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Abstract

Freshwater mussels (Bivalvia: Unionoida) are an integral component of freshwater ecosystems. Historically, they were an important part of the diet and material culture of indigenous peoples, including until recently the Karuk Tribe of California. This study represents the first systematic survey of freshwater mussels in the Klamath River Basin of northwestern California, where little is known about mussel distribution, abundance, habitat associations, or conservation status. We snorkel surveyed 82 sites on the mid Klamath River and sections of nine major tributaries to assess abundance, distribution, and habitat use of mussels at three different spatial scales. We identified all three western North American mussel genera (*Margaritifera*, *Gonidea*, and *Anodonta*) in the Klamath River, with *Gonidea* abundant and widely distributed within the mainstem, and *Anodonta* and *Margaritifera* present in low numbers and restricted in distribution. At the landscape scale we observed a negative relationship between mussel abundance and measures of hydrological variability. At the mesohabitat scale, bank type, channel unit type, and their interaction were important predictors of mussel distribution. At the microhabitat scale, bank type, substrate type, and flow refuge presence were important predictors of mussel distribution. Together, our results suggest the common influence of hydraulics and substrate stability as drivers of mussel distribution in the Klamath, which agrees with the findings of other recent studies of mussel distribution. Our results also illuminate where habitat protection and restoration efforts should be directed within the mid Klamath subbasin to aid in mussel conservation.

Key Words: freshwater mussels; Klamath River; Karuk Tribe; habitat distribution; mixed effects models

Introduction

Freshwater mussels (Bivalvia: Unionoida) face significant conservation challenges. In North America alone, over 70 percent of the estimated 300 species are either extinct or at risk of extinction (Williams et al. 1993, Neves et al. 1997). Declines of freshwater mussels are of concern in part because mussels provide valuable ecosystem services such as substrate aeration, nutrient depo-

sition, and water filtration within rivers and lakes (Vaughn and Hakenkamp 2001, Vaughn et al. 2004, Howard and Cuffey 2006). In many regions, the ability to manage and conserve mussel populations is hampered by limited knowledge of species distributions and habitat associations (Brim Box et al. 2006). Describing the presence, distribution, and habitat needs of freshwater mussel species is a necessary first step to protecting populations.

Western North America is home to far fewer genera (3) and species (6-8) of mussels than are watersheds east of the Rockies where most of the North American diversity is located. There are few

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comprehensive surveys and little basic knowledge of ecology, taxonomy, or zoogeography of mussels in the western United States (Brim Box et al. 2006). However, based on recent survey efforts, we know that some western mussels, including *Gonidea angulata* and one or more species of *Anodonta*, have likely been extirpated from parts of their former ranges (Nedeau et al. 2009, Howard 2010).

Despite intensive anthropogenic use of freshwater ecosystems in California, little is known about the conservation status or ecology of mussels in California. According to a recent synthesis of historical observations, all three genera of western mussels, *Gonidea*, *Margaritifera* and *Anodonta*, appear to be in decline statewide, with some populations completely extirpated (Howard 2010). The Klamath River Basin in Northern California is one example of a major western river basin where little is known about the distribution or ecology of freshwater mussels. Thirty isolated samples dating from between 1867 and the present day are recorded in the US Forest Service's Database of Freshwater Mollusks of the Western United States (USDA Forest Service 2004). However, to our knowledge, there had been no detailed, systematic study of mussels in the Klamath River prior to our work.

Besides their importance in aquatic ecosystems, freshwater mussels are also culturally significant. Historically, mussels formed an important part of the diet and material culture of indigenous peoples in North America (Parmalee and Klippel 1974), including, until the 1960s and 1970s, members of the Karuk Tribe of California (Kroeber and Barrett 1960, Ferrara 2004), whose homeland encompasses the middle Klamath Basin. Ethnographic accounts document Karuk use of freshwater mussels (*axthah* in the Karuk language) as food, tools, and game pieces (Gibbs 1860, Driver 1939, Greengo 1952). The cultural importance of mussels, coupled with their role in aquatic ecosystems and unknown conservation status, underscored the importance of initiating this study.

Inadequate knowledge of mussel habitat requirements and the factors that determine or constrain mussel distribution hinders mussel con-

servation (Strayer 2008). Mussel populations and the environments they inhabit are heterogeneous and fragmented (Newton et al. 2008), leading some researchers to suggest that principles of landscape ecology, including consideration of influences operating on multiple spatial scales, should be used to understand and manage populations (Newton et al. 2008).

There have been attempts to explain the patchy, aggregated distribution of mussel species at meso-habitat (10m—100m) and microhabitat (<10m) scales (Strayer 2008) using traditional microhabitat-scale variables such as water velocity and water depth, but those variables have been found to be poor predictors of mussel distribution (Strayer and Ralley 1993). More recently, complex hydraulic variables (shear stress, Reynolds and Froude's numbers) have emerged as better predictors and descriptors of mussel distribution, abundance, and patch suitability at meso and micro scales (McRae et al. 2004, Strayer 2008, Zigler et al. 2008). Hydraulic conditions at micro and meso scales can influence substrate stability, bed scour, presence of flow refuges (micro-eddies), and other variables relevant to benthic-dwelling organisms.

Mussel presence is also patchy at the landscape scale (>100m to many km), which can be attributed to a variety of factors such as host fish distribution, geology, climate, and land use (Arbuckle and Downing 2000, McRae et al. 2004, Vaughn and Taylor 2000). Some research has also shown that landscape-scale differences in mussel communities and distribution correspond with areas of differing hydrological variability. Hydrological variability can influence the presence or absence of certain substrates, the degree of siltation, the amount of scouring experienced at a site, and the presence or absence of host fish, all of which can in turn influence mussels (diMaio and Corkum 1995).

Our primary objectives were to: 1) identify mussel species of the middle Klamath River and its major tributaries, 2) quantify the relative abundance of these species, and 3) assess their distribution throughout the 250 river km of the study area. Our secondary objective was to investigate mussel habitat associations at macro (landscape, >100m to many km), meso (reach, 10 m—100 m) and

micro (local, < 10 m) scales. We examined mussel distribution at multiple spatial scales because research indicates that biotic and abiotic factors at different scales can interact with each other to produce a complicated suite of patterns (McRae et al. 2004). Accordingly, we investigated the influence of hydrological variability (macro scale), bank type and channel unit type (meso scale), and substrate type and flow refuges (micro scale) on the distribution and abundance of mussels.

Methods

Study Area

The Klamath River, located in northwestern California and southern Oregon (Figure 1), is the second-largest river basin in California, draining

an area of 40,632 km². The Klamath Basin is an unusual watershed, with an expansive alluvial and lacustrine upper basin transitioning to a steep, confined, erosive mountain river system in the lower basin—the opposite of many river systems (NRC 2004, VanderKooi et al. 2011). The boundary between upper and lower basins is generally defined based on the underlying geology (Williams and Curry 2011). The upper basin is semi-arid and primarily vegetated by shrubs, grasses, and ponderosa pine (*Pinus ponderosa*); the lower basin is more mesic and primarily vegetated by mixed conifer-hardwood forest. The dominant land use in the upper basin is agriculture, whereas the majority of land in the lower basin is forest managed by the US Forest Service and the Yurok and Hoopa Indian tribes.

