UNDERSTANDING FRESHWATER MUSSEL DISTRIBUTION, ABUNDANCE, AND

DEMOGRAPHY IN THE SOUTH UMPQUA RIVER BASIN, OREGON:

IMPACTS OF LAND USE AND STREAM HYDRAULICS

by

LAURA JOHNSON

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Student: Laura Johnson

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Dr. Lauren Hallett   Chairperson
Dr. Patricia McDowell   Member

and

Kate Mondloch   Interim Vice Provost and Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School.

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THESIS ABSTRACT

Laura Johnson

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Freshwater mussels are both keystone and indicator species within aquatic ecosystems and are declining across their historic ranges within the Pacific Northwest (PNW). This thesis provides baseline information necessary for conservation and management of native mussel populations in the South Umpqua River basin. We documented all three PNW genera within the basin, but only one species (*Margaritifera falcata*) was widespread. Species richness and mussel abundances were lowest at downstream sites. We found widespread evidence of recent *M. falcata* reproduction, but the lower South Umpqua River populations are likely non-viable. The percentage of forest cover within the drainage basin area was the best predictor of mussel abundance, and indicates that the cumulative impact of anthropogenic land use may be degrading mussel habitats. Our data also suggested a relationship between invasive Asian clams (*Corbicula fluminea*) and suppressed mussel abundances. Additional research is needed to understand the competition dynamics between these species.

CURRICULUM VITAE

NAME OF AUTHOR: Laura Johnson

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
Lane Community College, Eugene

DEGREES AWARDED:

Master of Science, Environmental Studies, 2020, University of Oregon
Bachelor of Science, Environmental Science, 2014, University of Oregon

AREAS OF SPECIAL INTEREST:

Biology

Geography

PROFESSIONAL EXPERIENCE:

Teaching Assistant, Environmental Studies Program, University of Oregon,
Eugene, 2017, 2019 – 2020

Internship Coordinator, Environmental Studies Program, University of Oregon,
Eugene, 2018

Project Manager, Environmental Leadership Program, University of Oregon,
Eugene, 2017 & 2018

Experimental Biological Aide, Oregon Department of Fish & Wildlife, June –
Sep. 2015 & Feb. 2016 – June 2017

GRANTS, AWARDS, AND HONORS:

Environmental Studies Summer Fellowship Award, University of Oregon, 2020

Teaching Excellence Award, University of Oregon, 2020

Barker Funds Award, Environmental Studies Program, 2018

The David S. Easly Memorial Award, University of Oregon, 2018

The Gary E. Smith Award, University of Oregon, 2018

The Brenda McGowan Grant, The Northwest Ecological Research Institute, 2018

PUBLICATIONS:

"In-stream Monitoring on the McKenzie River, Oregon" (Lead author), *Oregon Undergraduate Research Journal*, 6th ed., Spring 2014. Available from http://hdl.handle.net/1794/23421.

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I: INTRODUCTION

Freshwater mussels have been recognized as one of the most imperiled faunal groups in North America (Strayer et al. 2004; Haag & Williams 2014), and yet these animals have been persistently relegated to the sidelines of ecological inquiry in the Pacific Northwest (PNW). As a result, baseline information on species distributions and abundances is lacking in most watersheds. The dearth of information about PNW mussel species may be due to the relative lack of species richness in the west as compared to eastern North America: while there are about 300 species of freshwater mussels in North America (Haag & Williams 2014), the PNW is home to approximately 7 species within 3 genera (*Gonidea, Margaritifera,* and *Anodonta*). Recent efforts to assess the status of PNW species using criteria for the International Union for the Conservation of Nature's (IUCN) Red List have provided needed evidence that PNW species are in decline (Blevins et al. 2017). Baseline information is urgently needed in the PNW so that resource managers and scientists can effectively manage and monitor freshwater mussel populations.

Understanding current trends of freshwater mussel distribution and abundance in the PNW is a critical first step towards successful management and conservation efforts, but it falls short of determining whether extant populations are actually reproductively viable. Because freshwater mussel species in the PNW have long life spans (*M. falcata* can live 100+ years) and complex life cycles with a cryptic juvenile life stage (McMahon & Bogan 2001), it is difficult to determine whether populations are reproducing without including sampling methodologies designed to specifically target young mussels (Smith et al. 1999; Strayer & Smith 2003). A lack of juvenile mussels in some PNW mussel beds suggests an "extinction debt" in which their populations will inevitably decline without intervention (Tilman et al. 1994; Searles Mazzacano 2017, 2018). Extinction debts are a phenomenon impacting long-lived species wherein past habitat degradation negatively affects a population's ability to reproduce. Impacted populations do not go extinct until sometime in the future when relic individuals eventually die. Surveying mussel populations to determine baseline population parameters such as density and age structure can provide evidence of impending extinction debt phenomenon and allow comparison of how populations are changing over time.

Mussel populations are structured by both natural and anthropogenic drivers that influence the distribution, quality, and quantity of resources that mussels need to survive. These drivers operate at multiple spatial scales ranging in size from the patch (centimeters to meters) to the entire watershed (hundreds of kilometers). Freshwater mussels require species-specific host fish to complete their life cycle, stable stream sediments to embed within, adequate food resources within the water column, and water quality that is not excessively degraded by sediments or pollution (McMahon & Bogan 2001). Near-bed hydraulic conditions, including shear stress and stream power, are an important first-order natural control of freshwater mussel abundances because these long-lived animals can only persist in sediments that are not routinely transported downstream during high flow events (Layzer & Madison 1995; Gangloff & Feminella 2007). While natural drivers originally structured patterns of mussel distribution and abundance, anthropogenic alterations to terrestrial and aquatic habitats have modified hydrologic processes and drastically changed instream habitat conditions worldwide. Arguably the most influential anthropogenic driver of declining mussel abundances and contracting distributions is land use change and its concomitant impact on aquatic habitats and resources (Strayer et al. 2004). Understanding how natural and anthropogenic drivers interact to influence freshwater mussel populations is a critical component of developing successful conservation strategies and management plans, but relatively little research has been dedicated to this effort in the PNW.

This thesis provides a baseline understanding of freshwater mussel distributions, abundances, and population dynamics in the South Umpqua River basin located in southwestern Oregon. We sampled 13 sites distributed throughout the South Umpqua River and a major tributary, Cow Creek. Three western pearlshell (*Margaritifera falcata*) mussel beds were sampled to determine their densities, approximate age structures, and reproductive status. We tested the hypotheses that freshwater mussel abundance and demography within the basin are structured at the watershed scale by land use and at the reach scale by the specific stream power experienced during a 10-year peak flow event. We found all three western North American mussel genera (*Margaritifera*, *Gonidea*, and *Anodonta*) in the South Umpqua River and both *Margaritifera* and *Anodonta* in Cow Creek. *Margaritifera* were present at every site, *Anodonta* became increasingly common

with increasing distance upstream on the South Umpqua River, whereas *Gonidea* were rare and few in number. Recent evidence of reproduction was found at all mussel beds sampled and juveniles were widespread in basin, although this is not necessarily indicative of healthy populations because *M. falcata* are capable of self-fertilization at low population densities.

In the lower South Umpqua River, mussel aggregation abundances were suppressed as compared to aggregations in the upper South Umpqua River and Cow Creek. We found a significant negative relationship between freshwater mussel abundance in the South Umpqua River and the contributing drainage basin area of the aggregation. Freshwater mussel abundances significantly increased with increasing forest cover within the drainage basin and, somewhat paradoxically, were positively correlated to levels of timber harvest within the HUC12 subwatershed encapsulating each site. We found invasive Asian clams (*Corbicula fluminea*) were widespread and occurred in high densities in the lower South Umpqua River sites, but were absent from the upper South Umpqua River and Cow Creek. *C. fluminea* are likely to expand their range in the future, and additional research is urgently needed to understand the competitive dynamics between invasive clams and western North American native mussels species.

II: BACKGROUND

Ecological Importance of Freshwater Mussels & Conservation Status of PNW Species:

Freshwater mussels are unique animals that can be both keystone species and indicator species within aquatic ecosystems. In the PNW, 3 genera (*Margaritifera, Gonidea,* and *Anodonta*) and approximately 7 species of freshwater mussels occur. Both *Margaritifera falcata* (western pearlshell) and *Gonidea angulata* (western ridged) are easy to distinguish and identify in the field, but there is uncertainty about how many *Anodonta* species are present and field identification to species level is not reliable (Nedeau et al. 2009). Declining mussel populations in the PNW of North America not only indicate widespread deterioration of aquatic habitat conditions, but can also result in the loss of ecosystem function.

Freshwater mussels actively modify aquatic habitats by purifying water, bolstering aquatic food webs, and facilitating nutrient cycling processes. Mussels improve water quality by filtering bacteria, phytoplankton, and fine particulate organic matter from the water column (Vaughn & Hakenkamp 2001; Lummer et al. 2016). Abundant aggregations of mussels enhance aquatic food webs by depositing feces and pseudofeces on the streambed, thereby locally increasing the abundance of benthic zone food resources (Howard & Cuffey 2006a; Spooner & Vaughn 2006; Vaughn & Spooner 2006a). Mussel bioturbation of stream sediments enhances nutrient cycling between the water column and sediment layers and improves interstitial pore space habitat for a host of other species (Vaughn & Hakenkamp 2001). Whereas habitat degradation in the speciose portions of eastern North America (in which dozens of species commonly occur within a single watershed) has been linked to declining species richness and shifts in community assemblage (Morris & Corkum 1996; McRae et al. 2004; Hornbach et al. 2019), the PNW is home to comparatively few species of mussels and degradation in this region is likely to result in the extirpation of populations from previously suitable habitats.

Despite their ecological importance, freshwater mussels have been historically relegated to the sidelines of ecological inquiry and management in the Pacific Northwest (PNW) of North America. Baseline information regarding mussel species distributions, abundances, and population dynamics in the PNW are absent for many watersheds, and

when records do exist they are typically few in number (Adair & Miller, 2010; Blevins et al. 2017). What records of mussel occurrence do exist were compiled into the Western Freshwater Mussel Database (Xerces & CTUIR 2018). This database includes all freshwater mussel occurrence records from the western United States from as early as the 1800s (as documented by preserved museum specimens) up until the present. The collection of this data enabled the first comprehensive assessment of western North American mussel species statuses according to criteria for the International Union for the Conservation of Nature's (IUCN) Red List (Blevins et al. 2017). In the PNW, the western ridged mussel (*G. angulata)* and the winged floater mussel (*Anodonta nuttallina*) are Vulnerable to Extinction and the western pearlshell mussel (*M. falcata*) is Near Threatened (Blevins et al. 2017). In addition, the Xerces Society for Invertebrate Conservation petitioned to list *G. angulata* as an endangered species under the U.S. Endangered Species Act in August of 2020.

Freshwater Mussel Life Cycle & Implications for Bed Demographies:

Freshwater mussels have multiple life history traits that increase their vulnerability to both natural and anthropogenic disturbance and pollution. In particular, mussel's complex reproductive strategy, delayed maturity, low reproductive success and long life spans make them sensitive to environmental disruption and degradation (McMahon & Bogan 2001). Successful freshwater mussel reproduction requires an obligate parasitic life stage in which female mussels must attach their young mussel larvae (called glochidia) to a species-specific host fish (McMahon & Bogan 2001). In the PNW, *Margaritifera* use salmonids (salmon and trout) as host-fish, *Gonidea* likely uses a species of sculpin (*Cottus sp.*) but exact details are still unresolved, and *Anodonta sp.* are more generalist and have been shown to successful transform on various fish species including dace, shiners, and sculpin (Nedeau et al. 2009; O'Brien et al. 2013).The process by which glochidia encyst onto fish and transform into mature forms varies by species, but can last for days to many months and is an important dispersal mechanism for the species (McMahon & Bogan 2001; Barnhart et al. 2008). If larvae successfully transform and drop off their host fish, they typically remained fully buried in the substrate for several years and are thus undetectable by surface sampling methodologies (Neves &

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Widlak 1987; Yeager et al. 1994; McMahon & Bogan 2001). The odds of a glochidia successfully establishing in the substrate as a juvenile mussel are extremely unlikely: less than 1 in 1,000,000 for one natural population of pearl mussels (*Margaritifera margaritifera*), which is a close relative of *Margaritifera falcata* in the PNW (Young & Williams 1984). Stochastic natural disturbances have disrupted freshwater mussel populations over the millennia, but the rapid and pervasive human induced changes to aquatic ecosystems has resulted in a level of chronic disturbance that freshwater mussels are ill suited to tolerate.

When freshwater mussel populations are negatively impacted by either disturbance or degradation, their long life spans combined with delayed onset of maturity mean that it can take a long time for populations to recover. Although mussel lifespans are species specific, they are generally long lived animals that can persist for decades in stable environments. The average lifespan of *Anodonta sp.* is 10 – 20 years, whereas *G. angulata* can live 30 or more years and *M. falcata* can live for over a century (Nedeau et al. 2009; Blevins et al. 2018). Mussels also take a relatively long time to reach sexual maturity: populations of *G. angulata* were estimated to reach maturity at approximately 7 years old in British Columbia, Canada (Mageroy 2014), whereas *M. falcata* mature between 6 – 12 years of age (Toy 1998). *Anodonta sp.* experience higher growth rates as juveniles and reach sexual maturity relatively more quickly than either *G. angulata* or *M. falcata*. However, research on the reproductive biology of *Anodonta sp.* in the PNW is especially lacking and considerable uncertainties exist regarding when species reach sexual maturity. *Anodonta californiensis* was documented to be sexually mature at 4 years of age, but this estimate is based on two collections (n = 7 per collection) of animals from two populations in California (Heard 1975). The age of sexual maturity likely varies by species and even by population depending on whether the habitat is lentic or lotic and other habitat variables such as water temperature and productivity. Freshwater mussel's unique life history traits combined with their role as filter feeders and relative immobility once established as adults make them particularly sensitive to habitat disruption and degradation.

The juvenile life stage of freshwater mussel species is cryptic and generally poorly understood for most species, but juvenile mussels are likely more vulnerable to

disturbance then their adult counterparts. The demographies of some mussel beds indicate large variations in the annual recruitment of juveniles and indicate that particular environmental or flow conditions may be necessary for successful juvenile recruitment (Villella et al. 2004; Ries et al. 2016). In the PNW, *M. falcata* have been shown to recruit more successfully during low discharge years (Howard & Cuffey 2006b), with discharges in the spring and summer of most relevance because this is the period of mussel spawning and juvenile metamorphosis (Toy 1998). Anthropogenic pollution can also impact successful recruitment, with increasing levels of nutrient pollution and toxins linked to decreasing levels of successful juvenile metamorphosis from host-fish and decreased juvenile growth and survival (Valenti et al. 2006; Nobles & Zhang 2015; Moore & Bringolf 2018). Successfully metamorphosed juvenile mussels are typically buried within sediments for the first years of their life and feed from within the interstices of sediment grains, whereas adult mussels live at the substrate surface and filter from the water column (Yeager et al. 1994; Gatenby et al. 1996). Juvenile mussels require high concentrations of dissolved oxygen (DO) and low concentrations of suspended sediment and are susceptible to contaminants that may accumulate within stream sediments (Černá et al. 2018). Anthropogenic activities that increase suspended sediment loads and/or increase pollution levels within aquatic ecosystems have the potential to disrupt the recruitment and survival of juvenile mussels prior to reaching levels that negatively impact adults.

Locating freshwater mussel populations and determining whether successful recruitment of juveniles is occurring within them is a critical component of successfully conserving and managing mussel species in the PNW. Recently, there have been large *M. falcata* mussel beds documented on the Willamette River in western Oregon that contain no juvenile mussels and are likely experiencing an "extinction debt" in which their populations will inevitably decline without intervention (Tilman et al. 1994; Searles Mazzacano 2017, 2018). Extinction debts are a phenomenon impacting long-lived species wherein past habitat degradation negatively affects a population's ability to reproduce. Impacted populations do not go extinct until sometime in the future when relic individuals eventually die. Surveying known mussel populations to determine baseline population parameters such as density and age structure will provide evidence of

impending extinction debt phenomena and has been identified as a top priority with high conservation benefit in the PNW(Adair & Miller 2010). Additionally, knowing which mussel beds are reproductive can help guide conservation efforts since high density, reproductive beds are likely acting as source populations for dispersal and establishment in other areas (Vannote & Minshall 1982; Strayer et al. 2004). In absentia of baseline population data, land managers and researchers do not know how populations are changing over time and cannot develop appropriate management or conservation plans.

