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Freshwater mussels in a California North Coast Range river: occurrence, distribution, and controls

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Abstract. We report the occurrence and habitat of mussel populations within a continuous 8-km section of the South Fork Eel River in the Northern Coast Range of California. The primary goals of our study were 1) to compile information on species composition and population density, and 2) to examine whether spatial distribution and variability were related to geomorphology and hydrology. High discharges almost certainly provide more of a constraint on the distribution and persistence of mussels in the South Fork Eel than do low summer flows, so we used the Hydrologic Engineering Center's River Analysis System (HEC-RAS) hydraulic model to estimate physical conditions during high flows when in-channel investigations were not feasible. We found numerous individuals of 2 species (*Margaritifera falcata* and *Anodonta californiensis*), with the spatial distribution of both species characterized by high variability. Mussels in this system live almost exclusively in pools (with a few in runs), near the channel banks, and especially among sedge root-mat substrate. In all flow regimes (summer, winter, 5-y flood, and the largest floods on record), we found mussels in areas of lower boundary shear stresses and lower velocities. Our study suggests that, at various spatial scales, mussels appear to be distributed in a manner that protects them from the highest flow-induced stresses.

Key words: freshwater mussels, California, geomorphology, hydrology, hydraulic model, shear stress, microhabitat, South Fork Eel River.

Over the past decade, freshwater mussels have been the subject of numerous studies in many regions of the United States because of rapid mussel population declines (Bogan 1993, Williams et al. 1993, Nott et al. 1995, Neves et al. 1997, Brim Box and Williams 1999). Yet, little is known about the landscape-scale controls on habitat, and characterization of population distributions at this scale remains poor. We broaden this perspective by exploring the variability of mussel distributions in relation to physical constraints associated with flow conditions and channel character in the South Fork Eel River in the Northern Coast Range of California.

The conservation biology of freshwater mussels in this region is interesting for several reasons. First, mussels are sensitive to a wide variety of environmental changes (Williams et al. 1993) because their riverbed habitat depends on channel hydraulics and sediment transport. Mussels, therefore, provide a particularly rich opportunity to study the link between hydrology, geomorphology, and biology. Second, knowledge about California mussel populations is scant. The only distributional checklist of freshwater mollusks in the State speculated that

4 of the 5 mussel species that historically occurred (*Anodonta californiensis*, *A. wahlamatisensis*, *Gonidea angulata*, and *Margaritifera falcata*) were probably eradicated from most of their original ranges (Taylor 1981). The status of the 5th species (*A. oregonensis*) was not listed.

Third, watersheds in California have undergone massive urbanization, water diversion, logging, and agricultural development over the past century. Mussel populations are sensitive to changes throughout a watershed because they depend on suitable riverine habitat. *Margaritifera falcata*, a species with life spans >100 y, may provide long-term insights into the timing and impacts of watershed changes if the controls on their habitat and growth are understood. Fourth, mussels depend on fish hosts for larval development (Matteson 1955, Fuller 1974, Oesch 1984), so they may be seriously affected by the recent decline of salmonid populations in California.

The goals of our study were to compile information on abundance and species composition of mussels in the South Fork Eel River study area, and to examine whether the observed spatial distribution and variability within that area were related to characteristics of geomorphology and microhabitat. Four specific questions

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were addressed: 1) How are mussels distributed with respect to the pronounced longitudinal variations of channel type (the structure of pools, riffles, and runs)? 2) Are mussels uniformly distributed within a given channel type? 3) Do mussels preferentially occur in certain types of microhabitat? 4) Are mussels found in refuge areas of the river channel where hydraulic stresses are low during floods?

Methods

Study site

Our study area is an 8-km section of the South Fork Eel River and its tributaries in the Northern California Coast Range (Fig. 1). These rivers are part of the Eel River system, the 3rd largest in California, with a total watershed area of 1783 km², and an elevation range of 30 to 1370 m. The study area is within the Angelo Coast Range Reserve, part of the University of California Natural Reserve System, which protects natural land for research. Vegetation in the watershed is primarily old-growth Douglas fir (*Pseudotsuga menziesii*) and redwood (*Sequoia sempervirens*) forest with only minor human modifications.

Subduction zone tectonics cause high rates of rock uplift in this region, which, combined with mechanically weak bedrock (Lisle 1990, Seidl and Dietrich 1992), result in steep, unstable hillslopes. As a consequence, sediment yields and fluxes are variable and high (Clarke 1992, Mount 1995), among the highest in North America (Cleveland 1977, Lisle 1990).

The channel in the study area is 4th order and the average gradient is 0.0044 but is highly variable on the scale of 10 to 100 m. There is a well-defined alternating pool-riffle structure, with a few places along the channel having slopes intermediate between pools and riffles. These intermediate-slope sections are referred to as runs. Much of the study area lacks a floodplain, and is dominated by incised cobble river terraces and bedrock.

