Freshwater Mussel Distribution, Abundance and Habitat Use in the Middle Klamath River

Marie Louise Westover

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Certificate of Approval

This is to certify that the accompanying thesis by Marie Louise Westover has been accepted in partial fulfillment of the requirements for graduation with Honors in Biology.

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Timothy Parker

Whitman College
May 12, 2010

TABLE OF CONTENTS

ABSTRACT

Freshwater mussels of the Klamath River community filter water, provide habitat and food for other animals and are culturally important to the Karuk tribe. Mussels are disappearing at an alarming rate in the United States and worldwide; more information on mussel biology and habitat is crucial for conservation. As part of the first comprehensive study of mussels in the Klamath River, we identified habitat variables important to mussel conservation and provided baseline data for future studies. We hypothesized that long term habitat stability affected the distribution and abundance of *Gonidea angulata* (western ridged mussel), *Margaritifera falcata* (western pearlshell) and *Anodonta sp.* (floater mussel) in the Klamath River. We predicted that mussels would more commonly inhabit stable areas like pools, bar edges and bedrock and boulder substrates than less stable areas. We found that substrate and river edge correlated with *M. falcata* and *G. angulata* distribution, but mesohabitat did not. *M. falcata* preferentially inhabited boulder and gravel substrates whereas *G. angulata* lived in boulder and cobble; both commonly occupied stable bank edges. Our research suggests that river edge and substrate are important factors for mussel habitat, and that mussels prefer habitats that are stable for multiple decades. Continued research on the Klamath River mussels is necessary for effective monitoring and conservation of mussels as a cultural and biological resource.

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Freshwater Communities

Freshwater communities are important to ecosystems and humans, but are highly threatened by human activities. Lakes, streams, rivers and wetlands support a disproportionately large percentage of aquatic species, though only 1% of the world's water is held in these systems (Thorp and Covich 2001). They provide food, jobs, natural flood control and water purification for humans as well as habitat for plants and animals (Baron et al. 2002). Human activities also disproportionately impact freshwater communities. Freshwater communities face pollution, overexploitation of fisheries, habitat loss and habitat destruction. Scientists predict that climate change will adversely affect freshwater biodiversity through fragmentation of cold-water habitats, invasion and spread of exotic species, and water quality degradation from extended periods of low flow (Meyer et al. 1999). Because of these threats, freshwater animals might go extinct five times fasted than terrestrial animals in the next century (Ricciardi and Rasmussen 1999).

Freshwater Mussel Biology

Freshwater mussels (Bivalvia: Unionidea) are the most imperiled order of animals in North America, with over 70% of species extinct or in danger of extinction (Williams et al. 1993). Habitat loss, pollution, pesticides, dams, siltation, mining, dredging and introduced species all contribute to mussel extinctions and declines (McMahon and Bogan 2001). Although freshwater mussel populations are declining, their conservation remains inadequate due to limited scientific knowledge of mussel ecology.

Freshwater mussels are important inhabitants of lakes, rivers, streams and estuaries worldwide because they improve habitat and provide food for other animals (Bogan 2008). They anchor themselves into sediment with their muscular foot, unlike marine mussels that use sticky byssal threads to attach themselves to surfaces (McMahon and Bogan 2001). Mussels feed by taking in water with their incurrent siphon, trapping food particles on their gills and using cilia to move food particles from the gills to the mouth. They deposit excess or unwanted particles on the river bottom, which other invertebrates eat (Dillon 2000). Mussels decrease turbidity and improve water conditions by filtering phytoplankton and bacteria out of the water column. (Vaughn et al. 2008). They also improve habitat for macroinvertebrates by stabilizing and oxygenating sediments, and creating habitat with their shells and the spaces between their shells (Vaughn and Hakenkamp 2001, Vaughn and Spooner 2006). Bears, otters, mink, raccoons and other animals consume mussels as an important food source (Nedeau et al. 2000). By performing multiple ecosystem functions, mussels increase the biodiversity and abundance of invertebrates and vertebrates in streams (Vaughn and Spooner 2006).

Mussels have a complex life cycle, which can challenge conservation efforts. Male mussels expel sperm into the water, which females then take up with their incurrent siphon to fertilize their eggs (Dillon 2000). Successful fertilization requires a high concentration of sperm in the water, and may require high densities of mussels, which suggests that low-density mussel patches may not significantly contribute to reproduction (Bauer 1991). Females release larvae called glochidia into the water, where they are inhaled by a host fish and attach to its gills as a parasite, extracting nutrients from its blood supply (Dillon 2000). After several weeks, the glochidia mature into juvenile mussels, detach from the fish gills and settle to the river bottom. Each mussel species may rely upon a single species of host fish or many for their reproduction (Dillon 2000). The parasitic glochidial stage disperses mussels throughout the watershed, but makes mussel populations vulnerable to the loss of host fish.

Mussels in the Klamath River and the Western United States

Mussels in the western US are poorly studied, and lack of information on their ecology, life history and zoogeography hinders their conservation (Box et al. 2006). While the southeastern United States boasts the highest diversity of freshwater mussels in the world with 290 species, only seven species live west of the continental divide (Nedeau et al. 2000, Bogan 2008). Active geology, recent glaciations and aridity are all factors that have limited mussel dispersal and proliferation in the West (Nedeau et al. 2000).

The Klamath ecoregion of Northern California is biologically diverse and unique, but we know little about its freshwater mussels. The Klamath River flows from its headwaters in the Yolla Bolly Mountains in southern Oregon through cropland before passing through the Klamath Siskiyou Mountains and reaching the Pacific Ocean. Six dams block the river's flow and prevent fish from traveling upriver, which impede the distribution of mussel glochidia. The dams decrease water quality by creating eutrophication, toxic algae blooms and low dissolved oxygen content, which may negatively impact mussel populations downriver (Kann and Asarian 2002).

The USGS documented three species of mussels in the Klamath River in 1867: *Gonidea angulata,* (family Unionidae, order Unionoida) *Margaritifera falcata*, (family Margaritiferidae, order Unionoida) and *Anodonta sp.* (family Unionidae, order Unionoida), and these were again reported in 2008. (USDA Forest Service 2004, David 2008, Davis 2008). The three species are often found together because of their similar cool water needs (Frest and Hawks 2003).

G. angulata had a widespread historic range from southern British Columbia to southern California, including Idaho and Nevada. Its range no longer extends below northern California, and its populations are sparsely distributed. *G. angulata* lives 20-30 years and needs cold, clean water, which is increasingly uncommon in many rivers (Frest and Hawks 2003).

M. falcata are the most common mussel species in the Pacific Northwest, with a historic distribution reaching from California to southern Alaska (Nedeau et al. 2000). It has been decimated in many coastal and large rivers, like the Snake and Columbia Rivers, due to the loss of salmon and trout host fish (Nedeau et al. 2000). *M. falcata* can live to be over 100 years old, and requires cold, clean water. Because of its habitat and host fish requirements, dams, agriculture, pollution and siltation have all decreased *M. falcata*'s range.

The third species is a member of the genus *Anodonta,* but individual species are not identifiable based on shell morphology, which has created much taxonomic confusion (Nedeau et al. 2000). Therefore, the *Anodonta* species found in the

Klamath will be referred to as *Anodonta sp.*, although it is likely to be either *A. oregoniensis* or *A. californiensis* (Smith 2004, Nedeau et al. 2000). *Anodonta sp.* grows quickly in stable, nutrient rich waters such as lakes, and has a thin shell and short life span of 10-15 years. *Anodonta* species are generalists that can tolerate degraded water systems, low oxygen levels and siltation better than other mussels (Nedeau et al. 2000).

Although *Anodonta, G. angulata* and *M. falcata* are often found together, mussel communities in western rivers have variable species composition. In the John Day River, species composition changed from *M. falcata* dominance upriver, to greater numbers of *Anodonta* and *G. angulata* downriver. The Umatilla River had both *Anodonta* and *G. angulata*, but no live *M. falcata* (Box et al. 2006). Vannote and Minshall (2007) reported *M. falcata* and *G. angulata* in the Salmon River of Idaho, and Howard and Cuffey (2003) observed aggregations of *M. falcata* and *A. californiensis* in the South Fork Eel River of coastal northern California. The Klamath River has a relatively diverse mussel community compared to other rivers in the Pacific Northwest because it contains all three mussel genera.

