

Freshwater Mussels of the Klamath River:
A Personal and Scientific Account

Cristine Tennant
Bachelor of Arts Candidate
Environmental Studies - Biology
May 2010

I present this thesis in two parts. The first half takes the form of a personal non-fiction essay, in which I describe my experience working with the Karuk Tribe on the Klamath River through the lens of my research on freshwater mussels. In the second half, I present the results of my scientific study on the population demographics of *Gonidea angulata* in the Mid-Klamath basin. I hope that both parts work together to demonstrate that the issues surrounding the current state of the Klamath River are not simply biological, political or sociological. Rather, a full understanding of the Klamath River and the people who call it home requires that one synthesize knowledge from many intellectual disciplines. Additionally, I hope that this thesis accurately presents the positive impact that my experiences on the Klamath have had on me as a student, biologist, environmentalist, and humanist.

Yôotva!

TABLE OF CONTENTS:

Preface..... 2

PART I: Sitting Sentinel..... 4

PART I: A population demographic analysis of *G. angulata*
in the Mid-Klamath Basin..... 19

 Abstract..... 19

 Introduction..... 20

 Freshwater Mussel Ecology..... 20

 Life Cycle and Host Fish Relationship..... 20

 Evaluating Age Structure from Mussel Shells..... 22

 Mussel Fauna of the West..... 23

 Cultural Importance of Freshwater Mussels..... 24

Gonidea angulata: The Western Ridged Mussel..... 26

 Research Goals and Objectives..... 27

 Methods..... 28

 Study Region..... 28

 Study Species..... 29

 Mussel Surveys..... 29

 Evaluating the Relationship Between Mussel Length and Age..... 30

 Results..... 31

 Discussion..... 32

 Mussel Size..... 32

 Mussel Age Distribution..... 33

 Further Research and Conservation Concerns..... 36

 Figures, Graphs and Tables..... 38

Acknowledgements 44

Sources Cited..... 45

PART I: Sitting Sentinel

Somehow, until the age of twenty, I misunderstood what it meant to be a river. Aside from a few childhood camping trips along tributaries of the American in central California, rivers were largely missing from my outdoor vocabulary. I was a water child, certainly, but I preferred to spend my time in the great Pacific, where the salted water helped me float, and I never went out into waters past my shoulders – there were sharks out there.

I've always believed that my fear of open water was justified. The ocean is, of course, teeming with all kinds of dangers: stinging jellyfish, fierce-eyed sharks, and the ever-present threat of a good strong under-tow. Lakes and ponds are slightly more manageable. Innocuous crayfish and tadpoles replace jellies and sharks, and one is unlikely to be swept away. But rivers

are another story entirely. They are fast, cold, deep and dangerous. So it was with a tapping foot and a nervous stomach that I first came to the Klamath. To those who have not met it yet, the Klamath River is not friendly. It does not accept your trust willingly; you have to earn it.

I had been warned of the poison oak and mosquitoes. I had my calamine lotion and DEET. Yet despite my careful packing, when I got to the Klamath, ready for a summer of adventures and scientific discoveries, I found that I had no idea what to do with a river.

* * *

The landscape of the Mid-Klamath Basin ranges from arid agricultural lands in eastern Oregon, to low-elevation conifer forests as the river nears the Pacific coast. The Klamath river itself starts from a series of lakes and winds its way along the California-Oregon border, passing through six dams and joining forces with the Shasta, Scott, Salmon and Trinity rivers along the way. The Klamath region contains mountains older than those found in the Coast Range or the Cascades and boasts peaks as high as 9,000 feet. Standing at the river's edge and looking up at the jagged horizon can feel like being lost in a crowd of natural sky-scrapers; the river is barely above sea level, the mountains two miles high. Three national forests, the Shasta-Trinity, Six Rivers, and Klamath National Forests, all come together to maintain one of the most biologically diverse hotspots in North America. Like the land that surrounds it, the Klamath is wild.

The Klamath River once boasted the third most productive salmon runs on the West Coast, a feature that made the Klamath and its tributaries an attractive homeland for the Karuk, Hoopa, and Yurok tribes that call the region home. The discovery of California gold in the 1850's brought hoards of white miners to the region in search of an easy fortune. What they found was a rich river and a tribal community that became easy targets for rough-riding, bounty-hunting cowboys. Indian lands were stolen and bank-edge villages burned to the ground. Karuk

tribal numbers dropped to a quarter of the original population in the name of conquering the Wild West.

A first wave of genocide by murder and disease was followed soon after by ethnocide; native children were sent to boarding schools run by the Bureau of Indian Affairs starting in the late 1800's, where they were forced to forget their native language and learn English. As one tribal member said, the boarding schools functioned to beat the "Indian" out of anyone who tried to hold onto their culture. Possessing tribal knowledge became, for a time, taboo. Unlike their downriver neighbors, the Yurok and Hoopa tribes, the Karuk were never granted a reservation, despite the fact that they were once the second largest tribe in California. Instead, the U.S. Forest Service claimed Karuk land as its own, and many tribal members now live in government housing. Judging by how much regalia they had, the Karuk were also one of the richest tribes in the state. Now they are one of the poorest.

At the same time that tribal language and culture were under assault, the Klamath River was also changing dramatically. The first white explorers who passed through the Klamath region in the 1820's were fur trappers, who systematically removed all of the beavers from the river, significantly changing the river environment. Logging began in the upper Klamath Basin in the early 1900's, and continued until all the forests had been harvested. Starting around the same time under the guise of the Klamath Reclamation Project, several dams were put in place on the upper and mid-Klamath in order to supply water for newly established farmland in the Upper Basin. Later, in the 1950's, three more dams were built farther downriver on the Klamath in hopes of generating hydropower. Unfortunately, the people who built the dams didn't think to install fish ladders, thus cutting off almost seventy-five miles of habitat to migrating salmon. Along with the farms and dams came decreased water flows, raised water temperatures,

increased susceptibility to eutrophication, and drastically depleted salmon runs, the Karuk's biggest staple.