Natural Drivers and Freshwater Mussels:

Natural processes have been exerting controls on freshwater mussel distribution and abundance for thousands of years by heterogeneously distributing aquatic resources within streams at multiple spatial scales. Resources important to mussels are commonly investigated at the patch scale (centimeters to meters), the reach scale (tens to hundreds of meters), and at the watershed scale (one to hundreds of kilometers). Patch scale resources important to mussels include sediment size (Toy 1998; Brim Box & Mossa 1999; McRae el al. 2004; Davis et al. 2013), the presence or absence of flow refugia (Strayer 1999a; Davis et al. 2013; May & Pryor 2016), and water depths and velocities during low flow conditions (Layzer & Madison 1995; Gangloff & Feminella 2007). Freshwater mussels use a muscular foot to burrow into sediments layered upon the stream bed and generally require stable patches of sand or gravel-sand mixtures in which to embed (McMahon & Bogan 2001). Flow refugia are features, such as large boulders, that interrupt high flows and provide lower stress habitats within the channel. At the reach scale, channel unit type (Howard & Cuffey 2003; Davis et al. 2013), bank conditions (Davis et al. 2013), and riparian vegetation (Morris & Corkum 1996; Poole & Downing 2004; Degerman et al. 2013) have all been attributed to structuring mussel abundances, distributions, and richness.

The largest lens of consideration is at the watershed scale, where geology and gradient (Arbuckle & Downing 2002; McRae et al. 2004; Poole & Downing 2004), the distribution of host fish species (Watters 1992; Degerman et al. 2013), and the natural hydrologic variability due to regional climate patterns and tributary inputs are important drivers of mussel distribution and abundance (Di Maio & Corkum 1995; McRae et al.

2004; Davis et al. 2013). Recent research has focused on identifying patterns in mussel distribution, abundance, or community composition by analyzing variables across multiple scales (Howard & Cuffey 2003; McRae et al. 2004; Gangloff & Feminella 2007; Davis et al. 2013). Because mussel populations are structured by different variables depending on scale, it is important that researchers match the variables that they measure to the scale of their questions.

An emerging body of research demonstrates that hydraulic conditions exert a first order control on freshwater mussel distributions and abundances within high-energy gravel streams commonly found in the PNW. The probability that a mussel will remain alive and stationary is intricately linked to hydraulic processes that control the distribution and stability of the sand and gravel sediments within which mussels embed. High flow events (e.g. 5-year or 25-year peak flows) can re-distribute sediments and flush finer sediments downstream through grain entrainment and transport processes. Studies from the PNW, upper midwest, and Appalachia have demonstrated that mussels are preferentially located within low-stress habitats that experience relatively lower flow velocities, shear stress, and stream power values during high flow events (Layzer & Madison 1995; Howard & Cuffey 2003; Stone et al. 2004; Gangloff & Feminella 2007; May & Pryor 2016).

Shear stress is a measure of the force (N/m^2) the water column applies to the channel bed acting in the horizontal direction, whereas stream power is the rate of potential energy expenditure (watts/meter) against the channel bed and banks for a specific length of channel. Stream power measures the ability of the water column to perform the work of entraining and transporting sediments: stream power (and the likelihood of sediment transport) increases with decreasing channel width, increasing discharge, and increasing channel slope. Hydraulic conditions that impact sediment stability are considered a first order control because hydraulically unsuitable habitats cannot support mussels, but whether hydraulically suitable habitats contain mussels depends on other critical habitat components. When taken together, the consequence of mussels' complex habitat requirements is that they are patchily and non-randomly distributed within freshwater aquatic habitats.

Stream power forces are predominantly influenced by natural controls and can be analyzed at both the patch and reach scales. At the patch scale, the presence of flow refugia such as boulders, large woody debris structures, or sediments accumulated in bedrock pockets provide localized relief from high shear stress and stream power values (Strayer 1999a). At the reach scale, channel shape and gradient interact to form zones of higher and lower flow stress on the scale of tens to hundreds of meters. While changes in land use can have some influence on high stream power disturbance events by increasing the magnitude and frequency of peak flows (see following section on Anthropogenic Land Use), stream power is largely determined by natural conditions within the watershed (such as geology and gradient) that influence sediment size and composition, channel form and gradient, and the hydrologic response to precipitation events.

Anthropogenic Land Use and Freshwater Mussels:

Anthropogenic land uses within a watershed have the potential to modify naturally occurring patterns of freshwater mussel distribution and abundance by degrading water quality and aquatic habitat. Alongside the construction of dams, anthropogenic land use has been identified as one of the most pervasive threats to mussels because of its causal relationship to a myriad of other processes that degrade aquatic ecosystems (Strayer et al. 2004; Poole & Downing 2004; Gangloff & Feminella 2007). For example, anthropogenic land uses have been linked to the alteration of flow regimes (Paul & Meyer 2001; National Research Council 2008), increased influxes of suspended sediments and pollutants to streams (Lenat & Crawford 1994; Brim Box & Mossa 1999; Ha & Stenstrom 2003; Mallin et al. 2009), and degraded riparian zone vegetation (U.S. EPA 2016; Garcia et al. 2017) (Figure 1). Whether occurring individually or in tandem, these physical and chemical perturbations cause changes to the distribution and/or quality of aquatic habitat (Garcia et al. 2017; Anim et al. 2018) and thereby influence the composition and stability of aquatic communities (Lenat & Crawford 1994; Walser & Bart 1999; Walsh et al. 2005). The degradation of aquatic habitat that accompanies anthropogenic land uses has the potential to cause widespread contractions of freshwater mussel distributions and abundances from across species' ranges and to eliminate mussel populations from previously suitable habitats.
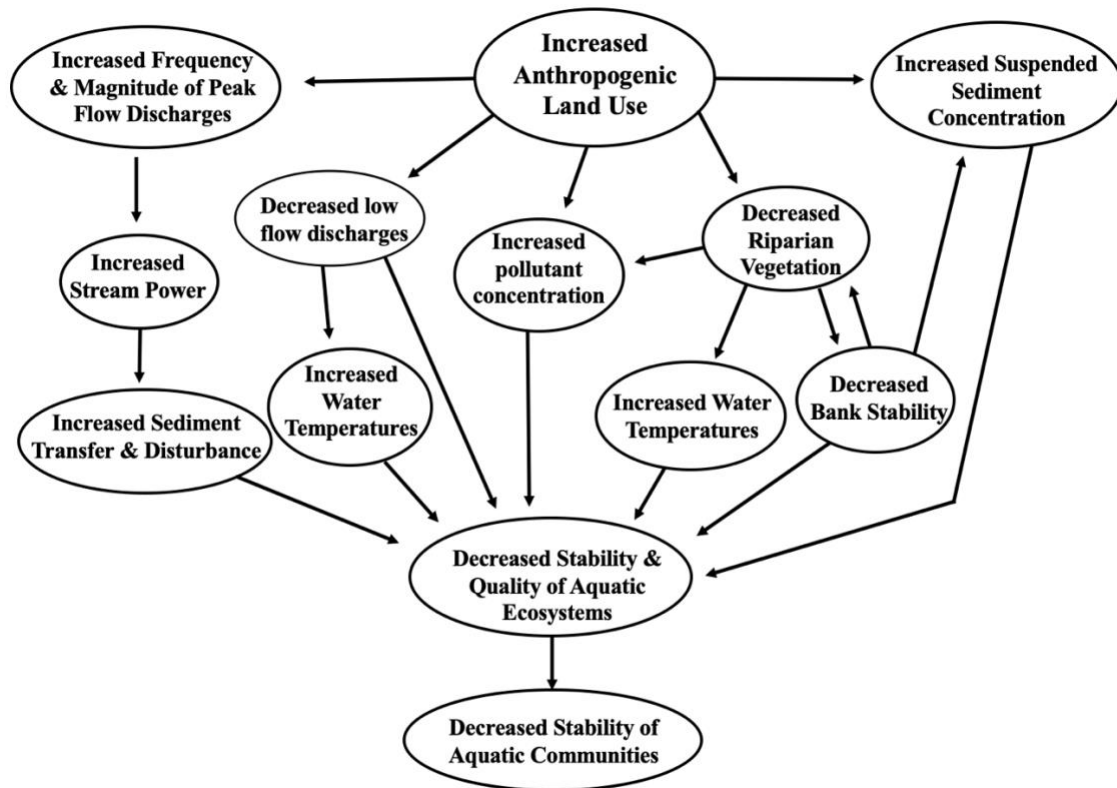
Figure 1: Conceptual figure linking anthropogenic land use change as a trigger of declining aquatic habitat stability and quality through its impacts on high and low flow discharges, riparian vegetation, and concentrations of both pollutants and suspended sediments.

Degraded aquatic habitats result in destabilized aquatic communities that commonly shift towards increased abundances of tolerant species (Resh & Unzicker 1975) and can result in the proliferation of invasive species (Havel et al. 2015). Invasive species can indirectly impact mussels by altering physical or chemical habitat features; for example, the invasive aquatic plant Eurasian watermilfoil (*Myriophyllum spicatum*) grows in dense colonies that alter benthic habitat by depressing water velocities at low flows and increasing the deposition of fine sediments (Wade et al. 2020). This can result in localized decreases in dissolved oxygen within the water column, decreases in the volume of food resources being delivered to mussels, and can even cause direct mortality if mussels are buried in accumulating sediments. Invasive species, especially other aquatic invertebrates such as Asian clams (*Corbicula fluminea*) or New Zealand mud snails (*Potamopyrgus antipodarum*), can directly compete with native mussels for food and space resources (Strayer 1999b). The common thread linking all of these drivers of

mussel declines is that they are caused by human interference in and modification of aquatic and terrestrial ecosystems.

In the PNW, the predominant anthropogenic land uses are for silviculture, agriculture and grazing, and various intensities of urban and industrial development (Wilson et al. 2014). Agriculture, grazing, and silviculture can all degrade aquatic ecosystems in similar ways by increasing influxes of suspended sediment and nutrient pollution into streams (Walser & Bart 1999; Binkley et al. 2004; National Research Council 2008; Hornbach et al. 2019). Suspended sediment loads are lethal to mussels at high enough concentrations, but also have sublethal impacts that inhibit mussel's ability to feed and respire (Hansen et al. 2016). Aquatic nutrient pollution, especially nitrogen and phosphorus, degrade habitats by causing large algal blooms and subsequent depletions of dissolved oxygen and increases in water pH. Excessive nutrients can also impact mussel fitness directly and have been linked to decreased abundances and failures in reproduction (Degerman et al. 2013; Hornback et al. 2019). Increased concentrations of nutrients and suspended sediments degrade aquatic habitat and can be especially detrimental to the survival of juvenile mussels living in the interstitial pore spaces of sediments within the channel bed.

In addition to degrading water quality, agriculture, grazing, and silviculture land uses can also alter the flow regimes of nearby streams. Agriculture and grazing can both result in increased peak flow discharges during precipitation events and decreased low flow discharges during the warm and dry summer months common in the PNW. Peak flows increase as a result of increased run-off from soil compaction (Brim Box & Mossa 1999), whereas low flow discharges decrease when water is diverted from streams to water crops and animals (López-Rodríguez et al. 2019). Silvicultural practices, including road building, can increase run-off and peak flows in adjacent streams (National Research Council 2008) with the potential impacts for channel change in the PNW being greatest in low gradient reaches with abundant gravel and sand sediments (Grant et al. 2008). Unfortunately, these low gradient reaches are the same areas that are most suitable for freshwater mussels and increased peak flows and sediment transport in these locations could shift the channel bed towards larger sediments potentially unsuitable for mussel habitat. The magnitude of impacts from silviculture and agriculture are complex and

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often context dependent, but both uses can lead to aquatic degradation through similar processes.

Although urban and industrial development account for a relatively small percentage of land use within typical PNW watersheds, they have a disproportionally large negative impact on water quality and aquatic habitat. Both uses increase the percentage of impervious surfaces draining to nearby streams, resulting in reduced infiltration and increased run off during precipitation events (Paul & Meyer 2001). Increasing impervious areas also disrupts sediment transfer processes from uplands into streams and tends to create long term sediment deficits (Paul & Meyer 2001). As a result of these changes, urbanized streams experience increased peak flows that frequently mobilize sediments and cause disturbance to instream habitats (Anim et al. 2018). The majority of sediments transported during high flows are sourced from within the channel, resulting in channel deepening and widening (Paul & Meyer 2001). Precipitation events are also linked to pollution pulses as a myriad of contaminants are flushed with stormwater into streams (Ha & Stenstrom 2003; Taebi & Droste 2004; Mallin et al. 2009). Another significant source of pollution is the discharge of effluent from wastewater treatment plants, which contains nutrients and other toxic compounds that inhibit mussel growth and survival downstream (Nobles & Zhang 2015; Gillis et al. 2017). Impacts from urban and industrial development have uniquely negative impacts on aquatic habitats that reduce mussel abundances and restrict their distributions.

One commonality amongst all of the anthropogenic land uses is their tendency to degrade or destroy the riparian vegetation adjacent to streams. In the United States, one quarter of stream lengths contain poor streamside vegetative cover and one fifth are impacted by high levels of disturbance within the riparian zone (U.S. EPA 2016). Intact, healthy riparian buffer zones can augment the negative effects of adjacent anthropogenic land use by reducing bank erosion (Brim Box & Mossa 1999), reducing the levels of suspended sediments and pollutants entering the stream (Castelle et al. 1994; Morris & Corkum 1996), and reducing adjacent water temperatures during the hot summer season (Castelle et al. 1994). Increasing water temperatures can directly impact mussels by altering their metabolic rates and decreasing the amount of energy available for survival, growth, and reproduction (Ganser et al. 2015). High water temperatures may also impact

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mussels indirectly by reducing populations of their host fish (i.e. salmonids). As forested riparian zones are lost, studies from the Midwest have documented shifts in mussel community structures towards species tolerant of degradation (Morris & Corkum 1996) and a loss of mussel species richness from otherwise suitable habitats (Poole & Downing 2004). However, PNW watersheds commonly harbor 4 or fewer species of mussel (as compared to the dozen or more species commonly found in Midwestern watersheds) and therefore the loss of one or more mussel species can easily result in localized extirpation in this region.

Linking land use to freshwater mussel declines has been complicated by the fact that the exact mechanisms driving degradation can change both temporally and spatially, and that the extent of changes are often dependent on pre-existing conditions within watersheds. Temporally, the processes linking anthropogenic land uses and streams are influenced by season and by precipitation events. For example, in the PNW, a preponderance of the processes that degrade aquatic habitats are activated by rains in the late-fall, winter, and early spring that generate run-off and spur erosion. Spatially, the magnitude of influence of anthropogenic land use changes dependent upon the scale of consideration. At the reach scale, localized effects have a disproportionately large effect on local waters and impacts tend to diminish downstream. For example, pollution levels are highest at a point-source of pollution and decrease downstream (Nobles & Zhang 2015) or the habitat condition of the riparian zone influences community composition within the adjacent stream reach (Poole & Downing 2004). Land use also influences water and habitat quality at the watershed scale through a cumulative effect. Land use impacts in the headwaters of a watershed become aggregated with impacts downstream. Depending on the unique configuration of land use within a watershed and ecosystem processes, water quality and habitat can progressively degrade downstream (Bolstad & Swank 1997; Černá et al. 2018). In the PNW, the conversion of floodplain valleys to agriculture, pastureland, and urban/industrial development is common as is increasing silvicultural land use in the forested, steeper headwaters of watersheds. There may be a threshold level of cumulative land use impacts on aquatic habitats at which instream conditions are no longer suitable for freshwater mussel habitation and mussel abundance declines toward extirpation in formerly suitable habitats.

III: HYPOTHESES

In the PNW, baseline information regarding freshwater mussel species abundances, distributions, and population demographies is missing in most watersheds. What limited information has been collected tends to only indicate species presence at a point location and lacks higher level details regarding abundances or demography. Given that anthropogenic land use change in the PNW is already widespread and projected to increase in the future (Wilson et al. 2014) and that PNW species ranges are currently declining (Blevins et al. 2017), research is urgently needed to identify existing trends of species distributions and abundances, understand what environmental drivers are responsible for these patterns, and to determine whether successful reproduction is occurring in populations. While studies investigating land use impacts on freshwater mussels have been conducted in eastern North America, to our knowledge there have been no studies investigating land use trends at the watershed scale within PNW watersheds.

Scale is an important consideration from an ecological perspective, but it is also critical to successful management and conservation action. In particular, understanding what scale may be predictive of mussel abundances is important and could be used to direct survey efforts. Mussels are patchily distributed in streams and rivers, and surveying for mussels to compile baseline information at the watershed scale is time consuming. The development of tools to indicate areas with high potential for harboring mussel populations is important, especially given the widespread deficit of information in the PNW. The development of a predictive indicator at the reach scale (10s to 100s of meters) would be ideal for directing future surveys. Because near-bed hydraulic forces are a first order natural control structuring mussel distributions and abundances, we sought to test the hypothesis that a reach-level representative specific stream power value could explain the variation in mussel abundances within an un-dammed watershed in the PNW.