Cultural Importance for the Karuk Tribe

Mussels have cultural importance for the native Karuk tribe. Mussels were traditionally harvested and eaten, and shells were used for women's spoons, tools, and jewelry. The Karuk have been denied traditional food sources, such as salmon, over the last 150 years, and have increasingly adopted western foods. This dietary shift has increased diabetes, heart disease and obesity (Norgaard 2005). As recently as the 1960s the Karuk ate mussels frequently (Davis 2008, David 2008). Today, the

Karuk eat small numbers of mussels during important ceremonies, but express concerns about potential toxins in the river and mussels (Davis 2008). Mussels are an irreplaceable cultural and biological resource in the Klamath River basin. Our study increased scientific and cultural knowledge of Klamath River mussels by identifying habitat variables important for their survival and conservation.

Research Goals

This research is part of the first comprehensive study on the freshwater mussels of the Klamath River in northern California, and our goal was to determine habitat factors affecting mussel distribution**.** We hypothesized that long term stability of features such as pools, bank edges, bedrock and boulder substrates, affect the distribution and abundance of *Gonidea angulata*, *Margaritifera falcata*, and *Anodonta sp.* in the Klamath River. We predicted that we would find mussels in stable areas more frequently than less stable areas. We surveyed 40 sites along the Middle Klamath River, recording all mussels encountered and the habitat variables of substrate, river edge, and mesohabitat.

METHODS

Study Area

We conducted our survey between June 24 and July 31, 2009 on the middle Klamath River in northern California's Humboldt and Siskiyou counties. The study sites were located between Iron Gate Dam and the confluence of the Klamath and Trinity Rivers (Fig. 1). Approximately half the sites were located in Karuk ancestral territory, which occupies about 100 miles between the borders of Aikens Creek to the south and Seiad Creek to the north (Fig. 2). We surveyed 40 sites for the distribution, abundance, and habitat use of *G. angulata*, *M. falcata* and *Anodonta sp.*

We randomly selected the 40 distribution and abundance survey sites from a previously performed U.S. Fish and Wildlife survey, which divided the Klamath River from Iron Gate Dam to the mouth into numbered sections, called reaches, according to changes in mesohabitat. Mesohabitat is the medium-scale habitat description of rivers that results from river flow interacting with local geology, which affects the slope and speed of the river. The USFW survey recorded the length of the reach, UTM coordinates and a brief description of landmarks at the site, with the sites sequentially starting at Iron Gate Dam and increasing in number towards the mouth of the river. To ensure an even distribution of sites along our survey area, we divided the river into 4 equal sub-segments and randomly chose 10 sites from each sub-segment. We entered these site numbers from Iron Gate Dam to the Trinity River into Microsoft's Excel randomize function to select our 40 survey sites. If the randomly selected sites were inaccessible or unsafe to survey, we replaced them with sites similar in location and mesohabitat.

We located the sites using a GPS, map, aerial photographs and landmarks, and accessed site by hiking from the roadside or by rafting to them. We surveyed upriver sites earlier in the summer to avoid poor visibility due to late summer algal blooms. We randomly selected five sites to survey twice to gauge the repeatability of our survey methods. We surveyed the repeated sites at the end of the field season, and researchers surveyed different sides of the river than they did in the initial survey to limit bias.

Survey Methods

At each site, we measured 50 meters of the reach with a taught survey tape, marking both upstream and downstream ends with flagging to ensure that boundaries were visible from both sides of the river. We generally measured 50 meters downstream from the beginning of the reach, unless access or safety concerns prohibited this. Alternatively, we would place our 50 m tape slightly upstream or downstream of the beginning of the site.

After securing the survey tape we recorded the location with a GPS, and took digital photographs from the upstream and downstream ends of the site looking both at the survey tape and directly across the river to identify the site in the future. We recorded the river edge on each side of the river as either a bank or bar. A bank edge has a steep slope to the water's edge, and is made of soil, boulders or bedrock, while a bar edge has a gentle slope, and is made of deposited material such as sand or cobble. We recoded the mesohabitat type as pool, low slope, medium slope, steep slope riffle, or rapid. A pool is a deep and slow moving section of river, a low slope riffle is shallow and faster moving with small whitecaps on the water's surface, a medium slope has larger whitecaps or small waves, a steep slope riffle is faster moving water with waves, and a rapid is steep with fast water and large waves.

Once we established the site, we systematically snorkel-surveyed both sides of the river. Typically, one teammate would survey each side of the river for mussels, while one person would record data. We started from the downstream end and worked up, surveying as far out into the main channel as was possible or safe. We counted mussels individually, and recorded the substrate in which we found them. We defined substrate categories as: bedrock, boulder (>25cm diameter), cobble (6.4 - 25cm), gravel (0.2mm - 6.3cm), sand (0.125mm - 1.9mm), silt (<0.125mm), and mud. We estimated the total percentages of each substrate at the site. For mixed substrates, we initially reported the components as dominant (comprising >50% of the mix) and subdominant (comprising 20-49% of the mix), but this method created complications. We later reported mixed substrates as being the larger particle size of the two categories, because we believe that the larger component of the two substrates is more likely to influence the hydraulics of the mussel microhabitat.

We recorded the species of each mussel and whether it was on the right or left river edge. We identified the species of each mussel by shell morphology (Smith 2004). We also drew a sketch of the site, including flow controls, bank features, landmarks, vegetation, and mussel and bed locations.

If mussels were too numerous to count individually, we designated the area as a 'bed,' and estimated numbers using quadrats. The snorkeler would use the survey tape to measure the length of the bed and estimate the width, because it was often too difficult to extend the survey tape perpendicularly into the current, and then we calculated the area of the bed. Next we determined how many 0.25 x 0.25m quadrats were needed to cover 10% of the bed area. We evenly spaced this number of quadrats in alternating locations within the bed. Each time we placed a quadrat, the snorkeler counted all of the mussels within the quadrat area and reported the substrate. We later used the quadrat mussel counts to estimate of the total number of mussels in the bed. We also searched the remainder of the site for individual mussels.

Analysis

We performed each statistical analysis for both *M. falcata* and *G. angulata,* but we did not include *Anodonta sp*. because sample size was too small. We attempted to explain the number of mussels using a single generalized linear mixed model using GLMMIX macro in SAS, combining the three fixed-effect predictor variables mesohabitat, river edge and substrate, with site and side of the river as random effects, but the models did not converge. Instead, we used G-tests to assess whether mussels were distributed according the relative availability of substrates. We determined the effects of river edge and mesohabitat type on mussel counts together in a single generalized linear mixed model with Poisson error. We controlled for the two counts per site (one from each side of the river) by including site as a random effect. We also assessed effects of mesohabitat type using G-tests to examine whether presence of mussel beds or mussel bed area are related to mesohabitat type.

We assessed the repeatability of our mussel counts on a per-site basis using the standard method (Lessells and Boag 1987). We also assessed repeatability of the proportion of each site estimated to belong to each substrate type using the same method.

RESULTS

Mussel Abundance and Wide Scale Distribution

Mussels were widely dispersed throughout the middle Klamath River. We found mussels at 37 of our 40 study sites, and recorded an estimated 127,341 *G. angulata*, 1,484 *Anodonta sp.*, and 492 *M. falcata* (Fig. 3)*. G. angulata* was abundant, common, and widely dispersed throughout our study area. Of the 40 sites surveyed, 36 contained *G. angulata.* Most *G. angulata* were situated in beds and the largest one contained an estimated 21,810 mussels. *Anodonta* was the second most abundant mussel, but was only located at three sites below Iron Gate Dam. We found a single bed with an estimated 1,308 *Anodonta sp.* immediately below Iron Gate Dam, and four individuals at two nearby sites*. M. falcata* was the least common mussel, but we found it at nine sites, mostly below the confluence of the Salmon and Klamath rivers. *G. angulata* dominated all of the sites where we found *M. falcata*. We found no beds of *M. falcata*, but instead we found them dispersed in congregations and beds of *G. angulata*.

Beds

We found beds of mussels at 18 out of the 40 sites surveyed. Two thirds of the beds were located in the upriver half of our sites.

River Edge

We determined that there was a significant relationship between river edge type and mussel counts using a generalized linear mixed model. Bank edges had significantly higher mussel abundance (*G. angulata* $p < 0.0001$, *M. falcata* $p = 0.03$)

(Tables 1, 2). Although we found large numbers of *G. angulata* on bar edges at a few sites, the vast majority of *G. angulata* lived on bank edges (Fig. 4). *M. falcata* occurred almost exclusively on bank edges (Fig. 5). A G-test showed that beds of mussels were significantly more common on bank edges than bar edges ($G = 4.5$, d.f. = 1, $p = 0.03$).