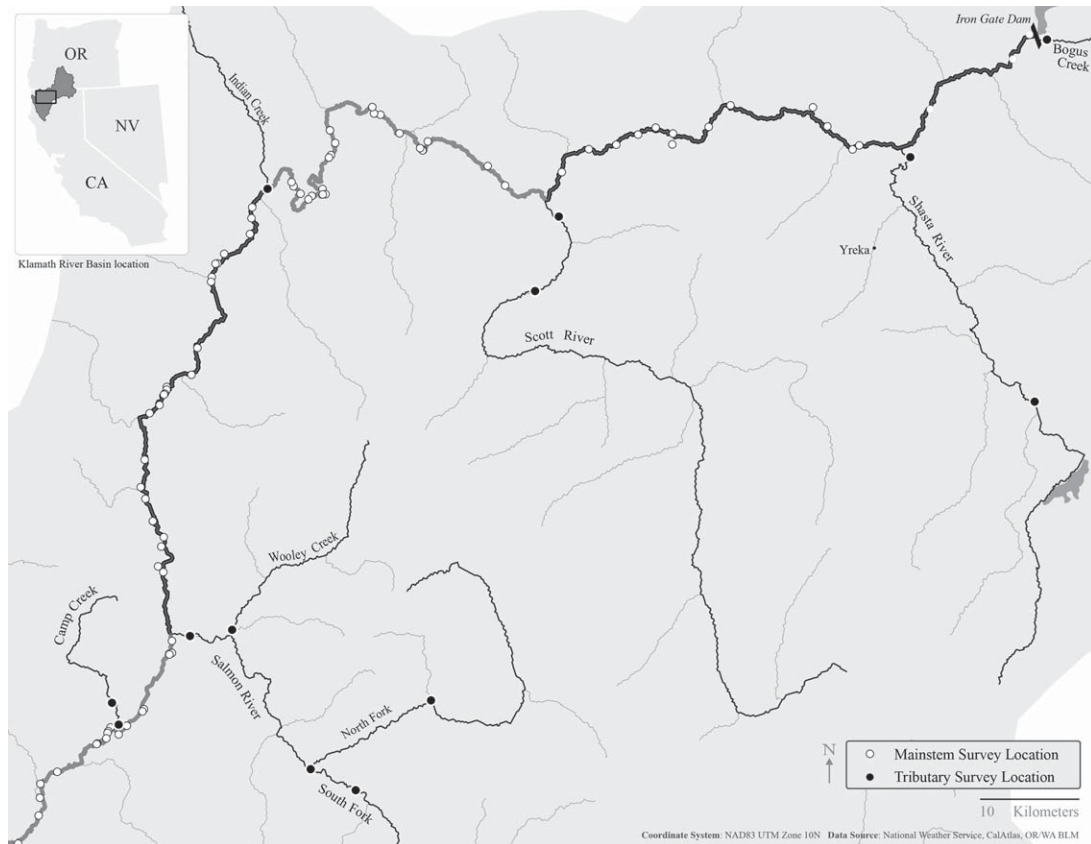


Figure 1. The middle Klamath basin with the mainstem study sections denoted with alternating gray and black lines. From upstream to downstream the sections are Irongate Dam—Scott River, Scott River—Indian Creek, Indian Creek—Salmon River, and Salmon River—Trinity River. Mainstem survey sites are identified as white points, and tributary surveys as dark points. The tributaries we surveyed are labeled and identified with darkened lines.

Four hydroelectric dams block the mainstem Klamath as it transitions from the upper to the lower basin. During summer, warm, nutrient-rich water from the upper basin is trapped behind the dams, promoting blooms of the hepatotoxic blue-green algae *Microcystis aeruginosa* (Kann 2006). Water quality improves downstream as the influence of major tributaries reduces nutrient and toxin concentrations (Asarian et al. 2010) and increases dissolved oxygen concentrations (Karuk Tribe 2008). The dams also alter the hydrologic regime, sediment transport, and the movement of aquatic animals (the dams lack fish ladders). Discharge from the lowermost dam, Irongate, is normally between 1,000 and 2,000 cf s⁻¹ (Williams and Curry 2011).

Our study area was the middle Klamath basin—the upper two thirds of the lower basin—between Irongate Dam and the Trinity River confluence (Figure 1). Much of this area overlaps Karuk ancestral territory. The geomorphic, climatic, and hydrologic character of the watershed changes dramatically between the upper and lower basins (Williams and Curry 2011), but also changes substantially within the study area itself. Differences in hydrological variability have been shown to influence the distribution and abundance of species such as juvenile coho salmon (*Oncorhynchus kisutch*) in the Klamath River (Hillemeier et al. 2009), and may influence patterns of mussel distribution. For this reason, we divided the 250 river km of our study area into four sub-sections with differing hydrologic regimes (Figure 1).

The furthest upriver section of the study area, between Irongate Dam and the Scott River, is characterized by a semi-arid climate, regulated flows year round, and a virtual absence of yearly peak flow events (Hillemeier et al. 2009). Moving downstream, the size and frequency of peak flow events, along with overall hydrological variability, all increase as the climate becomes more mesic, more tributaries enter the Klamath, and the system shifts from being dominated by groundwater and snowmelt to rain and snowmelt (Hillemeier et al. 2009). From upriver to downriver, the other three study area sections comprise the reaches between the Scott River and Indian Creek, between Indian Creek and the Salmon River, and between the Salmon River and the Trinity River (Figure 1).

Site Selection

We used a previous habitat survey of the Klamath River (USFWS 2002) to select survey sites and to evaluate the influence of channel unit type (i.e., channel geomorphology) on mussel distribution. The habitat survey divided the river into sequential channel units from Irongate Dam to the ocean, specified the length and georeferenced position of each unit and categorized these units as one of five types: low slope (LS), medium slope (MS), steep slope (SS), riffle, pool, or run. The channel unit types were defined using a series of habitat characteristics: gradient, active-channel confinement, surface disturbance, width to depth ratio, substrate composition, and the presence or absence of backwaters associated with hydraulic controls (Hendrix et al. 2011) (Table 1). This categorization

TABLE 1. Characteristics used to define channel unit types in a 2002 USFWS habitat survey of the Klamath River from Irongate Dam to the estuary. Adapted from table 4.3 in Hendrix et al. (2011). LS = low slope; MS = medium slope; SS = steep slope.

| Criteria | Pool | Run | LS Riffle | MS Riffle | SS Riffle |
|----------------|----------------------|----------|-----------------------|-----------------------------|-------------------------|
| Gradient | -- | <0.3% | <0.3% | 0.3%-0.8% | >0.8% |
| Channel width | -- | confined | relatively unconfined | moderately confined | confined |
| Backwater | yes | no | no | no | no |
| Substrate | finest, sand, gravel | -- | gravel, small cobble | large cobble, small boulder | small and large boulder |
| Standing waves | none | <1/2' | <1/2' | 1/2'-1' | >1' |

is similar to the stream channel unit classification system of Hawkins et al. (1993). From this dataset we used a random number generator to select channel units between Irongate Dam and the Klamath-Trinity confluence as our survey sites. We replaced units that were unsafe or inaccessible with nearby units of the same type.