Highway 96 traces most of the Klamath River from Iron Gate Dam to the town of Weitchpec, where the river has eroded the surrounding mountains into a deep gorge. Summer months can be hot and dry for the Klamath; Iron Gate Dam releases the bare minimum of 1,000 cubic feet per second from its reservoir. Low flows during the sweltering late summer and early fall cause Klamath River temperatures to spike, increasing stress on the dwindling salmon runs. During the winter months, rushes of snowmelt raise river output as high as 38,000 cubic feet per second or higher during flood years.

* * *

I made my way up from the San Francisco Bay to the tiny "town" of Somes Bar, where I would be stationed for the next two months, working closely with my employers, the Karuk Tribe Department of Natural Resources. After winding through three hours of hairpin turns and the brick red dirt of the Trinity Alps, I stopped in Willow Creek, the last town I would encounter with a stoplight. I pulled in at a gas station and went inside to ask for directions.

"Excuse me, how long will it take me to get to Somes Bar from here?" I was hot and sweaty from six hours of driving in the sun with a broken air conditioner.

"Somes Bar?" The woman behind the cash register gave me a look. "I've never heard of that place."

I glanced down at my map. Had I made a wrong turn somewhere? Quickly, I looked for the next closest town.

"Uh, okay, well what about Orleans? How far away is that?"

“Orleans?” She took a moment to think. “Well, a friend of mine went there once. It’s maybe ninety minutes away. You have to pass through the Hoopa Reservation. But there’s nothing up there. Why the hell would you want to go there?”

I wondered if I should be asking myself the same thing.

* * *

I ventured to the Klamath River as a budding scientist, sick of classrooms and eager for some hands-on learning. I came in search of the mysterious freshwater mussel, a creature so ordinary, actually, that many people don’t even notice its presence, even though mussels camp out on riverbanks inches below the surface in groups of up to sixteen thousand. They blend right into their surroundings, wedging their shiny black shells deep into bedrock crevices and the tangles of bank-side willow tree roots. The species I came to study, *Gonidea angulata*, had been studied only once before, by a pair of college students like myself, equally enticed by the wiles of these sedentary, brainless beings. No, mussels are not sexy. They have no interesting behavior to observe, nor are they particularly beautiful to look at. Though they simply sit there, they are a key component of any riverine ecosystem, because they filter pollutants and debris from the water column. These simple little creatures, only about three inches long on average, are the lungs of the river. They breathe in particulate matter, dissolved pesticides from upriver agriculture, and liver toxins borne of the algae produced in man-made reservoirs, and breathe out pure clean water, the kind that salmon and sturgeon cannot do without.

Not only do they play housekeeper, picking up all the things we humans throw into their river, they also play Mother Theresa. The biodeposits they accumulate and lay down into the riverbed are both home and dinner for other riverine invertebrates. They build up substrate and aerate habitat for the prey that juvenile salmon feed on, and create refuges from the strong river

flows that can push baby Coho and Chinook salmon downstream. They themselves feed the otter and mink that inhabit the river. These creatures, so confident and unassuming, don't ask for much in return. All they require is water in constant supply, and salmon to help them carry their babies upriver. Young mussels latch onto the gills of their host fishes, and, with little or no harm to the salmon, catch a ride to new habitat. There, they drop off into the water column and hope to secure themselves in a new patch of cobble or sand.

The students who came before me noticed something about these mussels when they studied them. No matter where they looked, they couldn't find any young ones. Mussels were abundant, certainly, but it seemed that the only mussels around were fully-grown. Where were all the babies? Either they were hiding, or they were missing. Something was keeping these mussels from reproducing. We knew that mussels around the world were threatened, and that many species had already been eradicated, mostly due to dams and human water diversion. I came to the river to see if I could detect whether this imminent extinction was happening to mussels on the Klamath, too. I wanted to figure out just how old the mussels living there were, and whether or not they were reproducing at a sustainable rate. No babies meant that in a few decades, there might not be any mussels left at all. And no mussels meant dirtier water, less food for wildlife, and a much different looking Klamath.

* * *

The Karuk tribe has more to lose from mussel extirpation than most. Freshwater mussels have cultural significance for the tribe; their shells are found throughout Karuk tradition. A women's spoon made of mussel shell is called *sikíhnuuk*, while a mussel tool used in traditional basket weaving is an *íshuvar*. Shells have also been used as fishhooks and children's toys. The *axthahá'iish*, or meat of the mussel, was a part of the traditional Karuk diet. Because of forced

assimilation into white culture, much of the traditional knowledge of when to harvest mussels and how to prepare them has been lost. Along with this cultural knowledge went much of the Karuk language. Today, very few people remember more than a few words. Like freshwater mussels, the Karuk people rely on salmon for their survival. While there are eight surviving Karuk words for mussels, there are eighty for salmon.

The first Karuk I met was a man named Ron Reed, my boss and fellow wildlife lover. Ron is tall and commanding, with piercing black eyes and a long ponytail he keeps immaculately braided and tucked under a bandana. I was eager to absorb as much as I could about Karuk history and culture, and Ron was always happy to answer my stream of questions. Ron has always known what to do with his people's river; he has a connection with the water and the salmon that I have never experienced before or since. Karuk means Upriver People, and for those living on the Klamath, both native and not, the river is inseparable from living. People give directions not by north or south, but by up or downriver. If you place a pot on a hot stove, you place it on the upriver burner. Ron told me again and again, "if the river is sick, the people are sick." As go the fish, so go the people. Ron makes no distinction between himself and his river. His surroundings are part of him. The river is a member of his family, and the salmon are his brothers and sisters. When his family is sick, he worries. This is why he asked me to come do research in the Klamath; he wanted to know if the mussels were another sick part of the river that needed to be healed. Ron knows that lawyers and politicians don't listen to feelings – they listen to facts. If I could document the mussels' sickness with science, he said, then maybe non-tribal people would help protect the mussels too. Right now, he's doing it almost on his own.