Mesohabitat

Although we found greater numbers of both *G. angulata* and *M. falcata* in low slope riffles than in other mesohabitats, we did not find a significant effect of mesohabitat on the distribution of either species (Tables 1,2, Figs. 6,7). We found that there were more square meters of mussel beds in low slope and medium slope riffles than expected ($G = 248.0$, d.f. = 3, $p << 0.0001$, Table 3, Fig. 8). However, mussel bed density was not significantly affected by mesohabitat ($G = 6.8$, d.f. = 3, $p = 0.08$).

Substrate

We performed G-tests to determine whether or not *G. angulata* and *M. falcata* were evenly distributed among substrates in proportion to the availability of each substrate. There were significantly more *G. angulata* in cobble and boulder substrates than expected, and significantly fewer in silt, sand, gravel and bedrock ($G =21487.5$, d.f. = 5, $p << 0.0001$, Table 4, Fig. 9). Similar G-tests on *M. falcata* revealed that they preferentially inhabited bedrock over all other substrates ($G = 932.4$, d.f. = 5, $p << 0.0001$). They also inhabited gravel more frequently than expected in an even distribution (Fig. 10). We found significantly fewer *M. falcata* in silt, sand, cobble and boulder substrates than expected (Table 5, Fig. 10).

Repeatability

Our counts of *G. angulata* were significantly repeatable, but not our counts of *M. falcata* ($r = 0.91$, $F = 22.8$, d.f. = 4,5, $p = 0.002$, $r = 0.31$, $F = 1.9$, d.f. = 4,5, $p = 0.25$, respectively). The repeatability of our initial estimates of percent coverage by dominant and subdominant was statistically significant, but low ($r = 0.55$, $F = 3.4$, d.f. = 109,110, $p << 0.0001$). The repeatability of our revised single substrate categories was significant and higher ($r = 0.86$, $F = 14.1$, d.f. = 24,25, $p << 0.0001$). When we excavated mussels in beds, we always found more mussels hidden under the substrate than counted on the surface per quadrat. Surface counts were a very strong linear predictor of the total number of mussels ($y = 1.80x - 34.80$, $R^2 = 0.83$, Fig. 11).

DISCUSSION

Our results from substrate and river edge data support our hypothesis that stability of physical features in the river positively effects mussel distribution. *Margaritifera falcata* more frequently live in bedrock and gravel substrates, *Gonidea angulata* mainly live in boulder and cobble substrates and both species more commonly live on bank edges. However, we did not find mussels more frequently in pools or other mesohabitats.

Mussel Abundance and Wide Scale Distribution

We found that the middle Klamath River provides habitat for thousands of freshwater mussels. Mussels were widely distributed throughout the river and found at almost every site. Our results on mussel abundance and distribution were similar to David (2008) and Davis's (2008) results. Both studies found that *G. angulata* comprised the vast majority of mussels, with limited numbers of *Anodonta sp.* and *M. falcata*. However, given that there are no studies of mussel distribution or abundance in the Klamath River prior to 2007, we cannot ascertain whether the mussel community has changed dramatically since the 1800s. Compared to other rivers in the Pacific Northwest, the Klamath appears unusual because *G. angulata* dominates its mussel community.

The variation we found in abundance and species composition between both sites and regions of the Klamath River provide insight in the different micro-habitats of each species. We found *Anodonta* primarily below Iron Gate Dam, *M. falcata* below the confluence of the Klamath and Salmon Rivers, and *G. angulata* almost everywhere, but with a large variability in its abundance. Our surface counts of mussels were a good predictor of total counts in beds, so even though we underestimated *G. angulata,* the relative abundances throughout our study are not affected. The different microhabitats of each species may help explain the different abundances and spatial distributions of the three species of mussels.

G. angulata has adaptations for tolerating mild sedimentation, but may be limited by other habitat challenges. These mussels prefer cold, clean water and their feeding may be limited under high temperatures, high sedimentation, or pollution

(Frest and Hawks 2003). *G. angulata* can tolerate seasonally turbidity and is well adapted to aggrading, or depositional areas because it can bury most or all of its shell in sediments without affecting filter feeding (Frest and Johannes 1992, Vannote and Minshall 1982). Its wedge shaped shell and strong muscular foot enable it to anchor securely in substrates (Vannote and Minshall 1982). Siltation and eutrophication from agricultural runoff have reduced populations in the Snake and Columbia River regions, and may affect populations in the Klamath River as well (Frest and Johannes 1999).

Although all three species reported by the U.S. Geological Survey in 1867 still live in the Klamath River, *Anodonta sp.* and *M. falcata* have limited distributions and abundances compared to *G. angulata*. According to our data, *Anodonta sp.* is the second most common species in the middle Klamath River, but it is localized to below Iron Gate Dam, which creates preferable water conditions for it*. Anodonta* species thrive in nutrient rich waters and can tolerate low dissolved oxygen levels better than other freshwater mussels (Nedeau et al. 2000). The stagnant and enriched water created by agricultural fertilizers and multiple dams on the Klamath River is beneficial for *Anodonta sp.* but unsuitable for *G. angulata* or *M. falcata.* Because of its absence, it appears that *Anodonta sp.* is unable to survive the higher and more variable flows far downriver from the dam.

Although *M. falcata* was the least abundant species in the Klamath River, it was more widely distributed than *Anodonta sp..* We only found *M. falcata* near cold tributaries such as the Salmon River and smaller creeks, indicating that the influx of cool, clean water may be necessary for it to colonize and inhabit the middle Klamath

River. This suggests that warm summer water temperatures may limit *M. falcata*'s distribution in the river. Alternatively, *M. falcata's* host fish could limit it to the downriver Klamath.

Sedimentation may in part explain the low numbers of *M. falcata* in our study. Vannote and Minshall (1982) found that increased sedimentation from mining and logging near the Salmon River in Idaho caused a shift in the river's mussel population from a *M. falcata* dominated community to a *G. angulata* dominated one. While *G. angulata* actively moves vertically under siltation, the larger *M. falcata* individuals failed to do so, and were entombed below sediment. Mussel communities in the Klamath River may be experiencing the same scenario in response to siltation, with *G. angulata* dominating the area because of its ability to vertically move through substrate. Perhaps the Klamath River once housed larger numbers of *M. falcata,* but siltation from historical and ongoing logging and mining has buried them, allowing *G. angulata* to dominate.

We witnessed suction dredge mining frequently over the summer, mostly in our upriver survey areas. Suction dredge miners use a gasoline motor to vacuum the riverbed and run the sediments over a sluice to separate gold flakes. On a summer day, there could be 200 suction dredges operating on the Klamath River and its tributaries, disturbing the river bottom and suspending sediments for hundreds of feet downriver (Harding 2009). A popular hobby since the 1960s, suction dredge mining became illegal in California in August 2009 until the California Department of Fish and Game prepares an environmental review (CDFG). Suction dredging in the Klamath River has likely displaced mussels from the river bottom, buried and suffocated mussels downstream from siltation, and may have altered the mussel community composition.

Influence of River Edge

Mussels may be more common on bank edges because they provide stable habitat. Although many factors such as channel shape, local geology and vegetation influence bank stability, banks are generally more stable than bars because they are less variable in shape and location over time (Ott 2000). *G. angulata* and *M. falcata* live for decades and need to inhabit areas that are stable over decades in order to reach maturity and for beds to accumulate (Nedeau et al 2000). When mussels are found in scour prone areas such as sand and cobble bars, they tend to be younger, while older mussels usually live in protected and stable areas (Hardison and Layzer 2001). Our data support this observation, since we found long-lived *M. falcata* only on bank edges. Howard and Cuffey (2003) also found that *M. falcata* inhabited banks, and attributed this to lower water velocity than mid channel areas. In the case of *G. angulata,* populations on bar edges are probably younger mussels that colonized the bars after major flood events, since floods are likely to periodically wipe out mussels on bars. The majority of *M. falcata* and *G. angulata* inhabit bank edges because they provide protection from scouring and erosion during high water, while mussels on bar edges are more likely to be buried under deposited substrate or washed away in a flood.