We did not select tributary sites randomly, as habitat mapping similar to the survey of the mainstem was not available for tributaries. We opportunistically selected sites using the goals of broad spatial coverage of the middle basin, site accessibility and safety, and anecdotal reports of mussel presence. From upriver to downriver along the Klamath we surveyed sites on Bogus Creek, the Shasta River, the Scott River, Indian Creek, the Salmon River (mainstem, North Fork, and South Fork), Wooley Creek (a tributary of the Salmon River), and Camp Creek.

We surveyed a total of 82 sites on the mainstem Klamath River and 19 sites on Klamath tributaries during the summers of 2007, 2009, and 2010. We also conducted within-season resurveys of 5 sites in 2009 and 10 sites in 2010 to assess the precision of our mussel counts.

Surveys

We defined a mainstem site as a 50 m segment of river within a single channel unit. Individual units could be hundreds of meters in length, making whole-unit surveys impractical. A 50 m length of channel struck a balance between accurately representing the larger channel unit and the time-intensive nature of the surveys. Once we arrived at a pre-selected channel unit and delineated the site within the unit, we systematically surveyed the site, covering as much riverbed as possible. One or more surveyors snorkeled each side of the river, moving parallel to the bank. We snorkeled as far out into the middle of the river as possible, but swift currents often prevented a detailed mid-channel survey. However, cursory surveys (e.g., while swimming across the main channel to the other bank) showed that the mid-channel held few if any mussels.

At each site we recorded the species present and the total number of individuals per spe-

cies. We counted only mussels visible on the surface of the river bed and did not excavate the substrate. Mussels were identified on the basis of shell morphology. Surveyors noted the side of the main channel (right or left) where each mussel or mussel bed occurred and recorded the bank type of both sides of the river at each site. The two bank types we used, bar edge and bank edge, were adapted from Beechie et al. (2005). Bar edges sloped gradually to the water's edge and consisted of loose, deposited cobble, gravel, or sand. Bank edges sloped steeply to the water's edge and consisted of stable, embedded boulders, bedrock, mud or other hardened substrate. Bank type is indicative of the hydrologic influence on the channel edge, such as the level of shear stress during peak flow events, whether scour or deposition dominates, and the stability of the substrate.

Any large, dense aggregation of mussels where it was not practical to count all individuals we defined as a "bed" and sampled with a 0.25 m² quadrat using an adaptation of systematic sampling (Strayer and Smith 2003). First, we determined the area of the bed to calculate how many quadrats would be needed to sample at least 10% of the total bed area. We then placed the quadrat at regular intervals along one or more linear transects within the bed, identifying and counting all mussels in each quadrat. Later we estimated the total number of mussels in the bed by extrapolation.

In 2010 we surveyed two new mainstem sites and resurveyed 19 sites previously surveyed in 2007 or 2009 to assess the effect of two micro-habitat variables, substrate and flow refuges, on mussel distribution. We used substrate type and presence of flow refuges, as well as bank type and channel unit type, as proxies for local hydraulic conditions and substrate stability. We were unable to observe these variables directly since most of the limiting hydraulic conditions for mussels occur during winter flooding, rather than summer low flows when we completed our surveys. We recorded the substrate occupied by each mussel and whether or not a mussel was associated with a flow refuge. For mussel beds we recorded the dominant substrate within each quadrat and whether or not that quadrat was associated with

a flow refuge. We used six substrate categories: bedrock, boulder (>256 mm), cobble (64-256 mm), gravel (2-63 mm), sand (0.125-1.9 mm), and silt. We defined a flow refuge (Strayer 1999) as the area immediately downstream of any physical element, such as a boulder, large cobble, or bedrock outcropping, which slowed or deflected the current's downstream flow, creating a micro-eddy.

At each site we also recorded the availability of substrate types and potential flow refuges. We sampled the substrate at a series of 30-40 points spaced evenly throughout the site. Surveyors placed the end of a pole on the river bottom at each point, recording the substrate that the pole touched and whether a physical bed element created a potential flow refuge at that point.

For the tributary surveys we focused only on the presence and abundance of mussel species, and did not assess habitat associations. In contrast to the mainstem surveys, tributary survey sites varied in length, often up to hundreds of meters. Some tributaries contained more than one site. We surveyed all tributaries in teams of at least three, with each person surveying a third of the channel. We identified and counted all mussels encountered, standardizing our counts as the number of mussels per 50 m of stream channel to make them comparable with our mainstem surveys.

For the four mainstem sections defined at the outset of the study (Irongate Dam—Scott River, Scott River—Indian Creek, Indian Creek—Salmon River, Salmon River—Trinity River) we calculated two measures of hydrological variability: high-to-low flow ratio and coefficient of variation (C_v) among daily mean flows, using flow data from the whole period of record for the gauges located within each of the sections (USGS 2011). We also calculated these measures for surveyed tributaries with gauges on them (four of nine). Coefficient of variation is a standard measure of hydrological variability that has been shown to influence aquatic communities (Jowett and Duncan 1990), and both C_v and high- to-low flow ratio influence the distribution of juvenile coho salmon (*O. kisutch*) in the Klamath River (Hillemeier et al. 2009). The high- to-low flow ratio is the ratio of the median

annual peak flow to the median annual low flow. Coefficient of variation (C_v) is defined as

$$C_v = \frac{SD_{df}}{\bar{df}} * 100$$

where SD_{df} is the standard deviation of daily mean river flow, and \bar{df} is the mean of daily mean flow.

No gauge exists for the Indian Creek - Salmon River section of the Klamath. To calculate measures of hydrologic variability for this section we combined the daily mean flows from the closest upriver mainstem gauge and from Indian Creek.

Data Analysis

We used the two surveys from each of the re-surveyed sites to calculate the precision (i.e., intraclass correlation) (Lessells and Boag 1987) of our counts of each species we encountered at those sites and our substrate coverage sampling. We assessed the relationship between the combined counts of all mussel species at each site ($\log_e + 1$ transformed), the distance downstream of Irongate Dam, and both measures of hydrological variability using linear regression. Adequacy of the fit of the hydrological variability regression models was assessed using analysis of variance. We also assessed the relationship between mussel counts (mussels per 50 m of channel length; $\log_e + 1$ transformed) and hydrological variability in the four gauged tributaries using linear regression. The criterion of $P \leq 0.10$ was used as the significance cutoff for all statistical tests.

We evaluated the relationship between mussel counts and meso and microhabitat variables using a series of generalized linear mixed models (GLMM) (reviewed by Bolker et al. 2009). We used the GLMM framework because it handles non-normal response variables and can account for nested, non-independent sampling. For all models we used a negative binomial error distribution (log link) because mussel counts were not normally distributed, and we included site as a random effect to account for the non-independence of counts within a site. We fit the models in R (R Development Core Team 2011) using the `glmmadmb` function in the `glmmADMB` package (Skaug et al. 2012). The `glmmadmb` function fits models

using a Laplace approximation of maximum likelihood estimation. Because *Margaritifera falcata* and *Anodonta* sp. had restricted distributions (see results) we performed these analyses for *G. angulata* counts only.

