Stone et al 2004

Spatial Distribution and Habitat Use of the Western Pearlshell Mussel (*Margaritifera falcata*) in a Western Washington Stream

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ABSTRACT

We investigated the spatial distribution and habitat associations of western pearlshell mussels (*Margaritifera falcata*) in a southwest Washington stream. Variation in mussel occurrence differed with the scale of the observations, being lower among study reaches and higher within reaches. Additionally, mussels exhibited a highly aggregated, non-random spatial distribution pattern. The distribution of mussels at large scales (across reaches) was associated with dissolved oxygen and shear stress. Mussel distribution at small scales (with the 50 m reaches) was associated with wetted width, canopy, abundance of small gravel substrate, and distance from the stream bank. Mussels were found in locations having reduced shear stress, turbulence, and gradient and increased wetted width, abundance of small gravel, dissolved oxygen, and conductivity. Optimum water depth was 0.2 – 0.6 m and optimum current velocity was 0.23 – 0.30 m/sec. Mussels preferred substrates where boulders increased bed roughness, allowing small gravel and sand to create a stable, heterogeneous substrate.

INTRODUCTION

Pearl mussels (*Margaritiferidae*) occupy lotic habitats of holarctic regions (Smith 2001). They are particularly long-lived, with life spans sometimes exceeding 100 years (Vannote and Minshall 1982, Bauer 1987). Like other unionid mussels, pearl mussels have a glochidial stage that is an obligate fish parasite (Smith 2001). Research to date has largely focused on life histories of the European populations of the family with limited investigations conducted in North America (Smith 2001).

Pearl mussels occur in small, stable, oligotrophic streams (Young and Williams 1983, Bauer et al. 1991, Johnson and Brown 1998) and typically exhibit aggregated, non-random distributional patterns (Vannote and Minshall 1982, Johnson and Brown 1998, Hastie et al. 2000). For example, Hastie et al. (2000) observed that *Margaritifera margaritifera* aggregated in boulder-dominated substrate and was generally more abundant in mixed substrate with high diversity. Pearl mussels can be susceptible to rapid stream aggradation. Vannote and Minshall (1982) observed that mussels covered during rapid depositional events were incapable of migrating to the surface and died.

Journal of Freshwater Ecology, Volume 19, Number 3 - September 2004

Like other members of the genus *Margaritifera*, the western pearlshell (*M. falcata*) has declined throughout much of its range (Frest and Johannes 1995), although its status is listed as undetermined by Williams et al. (1993). *M. falcata* originally occurred from southern Alaska south to central California and east to Montana, Wyoming, and northern Utah (Taylor 1981). *M. falcata* has been extirpated from much of the Snake River system and many coastal streams (Frest and Johannes 1995). One concern is that extant *M. falcata* populations are not successfully reproducing/recruiting (Young et al. 2001) and are therefore dominated by older individuals (Toy 1998). Factors attributed to their decline include streambed degradation and destabilization by channel diversion, poor land usage, and nutrient enrichment (Frest and Johannes 1995).

A more complete understanding of *M. falcata's* habitat requirements is needed by conservation and management agencies in western North America. Prior research (e.g., Roscoe and Redelings 1964, Stober 1972, Vannote and Minshall 1982, Toy 1998) focused on conditions within mussel beds (i.e., at the microhabitat scale) but did not systematically evaluate *M. falcata* distribution and habitat associations across multiple scales. Relatively little information is available about the longitudinal distribution of *M. falcata* at a drainage scale. Furthermore, we know little about how stream habitat parameters contribute to *M. falcata* density across spatial scales. Thus, we examined the distribution and habitat associations of *M. falcata* in Cedar Creek, Washington at two scales, reach (50 m) and subreach (1 m^2).

METHODS AND MATERIALS

Cedar Creek is a third-order tributary to the North Fork Lewis River within the Columbia River basin (Fig. 1). Land usage in the 89.3 km^2 drainage is primarily agriculture and silviculture. Stream elevation ranges between 10 and 290 m above sea level. Stream discharge was recorded at a fixed station approximately 4 km upstream of the mouth. Mean daily discharge for 2000, 2001, and 2002 was 4.84 m^3/s (Washington Department of Ecology, unpublished data). Potential fish hosts (Watters 1994) present in Cedar Creek include Chinook salmon (*Oncorhynchus tschawytcha)*, coho salmon (*O. kisutch*), coastal cutthroat trout (*O. clarki*), and steelhead trout (*O. mykiss*) (United States Fish and Wildlife Service, unpublished data).

