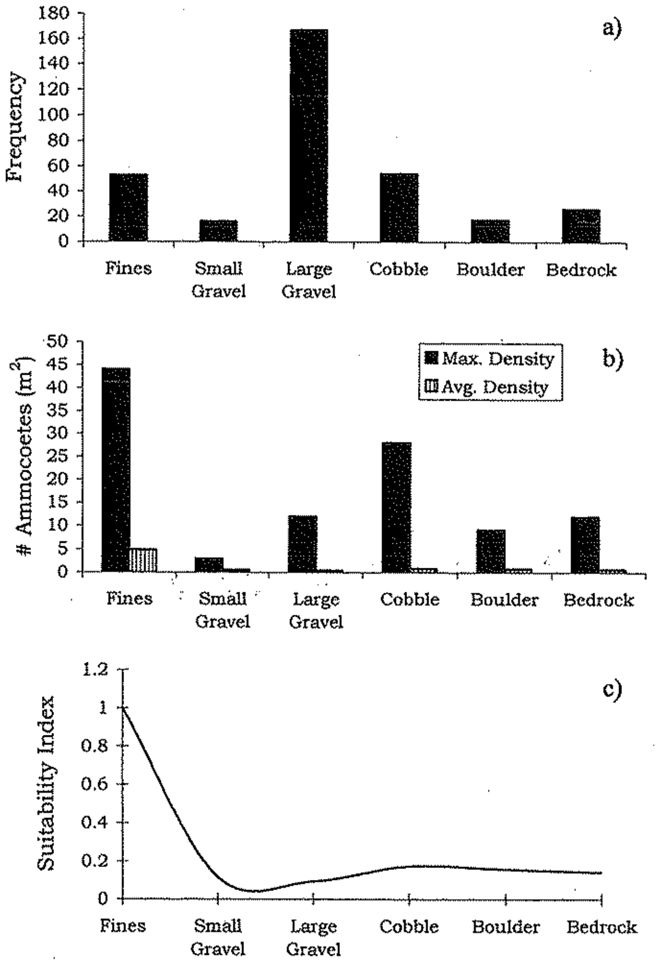

Figure 5. Overall availability (a), level of use (b), and preference (c) of ammocoetes for different dominant substrate types in Cedar Creek, Washington.

stream's headwaters are dominated by large gravel substrates, which favor the larger ammocoetes. Additionally, the ammocoetes residing in the upper reaches of Cedar Creek are subjected to higher velocities during run-off events, and it is likely that the smaller ammocoetes are more susceptible to downstream displacement.

The observed relationship of ammocoete presence to canopy and wetted width likely relates to the complex concepts described by the river continuum concept (Vannote et al. 1980). Increases in riparian canopy reduce autotrophic production by shading the stream (Vannote et al. 1980). The degree of shading along a stream determines the point at which a stream shifts from autotrophic to heterotrophic (Minshall 1978). This concept may help explain the negative relationship observed between ammocoete presence and riparian canopy. Dense canopy shades the stream, reduces autotrophic production, and limits the forage base of ammocoetes. Additionally, this process is tied into stream size (one characteristic of this is wetted width), which we found was positively associated with ammocoete presence, as did Roni (2002). As stream size increases, the reduced importance of terrestrial organic input coincides with enhanced significance of autochthonous primary production and transport of fine organic matter (ammocoete food as well as habitat).

Conductivity was the only reach-scale habitat value that was correlated with ammocoete presence as well as with the proportion of quadrats containing lamprey in each reach. Overall, conductivity was higher in reaches where more ammocoetes were captured. The conductivity values recorded at Cedar Creek were similar to those recorded by Pajos and Weise (1994) during their surveys in June 1989 and 1990 and are not considered excessively low. The relationship that we observed between conductivity and ammocoete presence or abundance might have a mechanical explanation, as will be discussed later. Conversely, it may be a true biological response to increased productivity that is often associated with higher water conductivities (Ryder 1974).