We considered two separate sets of models. Our first set of models evaluated mussel abundance at the mesohabitat scale using meso-scale explanatory variables. We constructed four models with different combinations of meso-scale variables that represented alternate hypotheses about which variables could be important to mussel abundance at this scale. The level of observation for the meso-scale models was the side of a site (i.e., the left or right half of a 50 m section of channel). For these models we used data from sites surveyed in 2007 and 2009, plus the two sites surveyed in 2010 that were not previously surveyed in 2007 or 2009. We included the explanatory variables channel unit type (Pool, LS riffle, MS riffle, and SS riffle), bank type (bank edge and bar edge), and the interaction between channel unit type and bank type as fixed effects in these models.

Our second set of models evaluated mussel abundance at the microhabitat scale using both meso- and micro-scale explanatory variables. We constructed 17 separate models with different combinations of meso- and micro-scale variables that represented alternate hypotheses about which variables could be important to mussel abundance at the microhabitat scale. The level of observation for the micro-scale models was individual substrate and flow refuge categories within each side of a site. For example, mussels counted in gravel associated with flow refuges on the left side of a site would be a single observation. For these models we used data from sites sampled in 2010 as these were the only sites where we collected microhabitat information. We included the explanatory variables channel unit type (Pool, LS riffle, and MS riffle), bank type, substrate (bedrock, boulder, cobble, gravel, sand, and silt), flow refuge presence/absence, the interaction between channel unit type and bank type, the interaction between substrate and flow refuge presence/absence, and the interaction between bank type and flow refuge presence/absence as fixed effects in these models. For models that included substrate and flow

refuge presence/absence as explanatory variables we included substrate-flow refuge coverage (the percent cover by a given substrate associated with and without flow refuges as determined by point intercept sampling on a given side of the site in question) as a covariate to account for differential availability of substrates and flow refuges among sites. We only evaluated models that seemed biologically relevant and interpretable, as opposed to evaluating every possible combination of explanatory variables, to reduce the probability of finding spurious effects (Anderson and Burnham 2002).

To determine which variables or sets of variables were most important in explaining mussel abundance we used an information-theoretic (IT) model selection approach (Anderson et al. 2000). The IT approach provides an alternative to traditional null-hypothesis based inference, which suffers from drawbacks when used with GLMMs (Bolker et al. 2009). We compared models using the Akaike information criterion with a bias correction term for small sample size (AIC_c) and AIC_c weights. For each model we report AIC_c for model_{*i*} - AIC_c min (Δ_i) and the AIC_c weight for model_{*i*} (w_i). We also report the model summaries for the best model (AIC_c min) for both the meso-scale and micro-scale models.

Results

Survey Precision

Our counts of *G. angulata* in 2009 were significantly precise ($r = 0.92$, $F = 22.77$, $df = 4, 5$, $P = 0.002$). Counts of *M. falcata*, by contrast, showed poor precision ($r = 0.31$, $F = 1.92$, $df = 4, 5$, $P = 0.246$). In 2010 our counts of *G. angulata* and *M. falcata* were significantly precise within substrate-flow refuge categories at each site ($r = 0.66$, $F = 4.85$, $df = 239, 240$, $P < 0.0001$; $r = 0.46$, $F = 2.69$, $df = 239, 240$, $P < 0.0001$, respectively). Substrate coverage estimated from point-intercept sampling was also significantly precise ($r = 0.67$, $F = 5.12$, $df = 239, 240$, $P < 0.0001$).

Large-Scale Patterns of Distribution and Abundance

We identified all three genera of western mussels in the mid Klamath River. We were able to identify

TABLE 2. The number of survey sites in each section and mean (SD) species abundance per site for each of the four mainstem Klamath sections. The bottom row shows the total number of each species counted at all survey sites.

| Mainstem Section | n | Mean (SD) | | |
|----------------------------|----|--------------------|-------------------|---------------------|
| | | <i>G. angulata</i> | <i>M. falcata</i> | <i>Anodonta sp.</i> |
| Irongate-Scott River | 16 | 4192 (6859) | 1 (3) | 95 (358) |
| Scott River-Indian Creek | 23 | 3838 (6322) | 5 (11) | 0 (0) |
| Indian Creek-Salmon River | 25 | 1110 (2253) | 2 (5) | 0 (0) |
| Salmon River-Trinity River | 18 | 796 (2408) | 95 (253) | 0 (0) |
| Total | 82 | 197418 | 1879 | 1515 |

G. angulata and *M. falcata* to the species level using shell morphology. However, western anodontines make up three distinct clades which are difficult to distinguish without a genetic analysis (Chong et al. 2008, Mock et al. 2010), so we were unable to assign the *Anodonta* specimens to a species or clade.

Mussels were abundant (Table 2) and widely distributed throughout the mainstem Klamath (Figure 2), though abundance varied widely among sites. We found mussels at 70 of 82 sites. *G. angulata* were more widely distributed (Figure 2) and more abundant than the other species by two orders of magnitude (Table 2). In contrast to *G. an-*

gulata, 95 percent of all *Anodonta sp.* we counted in this survey were located at the furthest upriver survey site—directly below Irongate Dam. During formal distribution surveys, we only observed *Anodonta sp.* in the furthest upriver mainstem section (Irongate Dam - Scott River) (Figure 2; Table 2); however, during an exploratory survey we did identify a few *Anodonta sp.* just upstream of a survey site located approximately 105 river km below the dam. We observed the opposite distribution for *M. falcata*, with low abundances in the upper three mainstem sections and the highest abundances in the furthest downstream section of the study area, between the Salmon

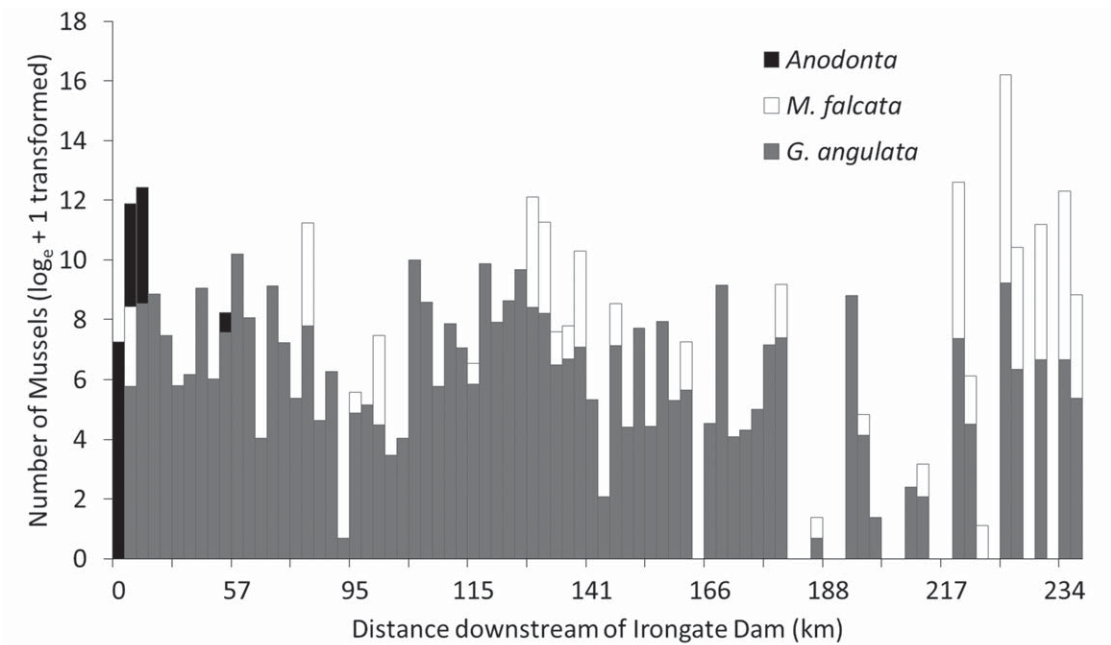


Figure 2. Longitudinal distribution of Klamath mainstem mussel abundance (log_e + 1 transformed).