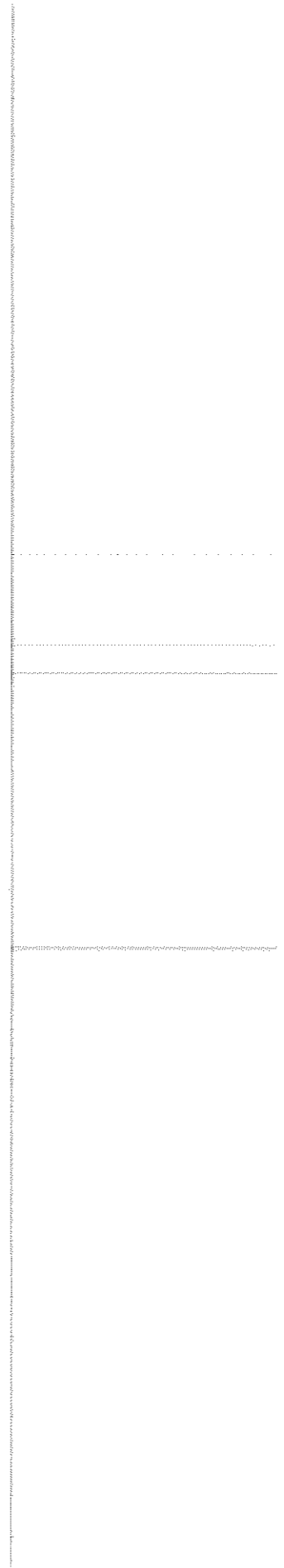
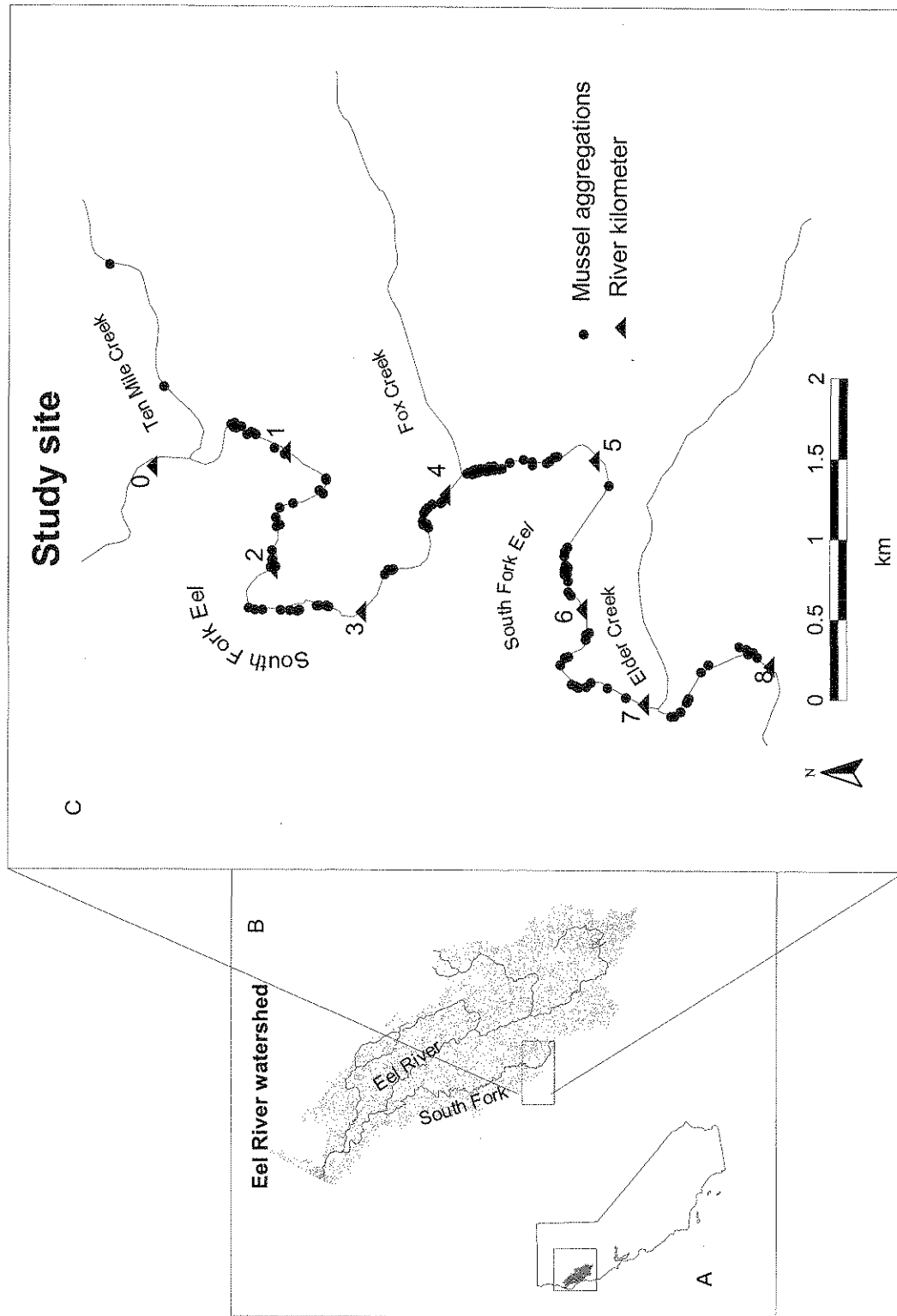
The hydrology of the basin is characteristic of

a Mediterranean climate: a seasonal cycle of warm and dry summers but wet and cool winters, during which high-intensity rainfalls produce high peak discharges. The hydrologic consequence is a seasonally predictable cycle of flooding in winter and near drought in summer. Lowest flows generally occur in September with means ranging from 0.03 to 0.25 m³/s (US Geological Survey [USGS] 35-y period). January is the wettest month with mean discharges ranging from 1 to 40 m³/s. The largest floods on record occurred in 1955 and 1964 with discharges of 478 and 469 m³/s, respectively.

Channel geomorphology

The topography of the study reach was intensively measured (2-m horizontal and <20 cm vertical resolution) using helicopter-based laser altimetry surveys (W. E. Dietrich, University of California, Berkeley, unpublished data). The 2-m horizontal resolution is 15× higher than the horizontal resolution of typical elevation data (e.g., digital elevation models, topographic maps). These data provided the topographic and spatial framework for the hydrologic model (see below), and ensured an accurate representation of the pool-riffle-run structure. Extensive ground-truthing was achieved by mapping channel geomorphology during the mussel surveys; all pools, riffles, and runs along the 8-km stretch were georeferenced with a global positioning system (GPS) and their dimensions directly measured during late spring flows. The velocity differences among pools, riffles, and runs in the study site are pronounced, with velocities in pools and riffles typically being 0.05 and 0.5 m/s, respectively. The velocity of runs fell between pools and riffles. Runs were easily distinguishable from riffles as areas with greater depths and less turbulent flow. Therefore, we had no trouble visually distinguishing among the channel types. The type of channel occupied by each mussel aggregation was identified as 1 of 3 geomorphic units: a pool, riffle, or run. Typical depths in riffles were <0.15 m, whereas depths in runs were generally 0.15 to 0.25 m.

FIG. 1. The study area. A.—Location of the Eel River watershed in northern California. B.—The Eel River watershed and the location of the Angelo Coast Range reserve. C.—Location of mussel aggregations in the South Fork Eel River.



Channel morphology was characterized for all geomorphic units for incorporation into the US Army Corps of Engineers' HEC-RAS (Hydrologic Engineering Center's River Analysis System) model (see below). Cross-sectional topography was measured (using a surveyor's rod and/or a total surveying station) along transects with locations selected so that they crossed the largest mussel aggregations, areas where mussels were absent, and riffles both upstream and downstream of the geomorphic unit. All cross sections were georeferenced and incorporated into the HEC-RAS model. Using an ArcView geographic information system (GIS), all mussel aggregations were assigned to the nearest cross section within the geomorphic unit.

In addition, velocities were measured every m across the channel with a Marsh McBirney Flo-mate Model 2000 portable flowmeter (6 cm above the bed and 6 cm below the water surface in pools; 0.6 depth below the water surface in riffles) to calculate average velocity at a cross section. Velocities were <0.05 m/s in pools, so mean velocities were calculated using the unorthodox 6 cm below the water surface in an attempt to characterize wind-driven velocities (not calculated by the model). Although both the flowmeter and the model readily identify zones of low velocity (<0.05 m/s), the accuracy of model and measured magnitudes <0.05 m/s was low.