The South Umpqua River basin, located in Douglas County, Oregon, is an ideal location for investigating trends of freshwater mussel distribution and abundance because it is particularly gravel rich and the South Umpqua River is not dammed. In dammed

rivers, it would be difficult to isolate the influence of anthropogenic land use from the large scale hydrologic and habitat changes caused by the dam. In addition, sediment supply and host fish distribution should not be liming factors within the basin. While there is a small dam on Cow Creek, a major tributary, the dam is located towards the headwaters and host fish distribution downstream from it and within the mainstem South Umpqua are unimpacted. Furthermore, the land use changes in the South Umpqua Basin are representative of the changes that have occurred in many forested watersheds in western Oregon: valley bottoms are primarily used for urban, industrial, and agricultural uses while silviculture dominates upland use. Given current land use conditions in the South Umpqua River basin, closed canopy forest cover is representative of the most undisturbed and stable use category. Overwhelmingly, if land is not forested, it is instead within an anthropogenic use such as agriculture or development.

This research aims to provide a baseline understanding of mussel species distributions, abundances, and population dynamics in the South Umpqua River basin, Oregon, and to test whether mussel abundances are structured by stream power at the reach scale and land use at the watershed scale. **(H1)** We hypothesize that stream power influences mussel distribution and abundance at the reach scale, and that mussel abundances will increase with decreasing stream power. (**H2)** We hypothesize that land use structures mussel abundance and population structure at the watershed scale. Mussel abundances will decrease with increasing levels of anthropogenic land use and decreasing percentage of forest cover in the drainage basin. In particular, the abundance of juvenile *M. falcata* mussels will decline with increasing levels of anthropogenic land use and decreasing percentage of forest cover in the drainage basin. **(H3)** We hypothesize that hydraulic conditions naturally structure mussel abundances, but that the cumulative effects of anthropogenic land use may supersede these effects at some threshold level of change. If this is the case, then mussel abundances will differ in response to stream power only in reaches in which land use impacts are not already a limiting factor.

IV: METHODS

Study Area:

The South Umpqua River basin drains approximately 4,660 km^2 of land and is located primarily within Douglas County in southwestern Oregon. Our study included 11 site locations on the South Umpqua River and 2 from the lower portion of its largest tributary, Cow Creek (Figure 2). To control for geology, we only included sites from within the Klamath Mountains geomorphic province. The entirety of Cow Creek and a substantial portion of the South Umpqua River from just south of Winston through Tiller drains this gravel-rich province characterized by its old and dissected rocks (Wallick et al. 2010). We further partitioned the South Umpqua River within the study area based on land use and population criteria: the lower South Umpqua River refers to sites downstream from Canyonville, while the upper river refers to sites upstream from Canyonville. The majority of both the population and anthropogenic land use is located downstream from Canyonville, therefore the lower section of river bears the largest cumulative anthropogenic impacts (Figure 2). For example, 3 wastewater treatment plants discharge effluent into the study area from Canyonville downstream as compared to only 1 treatment plant located above Canyonville in the town of Tiller.

The cumulative effect of anthropogenic land use in the South Umpqua River basin results in increasing levels of water quality impairment in downstream reaches with greater drainage basin areas. This trend is particularly pronounced in the South Umpqua River, where violations of established water quality standards increase downstream. For example, the South Umpqua River is 303(d) listed for bacteria (fecal coliform and *E. coli*) and aquatic weeds/ algae during the summer from river mile 57.7 (just upstream from Canyonville) downstream, and the most extreme violations for both pH and dissolved oxygen occur in the lowest reaches of the river (Turner et al. 2006). The majority of landcover in the South Umpqua River basin is forested and the most widespread anthropogenic land use is silviculture (Figure 2). Other anthropogenic uses tend to be concentrated within the wide floodplain valleys that flank the South Umpqua River and lower reaches of Cow Creek and include pasture lands, agriculture, and urban/ industrial development (Figure 2). Agricultural and urban/industrial development land

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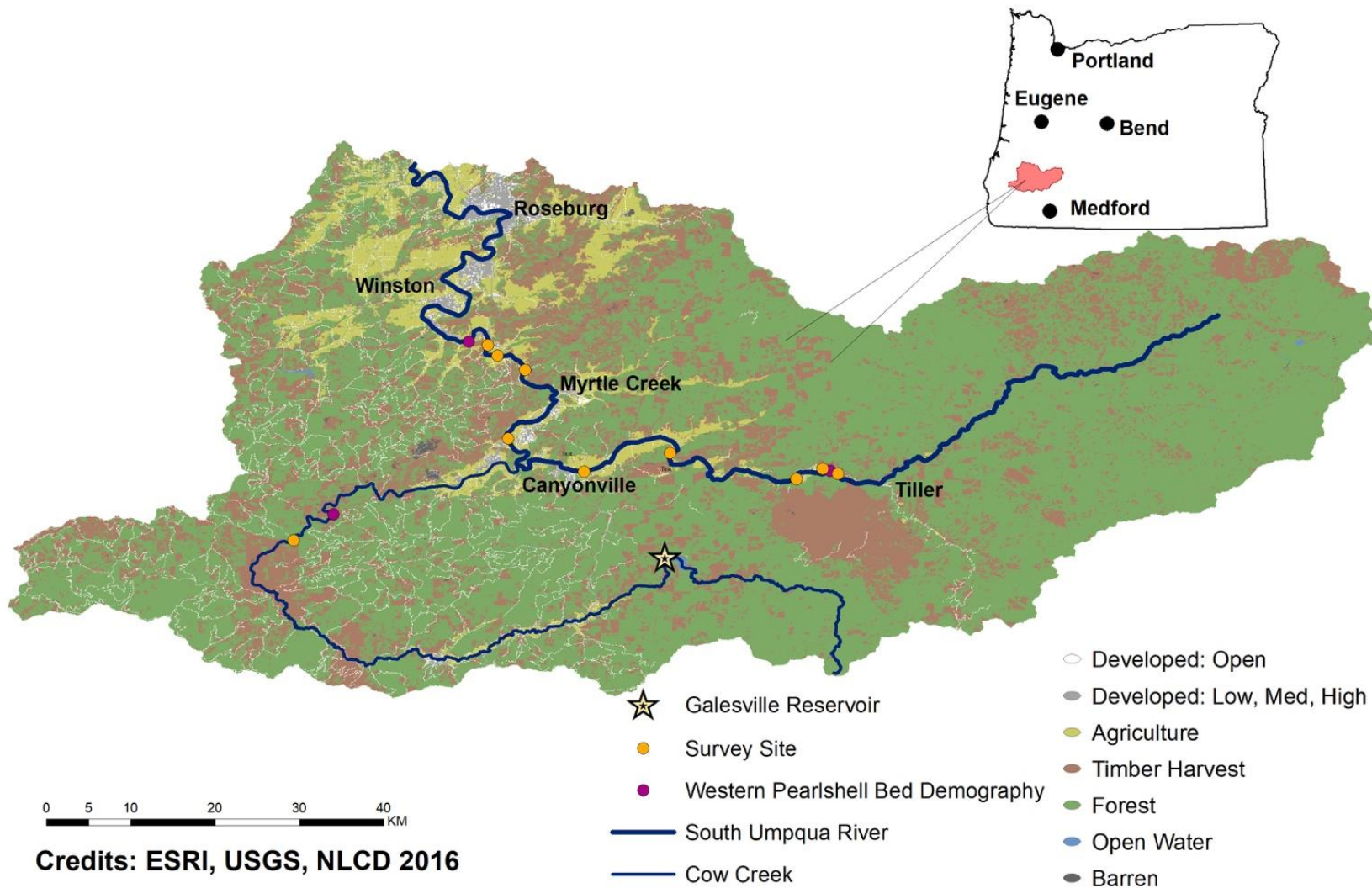
Figure 2: Land use map of the South Umpqua River basin, Oregon, showing locations of field survey sites and western pearlshell (*M. falcata*) mussel bed sampling locations to document baseline demographic parameters. Land use categories are represented by color.

uses exacerbate pre-existing channel conditions, and the entire South Umpqua River and lower Cow Creek are 303(d) listed for pH and temperature year-round (Turner et al. 2006).

The South Umpqua River basin experiences a typical Mediterranean climate: summers are hot, dry, and clear while winters are cold, wet, and cloudy. Precipitation in the basin is variable upon location but ranges between 30 – 70 inches of rain annually, with up to 90 inches falling at higher elevations (Geyer 2003). A combination of highly weathered parent material in the South Umpqua River basin and precipitation falling predominantly as rain results in a rapid hydrologic response to both wet and dry weather conditions (Wallick et al. 2010). Rivers and streams in this basin rise quickly in response to precipitation, sustain highest mean daily flow conditions in the late fall through early spring, and experience drastically reduced flow conditions in response to prolonged summer drought.

The average gradient of the South Umpqua River upstream from the Cow Creek confluence is 0.00249; downstream from Cow Creek the average gradient is 0.001 (Wallick et al. 2010). Below the confluence with Jackson Creek (upstream from Tiller), the South Umpqua River alternately flows over bedrock and coarse alluvium with gravel bar and terrace features present dependent on valley form. Lower Cow Creek (below the confluence with Middle Creek) is an alluvial stream with an average gradient of 0.05 and a floodplain that decreases in size with distance upstream from its confluence with the South Umpqua River (Geyer 2003). No dams have been constructed on the South Umpqua River, but Galesville Reservoir was constructed in the upper reaches of Cow Creek in 1985 to help reduce flooding downstream. The dam reduces peak flows in Cow Creek but has not noticeably impacted flows in the South Umpqua River as evidenced by USGS gaging records on the South Umpqua River downstream from its confluence with Cow Creek (Wallick et al. 2010). Galesville dam also limits bed material transport from the upper 192 km^2 of Cow Creek's drainage basin into downstream reaches of Cow Creek and the South Umpqua River, although this disruption in sediment supply is less impactful in a geomorphic province known for its propensity to produce and deliver sediments downstream.

Host-fish species important to freshwater mussel lifecycles are widespread in the South Umpqua River basin. A multitude of resident and anadromous salmonids (genus *Oncorhynchus*) utilize streams throughout the South Umpqua River basin, including Coho salmon (*O. kisutch*), fall and spring runs of Chinook salmon (*O. tshawytscha*), winter and summer runs of steelhead (*O. mykiss*), and anadromous and resident cutthroat trout (*O. clarkii*). Historically, greater numbers of salmon and steelhead returned to the basin to spawn as compared to present day and efforts to increase salmon populations are ongoing across all resource management agencies. In addition, fish species such as redside shiner (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), long-nose dace (*Rhinicthys cataractae*), and sculpin (*Cottus sp.*) are common throughout the South Umpqua River and Cow Creek.

Site Selection:

We selected all mussel site locations *a priori* from available databases and records indicating mussel presence at a site. We only considered sites with relatively recent records (dating back to 1990) to increase the likelihood that mussels were still present. All sites visited in 2018 were sourced from the Western Freshwater Mussel Database (Xerces/CTUIR 2018). After the 2018 field season, we discovered two additional sources of freshwater mussel records from the United States Forest Service Tiller Ranger District (Casey Baldwin, personal communication) and the Roseburg Bureau of Land Management (Duncan 2006) that were used to add additional sites in the summer 2020 field season.

Site Assessment Surveys (Summer 2018 & 2020):

The purpose of the site assessment surveys was to gather detailed information about freshwater mussel aggregation abundance and species presence from sites distributed throughout the lower and upper South Umpqua River and Cow Creek where previous mussel occurrence had been recently documented. Mussel aggregation abundances were used to investigate our hypotheses that land use structures mussel abundance at the watershed scale and that stream power is an important driver at the reach scale. We snorkel surveyed (Duncan 2008) eight site locations in summer of 2018

to locate mussels in the South Umpqua River and Cow Creek. In the summer of 2020, we surveyed an additional 5 sites in the South Umpqua River to increase the number of sample sites and their relative location within the study area. To complete a site assessment, a minimum of 2 surveyors navigated to the GPS point associated with each site record and spent a minimum of 5 person hours searching for mussels within all available habitats, including in the mid-channel. We attempted to survey at least one pool and one riffle habitat per site and snorkeled backwater habitats when present to ensure that a range of channel unit types were covered. Individual units, especially pools, commonly spanned hundreds of meters of river length.

We were not aware that invasive Asian clams (*Corbicula fluminea*) were present in the South Umpqua River basin prior to our summer 2018 field work. We observed high abundances of *C. fluminea* at sites on the lower South Umpqua River and decided to note the presence or absence of *C. fluminea* at each site location and provide a relative abundance estimate at each site. Low abundances of *C. fluminea* were recorded if less than 10 live animals were observed, moderate abundance indicated that between 10 – 100 live animals were observed, and high abundance referred to observations of greater than 100 live animals at a site.

For the purposes of this study, a mussel aggregation was defined as one or more mussels found within close physical proximity to one another. Mussel aggregations were considered separate entities when they occupied substantially different habitat zones and/or were separated by greater than 10 m of unoccupied substrate. Mussel beds were defined as being any mussel aggregation with 15 or more visible individuals at the substrate surface. When a mussel was found, surveyors identified the species of the animal and recorded a GPS location to mark the aggregation. Search efforts were intensified in the streambed adjacent to the animal, and the approximate stream area (in m^2) encompassing the aggregation was recorded in addition to observations regarding substrate, habitat, or demography.

Bed Demographies (Summer 2018):

We returned to mussel beds that were identified during the summer 2018 site assessment surveys to determine their population densities, approximate age structures,

and to assess whether reproduction was occurring. These demographic parameters were used to address our hypothesis that increasing percentages of anthropogenic land use in the drainage basin disproportionately impacts juvenile mussels and may result in a lack of reproduction entirely. We systematically sampled 3 *M. falcata* mussel beds from 3 unique locations in the South Umpqua River (shown on Fig. 2 as purple dots) and Cow Creek in the summer of 2018. In addition, we also systematically sampled one *Anodonta sp.* bed in the upper South Umpqua River. We only encountered two *M. falcata* mussel beds that met our definition of a bed (greater than 15 animals in an aggregation) while completing site surveys in 2018: one in Cow Creek and one in the upper South Umpqua River. In order to obtain demographic parameters from a mussel population in the lower South Umpqua River, the *M. falcata* mussel aggregation with the highest number of animals (n = 11) was selected for additional demographic sampling.

In order to avoid destructively sampling animals, we used mussel length as a proxy for age to infer each bed's approximate age structure and considered *M. falcata* mussels $\lesssim$ 3.0 cm to be juveniles. The correlation between length and age is linear for young mussels, and therefore this method is sufficient to answer questions about reproduction and juvenile size classes (Howard & Cuffey 2006b; Kunz et al. 2020). Juvenile *M. falcata* are considered to be animals that have not yet reached reproductive age and studies investigating length – age relationships in the PNW have found that juveniles are consistently less than 3 cm in length (Toy 1998; Howard & Cuffey 2006b). In addition, 1-year old *M. falcata* reared in an idealized laboratory setting reached an average shell length of 1 cm (Kunz et al. 2020). In contrast, the maximum shell size for this species ranges from 12 – 15 cm. Literature establishing length to age relationships for *Anodonta sp.* in the PNW is generally lacking, but recent efforts to culture *A. californiensis* in a lab setting demonstrated that 150-day old animals reached a maximum shell length of 2.8 cm (Kunz et al. 2020). This represents a maximum growth rate, but in the absence of species level identification we decided to conservatively use 2 cm length as our cut-off for delineating juvenile *Anodonta sp.*. The maximum shell length for *Anodonta sp.* is dependent on species and on habitat features, such as water temperature and productivity, and ranges from 10 – 18 cm in length (Nedeau et al. 2009; Blevins et al. 2018).

Our sampling methodology was derived from protocols developed by Strayer and Smith (2003) and designed to ensure that we sampled a minimum of 50 animals from each bed. We delineated each mussel bed using animals visible at the substrate surface, therefore each bed area is likely an underrepresentation because mussels at the bed margins were either buried or too cryptic to locate. We employed a unique sampling design at each mussel bed dependent on bed size: a complete census of animals available at the substrate surface was conducted in beds with an area of 50 m^2 or less, and a systematic sampling design was utilized for beds with an area of greater than 50 m^2. Regardless of sampling methodology, our goal was to sample at least 50 animals per population.