We sampled 19, nine, and three reaches at base-flow conditions during summer 2000, 2001, and 2002, respectively (Fig. 1) using a systematic sampling design with one random start to evaluate heterogeneity in mussel abundance and distribution. Sample reaches were selected using a Geographic Information System (ArcView) and occurred every 1000 m along the 32 km long stream. Sample reaches were found using a Trimble® Global Positioning System having sub-meter accuracies. Each 50 m reach was divided into six cross-sectional transects spaced 10 m apart. Two 1 m^2 quadrats were positioned along each transect. We placed quadrats in odd-numbered transects at the water's edge and at 1/3 and 2/3 of the wetted width in even-numbered transects. This technique allowed us to sample areas along the stream bank and at a distance from the stream bank. Twelve quadrats were sampled in each 50 m reach.

Water quality parameters (temperature, pH, dissolved oxygen, and conductivity) and stream gradient (surface slope) were recorded at all sample reaches. Wetted width and canopy cover (measured by spherical densiometer; Platts 1987) were recorded for each transect. We measured water depth, velocity (at 60% depth), and substrate type (modified Wentworth, Wentworth

1922) at each quadrat. We removed and measured (total shell and hinge ligament length to the nearest 0.1 mm) all visible mussels but did not disturb the sediment within the quadrats. A maximum of 30 mussels was measured at each quadrat and the remaining mussels were enumerated. All mussels were returned to the stream after measurement. When we did not observe mussels in any quadrats, the reach was carefully searched to assess presence or absence of mussels.

We calculated complex hydraulic variables (e.g., bed shear stress, Froude number, and Reynolds number) because they have been found to be important factors affecting the distribution of mussels and other lotic macroinvertebrates (Hardison and Layzer 2000, Statzner et al. 1988). Unlike other simple habitat measurements (e.g. depth, velocity, substrate), complex variables are generally unrelated to stream size and can therefore provide a more integrative assessment of physical conditions at the water-substrate interface (Hardison and Layzer 2000).

We calculated shear stress (dynes/cm^2) for each reach using the following equation (notation modified slightly from Statzner et al. 1988):

$$t = rgRSe$$

where t is the force per unit area exerted by flowing water on the stream bed, r is the density of the water (1000kg/m^3), g is gravitational acceleration (9.81 m/s), R is the hydraulic radius (defined as channel cross-sectional area divided by the wetted perimeter), and Se is the energy slope (bed slope for the reach). Cross sectional areas were calculated at each transect and were averaged over the reach. Reynolds and Froude numbers were calculated for each quadrat using the following equations (Statzner et al. 1988):

$$\text{Reynolds number: } Re = UD/\upsilon$$

$$\text{Froude number: } Fr = U/(gD)^{0.5}$$

where U is mean current velocity (cm/s), D is mean depth of water (cm), g is gravitational acceleration and υ is the kinematic viscosity of water (cm^2/s).

We assessed the uniformity in the mussel distribution at two scales by examining the percent of reaches (large scale) and quadrats (small scale) with and without mussels. To assess whether mussels were distributed randomly,