HEC-RAS hydrologic model

Cross-sectional topography and velocity were measured during June low discharges. However, higher discharges may constrain the distribution and persistence of the mussels. To estimate physical conditions during higher flows when in-channel investigations were not feasible, a 1-dimensional steady flow hydraulics model was adopted using a combination of Arcview GIS and the HEC-RAS software. The model calculates flow depth and velocity using conservation of mass and energy, and a boundary friction formulation for an open-channel, turbulent flow (Hoggan 1989, 1997, US Army Corps of Engineers 1995). Given a discharge, this model provides estimates of spatial patterns of velocity, boundary shear stress, and surface slope along the channel. Model results are useful for estimation of general patterns, but are approximate

because the details of small-scale topographic and substrate variability are not resolved.

Three types of data are needed to construct the model: 1) basic geometric data consisting of a river network (including tributary junctions), measured cross-sectional data, and cross-section positions along the channel; 2) discharge data; and 3) roughness factors (Manning's n). The high-resolution laser altimetry data provided the 3-dimensional representation of the land surface used to specify mainstem channel elevation and bank topography.

The variability of the types of flows mussels may experience over their lifetimes was captured by performing model runs for typical winter flows, for the 5-y flood, and for the exceptionally large flood that occurred in 1964. Results were also calculated for summer flows for comparison with our measurements.

Discharge data were provided by the USGS Water Resources Division. A gauging station is located on the reserve (station # 11475500, identified as the Branscomb station by the USGS), and daily flow data were available from 1946 to 1970 and from 1991 to the present. The average summer-month and winter-month flows from this data set were henceforth used to represent summer and winter discharge regimes. The 5-y flood magnitude was estimated from the 35-y annual flood data as the flood of rank given by $(N+1)/5$, where N is the number of years of record.

The following Manning's n values were initially used at all cross sections: pools = 0.03, runs = 0.04, and riffles = 0.045. The HEC-RAS model was sequentially refined by adjusting Manning's n values until observed and predicted velocities at the cross sections during summer flows were reasonably well matched ($r^2 = 0.78$, $p < 0.001$). For the remainder of this paper, summer flow velocities are those actually measured, and velocities for higher-discharge conditions are model results.

Survey of mussels and their locations

Detailed field surveys were conducted during the spring and summer of 2000 and 2001 to document the occurrence of mussels along the study reach. Two km on each of the 3 main tributaries, Ten Mile, Elder, and Fox creeks were also included. Surveys were conducted by snorkel

keling and wading shallow reaches, and diving in the deepest pools (up to 7 m).

The channel was divided into geomorphic units (pools, riffles, and runs) for the mussel surveys, which began at the downstream end of each unit near the right ascending bank. The surveyor moved upstream looking left and right. At the upstream end of the geomorphic unit, the surveyor turned and moved downstream along a path ~2 m offset from the previous path (peripheral vision was clear for at least 1 m). This method was continued until the entire geomorphic unit was searched. For example, if a channel reach was 20 m wide, the surveyor would make 10 passes in the reach. In areas too shallow to snorkel, the investigator walked the reach in the same manner. SCUBA was used in pools too deep to view the substrate.

Mussel aggregations were marked with flagging tape at either the upstream or downstream end of an aggregation. Once the entire geomorphic unit had been visually searched, the flagged areas were revisited and the area of the mussel aggregations marked and measured. The visible mussels within each aggregation were counted and identified to species.

Mussel aggregations were defined as ≥ 10 individuals, separated from adjacent groups by > 1 m of unoccupied substrate. Approximately 100 isolated individuals (0.5% of the total number of mussels) did not fit our definition of an aggregation and were excluded from our analyses. Georeferenced coordinates for each aggregation were obtained with a handheld GPS for incorporation into the GIS.

Buried mussels may have been missed by using visual searches, but most mussels within the study reach were probably found. The study reach was inspected for mussels on 3 separate occasions to ensure that mussel aggregations were not missed. Additional aggregations were never found in the study area, and the reproducibility of visual counts of individuals was high ($< 5\%$ maximum error). In addition, $\sim 5\%$ of the study area was surveyed by an independent researcher (Jayne Brim Box, US Forest Service, Logan, Utah) who located the same aggregations within specified reaches.

Mussel densities.—Mussel survey data were used to calculate the total linear density (number of mussels per m length of channel) along the 8 km of the South Fork Eel, using 50-m sec-

tions ($D_L^{(50)}$). Variations in linear densities could arise from variations in channel width if mussels were uniformly distributed across the channel. Likewise, variations in areal densities could arise from variations in channel width if mussels only inhabited a zone of uniform width along channel banks. Linear densities were used in our calculations because the latter scenario more accurately reflected mussel distribution in our study system (see results). Nevertheless, linear and areal densities were highly correlated ($r^2 = 0.90$, $p < 0.001$), so results presented below are valid for both of these measurements.

For analyses using HEC-RAS results, the density of mussels assigned to a cross section was characterized by defining a measure of linear density ($D_L^{(x)}$, individuals/m length of channel) for the portion of a geomorphic unit around the cross section as:

$$D_L^{(x)} = \frac{T_m}{\left(\frac{X_u - X_d}{2}\right)} \quad [1]$$

where T_m is total number of mussels assigned to the given cross sections, and $X_u - X_d$ is the distance between the nearest cross sections upstream and downstream from the given cross section.

It is conceivable that mussel aggregations could be assigned to an incorrect geomorphic unit, but this possibility did not occur in our analysis. A sufficient number of measured cross sections ensured that linear densities were assigned to correct geomorphic units.

Subset of aggregations for detailed characterization.—A subset of mussel aggregations was selected for more detailed measurements and analysis. First, all of the geomorphic units with > 500 mussels (there were 11) were selected. Between these areas were large gaps, and from these gaps additional geomorphic units were randomly selected so that no gaps > 500 m in length remained. The additional random selection was made before microhabitat characterization was conducted (see below). A total of 22 geomorphic units was selected for the characterization and analyses of microhabitat.