To census a population, the entire length of the mussel bed parallel to the stream bank was broken into individual blocks 0.25 m in length. At the downstream margin of each block, a transect perpendicular to the bank was established with units laid out every 0.25 m up to the maximal width of the bed. For example, a mussel bed that is 8 m long by 5 m wide would be broken into 32 consecutive blocks each containing 20 units along the transect. Within each block, we placed a 0.25 m^2 quadrat over every unit and a snorkeler collected all animals visible at the substrate surface. If any portion of a mussel shell fell within the boundary of the quadrat it was included in sampling. We identified mussels to species (*M. falcata* or *G.* angulata) or clade (*Anodonta sp.*) and measured their length as the maximum anterior to posterior extent of the shell. Length was measured to the nearest 0.1 mm using dial calipers. After all animals in a quadrat were sampled, mussels were re-positioned within the quadrat in as close to their original orientations as possible.

We included excavation within each sampling plan to answer questions about burial rates and the presence or absence of juvenile mussels. We double-sampled quadrats via excavation of the substrate to 13 cm depth such that 6% of the total bed size was double-sampled. Excavated quadrats were evenly spaced throughout the bed. For example, in an 8 X 5 m mussel bed we surface sampled 640 quadrats and every 64th quadrat would be double-sampled with excavation. Excavated substrate was sieved through 3.5 mm mesh screens, and all mussels collected were identified and measured. Excavated substrate and mussels were returned to the stream in as close to their original

orientations as possible. Juvenile mussels were buried 1-2 cm below the substrate surface, whereas adult mussels were repositioned at the substrate surface.

Systematic sampling designs were implemented to survey mussel beds larger than 50 m^2. Our sampling design used 3 random transect start locations at the downstream bed margin and placed subsequent upstream transects at equal intervals from each unique starting location. Each unique grouping of transects was considered a sample (transect groups A, B, and C with 3 samples per bed). Transects were oriented perpendicular to the stream bank and spanned the entire width of the mussel bed. Quadrats were placed along each transect using a random start position from the bank followed by equal placement along the transect; quadrats within each transect group had a unique start location and placement distance. For example, transects in Group A might start 1.5 m into the length of the mussel bed, be spaced 8 m apart for the remaining length of the bed, and have quadrats placed along transects starting 0.5 meters into the bed width.

For mussel beds greater than 50 m^2 or less than or equal to 250 m^2, each sampling plan was designed so that at least 20% of the bed was sampled at the substrate surface. Double-sampling of quadrats via excavation was completed in at least 33% of all quadrats sampled as per Smith et al. (1999) under the assumption that $50 - 60\%$ of mussels would be available at the substrate surface. Previous population studies of *M. falcata* have documented that between 50-60% (Searles Mazzacano 2017, 2018) or more (Howard & Cuffey 2006b) of *M. falcata* are typically available at the substrate surface. In mussel beds greater than 250 m^2, a similar sampling design based on random transect and quadrat starts within sampling groups was used. However, sampling plans were designed such that at least 200 quadrats total would be sampled at the substrate surface with at least 33% of quadrats double-sampled with excavation.

In addition to counting mussels within excavation units, we also counted live *C. fluminea* from within 6 randomly selected excavation units at the *M. falcata* bed on the lower South Umpqua River (site BKY01). This was the only systematically sampled mussel bed in which *C. fluminea* were present, and we wanted to approximate clam densities within the bed. We also collected habitat information at each bed including morphological stream unit type (i.e. pool, riffle, run), bank type, valley form, average water depth, water temperature, and associated riparian vegetation. The distribution of

substrate within each habitat unit within the bed was also estimated within six size classes: (1) silt and fine organic matter (>0.1 mm) (2) sand (0.1 – 2 mm), (3) gravel (2-64 mm), (4) cobble (64 – 256 mm), (5) boulders (greater than 256 mm), and bedrock.

Stream Power Analysis:

We calculated generalized specific stream power values for the stream reach encompassing each mussel site using remotely collected LiDAR data and ArcGIS. Stream power (Ω) is the rate of potential energy expenditure against the stream channel and bank for a specific unit length of channel and is calculated as: $\Omega = \rho * g * Q * s$, where ρ is the density of water (1000 kg/m^3), g is the rate of acceleration due to gravity (9.8 m/s^2), Q is the discharge (m^3/s), and s is the water surface slope. Stream power is expressed as watts/ meter and represents the potential energy available to entrain and transport bedload particles within a 1 m wide strip of channel stretching from bank to bank. Stream power increases with discharge at a particular site; higher flows result in higher stream power values and therefore more potential to move bedload particles. Specific stream power (ω) is calculated as: $\omega = \Omega / w$, where w is the active channel width of the water surface. Specific stream power corresponds to the energy acting upon a single m^2 section of the channel bed (watts/m^2). Specific stream power decreases with increasing channel width because the potential energy available for sediment transport is spread out over a larger area.

We used the 10-year peak flow discharge (Q_{10yr}) at each site to test the relationship between mussel abundance and naturally controlled stream power (Hypothesis 1). While anthropogenic land use can influence stream power through changes in the magnitude and frequency of peak flow events, our stream power analysis held discharge constant. The stream power values we calculated are instead the result of naturally controlled site specific channel gradient and active channel width measurements. Peak flow values are infrequent disturbance pulses with the potential to cause significant channel change in a short amount of time. The Q_{10yr} is considered large enough to influence sediment transport and structure instream habitat while also occurring frequently enough to occur one to many times during the average mussel's lifespan. We wanted to test whether a reach-level representation of disturbance could

explain variation in mussel aggregation abundance and be used to direct future mussel surveys within the South Umpqua River and Cow Creek. Because the average Q_{10yr} stream power for each site was calculated using reach-level measurements, it provides a generalized estimate of hydraulic disturbance upon the stream bed that does not represent the actual stream power occurring at smaller scale patches with the reach. At the patch scale, variables such as average particle size and bedform resistance also control whether particles are entrained at a certain location for a given discharge.

We identified a stream reach and calculated water surface slope and average active channel width remotely in ArcGIS (desktop version 10.5) for each of the 13 sites. We delineated reaches that were the same length or slightly longer than survey lengths at each site except for sites BKY02 and COW01. At these sites survey lengths were exceptionally long and reaches less than the field survey length were delineated; at both sites the delineated reaches encompassed all mussel aggregations at each site. We marked the extent of each reach with downstream and upstream points positioned along the stream's centerline; points were chosen within pool habitats with laminar flow. We derived water surface slope from LiDAR-derived bare earth digital elevation models (DOGAMI n.d.): at both the down and upstream point locations we recorded elevations within a 20 ft radius; all elevation measurements were taken from point returns at the water surface. We calculated both a high and low estimate of slope between the up and downstream extent of each reach, and used the average of these values as our slope gradient value. We calculated the average active channel width for each reach by averaging 3 active channel width measurements from the upstream, middle, and downstream sections of each reach. Q_{10yr} values for all sites were obtained from the United States Geological Survey's StreamStats program (U.S. Geological Survey n.d.), which is a web based GIS application that solves regression equations to estimate flow statistics at ungaged sites. Peak flow values represent the largest magnitude of flow that a site is probable to experience within a given timeframe. Peak flow is an instantaneous value and gives no indication as to how long a discharge of that magnitude would last. Peak flow values for a given site are correlated, such that the site experiencing the highest magnitude 2-yr flows would also have the highest magnitude 25-yr and 100-yr peak flows.

Land Use Analysis:

We determined the percent of land use within the South Umpqua River basin in 7 unique categories at two spatial scales to determine whether observed patterns of freshwater mussel abundances were linked to land use at the watershed scale (Hypothesis 2). At the largest scale, percent land use was quantified for each site's unique drainage basin, which begins at the downstream end of each site and extends upstream and upland to include all land that drains to that point. Drainage basins were delineated using the StreamStats web application (U.S. Geological Survey 2020). At the smaller scale, we quantified land use using the hydrologic unit code (HUC) 12 digit subwatershed that encompasses each site. The HUC12 represents the smallest watershed unit delineated by the National Resources Conservation Service (NRCS) and is referred to as a subwatershed. Both the drainage basin and subwatershed areas represent land use at the watershed scale (10's – 1000's of km), but the drainage basin unit is more likely to correspond to cumulative land use impacts whereas the subwatershed unit is representative of more localized land use impacts. Land use categories were derived from the USGS's National Land Cover Database 30-m resolution 2016 imagery (Dewitz 2019) and reclassified into the following 7 categories in ArcGIS: (1) open water; (2) barren; (3) developed: open space; (4) developed: low, medium, and high intensity; (5) agriculture; (6) forest; and (7) timber harvest.

Data Analysis:

For all analysis investigating trends of mussel abundance, we used mussel aggregations as the sampling unit and combined the total count of mussels from across species at each aggregation. Mussels are patchily distributed within aquatic habitats and populations likely experience sink – source dynamics that make the aggregation level most relevant for understanding abundance trends and inferring population level consequences. In addition, while we established a minimum search effort standard, we did not limit searches to a certain time nor did we standardize survey lengths at each site. Because maximum search effort varied by site, it was not possible to contrast total abundances per site in a meaningful way. Multiple aggregations frequently occurred within one site separated by a distance of 10 – 100s of meters, but stream power and land

use variables were calculated at the site level and therefore applied equally to all aggregations within a site. While aggregations were far enough apart to be ecologically meaningful, they were close enough that the percentage of change in drainage basin land use variables between them was negligible. We did not include mussel aggregations with only 1 mussel in our analysis because other processes, such as re-establishment of a dislodged animal downstream due to high flows, are likely driving these occurrences.

We used Pearson's correlations to reduce the number of landscape variables for use in step-wise regression models. Correlation coefficients greater than 80% were considered significant correlation and resulted in the elimination of at least one variable. Land use was significantly correlated at the drainage basin scale; in particular, the percent of forest cover was significantly negatively correlated with the percent of all anthropogenic land use categories (agriculture, timber harvest, and development). Land use categories were also significantly correlated at the smaller HUC12 scale: agriculture was positively correlated with development and negatively correlated with forest cover. Significant levels of correlation were much less common when comparing land use categories between the drainage basin and HUC12 scales. Only land use categories that were not correlated with one another were candidate variables in analysis comparing trends of mussel abundance with land use.

We log-transformed mussel abundance data prior to analysis (log(mussel abundance + 0.01)). We assessed the relationship between mussel abundance and the drainage basin area of each site using linear regression. We used the stepAIC() stepwise regression function in R (R Core Team 2018) to evaluate the relationship between mussel abundances, stream power, and land use variables. This function selects the most parsimonious model by reducing the Akaike Information Criteria (AIC) through systematic elimination of candidate variables. Candidate variables included the Q_{10yr}, the percent of forest cover within the drainage basin area of each site, and the percent of either forest cover, agriculture, or timber harvest within the HUC12 subwatershed encompassing each site. We decided to use forest cover at the drainage basin scale because it was the best representation of total anthropogenic land use; as forest cover decreased, anthropogenic land use increased. The criterion for significance in all statistical tests was a P value ≤ to 0.05.

V: RESULTS

Freshwater Mussel Distribution & Abundance:

In total, we searched 4.2 km of the lower South Umpqua River, 2.53 km of the upper South Umpqua River, and 1.38 km of Cow Creek and documented 49 mussel aggregations across 13 site locations (Table 1). In the South Umpqua River, our sites spanned approximately 95 km of river length. We found a significantly negative relationship between mussel abundance and the contributing drainage basin area of a site ($F_{1,32}$ = 8.371, Adj. R^2 = .18), which correlates to increasing mussel abundance with increasing distance upstream in the South Umpqua River (Figure 3, Panel A). In addition, we found the lowest species richness in sites with the greatest drainage basin areas (only *M. falcata* present in BKY sites 1 – 4) and that mussel species richness increased as the drainage basin area of sites decreased. *M. falcata* were widely distributed in the South Umpqua river basin and we found at least 1 live animal at every site location visited, but aggregation abundances significantly increased upstream on the South Umpqua River (Table 1).

Juvenile *M. falcata* were also widely distributed in the South Umpqua River basin, and bed demographies from 3 distinct populations revealed that they represented between 3 – 13% of their respective populations (Table 2). *Anodonta sp.* were the second most common freshwater mussels found in the basin and were documented on Cow Creek (site COW01), at one site in the lower South Umpqua River (BKY05), and in the majority of sites in the upper South Umpqua River (Table 1). *G. angulata* were found at only 2 site locations (TIL01 & TIL02) in the upper South Umpqua River in low abundances of <= 5 animals per aggregation (Table 3, Supplemental Figures). Of the 19 mussel aggregations located in the lower South Umpqua River sites, only 2 had greater than 10 animals and 84% of the aggregations contained less than 5 animals. In comparison, we located 24 aggregations in the upper South Umpqua River, of which 42% contained less than 5 animals but 50% contained more than 10 animals. In aggregations of greater than 10 animals, over half contained more than 350 animals and a third contained greater than 1,000 animals (Table 3, Supp. Fig.). The largest aggregation of mussels was an *M. falcata* bed with almost 87,000 animals at the TIL05 site in the upper South Umpqua River.

Table 1: Summary information for all sites including site ID, site location within the basin, the total river distance searched (km), the site's drainage basin (D.B) area (mi^2), the approximate river kilometer (increasing upstream), abundance (sum of all mussels from all aggregations), the number (Num.) of aggregations (Agg.) found at each site, and abundances for each species (western pearlshell and western ridged) or clade (floater).

Site ID	Location	Distance Searched (km)	D.B. Area (mi^2)	River km	Abundance	Num. Agg.	Species Abundances		
							Western Pearlshell	Floater	Western Ridged
BKY01	Lower S. Umpqua	0.44	1430	65.0	47	3	47	0	0
BKY02	Lower S. Umpqua	1.10	1410	71.0	4	1	4	0	0
BKY03	Lower S. Umpqua	0.85	1410	74.0	27	4	27	0	0
BKY04	Lower S. Umpqua	0.93	1410	78.5	6	4	6	0	0
BKY05	Lower S. Umpqua	0.88	1270	97.0	12	8	10	2	0
TIL01	Upper S. Umpqua	0.29	699	113.5	58	6	50	5	3
TIL02	Upper S. Umpqua	0.62	643	130.0	2661	8	1642	1012	6
TIL03	Upper S. Umpqua	0.47	571	152.5	365	2	1	364	0
TIL04	Upper S. Umpqua	0.37	565	157.5	1398	2	1397	1	0
TIL05	Upper S. Umpqua	0.26	564	159.0	87038	2	87038	0	0
TIL06	Upper S. Umpqua	0.52	545	160.0	3471	4	3465	6	0
COW01	Cow Cr.	0.95	474	36.5	115	4	114	1	0
COW02	Cow Cr.	0.43	394	46.0	2	1	2	0	0

Invasive Asian clams (*Corbicula fluminea*) were found at all sites in the lower South Umpqua River and at one site in the upper South Umpqua River immediately upstream from Canyonville (TIL01). When present, *C. fluminea* were most abundant in the finer sediments within pools but were distributed throughout sites in a range of sediment sizes and in both fast and slow water habitats. *C. fluminea* abundances decreased upstream with decreasing drainage basin area. We quantified *C. fluminea* densities within the *M. falcata* bed sampled in the lower South Umpqua River (site BKY01) and counted an average of 183 live *C. fluminea* per 0.25 m^2 quadrat, which equates to roughly 99,000 animals in the 135 m^2 bed area.
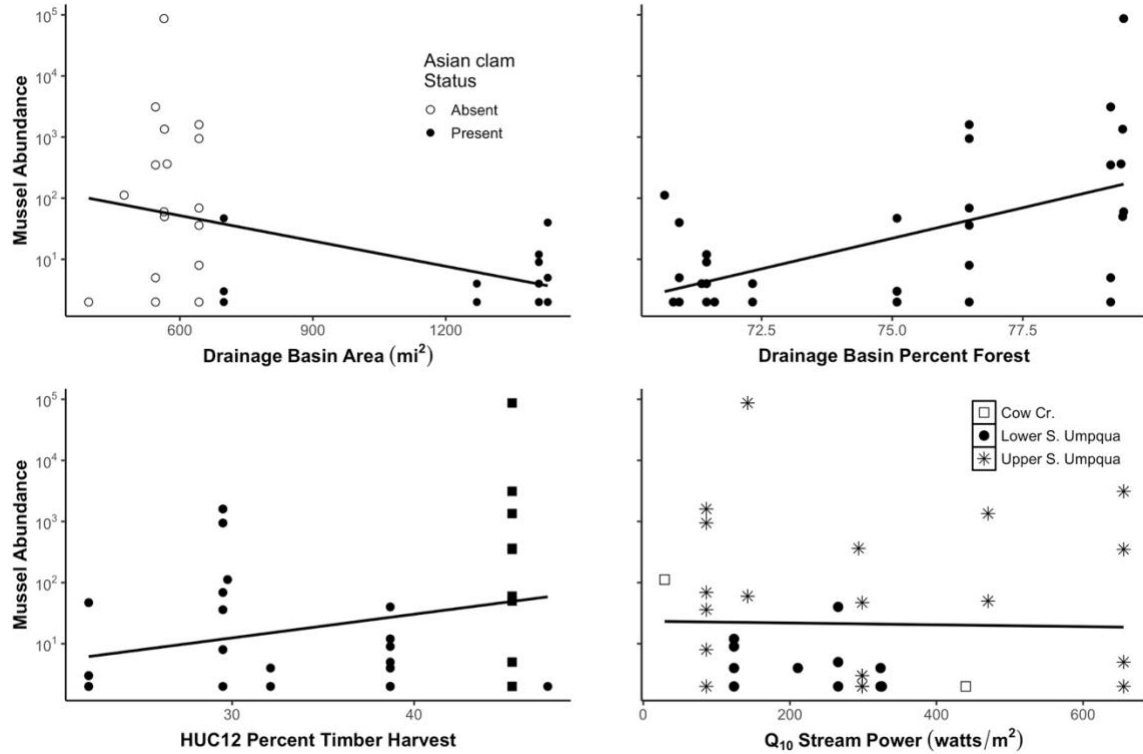
F**igure 3:** The relationship between mussel abundance and **(A)** the contributing drainage basin area of a site (mi^2), **(B)** the percentage of forest within the drainage basin, **(C)** the percentage of timber harvest within the HUC12 subwatershed unit, and **(D)** the representative reach scale Q$_{10}$ specific stream power (watts/m^2). In panel **(C)**, the squares represent sites within the same HUC12 unit on the South Umpqua River.