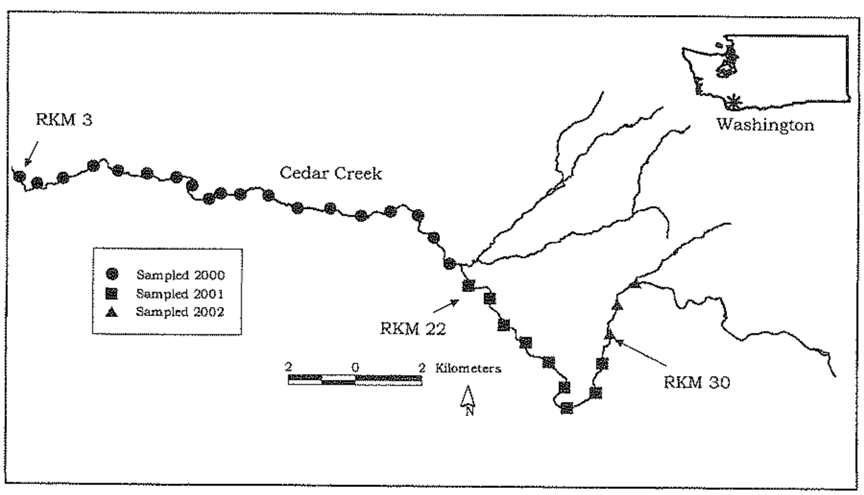

Figure 1. Map of Cedar Creek, Clark County, Washington, with dots indicating location of reaches sampled during 2000 (RKM 3 – 21), 2001 (RKM 22 – 29), and 2002 (RKM 30-33).

we first calculated the dispersal index (*I*= variance:mean ratio) for reaches where at least one mussel was present (Hastie et al. 2000). We then used a χ^2 test to detect non-random aggregations (Elliot 1977). Habitat associations were investigated by establishing habitat preference curves for depth, velocity, and substrate (Hastie et al. 2000) and by conducting two sample Kruskal-Wallis tests (SYSTAT 2002) of individual habitat variables measured in areas with and without mussels. Additionally, multiple regression analysis was performed for a more comprehensive model of the data. All multivariate statistical analyses were conducted using SAS software (SAS Institute 1999). Multicollinearity was assessed using both the collinearity diagnostics tool in SAS and by examining the variance inflation factor (VIF) for each variable. Variables with a VIF exceeding 10 were excluded from the final model (Belsley et al. 1980). Both linear (mussel density or proportion of quadrats containing mussels) and logistic (presence/absence data) models were evaluated using non-transformed and transformed data. Models having the highest AIC (Akaike's criterion) value or variance explained (F-ratio) were retained. Nagelkerke's R^2 was calculated for logistic regression models (Nagelkerke 1991).

RESULTS

A total of 842 mussels was collected from 372 quadrats and the overall mean mussel density was 2.26/m^2. *M. falcata* was abundant in lower Cedar Creek (downstream of RKM 20) but was less common at upstream sites (Table 1). Mussel density was greatest at the midway-point of the stream. At six sites, mussels were not found in the quadrats but were present in the reach at densities below the detection limit of our systematic sampling design. We found few, widely scattered mussels and only one small aggregation in the three most upstream reaches. Mussel density was greatest at the midway-point of the stream.

Mussel occurrence was less variable at the large scale (among reaches) than the small scale (within reaches). Although mussels were present in 21 of 31 reaches (68%) they were found in only 52 of 372 quadrats (14%). Mussel density in the reach was positively correlated with the proportion of quadrats containing mussels ($R^2 = 0.6055$, $P < 0.01$).

Mussels were distributed non-randomly within each reach. The dispersal index (calculated for 13 of the 31 reaches) indicates that mussels were distributed in a highly aggregated fashion and significantly different from a random pattern (X^2, $P< 0.01$) (Table 1).

Mussels were found in 20 to 60 cm water depths in a greater proportion than the depths that were available (Fig. 2). Optimal ranges of 23-38 cm/sec velocities were observed (Fig. 3). Mussels preferred boulder-dominated substrate with patches of small gravel or fine substrate (Fig. 4). This substrate comprised <20% of total available substrate. We observed the highest mussel densities (>120 mussels/m^2) in fine (1 – 8 mm) substrate. Although we did not differentiate between classes of fine sediments (sand vs. silt), this fine substrate seemed to be sandy rather than silty.

Several habitat parameters were significantly different between reaches with mussels and those lacking mussels. Reaches containing mussels had significantly lower shear stress and channel gradient ($P = 0.013$, $P = 0.008$, respectively) than those without mussels. Furthermore, reaches with mussels had higher conductivities ($P < 0.001$) and dissolved oxygen ($P = 0.006$). At the subreach scale, quadrats containing mussels had significantly higher percentages of small gravel, and were located on transects having larger wetted widths, than those without mussels ($P < 0.001$, for both variables). Additionally, quadrats with mussels had a lower Reynolds number than those without ($P = 0.014$).

Table 1. Average values of observed habitat variables and mussel densities in Cedar Creek. Dispersal Index = variance:mean ratio.