Microhabitat characterization.—Substrate type, spatial occurrence within the channel, channel cross sections, and flow velocities were examined to understand the physical conditions at the mussel beds within the microhabitat subset,

and to determine if mussels were randomly situated within geomorphic units. Aggregations within the representative subset were sampled by randomly placing 0.5-m² quadrats within them. A sufficient number of quadrats was used to ensure that $\geq 10\%$ of the aggregation was included. Quadrats included $\geq 50\%$ of the whole aggregation for aggregations with < 300 individuals. All mussels visible within the quadrat were measured. The top 10 cm of substrate within the chosen quadrats were excavated and examined using a 2-mm mesh sieve to uncover small individuals (< 10 mm) not visible from the surface. Less than 0.5% of individuals counted within the quadrats were found in this manner. Substrate type was identified and recorded for all individuals within the quadrats. Substrates were classified as bedrock, boulder (> 250 mm), cobble (60–250 mm), gravel (2–60 mm), sand (< 2 mm), or sedge root mats (*Carex nudata*).

For each aggregation, the inhabited area, distribution of water depths, distance of the mussel furthest from the bank (defined as the zone ≤ 3 m from the edge of water), and areas of substrate types were measured. The area of substrate types was also characterized at the larger scale for the entire geomorphic unit (pool, run, or riffle).

Preferential associations of mussels with certain substrate types were determined by calculating the average areal density (D_a , no./m²) for each substrate type as M_s/A_s , where M_s is the total number of mussels in a given substrate type, which has a total area of A_s in the entire study area. These densities were calculated for the entire channel and for the banks. For each pool and pair of banks, the null hypothesis was that the proportion of mussels in each habitat type was equal to the proportion of habitat available. Observed and expected frequencies were compared using χ^2 tests.

The extent to which variation in the total number of mussels between different geomorphic units resulted simply from variations in the total area of different substrate types was explored. If area of substrate of a given type is the dominant control on mussel occurrences, then number of individuals in a geomorphic unit should be predicted by a simple relationship:

$$M_p = [(D_{aB})(A_B)] + [(D_{aBo})(A_{Bo})] + [(D_{aC})(A_C)] \\ + [(D_{aG})(A_G)] + [(D_{aS})(A_S)] + [(D_{aR})(A_R)] \quad [2]$$

where M_p is the predicted number of mussels found in a given reach, D_a is average areal density computed over the entire 8-km study reach for a given substrate, and A is area of substrate type in the given geomorphic unit. Substrate types are bedrock (_B), boulder crevices (_{Bo}), cobble (_C), gravel (_G), sand (_S), and sedge root mats (_R). These predicted values were compared with the actual numbers of mussels in each reach.

Results

Mussel distribution and densities

Margaritifera falcata and *A. californiensis* were found living in the upper reaches of the South Fork Eel River. *Anodonta californiensis* has been identified by the State of California as a "species of special concern". One hundred and fourteen aggregations were found (Fig. 1), occupying 33 geomorphic units (out of a total of 80 pools, runs, and riffles), and totaling $\sim 12,000$ *M. falcata* (Fig. 2A) and $\sim 8,000$ *A. californiensis* (Fig. 2B). Only 2 small aggregations of mussels (10 and 7 *M. falcata*) were found on a 2-km reach of Ten Mile Creek, a tributary similar in drainage area to the South Fork Eel in the reserve (Fig. 1). No mussels were found on either Elder or Fox creeks.

Spatial variation of mussel density in the study area was high. Distributions of both species were patchy, with a few local areas of exceptionally high density and aggregate size. The frequency distribution of $D_a^{(50)}$ and aggregate size were approximately exponential (Figs 2C, D, 3A, B). Aggregations of *M. falcata* were distributed along the entire 8-km length of channel (Fig. 2B), whereas *A. californiensis* were completely absent from the upper 75% of the study area (Fig. 2A). Most aggregations of both species had between 50 and 100 individuals (Fig. 3A, B). The largest aggregation of *M. falcata* consisted of ~ 1100 individuals in a 78-m² area (Fig. 3B). The largest numbers of *A. californiensis* were found in a 100-m long pool at the downstream end of the study area where ~ 6300 individuals occurred in 2 aggregations (Fig. 3A).

Relationship to flow conditions and geomorphology

Some of the variability of mussel distribution was clearly related to physical constraints associated with flow conditions and channel char-