Table 2: Selected mussel bed characteristics and demographic parameters for the 3 western pearlshell (*M. falcata*) beds and 1 floater (*Anodonta sp.*) mussel bed that were sampled to determine baseline demographic parameters in the South Umpqua River and Cow Creek.

Site ID	Bed Area (m^2)	Species	Sample Type	Density / m^2	Perc. Juvenile	Burial Rate	Field Cnt	Est. Pop. Size	Mean Length (cm)
BKY01	135.0	*M. falcata*	Systematic	0.30	12.5	1.00	8	40	5.88
TIL05	932.0	*M. falcata*	Systematic	93.34	3.3	1.02	1151	86993	8.06
COW01	43.0	*M. falcata*	Census	2.60	7.2	1.17	97	112	4.85
TIL03	52.5	*Anodonta sp.*	Census	6.93	18.6	4.00	112	364	4.21

Land Use, Stream Power, and Freshwater Mussels:

Drainage basin areas ranged in size from 1430 mi^2 at the BKY01 site in the lower South Umpqua River to 394 mi^2 at the COW02 site on Cow Creek (Table 1). In contrast, HUC12 subwatershed sizes ranged in size from 86.9 mi^2 – 215.4 mi^2 (Table 4, Supp. Fig.). The most parsimonious model explaining mussel aggregation abundances in the South Umpqua River basin included forest land use at the drainage basin scale, timber harvest at the HUC12 scale, and the Q_{10} stream power value ($F_{3,30}$ = 8.594, adj. R^2 = .41). We found a significant positive relationship between mussel aggregation abundance and both the percentage of forest at the drainage basin scale (ß = 0.531, SE = 0.118, p-value = 9.86 x 10^{-5}) and the percentage of timber harvest at the HUC12 subwatershed scale (ß = 0.104, SE = 0.049, p-value = 0.044)(Figure 3, Panels B & C). There was also a significantly negative relationship between mussel abundance and the Q_{10} specific stream power value (ß = -0.006, SE = 0.002, p-value = 0.014) (Figure 3, Panel D). These results support our hypothesis that land use structures mussel abundance at the watershed scale. However, while including the stream power variable helped to improve model fit overall, its ability to predict mussel abundances was weak and indicates that we did not measure stream power at the right scale to explain the full range of variation in abundance due to hydraulic forces.

In the South Umpqua River basin, the percentage of forest within the drainage basin is strongly negatively correlated with the percentages of all anthropogenically derived land uses including various intensities of development, agriculture and rangeland, and timber harvest. Therefore, as the percentage of forest declines, the percentage of anthropogenic land use increases. The highest concentration of both development and agriculture in the basin are in lands adjacent to the lower South Umpqua River (Figure 2). The upper South Umpqua River flows through lands increasingly dominated by either forest or landscapes produced by timber harvest (Figure 2). Cow Creek flows through a landscape similarly dominated by a mosaic of forest and timber land uses, with the exception being the farthest downstream reaches which have increasing influence from both agriculture and urban development (Figure 2). Our analysis is not able to discern the impacts of particular anthropogenic land uses on mussel abundances and instead

measures the cumulative effect of anthropogenic land use at the drainage basin and HUC12 watershed scales.

The 10-year peak discharge (Q_{10}) specific stream power value at each site location varied from a low of 29 watts/m^2 at the downstream Cow Creek site (COW01) to a high of 655 watts/m^2 at the TIL06 site in the upper South Umpqua River (Table 4, Supp. Fig.). High abundance mussel aggregations were found in reaches experiencing a large range of stream power values (Figure 3, Panel D), which does not support our hypothesis that stream power structures mussel abundance on the reach level. We hypothesized that high abundance aggregations would only be found in reaches that experience the lowest values of Q_{10} stream power. Both *M. falcata* and *Anodonta sp.* occurred in high abundance aggregations in reaches spanning the full spectrum of possible Q_{10} stream power values. Two site locations in the upper South Umpqua River, TIL04 and TIL06, were notable for harboring high abundance aggregations (> 1,000 animals per aggregation) and having the two highest stream power values of all sites surveyed (Table 4, Supp. Fig.).

Mussel Bed Demographies:

Three *M. falcata* beds at sites BKY01, TIL05, and COW01 were systematically sampled with excavation to determine baseline demographic parameters including population size, density, age structure, and to assess whether reproduction was occurring (Figures 2 & 4). In addition, one *Anodonta sp.* bed located in the upper South Umpqua River was also systematically surveyed at site TIL03 (Figure 5). All *M. falcata* beds had a very low burial rate of animals ranging from 1 at the BKY01 site (all animals available at the substrate surface) to 1.17 at the COW01 site (Table 2). Despite this low burial rate in the *Margaritifera* beds, when mussels were found buried they were predominately within the juvenile size classes (Figure 6, Panels A & B, Supp. Fig.).

The *M. falcata* bed in the upper South Umpqua River at site TIL05 is comprised of approximately 87,000 animals and has a bed density of 93 mussels/ m^2 (Table 2). The bulk of this bed's population are older animals over 6 cm in length; the mean mussel length was 8.06 cm. All length categories are represented, which indicates that continual recruitment of new animals has been occurring at this location. However, juvenile mussels $\lesssim$ 3.0 cm comprised only 3.3% of the total population (Table 2). In stark

contrast, the *M. falcata* bed from site BKY01 contained approximately 40 mussels with a bed density of 0.3 mussels/ m^2 (Table 2). Only 8 live mussels were found while sampling the bed, which is much less than the 50 animal minimum specified in our sampling protocol. One of the mussels sampled from within the bed was 2.25 cm in length and indicative that juvenile mussels are present in the lower river.
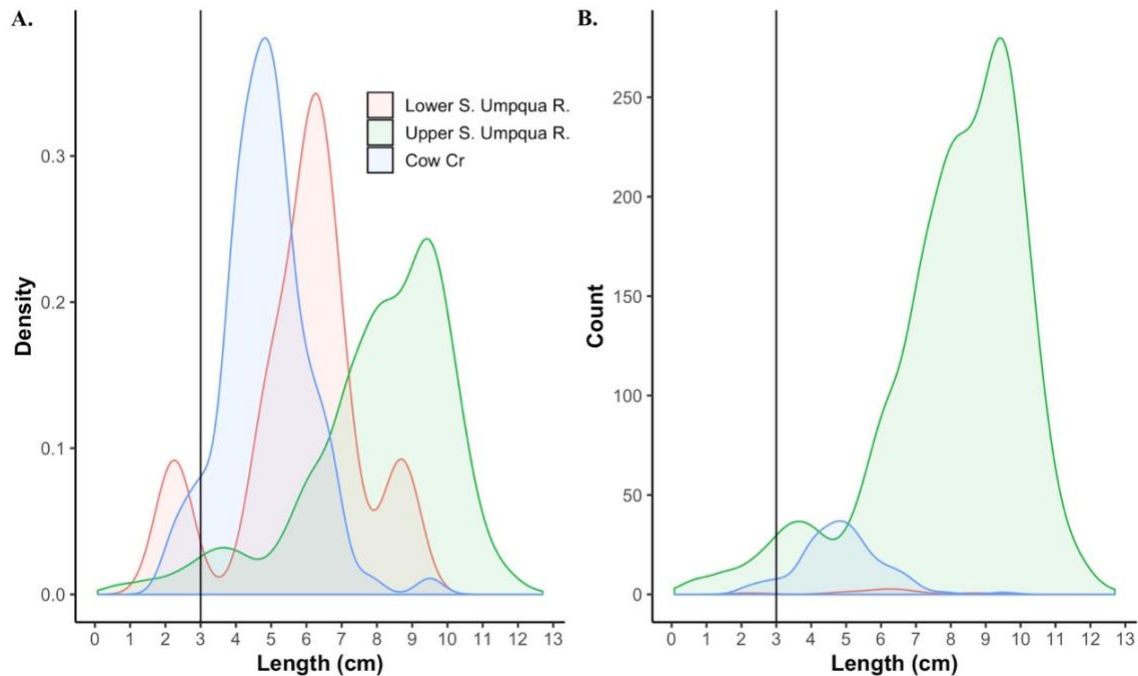
Figure 4: Age structures of each of the 3 *M. falcata* (western pearlshell) beds systematically sampled from site BKY01 in the lower South Umpqua River (red), site TIL05 in the upper South Umpqua River (green), and site COW01 from Cow Creek (blue). **Panel A** emphasizes the relative density of mussels found within each size class by normalizing the area underneath each curve to equal one. **Panel B** provides the actual count of mussels found within each size class. Juvenile *M. falcata* are animals 3 cm or less in length.

The mussels sampled from the lower South Umpqua bed (BKY01) represented a range of ages spanning from juvenile through mature adulthood (Figure 4, Panel A). We found and measured 11 mussel shells from recently deceased animals within the bed: these shell lengths were all 6 cm or greater (Figure 6, Panel D, Supp. Fig.). If all *M. falcata* mussels that we measured at the four farthest downstream sites during site assessment surveys (BKY01 – 04) are considered together (n = 18), juvenile mussels represent 22% of the total population. However, overall sample size from sites on the

lower South Umpqua River remain too low to confidently assess the abundance of juveniles in this area of the river and additional surveys are needed in that regard.

The *M. falcata* bed in Cow Creek had approximately 112 mussels and a bed density of 2.6 mussels/ m^2 (Table 2). The Cow Creek bed was the youngest of the *M. falcata* beds sampled, with a mean mussel length of 4.85 cm and almost no mussels larger than 7.5 cm in length (Figure 3). No mussels less than 2 cm in length were present,
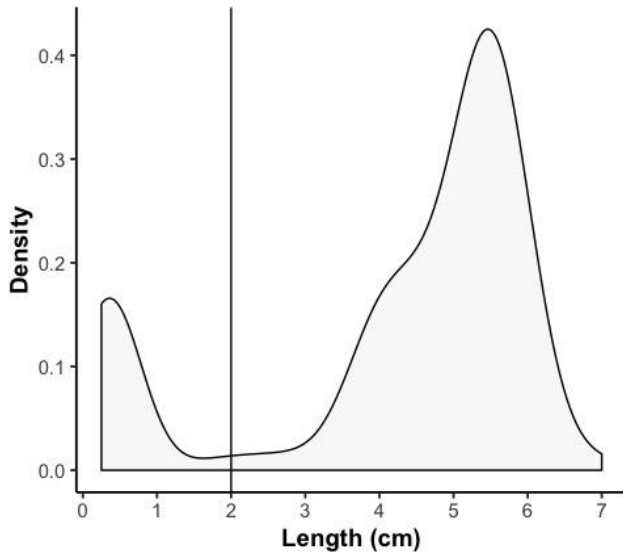
Figure 5: Age structure visualized as relative densities in the Anodonta sp. bed sampled from the TIL03 site in the upper South Umpqua River. We considered juvenile Anodonta sp. to be ≤ 2.0 cm in length.

indicating that there has likely not been successful recruitment to the bed within the past several years. However, there were enough mussels between 2 – 3 cm in length that juveniles comprised 7.2% of the total population (Table 2).

The *Anodonta sp.* bed sampled at the TIL03 site contained approximately 364 animals within a 52.5 m^2 bed area and had a density of 6.9 mussels/m^2 (Table 2). The burial factor of mussels within the bed was 4, meaning that for every 1 mussel available at the substrate surface another 4 were buried in the substrate. Buried mussels were overwhelmingly juveniles < 1.0 cm in length (Figure 6, Panel C, Supp. Fig.). The bed was predominately sand substrate with deposition of fines and organic matter near the bank edge. The bed had a bimodal age distribution with two peaks centered around roughly 0.38 cm and 5.4 cm in length (Figure 5), which suggests that this *Anodonta sp.* bed experiences pulses of successful juvenile recruitment followed by periods of low juvenile survivorship.

We hypothesized that juvenile abundances would decline with decreasing forest cover and increasing levels of anthropogenic land cover within the watershed (Hypothesis 2). The trend of widespread suppressed abundances in the lower South Umpqua River (where anthropogenic land use is greatest) supports this hypothesis. However, because both juveniles and adults occur in low numbers in the lower river, the relative proportion of juveniles within the population may actually be higher than in mussel aggregations in the upper South Umpqua River or Cow Creek. Successful recruitment of juvenile *M. falcata* is still occurring in the lower South Umpqua River, but altered habitat conditions may not be able to support large aggregations of mussels or may have increased mortality rates for this species.

VI: DISCUSSION

The distribution and abundance of freshwater mussel species in the South Umpqua River basin, as with most river basins in the PNW, was largely unknown prior to our study despite the important ecological function mussels provide and their imperiled status. We found widespread suppression of *M. falcata* abundances in the lower South Umpqua River that were concomitant with high abundances of Asian clams (*C. fluminea*), an invasive species that was previously undocumented in the basin. In addition, *Margaritifera* was the only genera present at the downstream sites BKY01 – BKY04. This is despite the fact that gradient decreases and channel width widens with increasing drainage basin area, so hydraulically suitable habitats for mussels should be greater in the lower river. Although historical evidence is limited, all 3 mussel genera were historically found in the lower river and historic habitat conditions likely supported large, dense mussel beds. Although we found evidence of recent reproduction of *M. falcata* throughout the South Umpqua River and Cow Creek, the presence of juveniles does not necessarily indicate healthy populations because *M. falcata* are known to be hermaphroditic at low population densities. The strongest predictor variable of mussel abundances was the percentage of forest within the drainage basin area of a site, indicating that the cumulative impacts of anthropogenic land use may be contributing to degraded aquatic habitat conditions for mussels within the basin. However, this study was not designed to determine which anthropogenic land uses are having the greatest negative impact. It is unclear at this time if the invasive Asian clam (*C. fluminea*) is also suppressing mussel abundances and species richness in the lower South Umpqua River either directly or indirectly through competition and habitat disturbance.

Mussel Distribution & Abundance:

We found a distinct pattern of decreasing mussel abundance and species richness with increasing contributing drainage basin area in the South Umpqua River. Mussel species richness is usually known to increase with drainage basin area, largely as a consequence of the increasing number of fish species that serve as their hosts (Strayer 1983; Watters 1992; Gangloff & Feminella 2007). Relatively few studies have assessed how mussel abundances change along a longitudinal gradient within a single river in the

PNW, and of these half of the rivers investigated are impacted by dams. On the undammed Middle Fk. and North Fk. John Day Rivers in Eastern Oregon, the relative abundance of *M. falcata* also declined downstream with increasing drainage basin area. However, this decline was balanced by increasing abundances of both *G. angulata* and *Anodonta sp.* in the downstream reaches of both rivers (Brim Box et al. 2006). In an 8-km section of the S. Fk. Eel River in Northern California, *M. falcata* were distributed throughout the study area and abundances were correlated with zones of low hydraulic stress during high flows, but *Anodonta californiensis* were only found in the farthest downstream 2-km (Howard & Cuffey 2003). In comparison with these studies, our finding of widespread low abundances of *M. falcata* within downstream reaches of the South Umpqua River and increasing species richness upstream appear to be unique.