Influence of Substrate

Biologists debate the importance of substrate in influencing mussel distribution. Many found substrate to be a significant factor affecting mussel distributions, whereas others reported no significant effects of substrate on mussel populations, or determined that other factors far outweighed the role of substrate. (Strayer and Ralley 1993, Layzer and Madison 1995, Hornbach et al. 1996, Box 1999, 2002, Howard and Cuffey 2003). Maybe substrate is more important to certain species of mussels, or may be more important in areas where scouring flows cause significant mortality. We found substrate to be an important factor influencing *M. falcata* and *G. angulata* distribution. Mussels may settle non-randomly in the river as a function of substrate and other hydraulic variables, and/or may suffer differential mortality as a function of substrate. *M. falcata* and *G. angulata* mainly occur in different substrates, indicating that they do not compete for the same microhabitat, but instead are specialized for the substrates that they inhabit.

It appears that bedrock, the most stable substrate, enables *M. falcata* individuals to remain secure and survive floods throughout its long life. Hydrologically stable areas are favorable for populations of *Margaritifera margaritifera*, a closely related species, because major floods, which upset less permanent substrates limit this species (Hastie et al. 2001). While boulder and cobble substrates provide a stable environment for *G. angulata*, we frequently found *G. angulata* clustered on the lee side of boulders in the river, which suggests that the mussels may be using the boulders as refuges from strong flows. Strayer (1999) demonstrated that mussels frequently inhabit flow refuges, or places were currents and shear stresses are stable even during floods. *G. angulata*'s distinctive ridged shell enables it to wedge securely under and between boulders and cobbles (Frest and Hawks 2003). Although boulder and cobble are not as stable as bedrock, *G. angulata's* adaptations enable it to remain secure in these substrates.

The different substrate preferences of *G. angulata* and *M. falcata* partially explain their distributions in the Klamath River. Vannote and Minshall (1982) found that mussel community composition in Idaho's Salmon River depended on substrate materials. *M. falcata* comprised 95% of the mussels in large boulder regions, while *G. angulata* comprised 97% of the mussels in sand and gravel. As finer sands replaced gravel over time, *G. angulata* replaced *M. falcata* in those areas. Our data support their findings, and indicate that substrate is an important factor determining the distributions of *G. angulata* and *M. falcata* in the Klamath River.

Influence of Mesohabitat

We found no statistically significant effect of mesohabitat on the local abundance of *M. falcata* or *G. angulata*. However, we did find significantly greater *G. angulata* bed area and more mussels within beds in low slope and medium slope riffles. Although many low slope riffles had many thousands of mussels in them, some low slope riffles had very few. It is possible that the wide variability of mussel abundance between sites reduced the generalized linear mixed model's ability to report any effect of mesohabitat on mussel abundance.

The extent to which mesohabitat affects mussel populations is debatable, and probably differs between rivers. Howard and Cuffey (2003) found *M. falcata* almost exclusively in pools, which are areas of low shear stress. In contrast, Vannote and

Minshall (1982) found *M. falcata* and *G. angulata* predominantly in shallow runs, which are similar to our definition of low slope riffle. They attributed higher mussel density in runs to optimal filter feeding, and found that pools scour during floods.

Perhaps riffles provide more food to support larger aggregations of mussels, which could explain why low and medium slope riffles contained greater mussel bed area than expected. Other research has suggested that riffles or moderately fast moving water allow for more efficient filter feeding by mussels, and deliver more food than slow moving pools or circulating eddies. Bolden and Brown (2002) found that *Margaritifera hembeli* grew faster in riffles than in pools, potentially because of greater food availability. Mussels in pools may deplete available food faster than the current can replenish it (Strayer 2008). In addition, sediment particles settle out in slow moving pools, which can result in detrimental siltation. While mesohabitat may play a role in determining the local abundance of mussels, our data do not provide strong support for this idea.

Repeatability

Although many of our results were highly significant, our low repeatability of *M. falcata* counts introduces uncertainty not reflected in our statistical analyses of river edge, mesohabitat, and substrate effects on *M. falcata* abundance. *M. falcata* was rare, so small differences in mussel counts within repeated sites had a large impact on our repeatability, making our first *M. falcata* counts at some sites an ineffective predictor of the second count. For example, at one site we found two *M. falcata* the first count and 30 the second time we surveyed it. We had a high repeatability of *G. angulata* counts because *G. angulata* abundances varied by several orders of magnitude between sites, and we found the same order of magnitude within repeated sites.

Future Research

Mussel research on the Klamath River has only recently begun, thus our research methods could be improved in future studies. For consistency in surveys, we suggest defining beds as any area over two meters squared with a density of over 40 mussels per meter squared. To improve substrate repeatability, we suggest using only single substrate categories as opposed to dominant/subdominant mixed substrate categories. Also, having the same surveyors work together over long periods of time probably increases the repeatability of both substrate and mussel counts.

Additional variables likely to affect the distribution of mussels should be examined, including the effects of shear stress and the use of flow refuges. Zigler et al. (2007), Steuer et al. (2008) and Morales et al. (2006) found that models reporting shear stress (the parallel stress created by water flowing over substrate) calculated from substrate roughness and flow velocity were good predictors of mussel distributions. Howard and Cuffey (2003) found *M. falcata* in areas of low velocity and low shear stress during winter flows and floods. Strayer (1999) reported that mussel beds were significantly more frequent in flow refuge areas. We observed mussels congregated on the lee sides of boulders and other hydraulic controls, and it seems likely that flow refuges and low shear stress are good habitat indicators for mussels.

In addition to analyzing which physical factors affect freshwater mussels, more work is needed in learning about the life histories of each species, which would allow for more effective conservation. We need genetic analyses to properly classify and identify the species of *Anodonta* in the Klamath River, because *A. californiensis* is a threatened species (Nedeau et al. 200). Also, knowing the host fish species of *G. angulata* and *Anodonta californiensis* is important for their conservation. Tennant (2010) analyzed the population age class structure to give insight into reproduction rates and historical limitations on *G. angulata* population or reproduction.

Klamath River dams negatively impact salmon, human and mussel populations. Summer blooms of the cyanobacterium *Microsystis aeruginosa* in Iron Gate and Copco reservoirs in the upper Klamath Basin produce unsafe levels of the liver toxin microcystin (Kann and Corum 2006). Microcystin accumulates in mussel tissues as they filter contaminated water, and mussels can contain unsafe levels of toxin in late summer, potentially exposing Karuk in their summer ceremonies (Davis 2008, Kann 2008).

The recent agreement to remove Iron Gate Dam in the year 2020 will surely have repercussions for water quality and all three species of mussels in the Klamath River. While the negative effects of dams on mussels are well documented (Vaughn and Taylor 1999), the effects of dam removal are not. Removal of Iron Gate Dam may negatively impact the mussel community in the Klamath River at first. Doyle et al. (2005) reported that transport of sediment downstream, burial and death of mussels resulted from multiple small dam removals in Wisconsin. Sethi et al. (2004)

reported an increase in percent cover of sand and silt downstream from a dam in Wisconsin, dead mussels buried under sediment, decreased mussel diversity and the extirpation of one species of rare mussel after dam removal. Because of their low mobility and dependence on host fish for reproduction, mussels are slow to recover from disturbances caused by dam removal (Sethi et al. 2004). While dam removal is necessary for the recovery of host fish populations and river restoration, efforts to limit the disruptive effects, such as a slow drawdown of the reservoir, must be taken to avoid irreparable damage to the Klamath River's mussel community.

Once the artificially warm and eutrophic conditions created by the dam are removed, the population of *Anodonta sp.* is likely to be negatively affected. In addition, because of their location immediately below the dam, the population of *Anodonta* risks burial from released sediments. If the water in the middle Klamath River becomes cooler and cleaner after the removal of Iron Gate Dam, then *M. falcata* may begin to inhabit more upriver sites, or become denser and more populous in the river. *G. angulata* also prefers cool water, so the removal of Iron Gate Dam might have a positive impact on its population, given its absence immediately downriver of the dam. Continuing to survey the populations of *M. falcata*, *G. angulata* and *Anodonta sp.* following the removal of Iron Gate Dam will provide valuable information on the effects of dam removal on these three species.

Wildlife managers and conservation groups currently aim restoration measures towards the salmon in the Klamath watershed, but they must also protect freshwater mussels to ensure the stability and biodiversity of the river ecosystem. Quality mussel habitat comprising stable substrate and river edges, cool water, appropriately low levels of siltation and host fish populations must be maintained to conserve mussel populations in the Klamath River.