The Karuk call themselves the “Fix The World People.” The place outsiders have named Somes Bar is for the Karuk the Center of the Universe. It is here that the Klamath and Salmon rivers come together at Ishi Pishi Falls, the Karuk’s most sacred fishing grounds, revered for an abundance of salmon. It is also where spirits go after death. My white skin prohibits me from seeing the falls; the tribe asks that non-Native people stay away, but I hear they are beautiful. Every August, the Karuk people come together at the falls to camp, fish, play games and dance. But mostly they are there to make medicine. Ron knows that he and his tribe are part of the Klamath ecosystem web; they are the predators that rely on their prey, yes, but they are also the protectors. They call the ceremonies *Pikyavísh*, or “World Renewal,” and they are meant to replenish, restore, and revive not just the Karuk people, but the entire world. This has been the responsibility of the Karuk since time immemorial. When Ron first told me about the ceremonies, I thought to myself, *thank goodness these river people understand how much this world needs mending. I certainly hope it’s working.*

* * *

On an average day that summer, I was covered from head to toe in neoprene. It wrapped thirteen millimeters thick around my torso, so much insulation that I certainly wouldn’t sink, but I still was not guaranteed protection against hypothermia. I wore deep-sea diving fins and a snorkel, because the Klamath is strong, and I needed all the help I could get if I wanted to have any say at all in where it sent me. Klamath water is cold and green. I’d tell you how deep it is, but I couldn’t see the bottom unless I dove down –fifteen feet at least in the middle. Years of practicing hand-stands in swimming pools finally came in handy; complete inversion, knees and fins out of the water and suctioned to the surface, legs split, was the only way to keep me from bouncing back to the surface while I counted mussels. I hung suspended in a sea of murky green.

If I didn't hold on to something – a boulder, a shelf of overhanging bedrock, a willow root – I'd get sucked into rapids, slammed against rocks or pulled down to the cold dark bottom.

Sometimes, I wondered how long it would take me to get to the ocean.

Occasionally, our surveys led us to sites where there was no road access, and so we would take out the tribal cataraft. It was always hot outside, even on the river, and so we sometimes jumped out to cool off, floating alongside the boat in our flippers and neoprene. There was one hole I was dying to swim in; I could see it from the highway, but there was no way to get down to it from the road. When we approached it in the cataraft, I got ready to jump out. We were working with Binx and J.J. that day, two burly tribal members who were part of the fisheries crew.

“*Apsunxárah* lives in there,” J.J. told me, as I de-fogged my goggles with some spit.

“Excuse me?” I asked. A chill of fear went down my spine.

“Yeah, this hole is his home. You jump in there and he'll get you.”

I looked to Binx to see if J.J. was pulling my leg. *Apsunxárah* is the mythical Karuk serpent who eats people if they pee in the river. If you disrespect the river, *Apsunxárah* is there to remind you that there are consequences. I'd peed in my wetsuit enough times to know he had in out for me. After generations of non-Natives disrespecting his river with more than just urine, why wouldn't he be eager to eat someone who looked like me? He's as long as a football field and slinks along the bottom of the river, waiting for anyone who doesn't know the rules. He never dies. I'd rather run into a bear than *Apsunxárah*.

“Oh, yeah, I dare you,” replied Binx, returning my inquisitive stare with a wink and a mischievous grin. I looked out over the glassy black water. The hole was at least thirty feet deep.

There was no doubt in my mind that at the bottom rested a huge serpent, coiled and ready to strike. I stayed in the boat.

There is a Karuk superstition not to swim in the river when a dead body is in it. It makes sense; any dead things upriver can float downstream. You could inhale them. The Klamath takes lives all the time if people are careless. Drunk drivers crash over the highway guardrails separating Highway 96 from the steep cliffs that line the river channel. River rafters and kayakers get sucked into holes and can't get out. If someone dies, no one in the tribe will go in the river until the body has been removed. The tribal fisheries crew cannot complete their river surveys. Work stops.

In September 2002, the Klamath River had a crisis. Because of an upriver need for agricultural water diversions, the mid-river reservoirs did not fill up with spring runoff, and Iron Gate Dam released some of the lowest flows ever recorded. Salmon returning from the Pacific found river flows so low that they had to cluster together in tight packs, in the narrow strips where cold flows from mountainous streams joined the body of the river. Their proximity to each other allowed gill rot to spread quickly, and salmon died by the thousands. The official count says 34,056 fish died, but the actual count was likely twice that; of a normal run of about 80,000 fish, only 12,000 survived. Bloating and bloody fish floated belly-up in the river, mouths gaping open. They drifted into eddies, congregating in rotting masses, or washed up onto shore. Disease made their flesh inedible. Tribal fishermen, with no fish to catch, found themselves unable to feed their families. Work stopped. The fishermen went into mourning for the genocide of their salmon brothers.

* * *

I am happy to report that of the 4,000 mussels my field partners and I plucked from the riverbed, measured, and returned to their homes over a summer's worth of research, we did find some young ones. There were very few young mussels in relation to their older aunts and uncles, but there were enough to give us hope that maybe the Klamath population is still recruiting new mussels. We don't know enough about this particular species, *G. angulata*, to determine if their reproductive strategy is still viable in a changing environment. We need to do much more research if we want to be able to make any conclusive statements. One curious thing we did find, however, was that these particular mussels are living to less than half of the age they reach in other river systems; they reach maximum size sooner and die earlier. Instead of living late into their twenties, they are dying at eleven, twelve, or thirteen years. It seems that the warmer temperatures of the Klamath are increasing their metabolism, causing them to grow more quickly but to give up the fight for survival sooner. Like the rest of the Klamath, they are being pushed to their physiological extremes, but so far, they are surviving. They will continue to sit sentinel on the riverbanks, watching as their world evolves around them.

* * *

What we see of the Klamath River today is only a single snapshot in time, a Polaroid moment of still water and solid rock. Around the water, we can count the eighteen different species of conifers that surround the Klamath. In it, we see the salmon, fighting their way upstream. We see mussels tucked into their beds, their pink gills frozen mid-breath. Klamath lamprey suction their mouths to river rock as they wiggle their way upstream. Giant sturgeons guard the depths. Maybe *Apsunxárah* casts a shadow over the frame. Maybe we see a family of otters playing at the bank's edge, or a black bear ambling along the shore, hunting for bright orange crayfish.