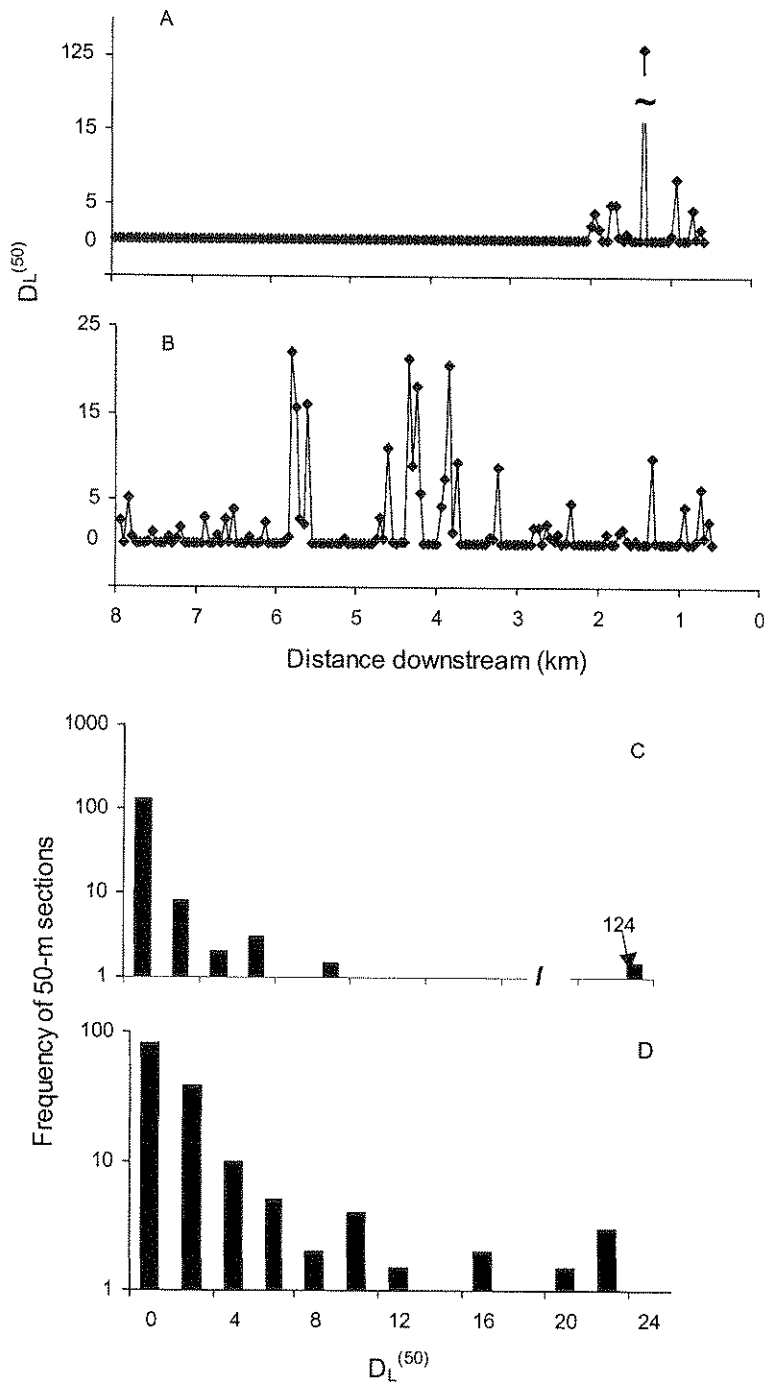


FIG. 2. Distribution of mussels in the South Fork Eel River. A, B.—Density of *Anodonta californiensis* (A) and *Margaritifera falcata* (B) in 50-m channel sections ($D_L^{(50)}$). C, D.—Frequency distribution of *A. californiensis* (C) and *M. falcata* (D) densities. Note the log scale on the y axis.

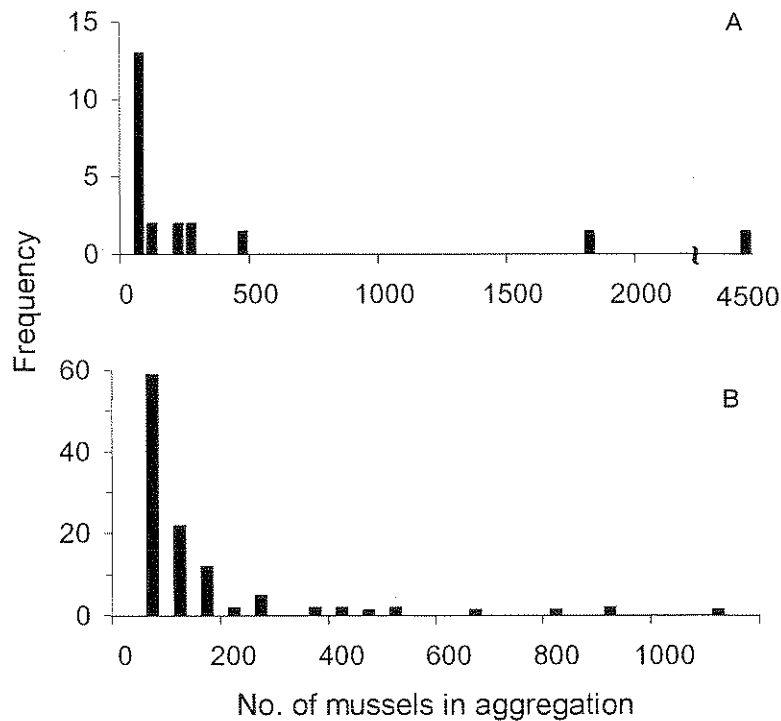


FIG. 3. Number of individuals in aggregations of (A) *Anodonta californiensis* ($n = 22$, $\bar{x} = 363$), and (B) *Margaritifera falcata* ($n = 114$, $\bar{x} = 112$).

acter. Mussels occurred where the chance of their displacement during high discharge was low, at both the scales of the entire study area and within geomorphic units.

Mussels were found almost exclusively in pools (Fig. 4A, B). Aggregations were completely absent from riffles, and only 6 of the 114 aggregations (3.5%) inhabited runs. We found ~50 isolated individuals in riffles throughout the study site. The 22 geomorphic units examined for more detailed analysis contained 99 aggregations. Only 22 aggregations of *A. californiensis* were found in the study area, with most individuals in one of these aggregations, so we did not analyze variability of this species with respect to higher flows and substrate characteristics.

HEC-RAS results showed that the locations inhabited by *M. falcata* also were areas of relatively low velocity and boundary stress during high discharges, including average winter flows, 5-y floods (Fig. 5A, B), and the 1964 flood. The clear segregation of *M. falcata* into these low-

stress habitats suggests that these mussels survive in portions of the channel where they are protected from displacement and possibly bed-load transport. Nonetheless, the model results suggested that mussels do survive in proximity to flow velocities of 1 to 3 m/s (Fig. 5A), significantly more vigorous flow conditions than observed during summer conditions (Fig. 4B).

The 2 regions of highest *M. falcata* population densities (between km 5.5–6 and 3.5–4.5; Fig. 2B), did not have distinctly lower velocities and boundary shear stresses compared to other pools as estimated by the model; specific physical conditions that favored such abundance could not be identified. However, these regions were the 2 areas of lowest average channel gradient in the study area, which hinted that these areas of high mussel densities were related to geomorphology (Fig. 6).

Further evidence of flow constraints on mussel distribution was seen at the scale of single channel cross sections. *Margaritifera falcata* were largely confined to a zone near channel banks

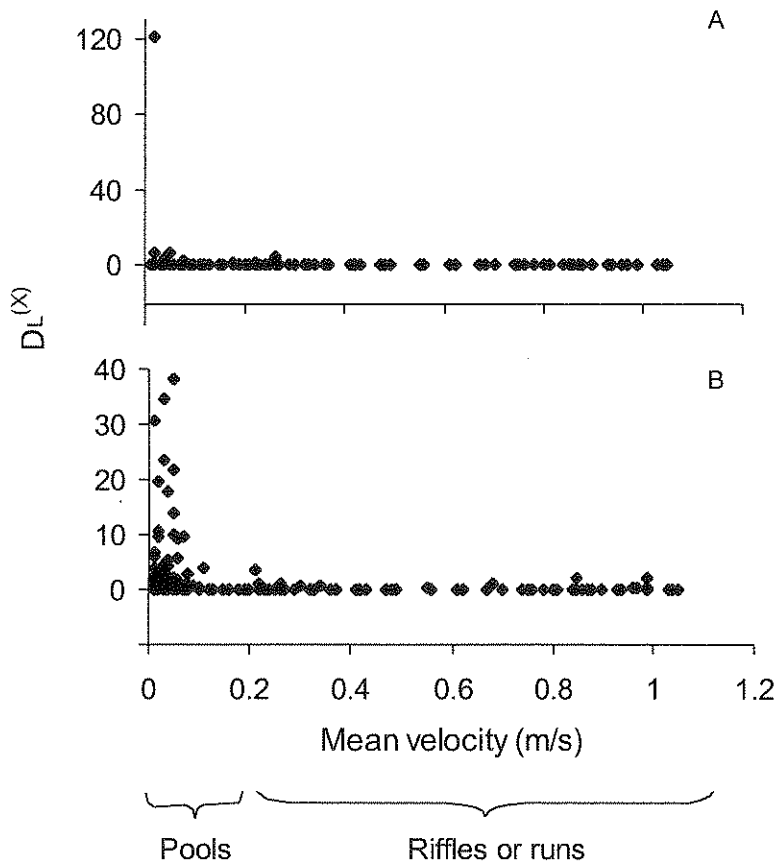


FIG. 4. Linear density (individuals/m length of channel, $D_L^{(\infty)}$) as a function of mean summer water velocity at each cross section. A.—*Anodonta californiensis*. B.—*Margaritifera falcata*.