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TABLES AND FIGURES

Table 1. Generalized linear mixed model for river edge and mesohabitat effects on *Gonidea angulata* abundance in the Middle Klamath River.

Effect	River Edge	Mesohabitat	Estimate	Standard Error	d.f.	F Value	p Value
River edge	bank		2.4	0.56	39	18.5	0.0001
River edge	bar		0	X			
Mesohabitat		low slope riffle	0.11	1.84	36	0.7	0.58
Mesohabitat		medium slope riffle	-0.03	1.95			
Mesohabitat		pool	-0.91	1.88			
Mesohabitat		steep slope riffle	0	X			

Table 2. Generalized linear mixed model for river edge and mesohabitat effects on *Margaritifera falcata* abundance in the Middle Klamath River.

Effect	River Edge	Mesohabitat	Estimate	Standard Error	d.f.	F Value	p Value
River edge	bank		5.84	2.56	39	5.22	0.03
River edge	bar		0	X			
Mesohabitat		low slope riffle	-2.85	2.47	36	0.45	0.72
Mesohabitat		medium slope riffle	-2.69	2.71			
Mesohabitat		pool	-2.5	2.5			
Mesohabitat		steep slope riffle	0	X			

Table 3. G-test comparing observed and expected mussel bed area (m^2) in different mesohabitats in the Middle Klamath River.

Mesohabitat	Expected Bed Area m^2	Observed Bed Area m^2	G Value	p Value
Pool	481.3	135	228.6	<<0.0001
LS Riffle	721.9	924.5	203.6	<<0.0001
MS Riffle	309.4	475	-12.6	<<0.0001
SS Riffle	34.4	12	-171.6	<<0.0001

Table 4. G-test comparing observed and expected *Gonidea angulata* abundance in each substrate in the Middle Klamath River.

Substrate Type	Observed *Gonidea. angulata*	Expected *Gonidea. angulata*	G Value	p Value
Silt	210	3088	-1129	<<0.0001
Sand	3224	10219	-7438.6	<<0.0001
Gravel	1247	2165	-1375.3	<<0.0001
Cobble	47523	41354	13216.8	<<0.0001
Boulder	68985	55998	28777.3	<<0.0001
Bedrock	6151	14517	-10563.7	<<0.0001

Table 5. G-test comparing observed and expected *Margaritifera falcata* abundance in each substrate in the Middle Klamath River.

Substrate Type	Observed *Margaritifera falcata*	Expected *Margaritifera falcata*	G Value	p Value
Silt	1	12	-5	<<0.0001
Sand	9	39	-26.8	<<0.0001
Gravel	18	8	28.1	<<0.0001
Cobble	100	160	-94	<<0.0001
Boulder	36	216	-129.2	<<0.0001
Bedrock	328	56	1159.1	<<0.0001

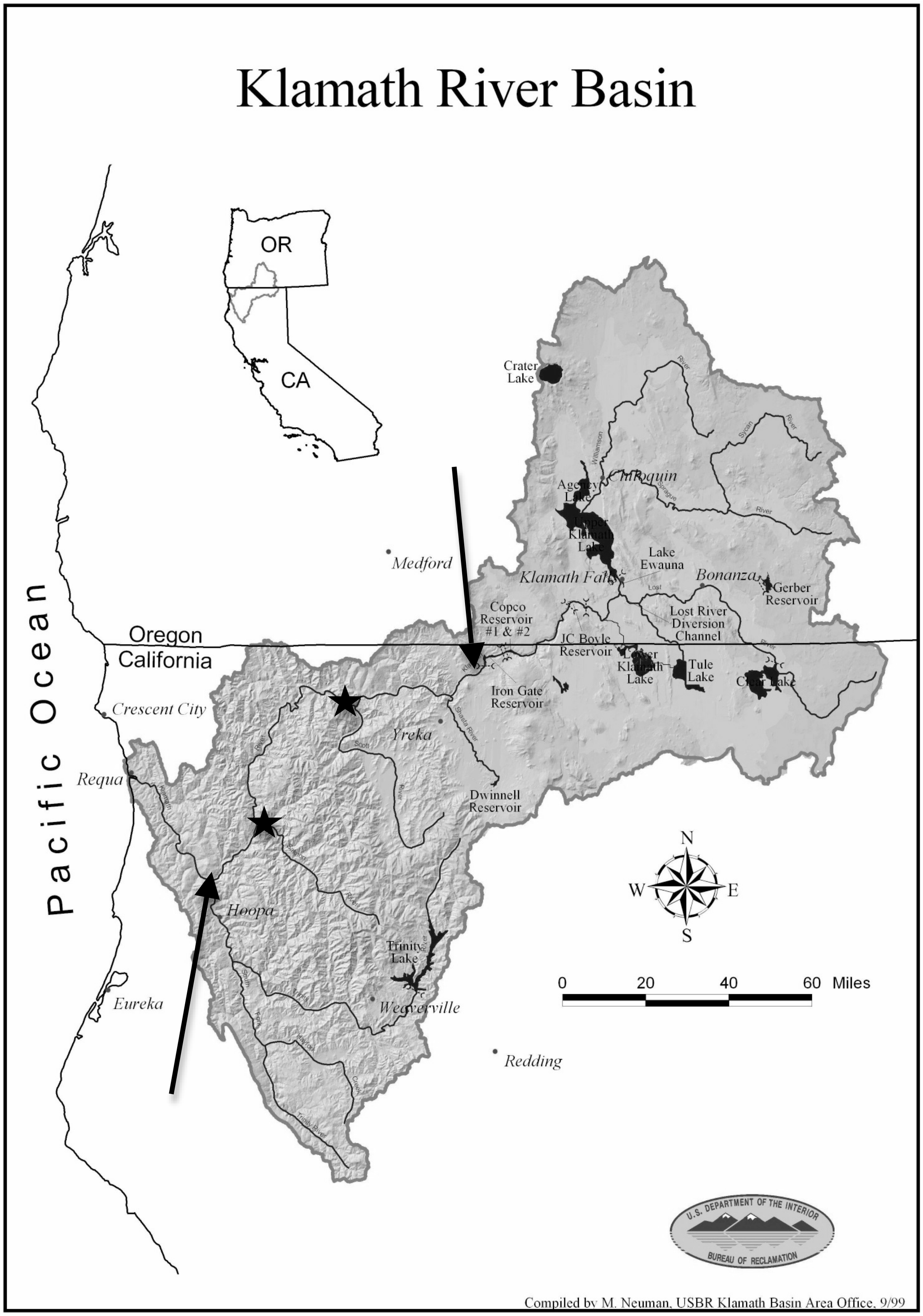

Fig. 1. Klamath River watershed with study area Iron Gate Dam to the confluence of the Klamath and Trinity Rivers marked by arrows. The stars indicate the section of the river encompassed by Karuk ancestral territory.