But we also see dry forests, full of underbrush waiting to catch fire and choke out elk and osprey because of years of no-burn policies and mismanagement. We see dam after dam after dam, creating reservoirs of soupy neon green algae caused by agriculturally induced eutrophication, ready to spill over and infect the lower reaches of the wild river. We see the effects of increased water temperatures and decreased water flows, as baby Chinook suffocate from too much heat and become easy targets for thermophilic parasites. We have disrespected the river, and we are seeing the consequences.

What we don't see right away is the devastation of the Karuk people. At the same time that white people destroyed their resources, the Karuk were told that their ancient river and forests were being managed better than a native person could. Despite their status as a sovereign nation, Karuk people are routinely denied full access to their traditional hunting and fishing grounds by the State of California. We cannot capture in a photograph the depression and grief that come with the loss of their salmon, or the obesity and diabetes that result from such a dramatic nutritional shift away from life-giving salmon to government supplied commodities. As go the fish, so go the people. We cannot visually see the deterioration of pride and self-worth that descends on a people after their language has been taken away and their customs ignored. For over 8,000 years, the Karuk demonstrated that there was a way to live on this land without cutting it all down, damming it all up, and devastating local flora and fauna. Their country is so abundant that they never needed agriculture to sustain themselves. Yet in less than two hundred years, non-native Americans have changed the landscape of the Klamath in a way that may not be recoverable. Some of the damage is reversible, yes, but some of it is not. And though they continue to try, Karuk medicine may not be strong enough to heal the entire world.

The problem is that this river still looks like a river on the surface. When we look at the Klamath, we see it only as it is today. But the Karuk know it to be more, an entity with a past and a future, whose fate is intertwined with their own. If we want to see the full spectrum of damage caused by outside influence, we need to look not solely at the river, but at the people who love it. Nature may be resilient, but culture is easily lost.

Bibliography:

- . 2004. September 2002 Klamath River Fish-Kill: Final Analysis of Contributing Factors and Impacts. California Department of Fish and Game. <www.pcffa.org>
- . 2009. The Klamath Fish Disaster and Improving the Management of the Wildlife Refuges. Earthjustice. <http://www.earthjustice.org/library/background/the_klamath_fish_disaster_and_efforts_to_improve_the_management_of_the_klamath_basin_national_wildlife_refuges.html>
- . 2006. You Tube – Klamath River Fish Kill 2002 (Earthjustice). Earthjustice. <<http://www.youtube.com/watch?v=WaHwESoaRAw>>
- Brink, Kenneth. Karuk Tribe Department of Natural Resources Fisheries crewmember and Tribal member. Personal communication.
- Harding, S. 2006. Mid Klamath Watershed Council (MKWC) – Watershed & fisheries restoration, education, fuels reduction & invasive species management in the middle Klamath River subbasin, Northern California. <<http://www.mkwc.org/>>
- Harling, Adrienne. Klamath-Salmon Natural History Library Librarian. Personal Communication.
- Norgaard, Kari M. The Effects of Altered Diet on the Health of the Karuk People. Federal Energy Regulatory Commission Docket #P-2082. 2005.
- Reed, Jayson. Karuk Tribal Member. Personal communication.
- Reed, J.J. Karuk Tribe Department of Natural Resources Fisheries crewmember and Tribal member. Personal communication.
- Reed, Ronald. Karuk Tribe Department of Natural Resources Cultural Biologist and Tribal Member. Personal communication.

PART II: A population demographic analysis of *G. angulata* in the Mid-Klamath Basin

ABSTRACT:

This preliminary study examines the population age structure of *Gonidea angulata*, the western ridged mussel, in the Klamath River of northern California. *G. angulata* is a traditional food and cultural resource for the Karuk Tribe. This species of mussel is very understudied, and this is the first study of its kind to be completed in the Klamath River system. I estimated mussel ages from measurements of mussel lengths from 16 sites, and constructed a population age distribution for *G. angulata*. My findings indicate that, unlike other *G. angulata* populations, Klamath River *G. angulata* are relatively large and short-lived; they grow to over 100 mm long, and live to between 11-14+ years old. Larger *G. angulata* are found more frequently on the thalweg edges of beds, while smaller mussels are found in the middle. *G. angulata* size distributions are similar to those found in other studies of apparently stable mussel populations, though recruitment in the past few years may have been lower than in years previous. Because of the slated removal of Iron Gate Dam, further baseline data need to be collected to ensure proper conservation and restoration of the species during and after dam removal.

INTRODUCTION:

Freshwater Mussel Ecology

Freshwater mussels are an important component of many riverine ecosystems. Mussels are largely sedentary filter feeders that remove large quantities of phytoplankton and organic debris from the water column, reducing turbidity. A single mussel can filter up to a liter of water per hour, and so contributes substantially to water quality maintenance (Nedeau et. al 2005). They deposit organic detritus, creating both food and habitat for macro invertebrates that otherwise would not have access to suspended particles (Howard and Cuffey 2006). Mussels also provide food for wildlife, such as raccoons, beavers, and mink, and can indicate freshwater system clarity (Helmstetler 2006, Williams et al. 1992). Mussels benefit fish by improving water quality, creating habitat for salmonid prey, and providing water flow refugia for juvenile salmonids (Gustafson and Iwamoto 2005, Hastie and Young 2003).

Lifecycle and Host Fish Relationship

The reproductive cycle of freshwater mussels is closely linked to host fish species. Sperm released by male mussels are ingested via female incurrent siphons, where they fertilize eggs and develop into embryos. Environmental cues, such as day length and water temperature, trigger reproductive cycles (COSEWIC 2003). Juvenile mussels, called glochidia, are released from females in packets, which often mimic the food of the host fish and can survive from 10-14 days after release (COSEWIC 2003). Glochidia parasitize fish gills, skin, or fins (COSEWIC 2003). Host fish vary among mussel species, as does host specificity; some species parasitize only one fish species, while others are generalists. Glochidia can remain attached to their host fish for weeks to months, while their internal organs develop and they acquire nutrients from the blood of their host (COSEWIC 2003). With glochidia attached, host fish continue to travel, often

moving upriver, and bring glochidia to new habitat. Once glochidia mature, they drop off the host fish and establish in the substrate, where they remain buried deep in the interstitial zone of the riverbed for their first year.