(Fig. 7A), which was generally shallower than mid-channel regions (Fig. 7B). Near-bank environments in channels of this form (lacking planform curvature that induces high velocity flow against cutbanks) are regions of low stress and velocity. The model results were not precise at this scale, but they showed that modeled winter-flow velocities over mussel beds were lower than the channel cross-sectional mean velocity (Fig. 8).

Pools with higher centerline velocities would be expected to have mussels more closely confined to the banks if the preference for channel banks is, in fact, a result of a stress constraint. An examination of measured fractional distance from banks of *M. falcata* vs modeled winter-flow centerline velocities divided by width (a proxy for bank shear stress) provided tentative support for this expectation (Fig. 9).

Relationship to substrate character

Some of the variability in *M. falcata* density was related to substrate character, although at the inter-pool scale little of the variability could be explained by variations in substrate. Sedge mats constituted only 1.6% of all habitats, but contained 38% of the mussels in the study area.

The differences in *M. falcata* densities and total numbers for different types of habitats were statistically significant, implying a preferential association with substrate type ($\chi^2 \approx 10^3$, $p \ll 0.0001$, $df = 5$) (Table 1). Nevertheless, relative proportions of substrate type were not useful predictors of the total number of mussels in a given pool or run. Only 15% of the inter-pool variation was explained by proportion of the substrate (equation 2) because of strong patchi-

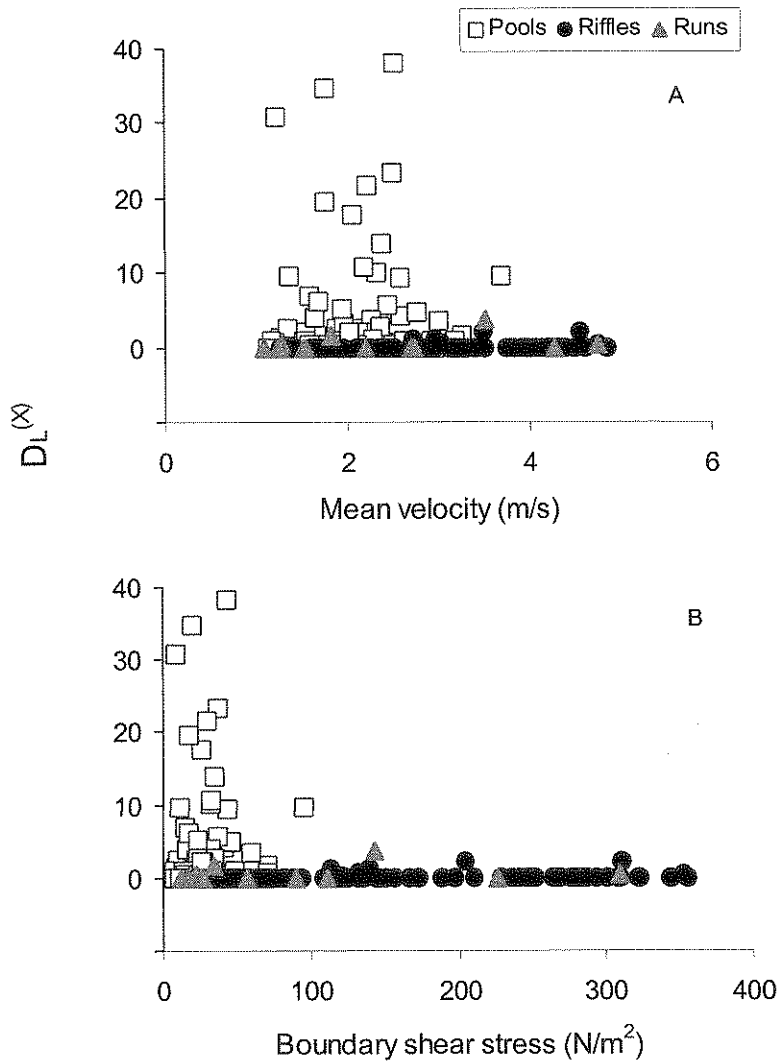


FIG. 5. Linear density (individuals/m length of channel, $D_L^{(\infty)}$) of *Margaritifera falcata* as a function of 5-y flood velocities (A) and 5-y mean boundary shear stresses (B) at each cross-section location. N = Newton.

ness of mussel occurrence within a substrate type ($r^2 = 0.15$, $p = 0.07$). In particular, large areas of apparently favorable substrate did not contain mussels.

Discussion

The spatial distribution of freshwater mussels in the South Fork Eel River was characterized by high variability as described elsewhere (Layzer and Madison 1995, Haag and Warren 1998, Strayer 1999). However, our study is

unique in that it captured the variability within a larger and more continuous framework (an unbroken 8-km stretch of channel). Unlike other studies, mussels were located primarily in pools, with a few in runs, and none in riffles. Our study also explained some of the variability by considering different spatial scales: the macro scale (from the entire length of channel down to distinct pools, riffles, and runs), the meso scale (within these geomorphic units and at single cross sections), and the micro scale (local substrate type).