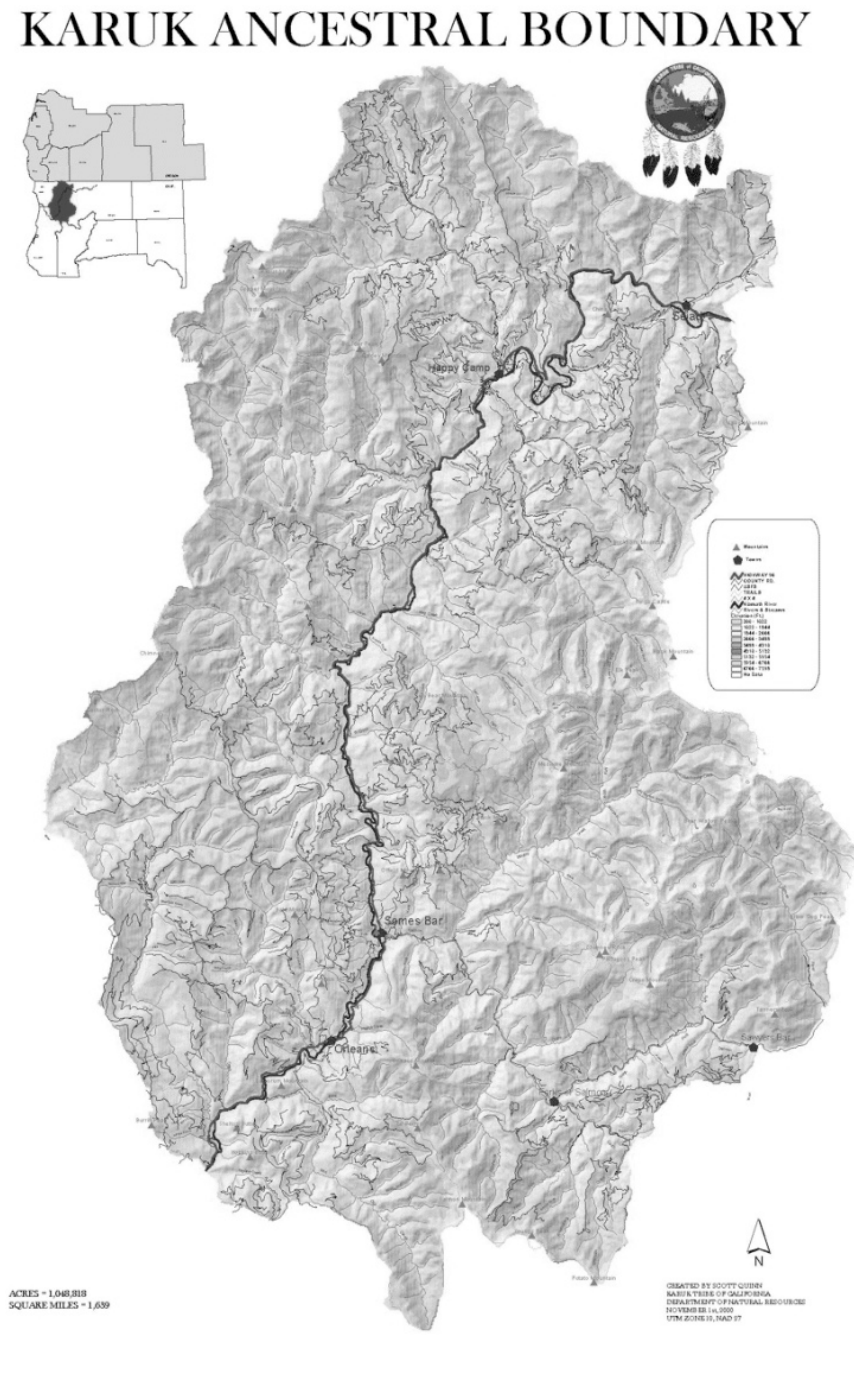

Fig. 2. Extent of Karuk ancestral territory in the Klamath River basin, northern California.

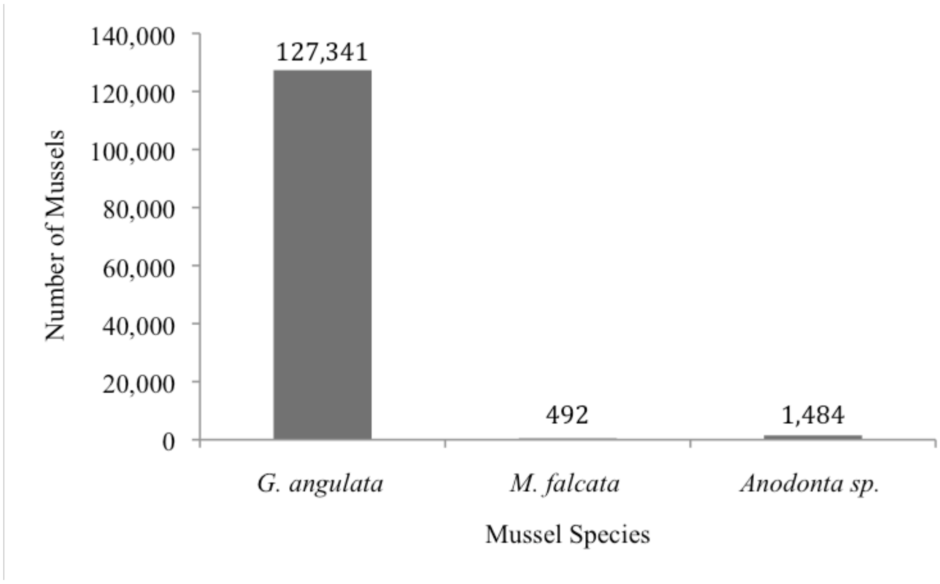

Fig. 3. Relative abundance of *Gonidea angulata, Margaritifera falcata* and *Anodonta sp*. in the Middle Klamath River.

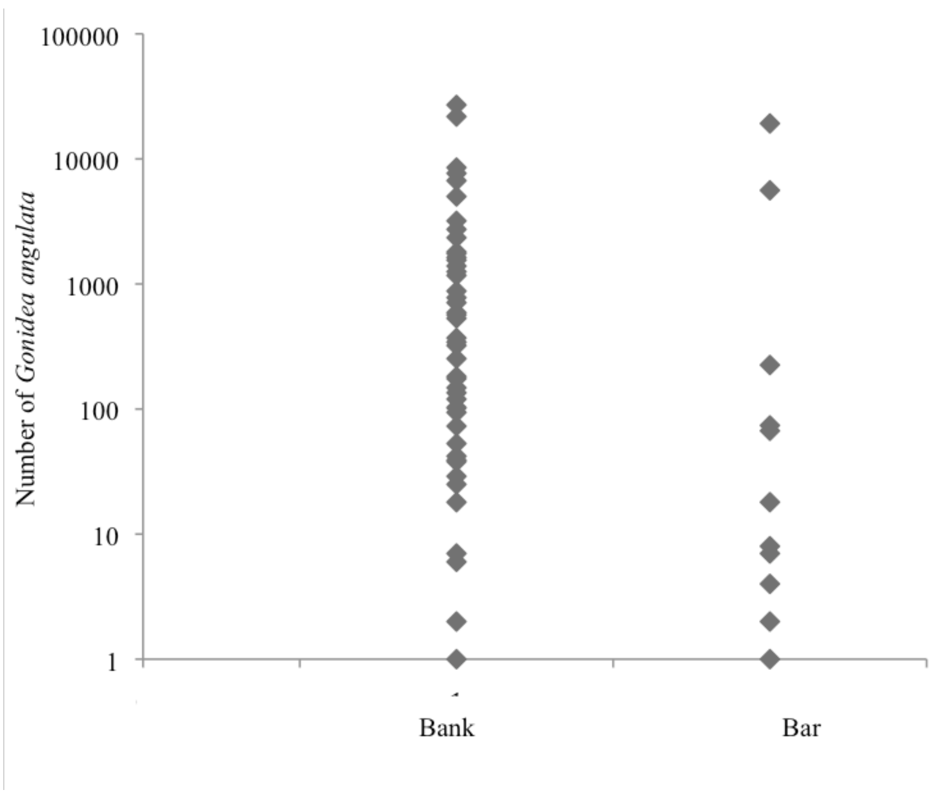

Fig. 4. Number of *Gonidea angulata* on bank and bar river edges in the Middle Klamath River.

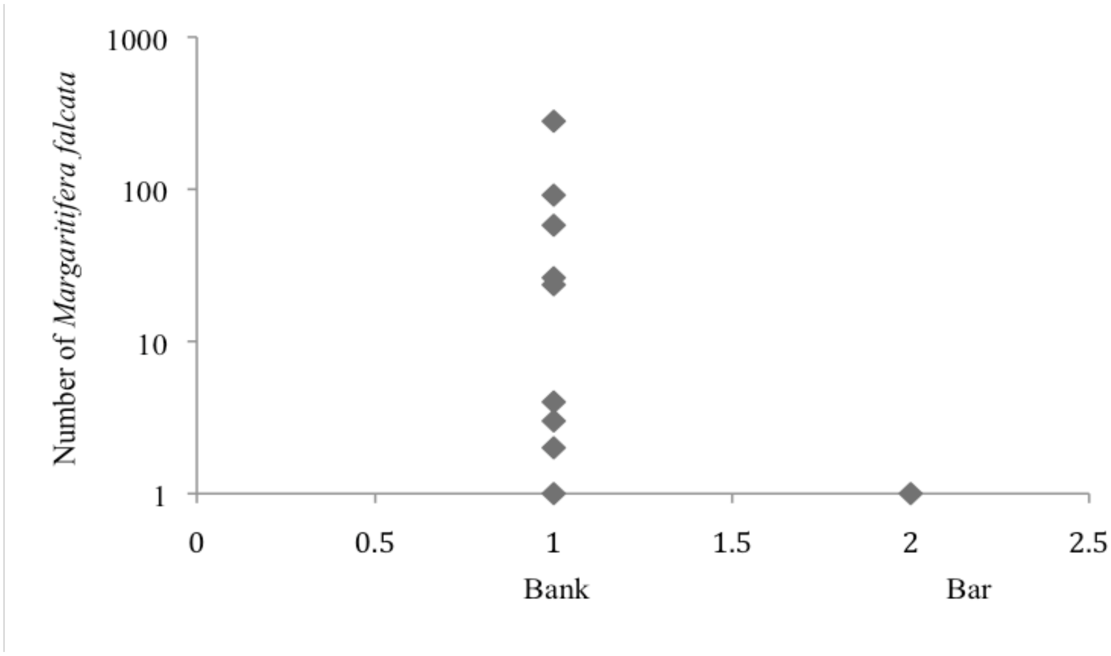

Fig. 5. Number of *Margaritifera falcata* on bank and bar river edges in the Middle Klamath River.