TABLE 3. Measures of hydrological variability for the four mainstem river sections and four gauged mid Klamath tributaries, plus the length of each of the four mainstem sections (km) and the distance surveyed on each mainstem section and tributary¹. The high- to-low flow ratio is the ratio of the median annual peak flow to the median annual low flow. Coefficient of variation (C_v) is the ratio of the standard deviation of daily mean river flow to the mean of daily mean river flow and is represented as a percentage. The length of the period of record (years) used for each calculation is noted.

| Mainstem section/tributary* | Length (km) | Distance surveyed (m) | High-low flow ratio | C_v | Years of record |
|-----------------------------|-------------|-----------------------|---------------------|--------|-----------------|
| Irongate-Scott River | 77 | 800 | 8.4 | 83.7% | 52 |
| Scott River-Indian Creek | 59.25 | 1150 | 17.0 | 101.0% | 100 |
| Indian Creek-Salmon River | 67 | 1250 | 23.5 | 111.8% | 56 |
| Salmon River-Trinity River | 37 | 900 | 38.2 | 122.7% | 84 |
| Shasta River* | | 1700 | 103.3 | 128.0% | 78 |
| Scott River* | | 1500 | 175.1 | 167.8% | 71 |
| Indian Creek* | | 1000 | 162.9 | 162.4% | 56 |
| Salmon River* | | 2600 | 134.7 | 140.7% | 101 |

¹Ungauged, surveyed tributaries and distance (m) surveyed: Bogus Creek (350), N. Fork Salmon (3000), S. Fork Salmon (3000), Wooley Creek (1000), and Camp Creek (1600).

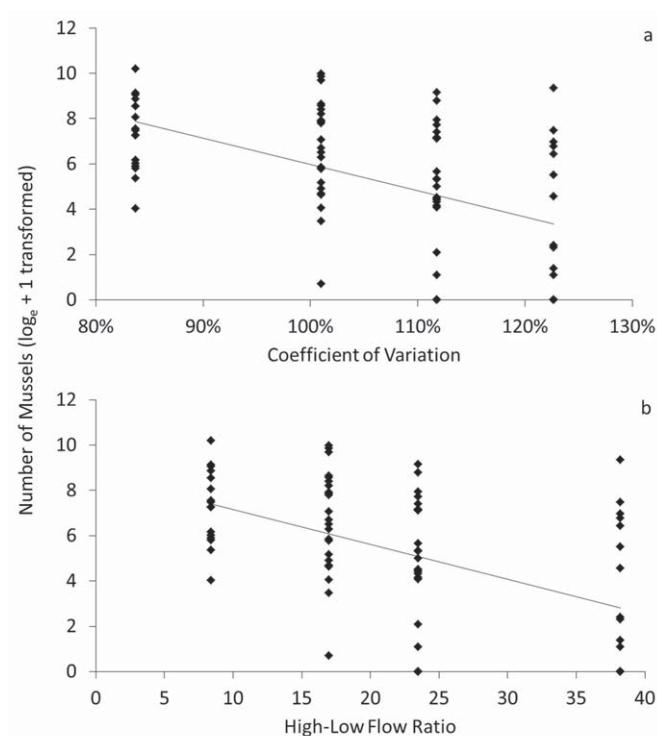


Figure 3. The relationship between two measures of hydrological variability in the mainstem Klamath River and the site counts of all mussel species combined ($\log_e + 1$ transformed). (a) Coefficient of variation. (b) High-low flow ratio.

and Trinity Rivers (Figure 2; Table 2). Where *M. falcata* was present, it co-occurred with *G. angulata* at all but one site. *Anodonta sp.* co-occurred with *G. angulata* at two sites and with *M. falcata* at a single site. *G. angulata* was the only species found at 44 sites, while *M. falcata* and *Anodonta sp.* were each found alone at a single site.

Mussels declined in abundance with increasing distance downstream of Irongate Dam ($r^2 = 0.24$, $F = 24.66$, $df = 1, 80$, $P < 0.001$) (Figure 2). Both measures of hydrological variability, the high-to-low flow ratio and C_v , increased with increasing downstream distance from Irongate Dam (Table 3). We found a negative relationship between both measures of hydrological variability and the site counts of total mussels (C_v : $r^2 = 0.25$, $F = 26.97$, $df = 1, 80$, $P < 0.001$; High-Low: $r^2 = 0.26$, $F = 27.96$, $df = 1, 80$, $P < 0.001$) (Figure 3a, 3b). Both linear models of hydrological variability and mussel counts adequately fit the data (C_v : $F = 1.51$, $df = 2, 78$, $P = 0.227$; High-Low: $F = 1.14$, $df = 2, 78$, $P = 0.326$).

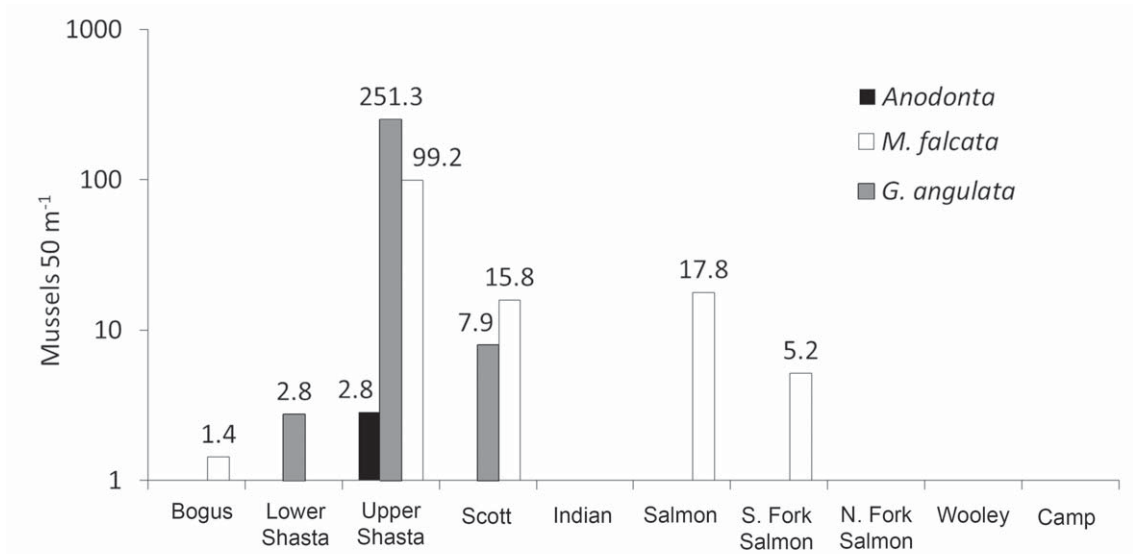


Figure 4. Mussel counts (mussels per 50 m of tributary channel) within mid Klamath tributaries. Note that the y-axis is a logarithmic scale.