Juvenile survivorship is very low. For every billion glochidia released, only between ten and 18,000 survive past the first year (COSEWIC 2003). Glochidia that parasitize an incorrect host fish cannot establish themselves and do not develop (Gustafson and Iwamoto 2005). Factors such as water temperature and strength and consistency of the current where host fish are swimming during time of host fish attachment affect juvenile establishment. Hruska (1992) found that low water temperatures can slow or stop glochidial development completely. Hruska also found that glochidia consistently release from host fish in river stretches where the current is consistent and flows are minimal, to reduce the risk of being displaced after establishment (Hruska 1992). Eutrophication of river systems can also reduce the success of juvenile mussels, and high turbidity slows mussel growth in general (Bauer 1987, Hruska 1992). Bivalves living in conditions with lowered pH and insufficient dissolved oxygen have thinner shells and grow more slowly than those found in less polluted rivers (Dunca et. al 2005).

Evaluating Age Structure from Mussel Shells

Mussel growth depends on multiple factors. Mussels grow rapidly during their first few years, and continue to grow throughout their life, though growth rate decreases over time (San Miguel et. al 2004). Mussels in systems with higher annual average temperatures grow faster than those with lower annual average temperatures. Because mussels are poikilotherms whose

body temperature varies with their surroundings, their growth rate changes throughout the year. Mussels grow more during the warmer summer months, when river productivity and food availability is higher (Dunca et. al 2005). This pattern of annual slow and fast growth is visibly recorded in the depositional layers of mussel shells. Dark rings, called annuli, represent winter periods of low growth, while lighter rings represent summer growth (Black 2009). Growth rates of individuals within a given population are highly correlated, and can be used to extrapolate the growth rate of an entire population (Black 2009).

When evaluating the age of a mussel from its shell annuli there are several factors to consider. Mussels are incredibly sensitive to disturbance, and any removal or displacement, either human or fluvial, can cause disturbance rings: thin dark bands that resemble annuli. Dark bands of unknown origin are also commonly found in mussel shells, and can be mistaken as annuli (San Miguel et. al 2004). In some species, growth rings can be observed from the outer prismatic layer, but they become more difficult to distinguish as the mussel ages. Thus cross sections of shells are the best guarantee for accuracy; only bands that go through both the nacreous inner layer and the prismatic outer layer provide reliable markers of annual growth (Helama and Valovirta 2007). Disturbance rings, dark bands and daily growth lines do not continue through to the prismatic layer, and it is possible to distinguish between true growth rings and disturbance rings.

Mussel Fauna of the West

There are eight species of freshwater mussels west of the continental divide, three of which are found in the main stem of the Klamath River (David 2008, Davis 2008, Taylor 1981). Though North America hosts some of the most diverse mussel fauna in the world, most of that

diversity lies in the East; few species are common to both the East and West of North America (Frest and Johannes 1995). Multiple recent formations of land west of the Rocky Mountains have contributed to frequent drainage shifting and evolution (Frest and Johannes 1995). Freshwater mollusks from the Great Basin historically entered the Klamath River drainage through a connection to Upper Klamath Lake (Frest and Johannes 1995).

Klamath River mussels fall into two families: Unionidae (*Anadonta* sp., *Gonidea angulata*) and Margaritiferae (*Margaritifera falcata*). *G. angulata* is the only species of its genus (Williams et al. 1992). Freshwater mussels were first collected from the Klamath River Basin in 1867, and from the thirty samples collected in the entire basin since then, seven species have been identified (Harling 2006). Four of these species are exclusive to the Klamath Lakes, and have not been identified in the river. The three species collected from the Klamath River in 1948 are the same three found today, indicating a recorded history of all three species of at least 60 years, though the record for *G. angulata* goes back to 1867 (Harling 2006).

Cultural Importance of Freshwater Mussels

I conducted this research in conjunction with the Karuk Tribe of California as part of a collaborative Tribal Wildlife Grant with Whitman College and the Confederated Tribes of the Umatilla Indian Reservation. The majority of our survey sites fell within Karuk ancestral territory. The abundance and sustainability of freshwater mussels in the Klamath are of particular interest, as no scientific research on Klamath mussels has been previously completed.

Freshwater mussels were an important food and tool resource for Native American tribes including the Karuk through the mid 20th century (Davis 2008, Parmalee & Klippel 1974). Mussel shells served as the traditional woman's spoon, as opposed to antler spoons used by men,

as well as a woman's tool for scraping iris fibers to be used in basket weaving (Harling 2006; Ron Reed, Karuk Tribe Cultural Biologist personal communication). Shells were also used decoratively for jewelry and ceremonial regalia, turned into children's toys, and sharpened into tools (Harling 2006, Heizer 1949).

Freshwater mussels continue to be an important cultural resource for the Karuk. Though much traditional knowledge has been lost in the past century due to Western influence and forced assimilation, a limited knowledge of the cultural role of mussels has been maintained through oral tradition. At least eight words pertaining to mussels still exist in the Karuk language dictionary (Karuk Dictionary – April 18 2010). Davis (2008) and David (2008) interviewed several Karuk tribal members in 2007 in an effort to record tribal knowledge about freshwater mussels. Older tribal members recount eating mussels several times a week during certain seasons, though which seasons these were has been forgotten. Tribal members younger than sixty reported much less frequent mussel consumption (Davis 2008). Some interviewees told of harvesting and preparing mussels for mussel stew as children, possibly indicating that mussel preparation was traditionally a women and children's chore. Another interviewee described selectively harvesting smaller mussels and avoiding larger ones because their meat was tougher (Davis 2008). Timing and methods for mussel harvesting have generally been forgotten, but some Karuk people continue to harvest and prepare mussels during World Renewal ceremonies in August (Davis 2008; Ron Reed, Karuk Tribe Cultural Biologist personal communication; JJ Reed, Tribal Fisheries crewmember personal communication).