RKM	Temp	pH	D. O. (mg/L)	Conductivity (uS/cm)	% Gradient	Shear stress	Water velocity (cm/sec)	Water depth (cm)	% Fines	% Small gravel	% Large gravel	% Cobble	% Boulder	% Bedrock	Substrate diversity	Wetted width (m)	Canopy density (%)	Total length (mm)	# Mussels Observed	Dispersal index
3	15.2	7.8	9.28	63.6	0.1219	0.67	13.79	26.42	0.16	0.31	0.26	0.16	0.05	0.06	2.97	12.55	58.83	50.00	1	11.0
4	17.6	8.2	10.04	67.9	0.4877	1.43	15.75	16.26	0.16	0.26	0.22	0.14	0.10	0.12	3.08	12.37	87.50	48.87	67	737.0
5	15.4	8	8.9	61.7	0.8534	3.34	18.64	18.03	0.13	0.10	0.25	0.28	0.06	0.17	2.77	14.71	70.17	50.82	12	54.0
6	16.3	8.2	9.12	64.5	1.4265	5.99	12.62	22.86	0.10	0.03	0.22	0.30	0.16	0.18	2.70	11.49	83.25	-	0	0.0
7	13.7	7.6	10.22	63.2	1.3655	6.09	7.29	20.14	0.20	0.12	0.19	0.11	0.15	0.24	3.18	14.96	58.17	67.84	17	79.7
8	13.8	7.8	10.38	65.2	0.7803	5.04	9.40	27.56	0.21	0.12	0.24	0.30	0.11	0.02	3.00	14.20	34.33	38.39	16	83.0
9	14.3	7.5	9.77	60.5	0.6096	3.88	17.37	27.65	0.11	0.04	0.13	0.21	0.17	0.34	2.16	16.41	55.33	-	0[a]	0.0
10		8.1	7.29	75.7	0.5974	4.40	10.06	35.94	0.33	0.14	0.24	0.07	0.12	0.09	2.49	13.12	67.83	60.35	143	1155.8
11	16.2	8.1	9.57	69.4	0.4633	1.24	11.79	13.46	0.13	0.33	0.30	0.16	0.08	0.00	2.97	12.45	80.08	62.26	316	1709.0
12	13.1	7.6	10.18	68.1	0.5121	1.17	12.88	11.30	0.21	0.26	0.46	0.04	0.03	0.00	2.45	12.86	79.08	63.21	129	301.0
13	13.4	7.6	9.6	54.1	-	-	14.15	24.33	0.16	0.17	0.52	0.15	0.00	0.00	2.34	7.51	35.00	61.43	19	164.8
14	14.7	8.1	10.62	70.7	-	-	4.11	24.26	0.33	0.12	0.40	0.14	0.01	0.00	2.40	12.98	37.00	59.14	15	78.6
15	12.4	7.7	11.83	58.8	0.1524	0.49	11.02	19.51	0.16	0.15	0.43	0.23	0.03	0.00	1.99	10.32	72.08	66.19	42	294.6
16	13.4	7.8	9.84	67.6	0.2743	0.87	12.34	19.25	0.07	0.15	0.40	0.11	0.19	0.08	2.54	9.06	29.00	61.25	17	58.5
17	13	8.1	11.16	65.9	-	-	10.03	26.19	0.25	0.10	0.19	0.03	0.00	0.43	1.69	12.09	50.00	-	0[a]	0.0
18	12.2	7.8	9.72	42.3	-	-	9.28	25.15	0.21	0.21	0.55	0.04	0.00	0.00	2.22	8.94	41.17	-	0[a]	0.0
19	13.7	7.8	11.42	69.4	1.1948	2.68	22.94	14.02	0.17	0.29	0.54	0.00	0.00	0.00	1.99	8.67	67.50	62.69	19	186.3
20	13.2	7.4	10.98	69.6	0.4328	1.15	12.37	15.90	0.16	0.20	0.43	0.15	0.06	0.00	2.65	9.59	72.00	61.72	28	284.9
21	13.9	7.7	10.64	67.2	0.2499	1.25	13.23	30.15	0.15	0.15	0.52	0.10	0.08	0.00	2.52	9.32	31.33		0	0.0
22	12.6	7.6	7.25	51.4	0.955	0.56	18.95	14.61	0.18	0.10	0.31	0.21	0.01	0.19	2.46	6.25	49.08	41.00	1	11.0
23	13.2	7.6	5.53	54.7	1.5596	1.37	14.20	17.27	0.16	0.09	0.39	0.33	0.02	0.02	2.99	6.90	81.92	-	0	-
24	12.4	7.6	4.75	55.8	1.3259	1.06	13.87	14.35	0.09	0.07	0.39	0.42	0.03	0.00	2.46	7.44	70.00	-	0	-
25	12.9	7.8	7.12	55.6	1.209	1.38	11.96	21.34	0.17	0.04	0.38	0.38	0.02	0.01	2.49	7.04	38.00	-	0	-
26	13.6	7.6	5.3	35.2	0.9957	0.83	10.36	17.27	0.23	0.10	0.34	0.33	0.01	0.00	2.57	6.52	75.58	-	0	-
27	12	7.8	5.38	38	1.8085	1.31	6.63	15.11	0.23	0.13	0.33	0.28	0.03	0.00	3.42	6.57	85.25	-	0	-
28	16	7.4	4.24	39.6	0.9246	0.73	8.66	12.57	0.34	0.13	0.35	0.15	0.03	0.00	2.97	8.93	89.92	-	0[a]	-
29	15.5	7.4	7.28	38.4	0.1676	0.15	7.67	21.59	0.43	0.12	0.32	0.11	0.01	0.00	2.46	5.46	57.67	-	0[a]	-
30	15.6	7.6	4.63	41.5	1.1633	0.85	17.17	15.62	0.35	0.13	0.35	0.15	0.02	0.00	2.54	6.25	81.42	-	0	-
31	15.6		8.93	38.7	3.3976	1.18	19.90	12.83	0.13	0.07	0.58	0.17	0.01	0.04	2.02	3.67	60.42	-	0[a]	-
32	12.6	7.7	8.15	31.7	3.7856	2.90	7.70	19.94	0.21	0.09	0.57	0.13	0.00	0.00	2.00	5.09	52.83	-	0	-
33	13.6	7.8	9.57	28.1	4.6175	1.39	2.57	11.43	0.04	0.10	0.51	0.34	0.01	0.00	2.48	3.32	82.50	-	0	-