Several studies have investigated trends of mussel distribution and abundance on dammed rivers in the PNW, although the applicability of comparing results between dammed and undammed systems is unknown. On the dammed Umatilla River in Eastern Oregon, both *Anodonta sp.* and *G. angulata* were concentrated at the farthest downstream sites and *M. falcata*, although historically present, was found to be extirpated (Brim Box et al. 2006). In Northern California, freshwater mussel abundances were assessed along a 250 km length of the Klamath River for which the upstream extent of the study area was immediately downstream of the Iron Gate Dam (Davis et al. 2013). *G. angulata* was the most widespread and abundant species, but abundances progressively decreased downstream from the dam. In contrast, *M. falcata* abundances increased with distance downstream alongside increasing levels of hydrologic variability. *Anodonta sp.* were only found immediately below the dam (Davis et al. 2013). In 2011, 52 transects were snorkeled for mussels along the 90-km Hanford Reach of the Columbia River. Only *Anodonta sp.* were present and the highest levels of mussel abundance were found within backwater habitats, as compared to medium to low densities in downstream reaches and low densities within upstream reaches (Mueller et al. 2011). *M. falcata* were historically present in the study area but were determined to have been extirpated.

Juvenile *M. falcata* mussels ≤ 3.0 cm were present at each sampled bed location and indicate that recent reproduction has occurred in each population in Cow Creek and the lower and upper South Umpqua River. The large mussel bed in the upper South

Umpqua River at site TIL05 is similar to other large *M. falcata* beds that occupy hydrologically stable habitat in that it is exceptionally dense with an age distribution skewed towards older individuals (Vannote & Minshall 1982). In such populations, competition between animals is high and, above some critical density threshold, adult densities can exert a negative impact on juvenile abundances (Hastie 2011). The large *M. falcata* bed at site TIL05 is likely a viable population because of its large size, high densities, and recent and sustained recruitment of juveniles that has resulted in a population structure with animals within all length categories. However, repeat demography surveys in 5 – 10 years' time can confirm whether this population is viable despite having a small percentage of juveniles overall (Hastie & Toy 2008). If the population is viable, it represents a large and stable source population that should be of the highest conservation priority given the trends of suppressed abundance lower in the river. In contrast, the *M. falcata* bed in Cow Creek has an approximately normal distribution and the population is relatively young, which can indicate that this location is periodically scoured by high flows (Vannote & Minshall 1982).

Evidence of recent juvenile recruitment in the lower South Umpqua River is indicative that *M. falcata* are successfully reproducing despite their widespread low abundances. While most unionoidean mussels are gonochoristic and successful reproduction is reliant on localized high densities within aggregations (McMahon & Bogan 2001; Downing et al. 1993), *M. falcata* mussels are capable of self-fertilization and may do so at increased rates at low population densities when outcrossing is not possible and populations are isolated (Mock et al. 2013). As inbreeding and hermaphroditism increase in a population, allelic richness declines (Mock et al. 2013). If hermaphroditism is common in the lower river, inbreeding could be reducing fitness in these populations and making them increasingly unable to adapt to changing instream conditions. In the *M. falcata* bed in the lower South Umpqua River at site BKY01, we found more recently dead mussels (n = 11) than live mussels (n = 8) in sampling units and dead mussels were all greater than 6 cm in shell length. This may suggest increased rates of mortality for adult mussels in the lower South Umpqua River, but more research into the demographic parameters for populations are needed. The overall lack of high abundance aggregations in the lower South Umpqua River is cause for concern,

especially if freshwater mussel abundances have declined from historical levels. Freshwater mussels can be both a keystone species when they occur at high abundances and an indicator species when their populations decline. Declining mussel populations in the lower river could equate to both the loss of ecosystem function and deteriorating water quality and habitat conditions.

There is evidence to support the conclusion that *M. falcata*, *G. angulata*, and *Anodonta sp.* were historically present in the lower South Umpqua River, and it is reasonable to assume that at least *M. falcata* used to occur in high abundance aggregations. The Western Freshwater Mussel Database (Xerces / CTUIR 2018) contains historic records dating from between 1927 – 1963 for all 3 genera, although these records provide no indication of abundance. Records are sourced to the lower South Umpqua River near Roseburg and downstream from the Cow Creek confluence near Myrtle Creek (and our BKY05 field site). In addition, one longtime landowner recounted playing in a large mussel bed at the BKY03 field site near where their family would ford the river prior to the Booth Hill Bridge construction in 1965. Other than the cumulative impact from anthropogenic land uses, instream habitat conditions in the lower reaches of the South Umpqua River seem suitable for mussels: there are species appropriate host fish, widely abundant sand and gravel substrate, and on average a lower gradient and wider active channel resulting in lower levels of hydraulic stress. Anthropogenic land use change may be contributing to suppressed mussel abundances in habitats that were otherwise suitable for supporting dense aggregations of mussels in the lower South Umpqua River.

Effects of Land Use:

We found a significant positive relationship between the percentage of forest at the drainage basin scale and mussel aggregation abundance in support of our hypothesis that land use structures freshwater mussel abundances within the basin. In the South Umpqua River basin, land that is not forested is overwhelmingly in an anthropogenically derived use category such as timber harvest, agriculture, grazing, or various intensities of development. As the percentage of forested land cover in the drainage basin increases, the percentage of anthropogenic land uses and their cumulative impact on instream conditions decreases. Previous studies have documented negative impacts on mussel

abundances and species richness due to increasing levels of agricultural production (Poole & Downing 2004; Hornbach et al. 2019), urbanization (Nobles & Zhang 2015; Gillis et al. 2017), or combinations of land use change categories (Gangloff & Feminella 2007). In some study basins, geological variables overwhelmed the influences of land use (McRae et al. 2004), but differences in geology are unlikely to account for variation in our study because all sites were located within the Klamath Mountains Geomorphic Province. While mussel abundances were uniformly suppressed in the lower South Umpqua River, the upper portion of the river had the potential to host either high or low abundance aggregations. Land use may be constraining mussel abundances above some critical threshold of alteration, below which other ecological constraints that we did not measure are structuring trends of distribution and abundance.

Perhaps paradoxically, we also found a significant positive relationship between the percentage of timber harvest within the smaller HUC12 subwatershed surrounding a site and mussel aggregation abundance. Although the percent of forest and timber harvest at the drainage basin scale were highly negatively correlated (-0.931), the strength of this correlation did not carry through to the HUC12 subwatershed scale. However, there was a slightly positive correlation between the percentage of forest at the drainage basin scale and the percentage of timber harvest at the HUC12 scale (0.297). While this correlation was below the minimum threshold of +/-0.80 and therefore the variables were treated as independent, it is possible that the positive correlation between drainage basin forest cover and HUC12 timber harvest is at least partially responsible for the significant positive relationship between mussel abundance and HUC12 percent timber harvest in the final model. Our model could be improved by including more sites within the various HUC12 units in the basin so that all HUC12 units are included and have relatively even number of sites within them.

It is also possible that the impacts from timber harvest have not yet resulted in population declines in nearby mussel aggregations because there is often a time lag between environmental degradation and population level impacts. This is because the processes that link land use to instream degradation are temporally driven by season and precipitation events, and the full impact of adjacent land uses may not be realized until one or more exceptionally high precipitation events occurs. *M. falcata* can have

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extraordinarily long lifespans of 100+ years, and relatively recent habitat degradation may set up an extinction debt phenomenon in which degradation negatively affects a population's ability to reproduce (Tilman et al. 1994). Impacted populations do not go extinct until sometime in the future when relic individuals eventually die. We delineated the timber harvest land use category from the National Land Cover Database's herbaceous and shrub scrub land cover types (Dewitz 2019), which are only present on the landscape immediately after harvest and before replanted trees grow large enough to obtain a closed canopy. Therefore, the timber harvest classification in our analysis represents relatively recent timber harvest activity on the landscape and insufficient time may have elapsed for impacts to manifest in nearby instream habitats.

In our study, we located 4 mussel aggregations with greater than 1,000 animals and 3 of these were found within the HUC12 unit with the highest levels of timber harvest on the South Umpqua River (Figure 3, Panel C). Recent and widespread logging activity in this upper portion of the South Umpqua River may be setting the stage for population declines in dense, established mussel aggregations that have existed for many decades if not centuries. It is of high importance that baseline demographic parameters such as density, demographic age structure, and mortality are collected for the other large *M. falcata* beds in the upper South Umpqua River that are suitable candidates for sampling and that beds are re-assessed periodically to determine how their populations are changing over time. The extant large beds of *M. falcata* mussels in the upper South Umpqua River may represent the last remaining source populations of mussels and should therefore be of the highest conservation concern (Vannote & Minshall 1982).

Effects of Stream Power:

We found a significant negative relationship between mussel abundances and the reach-level Q_{10} specific stream power value in the South Umpqua River basin. The fact that stream power appears as a significant variable in the model but does not appear to explain patterns of measured mussel abundance suggests that stream power is important in this system but was not measured at the correct scale to capture the full range of variability present. Recent research correlating mussel distributions and abundances to hydraulic forces have generally focused on measuring shear stress values at much smaller spatial scales than in our study, including along channel cross sections (Gangloff &

Feminella 2007), at the 1-m scale for an entire 1.25 km study reach (May & Pryor 2016), and within 0.25 m^2 sampling units (Randklev et al. 2019). One study calculated generalized shear stress values for reaches 50 m in length and found that average shear stress values within reaches with mussels were significantly lower than in reaches without mussels, but that this value was not useful in predicting mussel densities within aggregations (Stone et al. 2004). Howard and Cuffey modeled hydraulic variables at multiple discharge levels at the patch, reach, and catchment scale for an entire 8-km segment of the S. Fk. Eel River in N. California and found that the highest mussel abundances at all scales were partitioned into areas of lower boundary shear stress and lower velocities during peak flows (2003). We intentionally calculated a reach-scale estimate of hydraulic stress because we wanted to explore the potential to use it as a predictive tool to guide future mussel surveys in the basin. Because we measured stream power at the reach scale, we were unable to capture how finer scale hydraulic forces may be structuring mussel abundances.

While completing site assessments for the high stream power and high mussel abundance sites (TIL04 & TIL06) we observed that mussels were only located in areas that would provide refuge from high flows. Mussels at these sites were almost exclusively found densely packed on the downstream end of large angular boulders that are too large for the river to move during even very large peak flow events. The angular boulders are likely remnants of road construction of the Tiller-Trail Highway that hugs the river closely at both locations. Abundant mussel aggregations at these locations provides evidence that moderately large mussel beds can exist within refuge habitats in stream reaches that otherwise experience high levels of hydraulic stress. In addition, any efforts to use a larger-scale estimate of hydraulic stress (i.e. stream power or shear stress) to identify reaches with high potential for hosting abundant aggregations of mussels will preclude the discovery of aggregations structured by patch scale dynamics within otherwise hydraulically stressful reaches. It is important that researchers match their questions to the scale of their variables, and our calculation of reach-level Q_{10} stream power was designed to assess differences in mussel abundances due to hydraulic conditions at the reach scale (100s of meters) and could not explain variability in abundances due to dynamics at the patch scale (centimeters to meters). Therefore, the

predictive power of the generalized Q_{10} stream power value is highly scale specific. While additional sites are needed to validify this relationship, this suggests that using a reach level measure of hydraulic stress to direct future mussel surveys may have some value.

Asian clams (*Corbicula fluminea*) & Freshwater Mussels:

Prior to the implementation of field surveys in the summer of 2018, we were unaware that invasive Asian clams (*Corbicula fluminea*) were present in the South Umpqua River. The USGS's Nonindigenous Aquatic Species Database did not contain any records of *C. fluminea* from within the basin, nor did any of the databases we sourced our sites from. Our observations while in the field prompted us to modify our site protocol to note whether *C. fluminea* were present at a site and provide a generalized indication of their relative abundance. *C. fluminea* abundances were highest at the sites in the lower South Umpqua River and progressively decreased upstream. Abundances of *C. fluminea* were low at the site in Pickett Park just upstream from the town of Canyonville, and clams were absent from sites farther upstream. No *C. fluminea* were seen at either site on Cow Creek. While systematically surveying the *M. falcata* mussel bed in the lower South Umpqua River (site BKY01), we counted the number of live *C. fluminea* found in the excavated substrate of 6 randomly selected quadrats throughout the bed. We counted an average of 183 clams per 0.25 m^2 quadrat, which equates to roughly 99,000 animals in the 135 m^2 bed area. In comparison, this mussel bed hosts approximately 40 native mussels. Our observations of high and moderate densities of *C. fluminea* in the South Umpqua River are concomitant with suppressed freshwater mussel abundances.

C. fluminea boast a number of generalist life history traits that make them well adapted to unstable habitats. These traits include their higher feeding efficiency (Boltovskoy et al. 1995), short live span of $1-5$ years with rapid growth and maturation (Strayer 1999b), hermaphroditic reproductive strategy with the potential for multiple reproductive events per year (McMahon & Bogan 2001), and ability to colonize a range of sediments including bare rock and silt (McMahon & Bogan 2001). *C. fluminea* have been shown to have increased locomotor activity as compared to native mussels, which may disrupt the stability of native mussels, especially during their sensitive juvenile life stage (Strayer 1999b). *C. fluminea* may also disproportionately impact juvenile mussels

by limiting food and space in the interstitial spaces of sediments where juvenile mussels remain buried (Yeager et al. 1994; Modesto et al. 2019). Especially dense populations of *C. fluminea* can even harm native mussel reproduction by consuming large quantities of sperm, glochidia, and newly metamorphosed juvenile mussels (Strayer 1999b). Where they co-occur, these life history traits may contribute to *C. fluminea* outcompeting native mussels, especially when they occur in high densities.

Although the potential clearly exists for *C. fluminea* to negatively impact native mussel populations, we could find no research from the PNW that investigated relationships between native mussels and invasive Asian clams. In the south central U.S., *C. fluminea* abundances were found to be negatively correlated with native mussel abundance at the patch scale (within 0.25 m^2 quadrats) but not at the larger reach scale (Vaughn & Spooner 2006b). The researchers hypothesized that the likelihood of successful *C. fluminea* invasion into native mussel beds declines as the density of native mussels increases. One paired field and laboratory study demonstrated that increasing densities of *C. fluminea* resulted in lower growth, physiological condition, and higher locomotor activity in the native mussel *Unio delphinus* (Ferreira-Rodríguez et al. 2018). Invasive *C. fluminea* may be outcompeting native mussels in the lower South Umpqua River for space and food resources. However, it is also possible that instream habitat conditions in the lower river are no longer adequate to support dense aggregations of native mussels, and that opportunistic *C. fluminea* are proliferating in these abandoned habitats. Research investigating the relationship between native mussels and invasive clams - in the PNW generally and the South Umpqua River basin in particular - is urgently needed, especially given that *C. fluminea* will likely continue expanding their range upstream into Cow Creek and the upper South Umpqua River.

Future Directions:

Future efforts should focus on surveying additional sites on both the South Umpqua River and Cow Creek to extend our findings within the basin. We sampled relatively few sites from within one geomorphic province of the river, and we did not sample sites on the South Umpqua River that were downstream from Winston or upstream from Tiller. In addition, we only sampled 2 sites from lower Cow Creek, so

additional surveys to assess distribution and abundance trends on this major tributary are needed. Surveys on the lower South Umpqua River (below Canyonville) should be conducted as early in the summer as flows permit because dense mats of aquatic algae obscure the channel bed later in the season and make visual identification of mussels at the substrate surface impossible in some areas.

We located and systematically sampled one *M. falcata* bed and one *Anodonta sp.* bed during the summer of 2018; these efforts provided evidence that successful juvenile recruitment is occurring for at least one population per species in the upper river. These mussel beds should be re-sampled in the near future to assess how populations are changing over time. Re-sampling of populations should be completed with the goal of eventually being able to determine population growth rates at each bed location, which would enable resource managers to complete population viability analysis. Population viability analysis would enable resource managers to make well-informed restoration and conservation decisions based on future population trajectories. Based on their life spans and unique reproductive biology, we recommend resampling *M. falcata* beds every 5 – 10 years and resampling *Anodonta sp.* beds every 2 – 4 years. We documented at least 3 additional high-density *M. falcata* beds (sites TIL02, TIL04, and TIL06) and 1 additional *Anodonta sp.* bed (site TIL02) in the upper South Umpqua River during our summer 2020 site assessments. We recommend that systematic sampling of these additional populations should be undertaken as soon as possible to document baseline demographic conditions and assess whether successful juvenile recruitment is happening within multiple populations in the upper South Umpqua River. Mussel beds in the upper South Umpqua River should be actively monitored and protected as they are likely viable source populations for both *M. falcata* and *Anodonta sp.*.