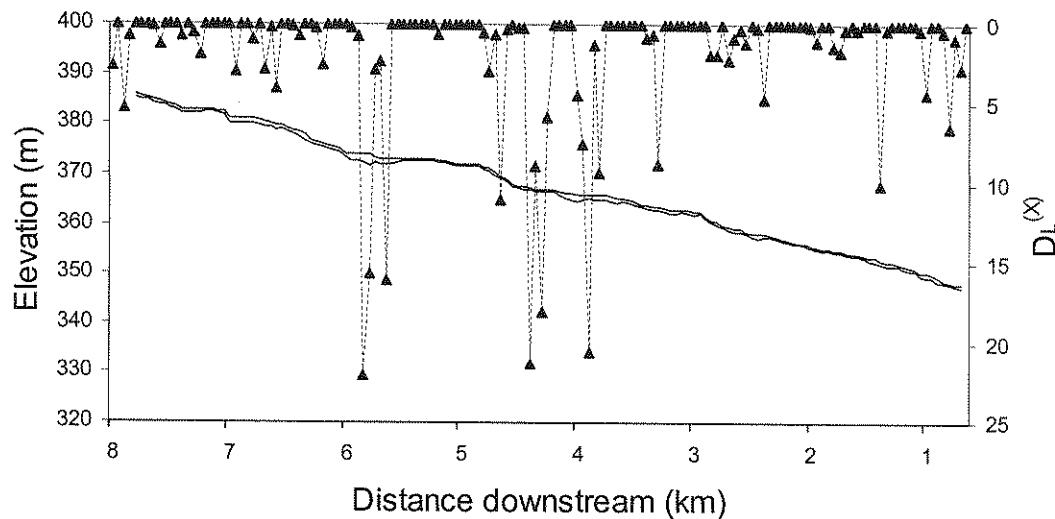


FIG. 6. Linear density (individuals/m length of channel, D_c^∞) of *Margaritifera falcata* along the channel (dashed/dotted lines) superimposed on the summer longitudinal profile of the South Fork Eel River (solid line: top line is water surface, bottom line is substrate surface). The water surface slope represents average summer discharge and was generated from the Hydrologic Engineering Center's River Analysis System (HEC-RAS) hydraulic model. High mussel occurrences (between river km \sim 5.5–6.0, and 3.5–4.5) are located in 2 areas of low channel gradient.

Macro and meso scales

There was a striking difference between the occurrence of *M. falcata* and *A. californiensis* within the study site. Although found in patches, *M. falcata* was widely distributed throughout the 8 km of the South Fork Eel River, and was the only species found in Ten Mile Creek. *Anodonta californiensis*, however, was restricted to the lower 2 km of our study area. The physical conditions examined provided no explanation for this difference.

Evidence clearly suggests that flow conditions constrained distributions of *M. falcata*; these mussels were almost exclusively found in pools and near banks (Figs 4, 5, 8). Direct measurements and the hydraulic model showed that, in all flows, mussels were found in areas of low boundary shear stresses and low velocities. Specifically, mussels were absent from locations of highest stress and fastest flow conditions, but their occurrence within low stress and flow locations was highly variable.

Shear stresses depend, in part, on channel gradient, so *M. falcata* was expected in areas of low slope. The higher average channel gradients on the 3 tributaries to the South Fork may explain why mussels were not found on either Elder (av-

erage slope = 0.03) or Fox creeks (average slope = 0.1), and only 2 small aggregations were found on Ten Mile Creek (average slope = 0.02).

The occurrence of mussels in pools in our study site, combined with the fact that pools are likely to be low stress environments at all flows (as supported by model results), suggests that it is the magnitude of stress that is most important. The occurrence of *M. falcata* almost exclusively in pools, with a few aggregations in runs and almost none in riffles, contrasts with most mussel distributions discussed elsewhere. The extreme changes in the hydraulic regime (floods in winter and drought in summer) may make riffles difficult habitat for long-lived species in the South Fork Eel River. Our model results showed that average winter shear stress in riffles is \sim 80 Newton/m², whereas average stress in pools is \sim 5 Newton/m². In addition, width and depth are highly reduced in riffles during summer flows. Pools may therefore act as both winter and summer refuges for mussels in this system. A similar refuge effect is seen at the local scale of channel cross sections, with *M. falcata* restricted to relatively protected areas near banks (Figs 8, 9).

These findings are consistent with Strayer's

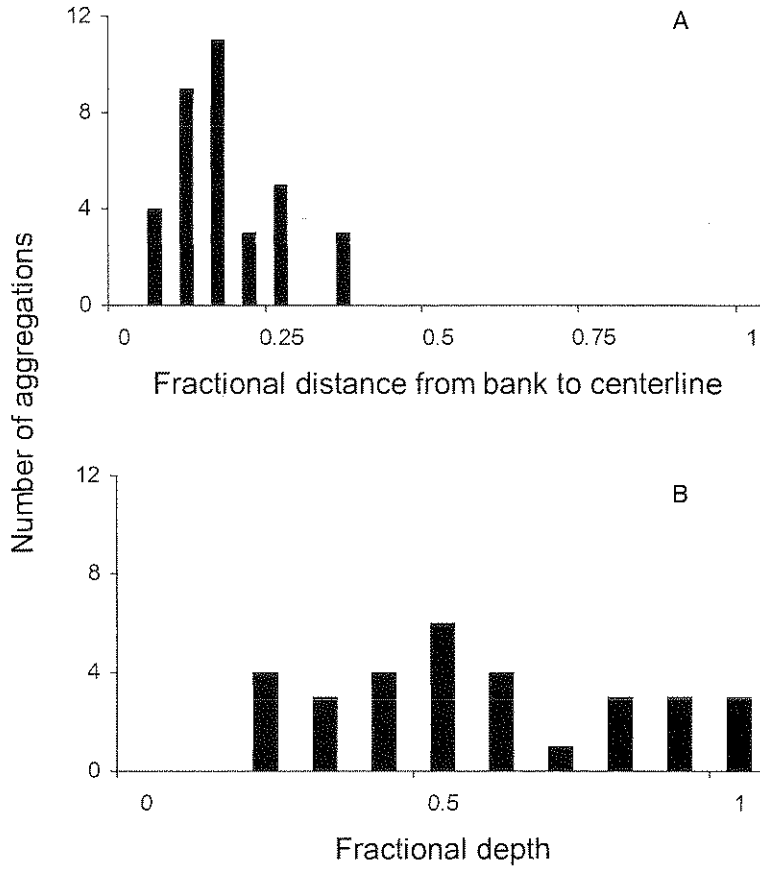


FIG. 7. Distribution of *Margaritifera falcata* with respect to distance from the bank and water depth. A.—Fractional distance from the bank (edge of water) to the centerline at all cross sections. B.—Fractional depth (maximum depth within a mussel aggregation divided by the maximum depth of the cross section).

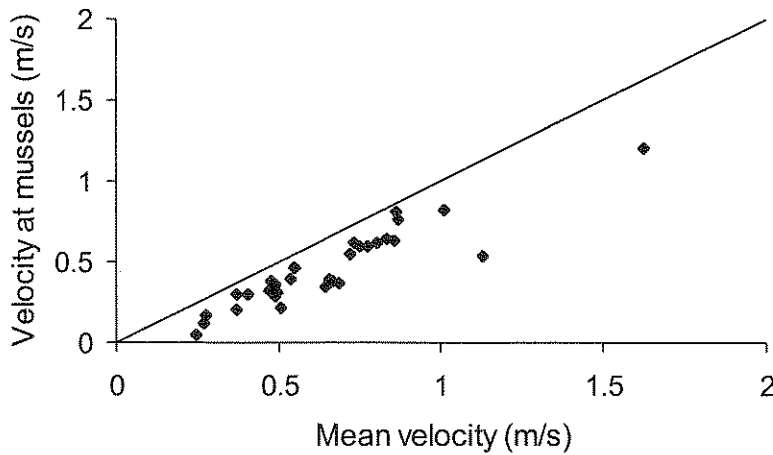


FIG. 8. Mean winter velocities generated from the Hydrologic Engineering Center's River Analysis System (HEC-RAS) model at each cross section versus the mean velocities at aggregations of *Margaritifera falcata* within the transect. The solid line is 1:1.