[a]Indicates that mussels were present but below the detection rate of our sampling design.

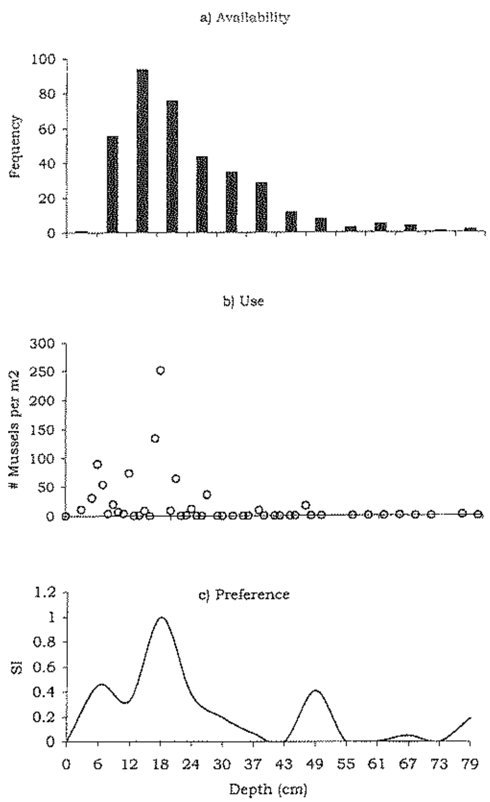

Figure 2. Overall availability (a), level of use (b), and preference of mussels (c) for different water depths in Cedar Creek. SI = habitat suitability index.