Today, tribal members rarely collect freshwater mussels, often citing concerns over high levels of microcystis, a liver toxin that reaches maximum density in the river in late summer due to spillover of warm and stagnant waters in the Iron Gate reservoir (Kann 2008; J.J. Reed, Tribal

Fisheries crewmember, personal communication). Four microcystis congeners were found in *G. angulata* samples taken from Seiad Valley during July and September, with 85% of samples testing positively for microcystis (Kann 2008). The samples contained levels of toxins far beyond a safe dose, between eight and 663 times above the recommended dose for children in all categories (lifetime, seasonal, and acute ingestion), and between 1.8 and 66 times higher for adults' seasonal ingestion limits (Kann 2008). Samples taken farther downriver of Iron Gate Dam also contained unsafe levels of microcystis, though the levels were not as high as in mussels from Seiad Valley. By November, microcystis was absent from mussel tissue, suggesting that all toxins had been cleared (Kann 2008). However, because the main ceremony season for the Karuk tribe is in August when microcystin levels are well beyond safe for human consumption, harvesting freshwater mussels for traditional ceremonies and feasts is dangerous to Karuk health.

Gonidea Angulata: The Western Ridged Mussel

I focused my research solely on *G. angulata*, the most abundant freshwater mussel species on the Klamath River (David 2008, Davis 2008). *G. angulata*, commonly called the western ridgeback mussel or rocky mountain ridged mussel, has a broad native range from southern California north into British Columbia, and from the continental divide west to the coast (see Fig. 1). This species has been eradicated in much of its southern range due in large part to water diversion projects, and populations in parts of Idaho are dying out as well (COSEWIC 2003). The rocky mountain ridged mussel is listed as a species of special concern in Canada, and is listed as “vulnerable” globally (COSEWIC 2003).

G. angulata is commonly found at lower elevations in clean cold rivers and streams where flow is constant and substrate is well oxygenated and stable. (COSEWIC 2003, Nedeau et. al 2005). Denser populations are generally found in areas with more pristine river conditions. The species shows more tolerance to pollution than *M. falcata*, though not as much as some other North American freshwater mussel species (COSEWIC 2003, Frest and Johannes 1995). Because *G. angulata* is chronically understudied, little is known about its reproductive cycle. Studies have found gravid females with developing glochidia from April through July, which suggests a 1-4 month gestation period. Glochidia are released sometime during this period, and attach onto host fish soon after, remaining there for one to six weeks. Though it has not been decisively ruled out, there is no evidence to suggest self-fertilization in *G. angulata* (COSEWIC 2003). This species is considered to be iteroparous.

The host fish of *G. angulata* is unknown, though based on its habitat preferences, it is likely a cold water salmonid, such as Chinook (*Onchorynchus tshawytscha*), Coho (*O. kisutch*), or steelhead (*O. mykiss*), all native to the Klamath Basin (COSEWIC 2003, Nedeau et. al 2005). Though the host species for *G. angulata* has not been specifically studied, Gustafson and Iwamoto (2005) genetically identified *G. angulata* glochidia taken from steelhead gills sampled from Washington. Because the historical range of *G. angulata* is so extensive, it is possible that it parasitizes more than one host fish species (COSEWIC 2003).

Research Goals and Objectives

Scientific interest in freshwater mussels emerged from tribal traditional ecological knowledge and cultural concern. My motivation behind this study was to answer two questions. First, how do Klamath River mussels grow with age? Past studies have aged *G. angulata* to be

between 20 and 30 years old, and have found individuals up to 125 mm (COSEWIC 2003). Thus, I predicted that if *G. angulata* in the Klamath were growing under conditions similar to other river systems, they too would be between 20 and 30 years old at their maximum size. The second question is: does the *G. angulata* population in the Klamath appear to be stable? To answer this question, I estimated the population age structure for this species in the river system. Freshwater mussels follow a type III survivorship curve with low juvenile survivorship and progressively fewer surviving mussels in each age class (Berg 2008). A commonly found size and age distribution shows few young mussels, many mid-sized mussels, and few old mussels (Cowles personal communication, Berg 2008). Thus, there were two possible outcomes for the population age structure of Klamath mussels: either *G. angulata* had a population with progressively fewer individuals in each size class, indicating consistent reproductive rates and mortality, or *G. angulata* had an unevenly distributed population, where age classes did not show a trend of many small individuals and progressively fewer in each size/age category, indicating inconsistent population reproduction. If found, this second scenario might imply that *G. angulata* are not reproducing at a sustainable rate in the Klamath River.

METHODS:

Study Region

My coworkers and I sampled 16 sites over 147 river miles on the main stem of the Klamath River from Iron Gate Dam to Weitchpec. The warm, nutrient rich waters exiting the Iron Gate Reservoir flow through an arid landscape. Along our study reach, cold tributaries including the Scott and Salmon Rivers cool the Klamath as it flows through progressively moister conifer forests, with less human influence and disturbance. Substrate along the Klamath

ranges from exposed bedrock to sand, with the most prevalent substrate a boulder/cobble mix (Westover 2010). We studied population age structure only at sites previously surveyed for mussel distribution.

From 40 reaches randomly selected for distribution surveying within the study area, we selected 16 sites with known mussel aggregations. We defined large aggregations, called beds, as areas in which there were more mussels than could be accurately counted within the allotted survey time of about two hours. We located study sites using GPS coordinates, satellite maps, river morphology notes and photographs, and previously recorded written descriptions and drawings. Each of the 16 reaches was 50 m long, and spanned the width of the river, though we confined our surveys to the areas in which beds were located.

Study Species

G. angulata is the most abundant species of freshwater mussel in the Klamath River. Though we did find some *Anadonta sp.* and *M. falcata* during our surveys, collecting samples of these species might have posed substantial risk to the small populations present in the river. Also, we encountered too few individuals to obtain any statistical power. Therefore, we focused solely on the population demographics of *G. angulata*.

G. angulata shells are characterized by a distinct ridge that extends from the beak towards the umbo, a dark prismatic outer layer, and a light pearly inner nacreous layer (Fig. 2). Often, the prismatic layer and parts of the nacreous layer are eroded on older specimens, creating a light stripe down the ridge of the shell.