Fewer ammocoetes were observed in Cedar Creek than in other stream systems where systematic sampling has occurred. Torgersen and Close (2004) observed average ammocoete densities of four ammocoetes per sampled meter and a maximum estimated density of $118/m^2$ ammocoetes in the Middle Fork of the John Day River. Their values most likely under-represent the true densities because they only used two passes to form their estimates (White et al. 1982). We observed an overall average of one ammocoete per sampled meter and a maximum abundance of $44/m^2$ in Cedar Creek. It is not likely that differences of this magnitude are entirely due to the different methodologies in reporting abundance. These differences may be related to differences in stream geomorphology and ecology. The Middle Fork of the John Day River is a fourth order, low-gradient, opened-canopied, and productive stream, whereas Cedar Creek is a third order, high-energy, oligotrophic system with a higher riparian canopy density. As we have noted, these variables interact to influence the presence and abundance of Pacific lamprey ammocoetes. However, the observed differences in ammocoete abundance between these two systems also may be influenced by electrofishing efficiencies as a result of water conductivity.

Conductivities recorded in the Middle Fork of the John Day River ranged between 125 and 170 µS/cm (Torgersen and Close 2004). The maximum conductivity recorded on Cedar Creek during sampling was 76 µS/cm. According to Koltz (1989), a fish will receive the maximum shock through its body when the conductivity of the water approaches that of the fish. It is possible that higher densities of ammocoetes were reported in the Middle Fork of the John Day River because water conductivities were closer to that of the ammocoete and sampling efficiencies were higher. This relationship has been documented with sea lampreys (Hintz 1993, Weisser 1994).

Though potentially fewer ammocoetes were captured in Cedar Creek than in the John Day River, overall distribution was similar between the two systems. Torgersen and Close (2004) observed ammocoetes in 93% of the reaches, but in only 31% of the quadrats. We observed ammocoetes in 90% of the reaches and in 24% of the quadrats.

By using this systematic sampling design we observed ammocoetes in unexpected habitats. Many ammocoetes less than 10 mm in length were recovered from bedrock habitats having a thin layer of silt. The silt is fine enough, and the water current in these areas slow enough, to allow these ammocoetes to settle out and burrow.

Dunham and Vinyard (1997) demonstrated the need for incorporating multiple spatial scales into studies that examine fish-habitat relationships. Torgersen and Close (2004) determined that habitat variables explained a significant proportion of variation in ammocoete abundance differently at large and small scales. In our study, we observed that ammocoetes were generally abundant when considered from a large-scale perspective but were relatively uncommon when examined at a smaller scale. Additionally, comparisons made to Torgersen and Close's study (2004), which was conducted in a separate watershed, revealed similarities in distribution and habitat use at both scales but uncovered potential differences in the overall number of ammocoetes present. When considering ammocoete habitat use and distribution, whether for the purpose of evaluating land-use or restoration effects or solely for descriptive purposes, it is important to take into account the scale of the observations.

Our findings, which further confirm the importance of slow water environments for the rearing stage of Pacific lamprey, should be considered in stream habitat restoration projects. Restoration activities should be designed to restore watershed function and process. For example, large woody debris reintroduction in Cedar Creek would both retain sediments and provide the slow water habitats that benefit many species including Pacific lamprey by providing velocity refuges, sediment retention, and increasing overall habitat complexity. These activities are more favorable than those that are designed to benefit one species assemblage, such as salmonid spawning gravel enhancement, which has been the focus in Cedar Creek.

Though our results provide useful information on general trends in ammocoete distribution and habitat use, future studies need to address gear functionality. Detection probabilities need to be determined for proper interpretation of absence events (Peterson and Dunham 2003). Catchability should be addressed for all age classes and across a variety of habitat types. A normalized curve for predicting the increase in power needed to maintain a constant transfer of power at different conductivity ratios (water:fish) needs to be determined as well as the conductivity of the Pacific lamprey ammocoete (Koltz 1989). Until these studies are completed, observations on ammocoete distribution and habitat use should be considered conservatively.

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