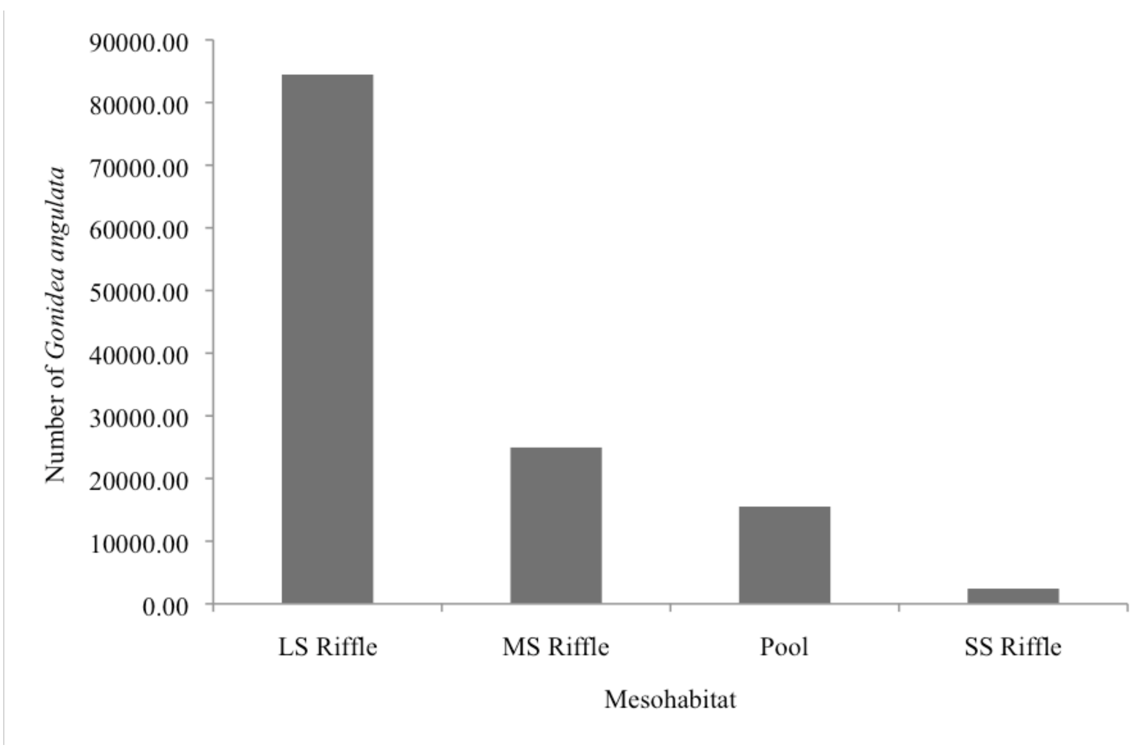

Fig. 6. Total number of *Gonidea angulata* in each mesohabitat in the Middle Klamath River.

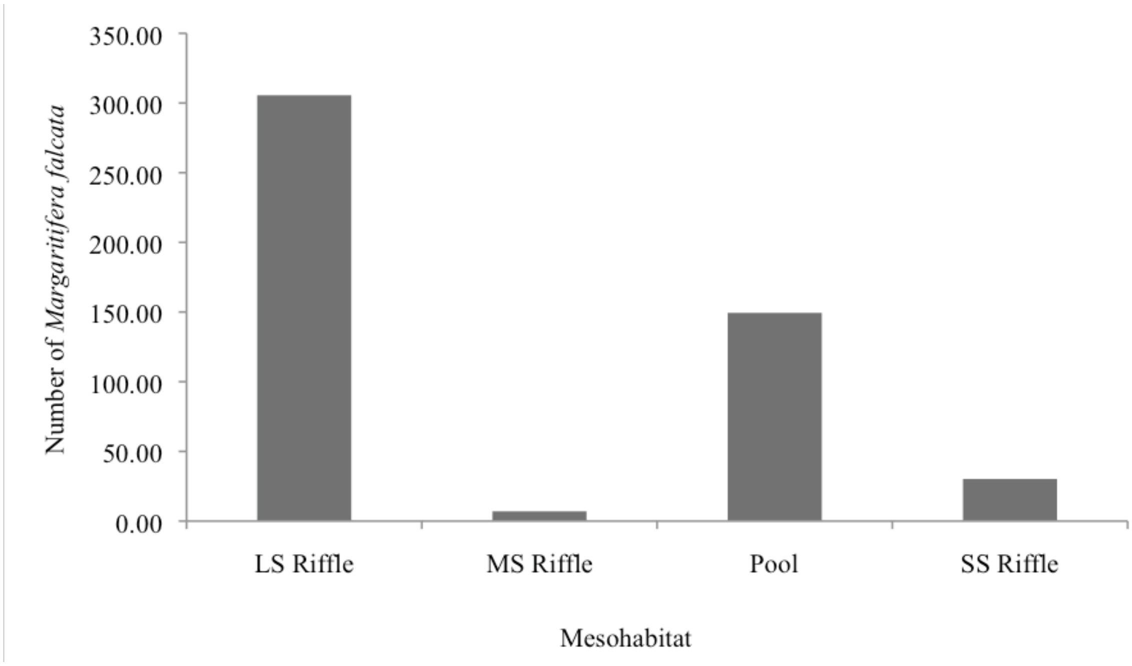

Fig. 7. Total number of *Margaritifera falcata* in each mesohabitat in the Middle Klamath River.

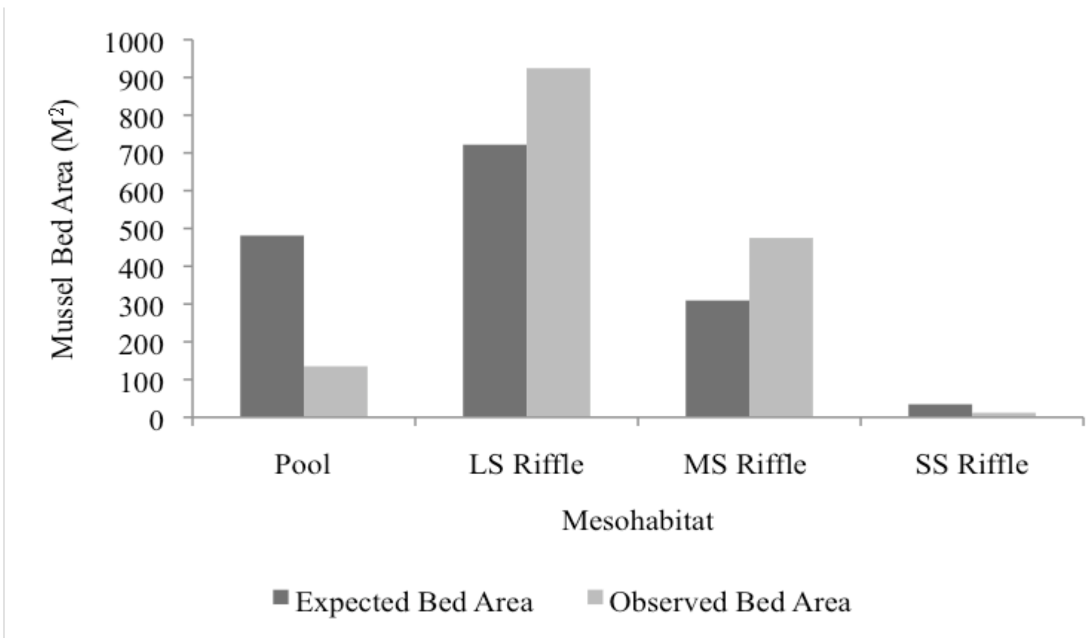

Fig. 8. Observed and expected mussel bed area (m^2) in different mesohabitats in the Middle Klamath River.