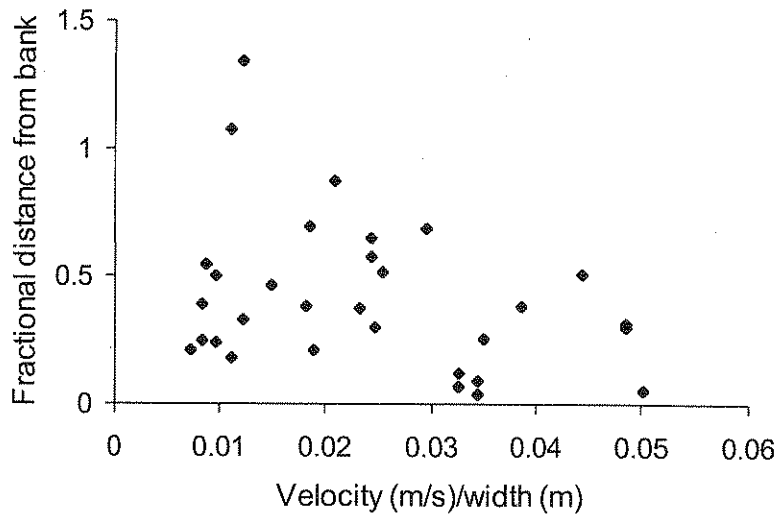


FIG. 9. Relationship between mean velocity divided by width of the channel (a proxy for shear stress at the banks) and fractional distance from the bank to the centerline for *Margaritifera falcata* at mean winter flows ($r^2 = 0.11$, $p = 0.07$). Mussels can be located at a fractional distance >1 in winter flows because the channel widens considerably at the 2 cross sections where this phenomenon occurs.

(1999) suggestion that mussel beds will generally be found in flow refuges where shear stresses during floods are too low to displace them or the sediments in which they are embedded. Similarly, Layzer and Madison (1995) found that in one 230-m section in Horse Lick Creek, Kentucky, mussels were located in areas of the channel estimated to have low shear stresses.

Other studies have shown that benthos is distributed in patches identified as refuges from

high flows (Lancaster and Hildrew 1993, Lancaster and Belyea 1997). The refuges are not absolute, but depend on discharge, which changes over the course of a year. These changes are especially pronounced in Mediterranean streams with seasonally predictable flood and drought stages (Gasith and Resh 1999). This flow regime, combined with high sediment yields and fluxes in this tectonic setting, create a highly variable environment. Stream organisms like *M. falcata* must develop strategies to deal with this high variability.

In contrast to our study, Vannote and Minshall (1982) found that *M. falcata* and *Gonidea angulata* were restricted to cobble/boulder ramp-like runs connecting deep pools to riffles in the Salmon River, Idaho. Mussels were, however, absent from riffles and deep pools as they were in our study site. Vannote and Minshall (1982) speculated that runs are the best habitat for mussels because the rate of seston transport increases in those areas, and that mussels avoid the alternating seasonal pattern of scour and sedimentation that occurs in pools. In our study, only 6 of the 113 populations were found in runs. Vannote and Minshall (1982) noted that reaches in the Salmon River were aggrading with sand and gravel from 100 y of mining, logging, irrigation, diversion, and grazing. In ad-

TABLE 1. Mean areal density (no./m²) of *Margaritifera falcata* for all habitat types at the pool and bank scales. Mean densities were calculated by totalling the number of mussels that occurred in each habitat type in each geomorphic unit and dividing by the area of each habitat type within those geomorphic units. Densities in sedges were the same at both scales because both mussels and sedges were found only along channel banks.

	Mean density	
	Pool	Bank
Bedrock	0.29	0.61
Boulder/cobble crevice	0.09	0.16
Cobble	0.23	0.74
Gravel/cobble/sand	0.12	0.46
Sand	0.09	0.22
Sedge	6.9	6.9

dition, they found relic populations buried under sand and gravel. Perhaps *M. falcata* was found only in runs in that study as a result of differential mortality (Strayer 1999) in which only those in runs survived, whereas those in pools were buried and killed by sedimentation. The difference between these 2 studies stresses the importance of understanding watershed-level controls on mussel variability.

Our observation that *M. falcata* were found almost exclusively in pools may seem puzzling if pools generally scour during floods, as is the case for alluvial channels (Leopold et al. 1964, Dunne and Leopold 1978, Resh et al. 1988, Knighton 1998). However, our study site is a mixed alluvial and bedrock channel. Most *M. falcata* here were either living in sedge root mats (which are very cohesive and, like mussels, may live for decades) or bedrock crevices, neither of which is likely to be entrained and transported according to normal granular sediment-transport relationships.

Micro scale

A number of researchers have found substrate to be a significant factor controlling mussel distributions (Salmon and Green 1983, Leff et al. 1990, Brim Box 1999, Brim Box et al. 2002), whereas others have found coincidental or no relationships between mussels and substrate composition (Strayer and Ralley 1993, Layzer and Madison 1995). Within our study area, *M. falcata* were associated with sedge root-mat substrates, and showed a weaker but still significant occurrence within bedrock and cobble interstices.

Although these relationships did not help explain inter-pool variability, the clear difference in population density between habitats demands an explanation. Possible explanations include similar settlement patterns, increased food supply at the sedge root mats, or sedge root-mat stability. Previous researchers have suggested that mussels may be indicators of (Amyot and Downing 1998, DiMaio and Corkum 1995) or contributors to (Johnson and Brown 2000) the stability of river substrates. Levine (2000) proved that sedges in the South Fork Eel River system provide critical stable substrate for other plants during winter floods. Perhaps *Carex nudata* provides stability for mussels as well.

In conclusion, long-lived species like mussels

must develop strategies to deal with extreme physical conditions in the Northern California Coast Range environment of highly variable discharge and moderately steep slopes. Our study suggests that, at various spatial scales, *M. falcata* appear to be distributed in a manner that protects them from the highest flow-induced stresses.

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