We recommend modifying our survey protocol for sampling mussel beds in several ways. Firstly, we recommend determining whether to census or systematically sample a mussel bed based on the number of animals counted in the preliminary bed survey and not based on bed size. The goal of sampling at least 50 animals per bed should remain, but choosing the correct sampling method to achieve this minimum count should be based on mussel density within the bed. For example, systematically sampling a high density mussel bed that occupies less than 50 m^2 of channel bed would be less time

consuming and less intrusive while still yielding the desired minimum sample size. In contrast, extremely low density mussel beds (such as the *M. falcata* bed at site BKY01) may require census sampling to produce the minimum sample size despite occupying more than 50 m^2 of the channel bed. Secondly, we recommend tagging sampled mussels during systematic survey efforts. While this effort would result in additional survey time, it would permit interesting analysis in the future including the assessment of whether handling results in increased mortality. Thirdly, we recommend that surveyors lethally collect at least one *Anodonta sp.* specimen from surveyed populations to determine species level identification.

Before sampling any mussel beds we recommend understanding the scale at which hydraulic forces structure the population. Our observations while in the field suggest that at some locations the process of sampling the bed may irrevocably impact the mussels and their habitat. Mussel beds that occurred within low stream power reaches (i.e. those at the TIL02 and TIL05 sites) extended into the channel towards the stream's thalweg. In these locations, a greater area of the streambed was suitable for mussel establishment and persistence. In comparison, mussel beds at the high stream power sites (i.e. at the TIL04 and TIL06 sites) were relegated to pockets of suitable habitat behind large boulders and most areas of the streambed were devoid of mussels. Although we did not explicitly measure water velocity, it seemed clear that velocities were considerably higher at the high stream power sites as we had to frequently cling to large boulders while surveying to avoid being flushed downstream despite the river being at extremely low flow conditions. Based on our observations, the process of briefly snorkeling above the high density pockets of mussels at the high stream power sites changed water currents sufficiently to cause localized transport of fine sand and gravel sediments from behind the large boulders. Therefore, the extended process of systematically sampling a bed whose stability is dominated by highly localized conditions is likely a habitat disruption with the potential to significantly threaten the population. Therefore, we recommend that systematically sampling mussel beds, especially with any excavation of sediments, should only be completed on beds occupying larger areas of hydraulically stable habitat.

Our survey efforts revealed widespread suppression of freshwater mussel abundances in the lower South Umpqua River. We were unable to make definitive

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conclusions about the cause(s) of low mussel abundances in the lower river, and we recommend that future research investigate the relationship between invasive Asian clams (*Corbicula fluminea*) and native mussels. Regardless of the exact reason, it seems unlikely that current conditions could support additional native mussels even if they were to be intentionally propagated and re-introduced. Therefore, we recommend that management efforts in the lower South Umpqua River downstream from Canyonville should be focused on reducing the impact of anthropogenic land use, primarily by increasing the width and condition of riparian buffers. Because the majority of land in the lower river is privately held, this will take a coordinated effort between private landowners, the watershed council (Partnership for Umpqua Rivers), and local management agencies. At present, awareness of the presence and importance of freshwater mussel species is lacking even for aquatic resource managers let alone for the general public. Therefore, a targeted education and outreach campaign will likely need to proceed any efforts to compel private landowners to change their land management practices for the benefit of freshwater mussels.

SUPPLEMENTAL FIGURES:

Table 3: Characteristics of mussel aggregations in the South Umpqua River basin, including the aggregation (Agg.) ID, observation (Obs.) type, total count of mussels within each aggregation, approximate area (m^2) of the aggregation, latitude, longitude, datum used to collect GPS information, and species (western pearlshell and western ridged) or clade (floater) specific counts. The first 5 characters of each aggregation ID indicates the site location. Observation type indicates whether aggregations were further sampled via systematic sampling or with a 30 minute timed counting effort. Visual observation refers to aggregations found within the course of a site assessment for which surveyor's increased their search effort within the local area but did not further quantify search efforts. The minimum area assigned to aggregations of 1 animal was 0.25 m^2.

Agg. ID	Obs. Type	Total Count	Area	Latitude	Longitude	Datum	Species Abundances Western Pearlshell	Floater	Western Ridged
BKY0101	systematic sample	40	120.00	43.07927	-123.3882	WGS84	40	0	0
BKY0102	visual	5	15.00	43.08073	-123.3864	WGS84	5	0	0
BKY0103	visual	2	60.00	43.07939	-123.3873	WGS84	2	0	0
BKY0201	visual	4	7.50	43.07161	-123.3712	WGS84	4	0	0
BKY0301	visual	9	75.00	43.06412	-123.3575	WGS84	9	0	0
BKY0302	visual	2	30.00	43.06336	-123.3573	WGS84	2	0	0
BKY0303	visual	4	200.00	43.06244	-123.3540	WGS84	4	0	0
BKY0304	visual	12	210.00	43.06369	-123.3521	WGS84	12	0	0
BKY0401	visual	1	0.25	43.04873	-123.3283	WGS84	1	0	0
BKY0402	visual	2	10.00	43.04727	-123.3287	WGS84	2	0	0
BKY0403	visual	1	0.25	43.04641	-123.3292	WGS84	1	0	0
BKY0404	visual	2	0.25	43.04546	-123.3296	WGS84	2	0	0
BKY0501	visual	1	0.25	42.97218	-123.3459	NAD83	0	1	0
BKY0502	visual	2	NA	42.97129	-123.3452	NAD83	2	0	0
BKY0503	visual	1	0.25	42.97030	-123.3450	NAD83	1	0	0
BKY0504	visual	1	0.25	42.97117	-123.3451	NAD83	1	0	0
BKY0505	visual	4	0.25	42.97049	-123.3446	NAD83	4	0	0
BKY0506	visual	1	0.25	42.97503	-123.3474	NAD83	0	1	0
BKY0507	visual	1	0.25	42.97510	-123.3470	NAD83	1	0	0
BKY0508	visual	1	0.25	42.97380	-123.3471	NAD83	1	0	0
TIL0101	visual	1	0.25	42.94022	-123.2662	NAD83	0	1	0
TIL0102	visual	3	6.00	42.94031	-123.2654	NAD83	2	1	0
TIL0103	visual	3	6.00	42.94034	-123.2653	NAD83	2	1	0
TIL0104	visual	2	2.00	42.94029	-123.2651	NAD83	2	0	0
TIL0105	visual	2	0.50	42.94024	-123.2651	NAD83	0	2	0
TIL0106	visual	47	90.00	42.94049	-123.2647	NAD83	44	0	3

Agg. ID	Obs. Type	Total Count	Area	Latitude	Longitude	Datum	Species Abundances		
							Western Pearlshell	Floater	Western Ridged
TIL0201	visual	2	10.00	42.95972	-123.1758	NAD83	1	1	0
TIL0202	visual	1	0.25	42.95959	-123.1761	NAD83	1	0	0
TIL0203	visual	1	0.25	42.95987	-123.1762	NAD83	1	0	0
TIL0204	timed search	1600	1600.00	42.95951	-123.1764	NAD83	1594	1	5
TIL0205	timed search	944	735.00	42.95853	-123.1759	NAD83	2	942	0
TIL0206	visual	69	150.00	42.95745	-123.1762	NAD83	2	68	0
TIL0207	visual	8	0.50	42.95864	-123.1765	NAD83	5	0	1
TIL0208	visual	36	10.00	42.95886	-123.1766	NAD83	36	0	0
TIL0301	systematic sample	364	52.50	42.93426	-123.0387	WGS84	0	364	0
TIL0302	visual	1	0.25	42.93349	-123.0379	WGS84	1	0	0
TIL0401	visual	1348	1950.00	42.94368	-123.0112	NAD83	1347	1	0
TIL0402	visual	50	120.00	42.94452	-123.0095	NAD83	50	0	0
TIL0501	systematic sample	86978	931.84	42.93944	-123.0024	WGS84	86978	0	0
TIL0502	visual	60	2.50	42.94003	-123.0033	WGS84	60	0	0
TIL0601	visual	2	3.00	42.93782	-122.9930	NAD83	1	1	0
TIL0602	timed search	3114	115.00	42.93765	-122.9923	NAD83	3114	0	0
TIL0603	visual	350	25.00	42.93738	-122.9921	NAD83	350	0	0
TIL0604	visual	5	10.00	42.93662	-122.9918	NAD83	0	5	0
COW0101	systematic sample	112	43.00	42.89284	-123.5347	WGS84	112	0	0
COW0102	visual	1	0.25	42.89189	-123.5352	WGS84	1	0	0
COW0103	visual	1	0.25	42.88960	-123.5377	WGS84	1	0	0
COW0104	visual	1	0.25	42.89333	-123.5335	WGS84	0	1	0
COW0201	visual	2	0.50	42.86585	-123.5789	WGS84	2	0	0

Table 4: Characteristics of mussel site locations in the South Umpqua River basin including site ID, location within the basin, survey length (km) completed in the field, reach length (km) used for the stream power analysis, slope gradient, average (Av.) width (m), the drainage basin (D.B.) area (mi^2), the HUC12 area (mi^2), the 10-year peak flow (Q_{10}) discharge (m^3/s), the reach-level Q_{10} specific stream power (watts/m^2), the percent (Perc.) of forest within the drainage basin (D.B.), and the percent (Perc.) of timber harvest (T.H.) within the HUC12 subwatershed unit.

Site ID	Location	Survey Length (km)	Reach Length (km)	Slope Gradient	Av. Width (m)	D.B. Area (mi^2)	HUC12 Area (mi^2)	Q_{10} Discharge (m^3/s)	Q_{10} Stream Power	D.B. Perc. Forest	HUC12 Perc. T.H.
BKY01	Lower S. Umpqua	0.44	0.65	0.00130	133.0	1430	83.2	2775.1	265.8	70.9	38.7
BKY02	Lower S. Umpqua	1.13	0.80	0.00147	188.0	1410	83.2	2749.6	210.9	71.4	38.7
BKY03	Lower S. Umpqua	0.85	0.85	0.00080	170.2	1410	83.2	2749.6	123.7	71.4	38.7
BKY04	Lower S. Umpqua	0.90	0.90	0.00115	95.0	1410	83.2	2749.6	325.4	71.6	38.7
BKY05	Lower S. Umpqua	0.88	0.88	0.00111	85.0	1270	41.5	2537.2	323.7	72.3	32.1
TIL01	Upper S. Umpqua	0.29	0.78	0.00191	87.4	699	77.3	1393.2	298.6	75.1	22.1
TIL02	Upper S. Umpqua	0.62	0.65	0.00046	93.3	643	50.5	1308.2	85.9	76.5	29.5
TIL03	Upper S. Umpqua	0.47	0.54	0.00258	91.2	571	35.0	1118.5	293.7	79.4	45.4
TIL04	Upper S. Umpqua	0.37	0.67	0.00322	74.2	565	35.0	1107.2	470.4	79.4	45.4
TIL05	Upper S. Umpqua	0.26	0.63	0.00083	63.0	564	35.0	1104.4	142.3	79.4	45.4
TIL06	Upper S. Umpqua	0.52	0.58	0.00500	78.3	545	35.0	1056.2	655.4	79.2	45.4
COW01	Cow Cr.	0.95	0.59	0.00029	66.1	474	33.6	1019.4	29.0	70.6	29.7
COW02	Cow Cr.	0.43	0.67	0.00330	64.4	394	51.6	957.1	440.0	70.8	47.3
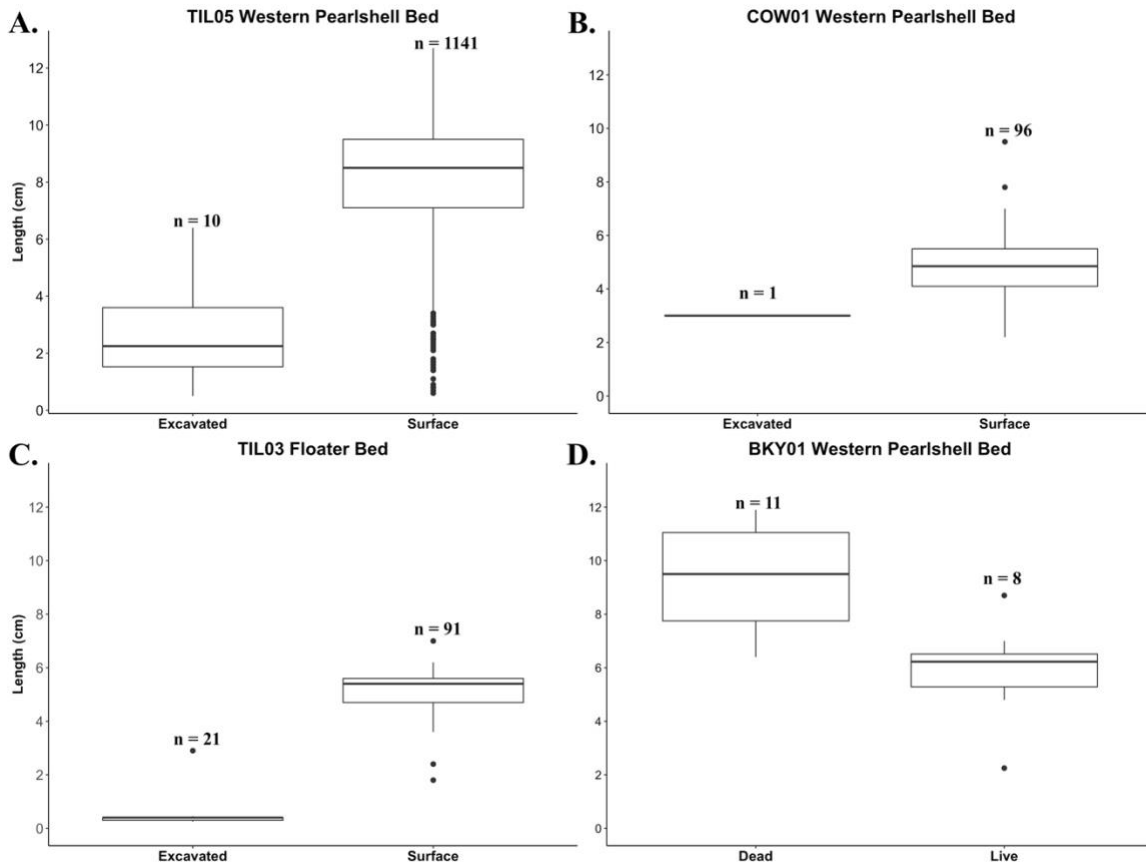
Figure 6: Comparison of mean lengths of live mussels located in excavated substrate versus at the bed surface for **(A)** the western pearlshell (*M. falcata*) bed sampled at the TIL05 site in the upper S. Umpqua R., **(B)** the *M. falcata* bed sampled at the COW01 site in Cow Cr., **(C)** the floater (*Anodonta sp.*) bed sampled at the TIL03 site in the upper S. Umpqua R., and **(D)** the comparison of mean lengths of dead mussels as compared to live mussels found within all sampling quadrats at the BKY01 *M. falcata* bed on the lower S. Umpqua R.

REFERENCES CITED:

Adair B, Miller S. 2010. Critical uncertainties for native freshwater mussels (Bivalvia : Unionidae) in the Pacific Northwest. Pacific Northwest Native Freshwater Mussel Workgroup.

Anim DO, Fletcher TD, Vietz GJ, Pasternack GB, Burns MJ. 2018. Effect of urbanization on stream hydraulics. River Research and Applications **34**:661–674.

Arbuckle KE, Downing JA. 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Canadian Journal of Fisheries and Aquatic Sciences **59**:310–316.

Baldwin C. 2019. Personal communication. U.S. Forest Service Tiller Ranger District, Fish Biologist.

Barnhart MC, Haag WR, Roston WN. 2008. Adaptations to host infection and larval parasitism in Unionoida. Journal of the North American Benthological Society **27**:370–394.

Binkley D, Ice GG, Kaye J, Williams CA. 2004. Nitrogen and phosphorus concentrations in forest streams of the United States. Journal of the American Water Resources Association **40**:1277–1291.

Blevins E, Jepsen S, Box JB, Nez D, Howard J, ... 2017. Extinction risk of western North American freshwater mussels: Anodonta Nuttalliana, the Anodonta Oregonensis …. Freshwater Mollusk Biology and Conservation **20**:71–88.

Blevins E, McMullen L, Jepsen S, Blackburn M, Code A, Hoffman Black S. 2018. Conserving the gems of our waters. Portland, OR.

Bolstad P V., Swank WT. 1997. Cumulative impacts of landuse on water quality in a southern appalachian watershed. Journal of the American Water Resources Association **33**:519–533.

Boltovskoy D, Izaguirre I, Correa N. 1995. Feeding selectivity of Corbicula fluminea (Bivalvia) on natural phytoplankton. Hydrobiologia **312**:171–182.

Brim Box J, Mossa J. 1999. Sediment, land use, and freshwater mussels: Prospects and problems. Journal of the North American Benthological Society **18**:99–117.

Brim Box J, Howard J, Wolf D, O'Brien C, Nez D, Close D. 2006. Freshwater mussels (Bivalvia: Unionoida) of the Umatilla and Middle Fork John Day Rivers in eastern Oregon. Northwest Science **80**:95–107.