Mussel Surveys

At each of 16 sites along the Klamath, we selected six plots for sub-sampling within the designated bed. Whenever possible given bed dimensions and river conditions, we sampled two plots each at the bank edge, the middle, and the thalweg edge of the bed, and we dispersed quadrat locations evenly along the length of the bed. We removed all the mussels within each 0.25 m² (0.5 m x 0.5 m) quadrat and thoroughly sifted through the substrate to remove all mussels. We measured the length (the longest dimension of the mussel) and width (from hinge to edge) of each mussel to 0.1 cm using digital or analog calipers (see fig. 2; San Miguel et. al 2004). Mussels spent no more than 2 minutes out of water for measuring, and no more than 20 minutes out of substrate. We kept all mussels in river water during processing to reduce stress. Once measured and recorded, we returned the mussels to the quadrat from which they were removed, and placed them with feet down and siphons up to promote proper reestablishment. I observed that in most substrates mussels re-established within 30 minutes or less.

At ten of the sites, I kept between two and eight samples for shell analysis. I collected a total of 39 shell samples. I did not take samples from beds that had low mussel counts or were in reaches that experienced more shear force and therefore more shell erosion. I chose shells of all sizes that were the most intact, with the least amount of wear, though the larger a mussel is; the more likely it is to be partially eroded.

Evaluating the Relationship Between Mussel Length and Age

I created thin sections of the mussel shells to analyze their ages. First, I applied JB KwikWeld epoxy to protect shells from breaking during processing. I used a diamond saw to cut a thin section of the shell across the axis of least growth, and sanded the sample down using progressively finer grit, from 120 to 600 to 1000. I then affixed the sample to a glass slide, used a

thin section machine to create even sections, and sanded the slides again. Once the thin sections were approximately 30 microns thick, I examined them under a light transmittance microscope and took photographs to determine mussel age. Two different viewers read each thin section twice to ensure accuracy (Black et. al 2009).

I analyzed all data using Microsoft Excel. I estimated the relationship between age and length using a linear regression model. I used regular t-tests to examine mussel distributions between sites and a single factor analysis of variance (ANOVA) to look at differences between different regions of the bed (bank edge, middle or thalweg edge).

RESULTS:

We measured a total of 4,298 mussels and processed 38 shell samples. Because size was the measurement taken for the entire sample population, rather than age, I used a linear regression model to assess how well size acts to predict age. Using a line of best fit, a regression analysis revealed the linear equation between shell length and age to be $y = 0.1124x - 1.1397$, where $x = \text{length}$ and $y = \text{age}$ ($F = 42.7$; $d.f. = 1,36$; $p < 0.005$; $r^2 = 0.54$; Fig. 3). For an estimated length-to-age guide as generated by this formula, see Table 1. Because of layers lost to erosion, it is likely that up to three years of growth have been lost per shell sample, making our age estimates as many as three years too young (Fig. 4) (Black 2009; Brett Blundon, Department of Fisheries and Wildlife: University of Oregon, personal communication). For consistency within this discussion however, I will use the minimum age possible for each mussel according to the length-age relationship.

The size distribution was bell-shaped, with many mid-sized mussels, and fewer small or large mussels (Fig. 5). Over half (59.6%) of mussels measured were between 59.1-76.8 mm long,

an estimated six to seven years old. Mussels up to five years composed 20.4% of the population, while mussels eight years or older composed 20.0%. The smallest mussel measured was 15 mm (min. age one year), and the largest was 104.1 mm in length (min. age 11 years). We also found a mussel shell that was 119.9 mm long (min. age 15 years).

Distribution of mussel ages between sites was relatively consistent (Fig. 6). Mean age in each bed was between 6-8 years old. Though there was not a significant difference, older mussels were slightly more frequent at upriver sites (sites 94, 163, 305), younger mussels were slightly more frequent at mid-river and downriver sites (Fig. 6, Fig. 7). Of mussels measured from the most downriver sample site, 40.8% were five years old or younger. There were slightly more three-year-old mussels (32.4-41.4 mm) than four-year-old mussels (41.4-50.4 mm).

There was a significant difference in mussel size between the bank edges, middle and thalweg edges of the beds. Mussels were significantly largest in the thalweg edge, smallest in the middle of the bed, and intermediately sized in the bank edge (Fig. 8; $F=33.54$; $d.f. = 2, 3665$; $p<0.005$).

DISCUSSION:

Mussel Size

I found that *G. angulata* in the Klamath River were slightly smaller and younger, and reached maximum size at a younger age than those recorded in other systems (Black et. al 2009, San Miguel et. al 2004). This variation between systems is not unusual, and can be explained by a physiological response to temperature. As latitude increases and temperature decreases, metabolic rate slows, and therefore growth rate decreases and lifespan increases (Bauer 1992). Conversely, a warm system leads to increased metabolism and decreased lifespan. Indeed, *G.*

angulata aged between 20-30 years came from a river system in British Columbia (COSEWIC 2003). It is likely that the high summer temperatures and productivity of the Klamath River have contributed to increased metabolic and growth rates of *G. angulata*. This same pattern has also been observed in geographically diverse populations of the related European species *Margaritifera margaritifera* L. (Bauer 1992). It is also possible that there are larger mussels in the Klamath than the ones we sampled.

Mussel Age Distribution

Despite finding few small *G. angulata* in this survey, the distribution in the Klamath is common in freshwater mussel surveys (Helmstetler and Cowles 2008, Berg 2008). There are several explanations for why younger size/age classes are less abundant than mid-size/age classes. This common pattern may be the result of sampling techniques; because young mussels are so small, it is likely that some were overlooked during sampling, and thus not all young mussels present were recorded. It is also possible that younger *G. angulata* simply were not located in areas where we looked (perhaps they were elsewhere in the bed, or buried deeper in the substrate). This is problematic, because if sampling techniques cannot accurately assess the frequency of younger mussels, it becomes difficult to understand the age distribution of mussels without several seasons of sampling. Because there was a significant difference in mussel size in different areas of the bed (bank edge, middle, and thalweg edge), perhaps uneven sampling could have lead to the age distribution observed, though we made every effort to sample consistently within all areas of the bed.