We observed lower abundances of mussels in the tributaries compared to the Klamath mainstem, with the exception of the upper Shasta River, where counts per 50 m were similar to some mainstem sites (Figure 4). The Shasta River was also the only tributary with all three western mussel genera (Figure 4). For the four gauged tributaries, there was no statistically significant relationship between mussel counts and hydrological variability (C_v : $r^2 = 0.35$, $F = 1.06$, $df = 1, 2$, $P = 0.412$; High-Low: $r^2 = 0.32$, $F = 0.94$ $df = 1, 2$, $P = 0.436$).

Mesohabitat and Microhabitat

Out of the 82 mainstem survey sites, we sampled 4 steep slope riffles, 17 medium slope riffles, 25 low slope riffles, 35 pools, and 1 run. We excluded the lone run from the GLMMs. We recorded 93 bank edges and 67 bar edges at survey sites. At two sites we failed to record on which side of the channel mussels were located, so those two sites were also excluded from the GLMMs.

We only developed GLMMs for *G. angulata* abundance. Of the four meso-scale GLMMs we considered, there was strong support for the model that included bank type, channel unit type, and the interaction between channel unit type and bank type as fixed effects (Table 4). Of the 17

TABLE 4. Summary of small sample size Akaike information criterion (AIC_c) ranking of *G. angulata* meso-scale abundance GLMMs for data collected from sites in all three years ($n = 79$ sites, $n = 158$ observations). Channel = channel unit type; Bank = bank type; * = interaction term. Δ_i = AIC_c of model_{*i*} - AIC_c min; k = number of model parameters; w_i = AIC_c weight for model_{*i*}. AIC_c weights sum to one for the set of models under consideration.

| Rank | Channel | Channel* | | Δ_i | k | w |
|------|---------|----------|------|------------|----|-------|
| | | Bank | Bank | | | |
| 1 | x | x | x | 0.0 | 10 | 0.996 |
| 2 | x | x | | 10.9 | 7 | 0.004 |
| 3 | | | x | 16.0 | 4 | 0.000 |
| 4 | x | | | 61.2 | 6 | 0.000 |

micro-scale GLMMs we considered, there was strong support for the model that included bank type, substrate, and flow refuge presence/absence as fixed effects (Table 5).

Information on how *G. angulata* abundance varies among the levels of each fixed effect is provided by figures and the parameter coefficients (and associated confidence intervals) for the top ranked models. *G. angulata* abundance was not significantly different among the channel unit types (Figure 5a; Table 6). We found significantly

more *G. angulata* on bank edges than bar edges (Figure 5b; Table 6, 7). Controlling for availability of substrates, *G. angulata* were found more frequently in sand than any other substrate, and second-most frequently in gravel; abundances were much lower in all other substrates (Figure 5c; Table 7). Controlling for availability of flow refuges, significantly more *G. angulata* were found in flow refuges than outside of flow refuges

(Figure 5d; Table 7). These results corroborated our qualitative observation that most mussels appeared positioned in microhabitats protected from the main current. Within these velocity refuges, mussels would often be embedded in sand or gravel that had settled behind boulders or in bedrock crevices. We rarely found mussels in the thalweg (lowest portion of the river channel) or more than two to three meters from the bank.

TABLE 5. Summary of small-sample size Akaike information criterion (AIC_c) ranking of *G. angulata* micro-scale abundance GLMMs for data collected from sites in 2010 (n = 21 sites, n = 504 observations). Channel = channel unit type; Bank = bank type; Sub = substrate type; Flow = flow refuge presence/absence; * = interaction term. Δ_i = AIC_c of model_i - AIC_cmin; k = number of model parameters; w_i = AIC_c weight for model_i, AIC_c weights sum to one for the set of models under consideration. Only the six highest ranked models out of 17 total models are shown.

| Rank | Channel | Bank | Sub | Flow | Sub*Flow | Channel*Bank | Bank*Flow | Δ_i | k | w_i |
|------|---------|------|-----|------|----------|--------------|-----------|------------|----|-------|
| 1 | | x | x | x | | | | 0.0 | 11 | 0.579 |
| 2 | x | x | x | x | x | | | 3.3 | 18 | 0.113 |
| 3 | x | x | x | x | | x | | 3.4 | 15 | 0.103 |
| 4 | x | x | x | x | x | x | x | 4.1 | 21 | 0.075 |
| 5 | x | x | x | x | | | | 4.2 | 13 | 0.071 |
| 6 | x | x | x | x | | | x | 4.5 | 14 | 0.060 |

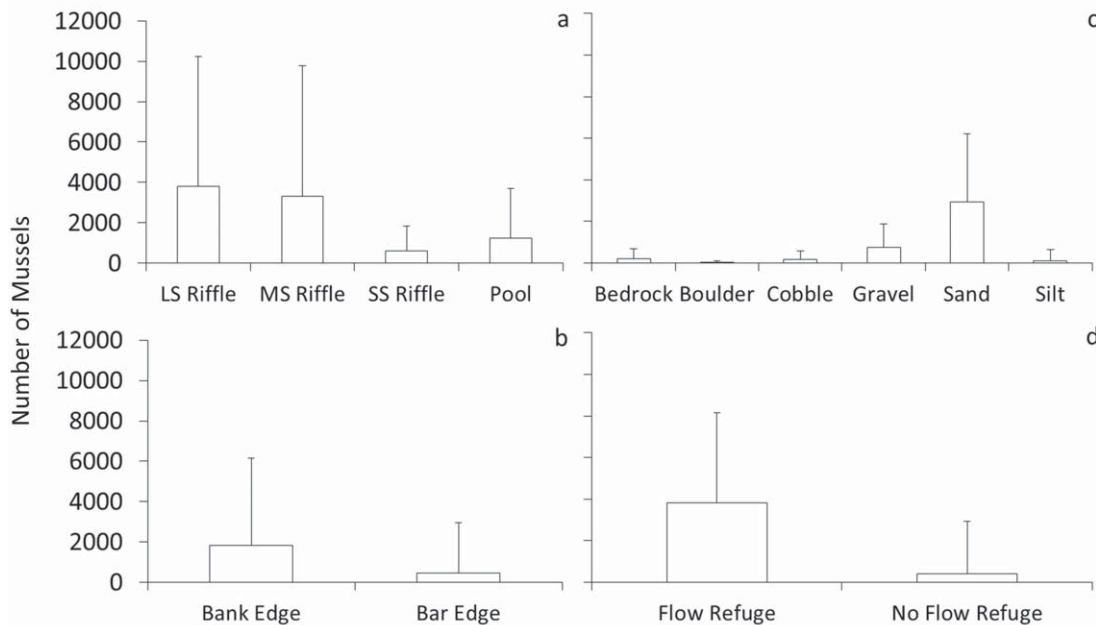


Figure 5. Mean (+SD) mainstem Klamath *G. angulata* abundance for meso- and micro-scale habitat categories. (a) Total site abundance in different channel unit types from sites sampled in all years. (b) Side of site (the left or right half of a 50 m section of channel) abundance in different bank types from sites sampled in all years. (c) Total site abundance in different substrate types from sites sampled in 2010. (d) Total site abundance associated with and without potential flow refuges from sites sampled in 2010.