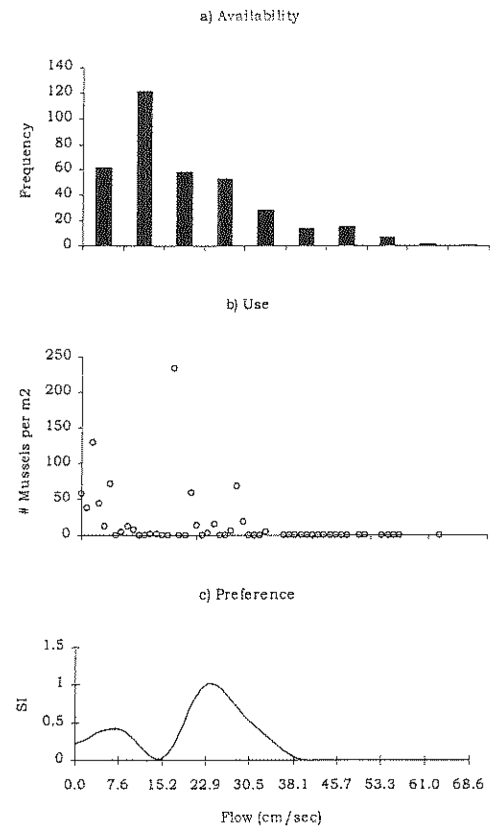

Figure 3. Overall availability (a), level of use (b), and preference of mussels (c) for different water velocities in Cedar Creek. SI = habitat suitability index.

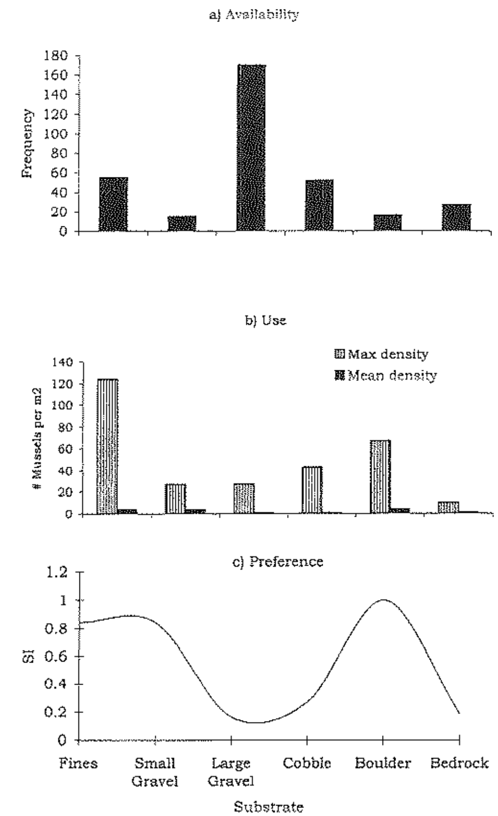

Figure 4. Overall availability (a), level of use (b), and preference of mussels (c) for different substrate types in Cedar Creek. SI = habitat suitability index.

Forward regression analysis conducted at the reach scale revealed that shear stress (-) and dissolved oxygen (+) could predict presence of mussels 92% of the time (Nagelkerke's $R^2 = 0.67$, $P < 0.05$). Conductivity was positively and significantly related to the proportion of quadrats containing mussels in each reach ($P = 0.006$), though these data were highly variable ($R^2 = 0.2888$). At the subreach scale, wetted width (+), percent small gravel (+), and location of quadrat (margin), could predict presence 83% of the time (Nagelkerke's $R^2 = 0.31$, $P < 0.001$). Only wetted width and canopy were positively correlated with mussel density at the subreach scale ($P = 0.0087$, $P = 0.035$, respectively), although they had low predictive capability ($R^2 = 0.0189$).

The length distribution of *M. falcata* was normally distributed but skewed to smaller individuals (Figure 5). Mean shell length was 61 mm (n = 470) and ranged from 8 to 95 mm. Average length of mussels per reach increased with increasing distance from the mouth ($R^2 = 0.4070$, $P = 0.0256$).