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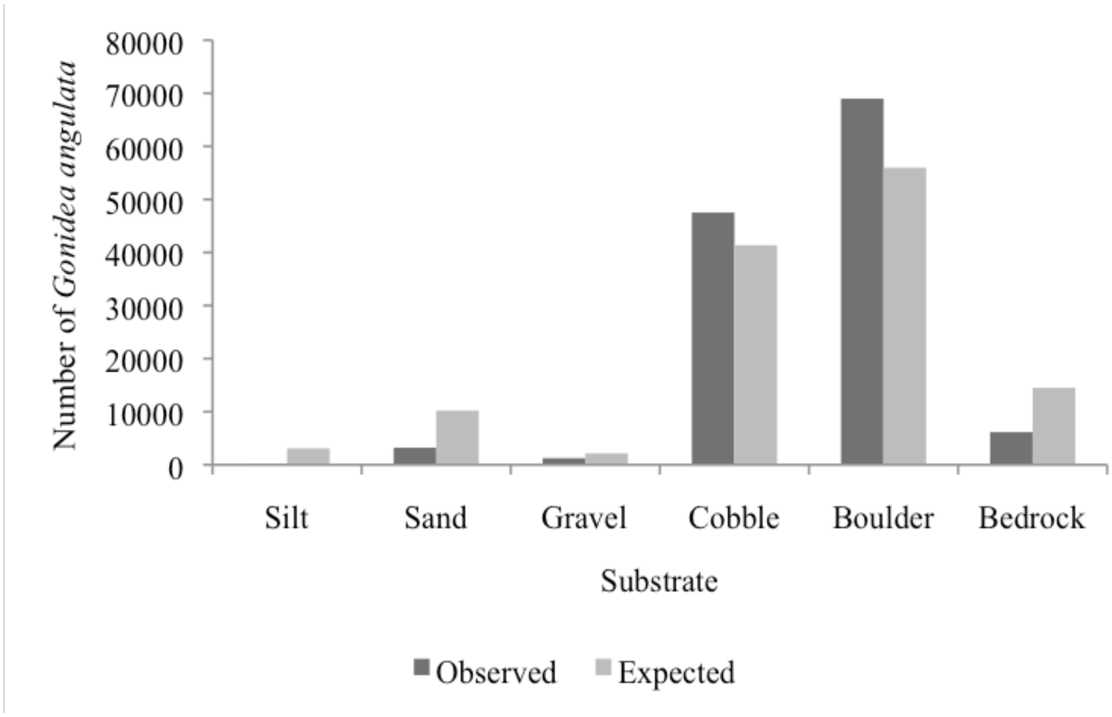

Fig. 9. Observed and expected *Gonidea angulata* abundance in different substrates in the Middle Klamath River

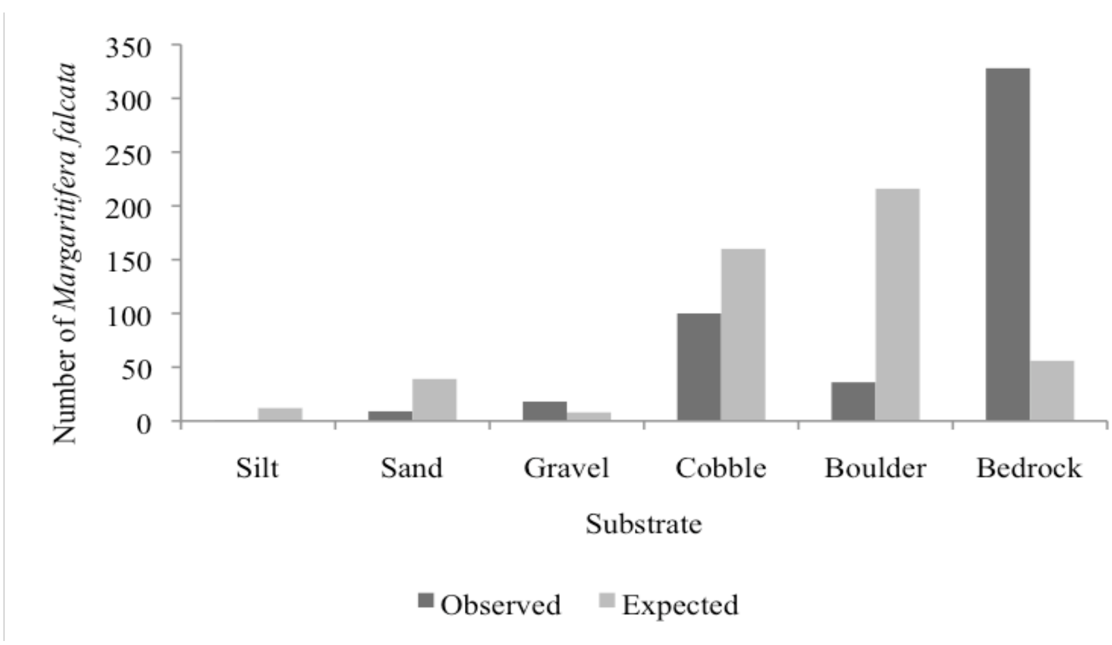

Fig. 10. Observed and expected *Margaritifera falcata* abundance in different substrates in the Middle Klamath River.

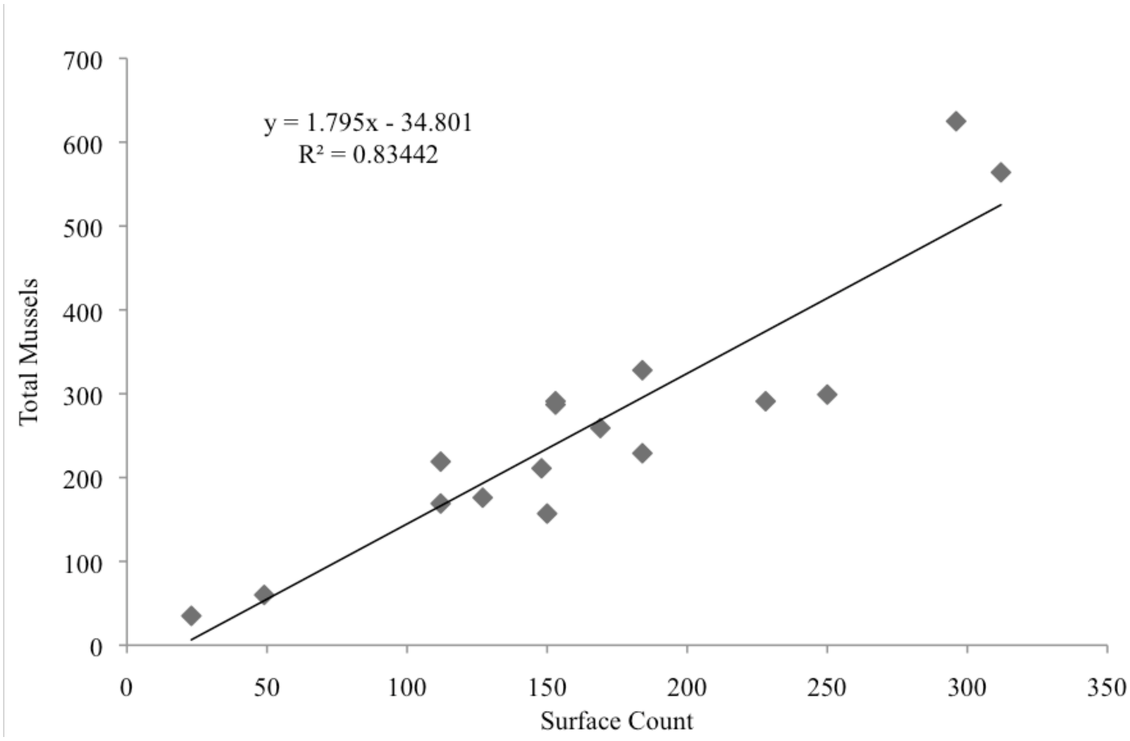

Fig. 11. Comparison and regression analysis of surface mussel counts and total excavated mussel counts in beds in the Middle Klamath River.