Castelle AJ, Johnson AW, Conolly C. 1994. Wetland and stream buffer size requirements - a review. Journal of Environmental Quality **23**:878–882.

Černá M, Simon OP, Bílý M, Douda K, Dort B, Galová M, Volfová M. 2018. Within-river variation in growth and survival of juvenile freshwater pearl mussels assessed by in situ exposure methods. Hydrobiologia **810**:393–414.

Davis EA, David AT, Norgaard KM, Parker TH, McKay K, Tennant C, Soto T, Rowe K, Reed R. 2013. Distribution and abundance of freshwater mussels in the mid Klamath subbasin, California. Northwest Science **87**:189–206. Available from http://www.bioone.org/doi/abs/10.3955/046.087.0303.

Degerman E, Andersson K, Söderberg H, Norrgrann O, Henrikson L, Angelstam P, Törnblom J. 2013. Predicting population status of freshwater pearl mussel (Margaritifera margaritifera, L.) in central Sweden using instream and riparian zone land-use data. Aquatic Conservation: Marine and Freshwater Ecosystems **23**:332–342.

Dewitz J. 2019. National land cover database (NLCD) 2016 products: U.S. Geological Survey data release. Available from http://doi.org/10.5066/P96HHBIE.

Di Maio J, Corkum LD. 1995. Relationship between the spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. Canadian Journal of Zoology **73**:663–671.

DOGAMI. n.d.. Oregon Department of Geology and Mineral Industries LiDAR program airborne LiDAR survey. Oregon Department of Geology and Mineral Industries (DOGAMI). Available from https://gis.dogami.oregon.gov/maps/lidarviewer/. Accessed December 2019.

Downing JA, Rochon Y, Pérusse M, Harvey H. 1993. Spatial aggregation, body size, and reproductive success in the freshwater mussel Elliptio complanata. Journal of the North American Benthological Society **12**:148–156.

Duncan N, Furnish J, Monthey R, Applegarth J. 2008. Survey protocol for aquatic mollusk species: preliminary inventory & presence/absence sampling. USDA Forest Service & USDI Bureau of Land Management.

Duncan N. 2006. Mussel survey techniques and results of 2006 surveys in the Umpqua basin, Douglas County, OR. Roseburg District Bureau of Land Management.

Ferreira-Rodríguez N, Sousa R, Pardo I. 2018. Negative effects of Corbicula fluminea over native freshwater mussels. Hydrobiologia **810**:85–95.

Gangloff MM, Feminella JW. 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, U.S.A. Freshwater Biology **52**:64–74.

Ganser AM, Newton TJ, Haro RJ. 2015. Effects of elevated water temperature on physiological responses in adult freshwater mussels. Freshwater Biology **60**:1705–1716.

García L, Cross WF, Pardo I, Richardson JS. 2017. Effects of landuse intensification on stream basal resources and invertebrate communities. Freshwater Science **36**:609–625.

Gatenby CM, Neves RJ, Parker BC. 1996. Influence of sediment and algal food on cultured juvenile freshwater mussels. Journal of the North American Benthological Society **15**:597–609.

Geyer NA. 2003. Lower Cow creek watershed assessment and action plan. Prepared for the Umpqua Basin Watershed Council, Roseburg, OR.

Gillis PL, McInnis R, Salerno J, de Solla SR, Servos MR, Leonard EM. 2017. Freshwater mussels in an urban watershed: Impacts of anthropogenic inputs and habitat alterations on populations. Science of the Total Environment **574**:671–679. Elsevier B.V. Available from http://dx.doi.org/10.1016/j.scitotenv.2016.09.110.

Grant GE, Lewis SL, Swanson FJ, Cissel JH, McDonnell JJ. 2008. Effects of forest practices on peak flows and consequent channel response: A state-of-science report for western Oregon and Washington. General Technical Report PNW-GTR-760. Available from http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.157.4363&rank=3.

Ha H, Stenstrom MK. 2003. Identification of land use with water quality data in stormwater using a neural network. Water Research **37**:4222–4230.

Haag WR, Williams JD. 2014. Biodiversity on the brink: An assessment of conservation strategies for North American freshwater mussels. Hydrobiologia **735**:45–60.

Hansen AT, Czuba JA, Schwenk J, Longjas A, Danesh-Yazdi M, Hornbach DJ, Foufoula-Georgiou E. 2016. Coupling freshwater mussel ecology and river dynamics using a simplified dynamic interaction model. Freshwater Science **35**:200–215. Available from http://www.jstor.org/stable/10.1086/684223.

Hastie LC, Toy KA. 2008. Changes in density, age structure and age-specific mortality in two western pearlshell (Margaritifera falcata) populations in Washington (1995-2006). Aquatic Conservation: Marine and Freshwater Ecosystems **18**:671–678.

Hastie LC. 2011. Are Scottish freshwater pearl mussel populations recruiting normally? Toxicological and Environmental Chemistry **93**:1748–1763.

Havel JE, Kovalenko KE, Thomaz SM, Amalfitano S, Kats LB. 2015. Aquatic invasive species: challenges for the future. Hydrobiologia **750**:147–170.

Heard WH. 1975. Sexuality and other aspects of reproduction in Anodonta (Pelecypoda: Unionidae). Malacologia **15**:81–103.

Hornbach DJ, Stutzman HN, Hove MC, Kozarek JL, MacGregor KR, Newton TJ, Ries PR. 2019. Influence of surrounding land-use on mussel growth and glycogen levels in the St. Croix and Minnesota River Basins. Hydrobiologia. Springer International Publishing.

Howard JK, Cuffey KM. 2003. Freshwater mussels in a California North Coast Range river: occurrence, distribution, and controls. Journal of the North American Benthological Society **22**:63–77.

Howard JK, Cuffey KM. 2006a. The functional role of native freshwater mussels in the fluvial benthic environment. Freshwater Biology **51**:460–474.

Howard JK, Cuffey KM. 2006b. Factors controlling the age structure of Margaritifera falcata in 2 northern California streams. J. N. Am. Benthol. Soc. **25**:677–690.

Kunz JL, Brunson EL, Barnhart MC, Glidewell EA, Wang N, Ingersoll CG. 2020. Pulsed flow-through auto-feeding beaker systems for the laboratory culture of juvenile freshwater mussels. Aquaculture **520**. Elsevier.

Layzer JB, Madison LM. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. Regulated Rivers: Research & Management **10**:329–345.

Lenat DR, Crawford JK. 1994. Effects of land use on water quality and aquatic biota of three North Carolina Piedmont streams. Hydrobiologia **294**:185–199.

López-Rodríguez MJ, Márquez Muñoz C, Ripoll-Martín E, Tierno de Figueroa JM. 2019. Effect of shifts in habitats and flow regime associated to water diversion for agriculture on the macroinvertebrate community of a small watershed. Aquatic Ecology **53**:483–495.

Lummer EM, Auerswald K, Geist J. 2016. Fine sediment as environmental stressor affecting freshwater mussel behavior and ecosystem services. Science of the Total Environment **571**:1340–1348. Elsevier B.V. Available from http://dx.doi.org/10.1016/j.scitotenv.2016.07.027.

Mageroy J. 2014. Rocky mountain ridged mussel (Gonidea angulata) in the Okanagan Valley, BC: Final report on juvenile recruitment, host fish field sampling, and the impact of rototilling against Eurasian watermilfoil (Myriophyllum spicatum). Kelowna, BC.

Mallin MA, Johnson VL, Ensign SH. 2009. Comparative impacts of stormwater runoff on water quality of an urban, a suburban, and a rural stream. Environmental Monitoring and Assessment **159**:475–491.

May CL, Pryor BS. 2016. Explaining spatial patterns of mussel beds in a northern California river: The role of flood disturbance and spawning salmon. River Research and Applications **32**:776–785.

Mcmahon RF, Bogan AE. 2001. Mollusca: Bivalvia. Pages 331–429 in J. P. Thorp and A. P. Covich, editors. Ecology and classification of North American freshwater invertebrates. Academic Press.

McRae SE, Allan JD, Burch JB. 2004. Reach- and catchment-scale determinants of the distribution of freshwater mussels (Bivalvia: Unionidae) in south-eastern Michigan, U.S.A. Freshwater Biology **49**:127–142.

Mock KE, Brim Box JC, Chong JP, Furnish J, Howard JK. 2013. Comparison of population genetic patterns in two widespread freshwater mussels with contrasting life histories in western North America. Molecular Ecology **22**:6060–6073.

Modesto V, Castro P, Lopes-Lima M, Antunes C, Ilarri M, Sousa R. 2019. Potential impacts of the invasive species Corbicula fluminea on the survival of glochidia. Science of the Total Environment **673**:157–164. Elsevier B.V. Available from https://doi.org/10.1016/j.scitotenv.2019.04.043.

Moore AP, Bringolf RB. 2018. Effects of nitrate on freshwater mussel glochidia attachment and metamorphosis success to the juvenile stage. Environmental Pollution **242**:807–813. Elsevier Ltd. Available from https://doi.org/10.1016/j.envpol.2018.07.047.

Morris TJ, Corkum LD. 1996. Assemblage structure of freshwater mussels (Bivalvia: Unionidae) in rivers with grassy and forested riparian zones. Journal of the North American Benthological Society **15**:576–586.

Mueller RP, Tiller BL, Bleich MD, Turner GK, Welch ID. 2011. Assessment of the species composition, densities, and distribution of native freshwater mussels along the Benton County shoreline of the Hanford Reach, Columbia River, 2004. Pacific Northwest National Laboratory. Prepared for the U.S. Department of Energy, Richland, WA.

National Research Council. 2008. Hydrologic effects of a changing forest landscape. The National Academies Press, Washington, DC. https://doi.org/10.17226/12223.

Nedeau EJ, Smith AK, Stone J, Jepsen S. 2009. Freshwater mussels of the Pacific Northwest: 2nd edition. The Xerces Society, Portland.

Neves RJ, Widlak JC. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. American Malacological Bulletin **5**:1–7.

Nobles T, Zhang Y. 2015. Survival, growth and condition of freshwater mussels: Effects of municipal wastewater effluent. PLoS ONE **10**:1–19.

O'Brien C, Nez D, Wolf D, Brim Box J. 2013. Reproductive biology of Anodonta californiensis, Gonidea angulata, and Margaritifera falcata (Bivalvia:Unionoida) in the Middle Fork John Day River, Oregon. Northwest Science **87**:59–72.

Paul MJ, Meyer JL. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics **32**:333–365.

Poole KE, Downing JA. 2004. Relationship of declining mussel biodiversity to stream-reach and watershed characteristics in an agricultural landscape. Journal of the North American Benthological Society **23**:114–125.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Randklev CR, Hart MA, Khan JM, Tsakiris ET, Robertson CR. 2019. Hydraulic requirements of freshwater mussels (Unionidae) and a conceptual framework for how they respond to high flows. Ecosphere **10**:1–19.

Resh VH, Unzicker JD. 1975. Water quality monitoring and aquatic organisms: the importance of species identification. Journal of the Water Pollution Control Federation **47**:9–19.

Ries PR, Newton TJ, Haro RJ, Zigler SJ, Davis M. 2016. Annual variation in recruitment of freshwater mussels and its relationship with river discharge. Aquatic Conservation: Marine and Freshwater Ecosystems **26**:703–714.

Searles Mazzacano CA. 2017. Assessing a freshwater mussel population in the Norwood Island backchannel. CASM Environmental, LLC. Prepared for the Willamette Riverkeeper, Portland, OR.

Searles Mazzacano CA. 2018. Characterizing a Freshwater Mussel Shoal in the Willamette River in Eugene, Oregon, ~RM 180. CASM Environmental, LLC. Prepared for the Willamette Riverkeeper, Portland, OR.

Smith DR, Villella RF, Lemarie DP, von Oettingen S. 1999. How much excavation is needed to monitor freshwater mussels? Pages 203–218. Proceedings of the First Freshwater Mollusk Conservation Society Symposium.

Spooner DE, Vaughn CC. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. Freshwater Biology **51**:1016–1024.

Stone J, Barndt S, Gangloff M. 2004. Spatial distribution and habitat use of the western pearlshell mussel (Margaritifera falcata) in a western Washington stream. Journal of Freshwater Ecology **19**:341–352.

Strayer D. 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia, Unionidae) distribution in southeastern Michigan, U.S.A. Freshwater Biology **13**:253–264.

Strayer DL, Downing JA, Haag WR, King TL, Layzer JB, Newton TJ, Nichols SJ. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. BioScience **54**:429–439.

Strayer DL, Smith DR. 2003. A Guide to sampling freshwater mussel populations. American Fisheries Society.

Strayer DL. 1999a. Use of flow refuges by Unionid mussels in rivers. Journal of the North American Benthological Society **18**:468–476.

Strayer DL. 1999b. Effects of alien species on freshwater mollusks in North America. Journal of the North American Benthological Society **18**:74–98.

Taebi A, Droste RL. 2004. Pollution loads in urban runoff and sanitary wastewater. Science of the Total Environment **327**:175–184.

Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. Nature **371**:65–66.

Toy KA. 1998. Growth, reproduction and habitat preference of the freshwater mussel Margaritifera Margaritifera falcata in western Washington. University of Washington.

Turner D, Kasper B, Heberling P, Lindberg B, Wiltsey M, Arnold G, Michie R. 2006. Umpqua basin total maximum daily load (TMDL) and water quality management plan (WQMP). Oregon Department of Environmental Quality.

U.S. Environmental Protection Agency (EPA): Office of Water and Office of Research and Development. 2016. National rivers and streams assessment 2008-2009: A collaborative survey (EPA/84I/R-I6/007). Washington, DC. http://www.epa.gov/national-aquatic-resource-surveys/nrsa.

U.S. Geological Survey. n.d.. The StreamStats program version 4.4.0. Available from http://streamstats.usgs.gov. Accessed February 2020.

Valenti TW, Cherry DS, Currie RJ, Neves RJ, Jones JW, Mair R, Kane CM. 2006. Chlorine toxicity to early life stages of freshwater mussels (Bivalvia: Unionidae). Environmental Toxicology and Chemistry **25**:2512–2518.

Vannote RL, Minshall GW. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. Proceedings of the National Academy of Sciences of the United States of America **79**:4103–4107.

Vaughn CC, Hakenkamp CC. 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshwater Biology **46**:1431–1446.

Vaughn CC, Spooner DE. 2006a. Unionid mussels influence macroinvertebrate assemblage structure in streams. Journal of the North American Benthological Society **25**:691–700.

Vaughn CC, Spooner DE. 2006b. Scale-dependent associations between native freshwater mussels and invasive Corbicula. Hydrobiologia **568**:331–339.

Villella RF, Smith DR, Lemarié DP. 2004. Estimating survival and recruitment in a freshwater mussel population using mark- recapture techniques. The American Midland Naturalist **151**:114–133.

Wade J, Stephen C, Robertson C. 2020. Mapping rocky mountain ridged mussel beds with preliminary identification of overlapping Eurasian watermilfoil within the Canadian range. Nature Conservation **42**:19–31.

Wallick JR, O'Connor JE, Anderson S, Keith M, Cannon C, Risley JC. 2010. Channel change and bed-material transport in the Umpqua River basin, Oregon. U.S. Geological Survey Open-File Report 2010-1314, 135 p. and 3 appendices.

Walser CA, Bart HL. 1999. Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River System. Ecology of Freshwater Fish **8**:237–246.

Walsh CJ, Roy AH, Feminella JW, Cottingham PD, Groffman PM, Morgan RP. 2005. The urban stream syndrome: Current knowledge and the search for a cure. Journal of the North American Benthological Society **24**:706–723.

Watters GT. 1992. Unionids, fishes, and the species-area curve. Journal of Biogeography **19**:481–490.

Wilson TS, Sleeter BM, Sleeter RR, Soulard CE. 2014. Land-use threats and protected areas: A scenario-based, landscape level approach. Land **3**:362–389.

Xerces Society for Invertebrate Conservation (Xerces) and the Confederated Tribes of the Umatilla Indian Reservation Mussel Project (CTUIR). 2018. Western freshwater mussel database. Available at http://www.xerces.org/western-freshwater-mussels/. List of contributors available at: http://xerces.org/western-freshwater-mussel-database-contributors/.

Yeager M., Cherry DS, Neves RJ. 1994. Feeding and burrowing behaviors of juvenile rainbow mussels, Villosa iris (Bivalvia: Unionidae). Journal of the North American Benthological Society **13**:217–222.

Young M, Williams J. 1984. The reproductive biology of the freshwater pearl mussel Margaritifera margaritifera (Linn.) in Scotland. I: Field studies. Archiv für Hydrobiologie **99**:405–422.