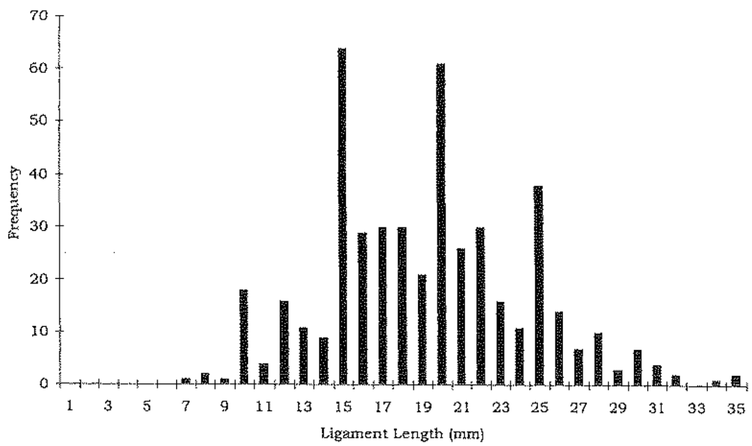

Figure 5. Ligament length frequency of sampled *M. falcata*.

DISCUSSION

M. falcata spatial distribution in Cedar Creek was non-uniform and aggregated and this aggregation was particularly pronounced at the subreach scale. These results are consistent with previous studies of this species at more localized scales (Roscoe and Redelings 1964, Stober 1972, Vannote and Minshall 1982), as well as studies of other *Margaritifera* species (Young and Williams 1983, Bauer 1987, Johnson and Brown 1998, Hastie et al. 2000). The water chemistry and physical factors observed in this study likely contributed to this aggregated distribution. However mussel occurrence and spatial distribution may also be limited by other factors, including host presence and previous hydrological changes to the stream (Hastie et al. 2000).

Numerous variables were recorded in this study to associate habitat with mussel presence and abundance. Many of these variables were highly correlated with each other and some were highly correlated with stream distance. Although few habitat variables directly affect mussel presence and abundance (i.e., substrate composition), many more variables have indirect and confounding effects (i.e., riparian canopy, water velocity). The physical variables within a stream are a continuous gradient of conditions determined by wetted width, depth, velocity, etc. (Vannote et al. 1980).

Shear stress was significantly lower in reaches with mussels than in those without mussels. However, this measure of streambed stability could not predict mussel density, as has been done with other benthic organisms (Hardison and Layzer 2000, Statzner et al. 1988). This suggests that the scale at which we calculated shear stress (50 m reach) may be too large to explain the variability in mussel density. Because mussels were highly aggregated within reaches, shear stress or other complex hydraulic characteristics measured at a smaller scale might reveal further relationships.

One complex hydraulic variable we measured at the subreach scale, the Reynolds number, was significantly lower in quadrats containing mussels and indicates a preference for less turbulent flow. Though all of the Reynolds numbers we calculated indicate turbulent flow (>10,000; Allan 1995), we speculate that conditions in quadrats having higher Reynolds numbers may reduce the settling ability of *M. falcata* after excysting from host fish. Quadrats having higher Reynolds numbers likely have lower substrate stability.

As with previous studies (Stober 1972, Vannote and Minshall 1982), we noted that mussels preferred habitats having small gravels and sand in association with boulders. Vannote and Minshall (1982) attribute this relationship to streambed stability and the mussel's ability burrow deeply and avoid displacement. Larger substrates, particularly boulders, are relatively rare in the watershed. Toy (1998) observed that large woody debris provided stable habitat for *M. falcata*. However, because large woody debris is rare in Cedar Creek, boulders are the most important factor affecting bed roughness and shear stress.

The range of depths used by mussels in Cedar Creek generally agrees with those reported in previous studies of *M. falcate*. Stober (1972) recorded water depths of 0.5 - 0.8 m and Vannote and Minshall (1982) observed mussels at depths of 1 - 2 m. Though similar, the minimum depths they observed were deeper than the minimum depths we observed. In some northern European habitats, minimum depth for *M. margaritifera* was not shallower than 0.5 m, presumably because of the effects of ice in shallower depths (Hendelberg 1961). Whereas the effects of ice may have influenced the minimum depths reported by Stober (1972) and Vannote and Minshall (1982), ice formation is very rare in Cedar Creek. The depth preferences of mussels observed (0.2-0.6 m) in Cedar Creek are similar to those reported for *M. margaritifera* (summarized by Hastie et al. 2000).

The observed water velocities used in Cedar Creek are consistent with the 0.38-0.69 m/s reported by Stober (1972) for *M. margaritifera*, the 1 m/s described by Vannote and Minshall (1982) for *M. falcata*, and the 0.25-0.75 m/s described for *M. margaritifera* by Hastie et al. 2000. The velocity preferences of mussels observed in Cedar Creek are similar to those reported for *M. margaritifera* (summarized by Hastie et al. 2000).