TABLE 6. Model summary for the AIC_c top-ranked *G. angulata* meso-scale model. For each categorical fixed effect, one level is set as the reference level for that effect (the intercept). Fixed effect parameter coefficient estimates are thus the difference between the mussel abundance of the reference level and the level in question (in log space). Wald Z scores and *P* values indicate whether a parameter coefficient is different from zero.

| Coefficient | Estimate | SE | Z | <i>P</i> |
|--------------|----------|-------|-------|----------|
| (Intercept) | 8.094 | 0.734 | 11.03 | <0.0001 |
| Pool | -1.352 | 0.850 | -1.59 | 0.11 |
| LSriffle | -0.547 | 0.891 | -0.61 | 0.54 |
| SSriffle | -1.736 | 1.659 | -1.05 | 0.30 |
| Bar | -7.388 | 1.146 | -6.45 | <0.0001 |
| Pool*bar | 0.765 | 1.304 | 0.59 | 0.56 |
| LSriffle*bar | 6.735 | 1.388 | 4.85 | <0.0001 |
| SSriffle*bar | -0.303 | 2.646 | -0.11 | 0.91 |

TABLE 7. Model summary for the AIC_c top-ranked *G. angulata* micro-scale model. For each categorical fixed effect, one level is set as the reference level for that effect (the intercept). Fixed effect parameter coefficient estimates are thus the difference between the mussel abundance of the reference level and the level in question (in log space). Wald Z scores and *P* values indicate whether a parameter coefficient is different from zero.

| Coefficients | Estimate | SE | Z | <i>P</i> |
|--------------|----------|-------|-------|----------|
| (Intercept) | -0.220 | 0.908 | -0.24 | 0.809 |
| Bar | -6.829 | 0.718 | -9.51 | <0.0001 |
| Flow refuge | 3.379 | 0.427 | 7.92 | <0.0001 |
| Boulder | -3.853 | 0.936 | -4.12 | <0.0001 |
| Cobble | 0.027 | 0.760 | 0.03 | 0.972 |
| Gravel | 1.630 | 0.729 | 2.24 | 0.025 |
| Sand | 3.827 | 0.756 | 5.07 | <0.0001 |
| Silt | -1.544 | 0.898 | -1.72 | 0.085 |
| Sub cover | 9.855 | 2.491 | 3.96 | <0.0001 |

Discussion

Landscape-scale Patterns of Distribution and Abundance

We found distinct, large-scale patterns of mussel species distribution in the Klamath. Within the mainstem mid Klamath, we observed *Anodonta* sp. occurring only in the furthest upriver survey sites, *G. angulata* almost throughout, frequently in high numbers, and *M. falcata* only present in high numbers downstream of the confluence with the Salmon River. The unusual “upside-down” nature of the Klamath watershed (NRC 2004, VanderKooi et al. 2011), specifically with regard to hydrological variability, may be responsible for some of the longitudinal variation in mussel distribution we observed. Hydrological variability has been shown to affect mussel distribution, abundance, and community composition in other watersheds, with distinct differences between rivers with different hydrological regimes (diMaio and Corkum 1995, McRae et al. 2004).

We observed an overall decline in mean mussel abundance per site as hydrological variability increased progressing downstream. High values for measures of hydrological variability mean an increase in the magnitude and frequency of high flows and extreme variations from the mean flow,

which mean an increased probability of riverbed scouring and/or high shear stresses that may prevent mussel recruitment. High shear stress is associated with low substrate stability and increased energy required by the mussel to maintain its position and feed (Rempel et al. 2000). Large variability in flows also reduces the proportion of the channel that is suitable for mussels during both high and low flow periods. Habitats suitable for mussels during peak flows (e.g., edge habitats) are dry during low flow periods and habitats suitable during low flow periods (e.g., the central channel) experience high shear stress and bedload transport during peak flows. Hence, the further downstream a site was located within our study area, the lower the probability that it would support mussel recruitment and persistence under a range of annual hydrological conditions.

The pattern of species distribution throughout the system may also be partially a function of hydrological variability. Research has shown that shell morphology, shell thickness, and other species-specific adaptations enable mussels to tolerate varying hydrological and substrate stability conditions (Stanley 1981, Allen and Vaughn 2009, Hornbach et al. 2010), and such adaptations may contribute to the observed pattern of species distributions in the Klamath. *Anodonta* is a soft-

substrate genus (Nedeau et al. 2009) with a thin shell, meaning that it has little ballast in fast currents and cannot withstand scouring. This could explain its relatively high abundance in the hydrologically regulated stretch of river just below Irongate Dam, which maintains a stable flow year-round (Williams and Curry 2011). As hydrological variability increases (and the availability of stable substrate presumably decreases) further downstream from Irongate, *Anodonta* disappear. *G. angulata* and *M. falcata* are more common in downstream areas, probably due to thicker shells which allow them to withstand scouring in high flow events (Burch 1973, COSEWIC 2003). We observed that *G. angulata* and *M. falcata* are also better able to wedge themselves tightly into substrate.

The pattern we observed in the Klamath is different from patterns of longitudinal distributions of mussel species found in the few published studies of mussels in other western rivers. *M. falcata* occurred in relatively higher numbers in the headwaters of the North and Middle Fork John Day, while *G. angulata* and *Anodonta sp.* were more common at downstream sites in this system; in the Umatilla system, both *Anodonta sp.* and *G. angulata* were collected only from the furthest downstream sites sampled (Brim Box et al. 2006). Howard and Cuffey (2003) observed a similar pattern in the upper South Fork Eel River drainage of California's North Coast range, with *M. falcata* occurring throughout the study area of the upper drainage, but aggregations of *Anodonta sp.* only occurring at the downriver end of the surveyed reach. Both the John Day/Umatilla and Eel systems have a more commonly observed watershed structure compared to the Klamath: steep mountain headwaters transitioning to low-relief mainstems. These differences in basin structure may contribute to the differences with the Klamath in how mussel species are distributed throughout the basins.

Although hydrological variability is one important factor constraining mussel distribution at the macro scale, it does not account for all the variation within and among species distributions, nor do the other physical habitat factors described in this study. To explain more of the variation in

mussel distribution, it may be necessary to consider additional variables and move to a functional rather than strictly physical view of mussel habitat. Such a "functional habitat" approach asks, "What does a mussel need from its habitat?" (Strayer 2008). For example, a combination of biotic and abiotic factors important to mussels includes stable habitat and protection from sediment transport; sufficient food; dispersal opportunity (via host fish availability); water chemistry; temperature; and protection from predators (Newton et al. 2008). Therefore, physical habitat variables such as substrate and hydraulics should be not be analyzed as the sole predictive variables, because they can only partially explain mussel distributions (Allen and Vaughn 2010). Other factors that could be influential in watershed-scale distribution of mussels which we did not measure include water quality (McRae et al. 2004), stream productivity/food availability (Brim Box et al. 2006), water temperature, host fish abundance/distribution (Vaughn and Taylor 2000), surrounding land use (Arbuckle and Downing 2002), and river aggradation (Vannote and Minshall 1982).

We observed all three western mussel genera in the major tributaries of the mid Klamath (although only a single tributary hosted all three together), but we were unable to identify clear patterns among tributaries due to the patchy nature of our tributary sampling and the inherent difficulties of making cross-basin comparisons without accounting for differences in geology and watershed size, as well as drastic anthropogenic alterations to basin hydrology in the Scott and Shasta watersheds. However, a few observations stood out from our surveys. Mussel abundance (standardized as counts per 50 m to be comparable with mainstem counts) was generally lower in tributaries and distribution was quite restricted as compared to the mainstem Klamath. The Shasta, with the lowest measures of hydrological variability of the four gauged tributaries, was the only tributary with all three western genera, and by far the highest counts of mussels, approaching abundances of some sites on the mainstem. The majority of the mussels we found in the Shasta were located at sites near its low-gradient, spring-fed, and hydrologically stable headwaters. Similarly, the low-gradient reach near

the confluence of the Salmon with the Klamath and the low-gradient reaches of the South Fork of the Salmon had relatively high densities of mussels, although not approaching those of the Shasta. Some tributaries such as Wooley Creek and Indian Creek had no mussels at all, and these had hydrologically unstable, high-gradient profiles. Scour during high flow events in the steep canyon reaches of these streams probably limits recruitment and long-term survival of mussels.

Mesohabitat Factors

Many researchers attempting to explain patterns of mussel abundance and distribution agree that shear stress, substrate stability, and flow refuges are three important meso- and micro-scale determinants limiting mussel recruitment and survival (Vannote and Minshall 1982, Strayer 1999, Morales et al. 2006).

Previous studies (Vannote and Minshall 1982, Howard and Cuffey 2003, Gangloff and Feminella 2007) found that channel unit type (i.e., whether a reach is a riffle, run, pool, etc.), influences mussel abundance, though the studies differed about which channel unit type was “best” for mussel habitat. Our best model of meso-scale mussel abundance included channel unit type as a predictor variable, though there was a high degree of variation in mussel counts among sites with the same channel unit type—indicating that additional variables are important at this scale of observation. Channel unit type was not an important predictor of mussel abundance at the micro scale when micro-scale habitat variables were included in a model, suggesting that channel unit types do not account for important fine scale habitat variation.

It may be that suitability of habitat types and the degree to which a physical habitat component influences mussel abundance differs from river to river depending on hydrological and geological conditions. If so, this underscores the importance of understanding watershed-level controls—hydrological variability, gradient and geology—on the abundance and distribution of particular mussel species. It also underscores the need to move to a “functional habitat” approach incorporating biotic and abiotic factors important to mussel life stages.

The habitat survey we selected our sites from used several criteria to define channel unit types. A functional habitat approach might identify the particular factors relevant to mussels (e.g., channel gradient) rather than using broad categories that incorporate multiple physical habitat variables, some of which may not be relevant to mussels. We suggest that future studies in the Klamath take a functional habitat approach.

In contrast to channel unit type, bank type—another meso-scale characteristic—was an important predictor of *G. angulata* abundance at both meso and micro scales. Mussels were significantly more abundant on bank edges than on bar edges. Bank type is indicative of the shear stress experienced by and substrate stability of edge habitats at scouring flows. Above a certain level of shear stress, mussels are dislodged or crushed/scoured by large mobile substrate (Strayer 1999). The loose cobbles and gravels that compose bar edges move during flood flows, while the boulders, bedrock, and other hard features that compose bank edges remain stable, with less sediment deposition, providing habitats where mussels can recruit and persist over the long term. Bank type is thus likely indicative of the availability of flow refuges, an important micro scale habitat variable.

The top-ranked meso-scale model also included the interaction between channel unit type and bank type. The importance of this interaction is not surprising: channel edges vary in their suitability as habitat depending on factors such as gradient, which is included in channel unit type. Thus, overall banks are more suitable than bars for mussel habitat, but vary in suitability depending on association with channel unit type.

Microhabitat Factors

Considerable debate and uncertainty remains regarding the strength of associations between sediments and mussels (Brim Box and Mossa 1999). More sediment particle size categories than the ones used in this study may be necessary to accurately describe habitat associations (Brim Box and Mossa 1999). Interpreting the results of mussel substrate distribution on their own can be difficult; however, if substrate size is considered

in conjunction with information on the hydraulic environment, the results may be more valuable (Allen and Vaughn 2010).

We found *G. angulata* more frequently in sand than all other substrates, and second-most frequently in gravel. Substrate size is a commonly reported habitat characteristic for studies of mussel distribution; however, substrate often fails to be a strong predictive variable (Strayer and Ralley 1993), especially in comparisons across drainages. Microhabitat factors such as substrate size may not themselves control mussel distribution; rather, they likely serve as a visible proxy for the real controls, hydraulics and substrate stability.

At the micro scale mussels tended to inhabit “flow refuges,” where long-term substrate stability is ensured by protective features like boulders and low-velocity regions on edges of islands (Morales et al. 2006). After accounting for the availability of potential flow refuges, we found significantly more mussels associated with flow refuges than with those microhabitats lacking flow refuges. It is important to note that in contrast to Strayer’s (1999) study of flow refuges, we did not actually map flow refuges during high flow events. We noted physical features which appeared likely to alter the flow of water over the riverbed. These physical features, such as boulders or bedrock ledges, often accumulate finer sediments, mostly sand or gravel, in the micro eddies on their lee sides. Mussels situated in flow refuges are protected from scouring flows and have substrate of a grain size small enough in which to embed themselves. Our results suggest that the association of mussels with specific sediment size classes and the distribution of mussels in relation to flow refuges are directly linked. This supports Vannote and Minshall (1982), Strayer (1999), and Gangloff and Feminella’s (2007) conclusions that mussel abundance at the reach and micro-scale levels is low in areas of high shear stress and is controlled by availability of flow refuges.

Summary

Our study, examining mussel distribution and abundance in the middle Klamath basin at three

nested spatial scales, demonstrates the need for a multi-scale approach when examining mussel habitat associations. We showed that distribution patterns can be partially explained by different physical variables at different scales. The patterns observed at each scale suggest a common influence of hydraulics as a major driver of mussel distribution. Hydrological variability, which changes longitudinally across the middle Klamath basin, limits the amount of the channel that is potentially suitable habitat. Hydraulics and hydrological variability are linked: part of a watershed with variable hydrological conditions (extreme high and low flows, high frequency of high flows) is likely to have small-scale hydraulic conditions (shear stress, scour) that are often unfavorable for mussels. At meso and micro scales, mussels are found predominantly along bank edges, which provide stable substrates, and in flow refuges where fine sediments accumulate. Further research that measures flow refuges, substrate stability and complex hydraulic variables during periods of high flow would likely corroborate our results by taking a direct rather than indirect look at these important variables. Additionally, future research should incorporate biotic, chemical, and anthropogenic variables such as land use to achieve a true functional habitat perspective.

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