Among physical habitat parameters, the positive relationship between riparian canopy density and *M. falcata* occurrence in Cedar Creek is most puzzling. Gittings et al. (1998) noted a similar relationship in a stream in Ireland for *M. margaritifera*, and Morris and Corkum (1996) noted that mussel species composition in southwestern Ontario streams changed between forested stream and reaches with grassy riparian zones associated with agriculture. In the latter study, the change in species composition was attributed to the differences in water temperature regimes and nitrogen concentrations, both attributes we did not measure.

Although stream width may influence mussel distribution, its influence in this study may be combined with changes in stream morphology and associated hydraulic parameters. Wetted widths in upper reaches of Cedar Creek (mean of 6 m) are similar to those Toy (1998) reported for *M. falcata* and

Johnson and Brown (1998) described for *M. hembeli* populations in Louisiana, where the species were present in high densities. However, they reported stream gradients of <1%, whereas in upper Cedar Creek, gradients averaged 2% or higher. Wetted widths in the lower reaches of Cedar Creek, where mussels were abundant, averaged 12 m with mean gradients <1%. Gradient strongly influences stream morphology, determining characteristics of substrate composition and stability, thereby influencing mussel distribution (Vannote and Minshall 1982, Hastie et al. 2000).

The mussels sampled in Cedar Creek were normally distributed in size with few small mussels observed. This observation is likely an artifact of our sampling technique and is not evidence to support recruitment deficiencies. Toy (1998) reported that juvenile *M. falcata* <30 mm were rare and she presumed they used different microhabitats than adults. In a later investigation, she found juvenile mussels by specifically targeting and sifting sandy sediment behind hydraulic controls, such as large woody debris structures. Hastie et al. (2000) reported that juvenile *M. margaritifera* were frequently buried and were not visible through surface examinations. Additionally, smaller mussels (<20 mm) are light-colored and difficult to see against the streambed. Thus, it is likely that juveniles were missed during our sampling efforts. Additionally, the relatively uniform size classes of smaller, mature-sized mussels indicate steady recruitment over recent years.
The normally distributed and apparently young *M. falcata* population in Cedar Creek may indicate a susceptibility of larger adult mussels to extreme flow events. Our results contrast most other studies of *M. falcata* (Stober 1972, Toy 1998) and *M. margaritifera* (summarized by Hastie et al. 2000), where age distributions were skewed towards larger, older mussels. Both Vannote and Minshall (1982) and Toy (1998) purported that *M. falcata* age distributions skewed toward older individuals was indicative of more stable habitats, whereas distributions similar to what we observed indicated less stable habitats. Cedar Creek is considered a hydrologically variable environment due to rain-on-snow events experienced during the winter months. Over the past three years, discharge in Cedar Creek has ranged between 0.22 and 40 m^3/sec (Washington Department of Ecology, unpublished data). Periodic streambed scour keeps populations relatively young with an approximately normal size distribution; additionally, unsuitable orientation after displacement and burial of mussels, especially larger mussels, is a known source of mortality (Vannote and Minshall 1982).

Our results show that assessing mussel occurrence and habitat use is highly dependent upon the scale of the observations, largely due to the aggregated structure of these populations. Regardless of scale, habitat stability was the driving force in determining mussel occurrence, abundance, and population structure in this study. Complex hydraulic characteristics, such as shear stress and turbulence (i.e. Reynolds number), need to be considered when associating mussels to their environment, as individual measurements of water velocity and depth, for example, can form an incomplete and inaccurate description of habitat.

ACKNOWLEDGEMENTS

We would like to thank Jodi Pirtle, Travis Collier, Tim Sundlov, and Donna Allard for field assistance, Christian Torgerson for his insights on study design, Henry Yuen and Matt Mitro for statistical assistance, and Travis Coley for administrative support. We are grateful to Columbia River Fisheries Program Office staff for their constructive reviews of an earlier draft of this manuscript. Finally, we thank the landowners on Cedar Creek for granting us access and allowing us to conduct this research. The U. S. Fish and Wildlife Service funded this project.

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Received: 1 November 2003

Accepted: 5 February 2004