Because this is the first survey of its kind in the Klamath, it is difficult to know if the pattern observed by this study indicates reduced or absent recruitment. Low numbers of young

mussels may also be due to episodic reproduction or reduced or absent recruitment. Certain species of mussels reproduce more in some years than in others. It is possible that the lack of smaller age classes represents a natural period of reduced recruitment, while the most abundant size classes represent years of high recruitment (Cowles personal communication, Berg 2008). If this is the reproductive cycle for *G. angulata*, an observable trend in frequency of different size classes suggests two periods of mussel recruitment: 6-7 years ago, and 3-4 years ago.

If *G. angulata* populations are decreasing, survival could be reduced during several stages: fertilization, glochidial infestation of host fish, settlement of juveniles into substrate, or maturation of juveniles into adults (Berg 2008). If food sources are low, female mussels invest less in reproduction (Berg 2008). The Klamath River is very productive and nutrient rich, so it is unlikely that females are choosing not to designate resources to reproduction. Eutrophication however, can lead to decreased growth (Bauer 1992). Reproductive failure can also occur if mussels are dispersed enough that likelihood of sperm encountering a female is too low. Because *G. angulata* are abundant in the Klamath, fertilization failure is also unlikely. Additionally, high turbidity can reduce the ability of females to brood larvae in their gills (Osterling et al 2008). This could be a problem in the Klamath River, but not enough is known about brood timing for *G. angulata* to know if it correlates with periods of high turbidity.

A lack of appropriate host fish can lead to failure of glochidial infestation, which can reduce recruitment (Osterling 2008). The larger the mussel population is in relation to the host fish population, the greater the negative impact of glochidia. Gustafson and Iwamoto (2005) note that glochidial infection, called glochidiosis, can reduce short and long term growth of host fish, increase their chances of fungal infection, and in some extreme cases, lead to host fish death due to asphyxiation (Karna et. al 1978). If a high density of mussels releases glochidia in an area

with a low density of host fish, glochidiosis rates are likely to be much higher. Too many glochidia can harm host fish, and at the same time too small a host fish population means the new generations of mussels cannot survive. This dynamic exists in many Pacific river systems, where long-lived mussels such as *M. falcata* continue to release glochidia onto dwindling salmonid populations (Gustafson and Iwamoto 2005). Because the host fish for *G. angulata* is unknown, and therefore the status of said host is likewise unknown, we cannot determine if this dynamic is a threat to freshwater mussels in the Klamath, where some salmonid species are threatened (Toz Soto, Karuk Tribe Fisheries Biologist, personal communication). High water temperatures in the Klamath caused by reservoirs and impoundments could affect the timing of glochidial release, and change the encounter rate with host fish (Hastie 2003, Osterling 2008). Increased water temperatures are not new to the Klamath, however, so this is likely not a critical factor in glochidial infestation rates.

It is possible that juvenile survival decreases during settlement. The juvenile stage of mussel development is the most difficult to measure, because mussels are small and hard to locate in the substrate (Berg 2008). Substrate suitability, sedimentation, hydrology, and turbidity are all factors that effect juvenile success (Berg 2008, Osterling et al 2008). High sedimentation and turbidity can reduce the capacity for young mussels to filter feed and breathe, providing perhaps the most likely cause of potential reduced mussel survivorship (Osterling et al 2008). There is little evidence for reduced survivorship of existing adults (older than four years) because older mussels appear to be abundant in the Klamath.

Further Research and Conservation Concerns

Freshwater mussels are the most endangered faunal group in North America (Williams et al. 1993). Of the 291 known species, 71.1% are listed as either endangered, threatened, or of special concern. Only 23.6% of all mussel species are considered stable. The conservation status of fourteen mussel species (4.7%) has not been determined; all three species extant in the Klamath fall into this category (Williams et al. 1993).

Impoundments and subsequent increases in water temperature, reduced flows from diversion projects, and pollution are the largest threats to freshwater mussels. Each of these negative factors is present on the Klamath system, and thus presumed to threaten the mussel population in the Klamath River (Strayer 2006). Iron Gate Dam is currently slated for removal in 2020 (Environmental News Service, 18 Feb 2010). If this initiative comes to fruition, it would mean a large habitat change for Klamath River mussels. All mussel species in the Klamath require further study, particularly population demographic analyses and host fish determination to increase the success of any conservation, restoration, or reestablishment efforts after dam removal. *M. falcata* and *Anadonta sp.* in particular have such low numbers in the Klamath that their populations are likely in jeopardy.

Much further research needs to be done to support the findings of this study, and to better evaluate the conservation needs of freshwater mussels in the Klamath. Expanding the number of survey sites as well as the project area and the number of shells sampled will increase the accuracy of and confidence in the data. I suggest that this survey be repeated in several years to confirm observed trends in mussel recruitment. If further research detects the same recruitment gap, it is likely that data from this study are in fact observing a pattern of diminishing recruitment rather than fluctuations from year to year. Further research can also illuminate if *G. angulata* reproduce in short intense bursts or consistently over time. Also, more research is

required to establish age composition of individual mussel beds and to determine whether bed sampling techniques can be improved. Because of the significant difference in mussel sizes in different areas of the bed, surveyors need to be sure they are sampling evenly from different bed areas.

Figures, Graphs and Tables:

Table 1: total mussels counted with observed lengths and extrapolated ages, using the formula $y = 0.1124x - 1.1397$, where x = length and y = age.

Frequency	Age (measured)	Age (with erosion)	Length (mm)
25	1	4	0-23.3
125	2	5	23.5-32.4
195	3	6	32.4-41.4
173	4	7	41.4-50.4
360	5	8	50.4-59.0
1112	6	9	59.1-67.9
1447	7	10	68.0-76.8
635	8	11	76.9-85.6
188	9	12	85.9-94.6
36	10	13	94.7-103.0
1	11+	14+	103.1 +1



Fig. 1: Historical range of *G. angulata* (COSEWIC 2003).



Fig. 2: *G. angulata* shell (Nedeau et al. 2006).

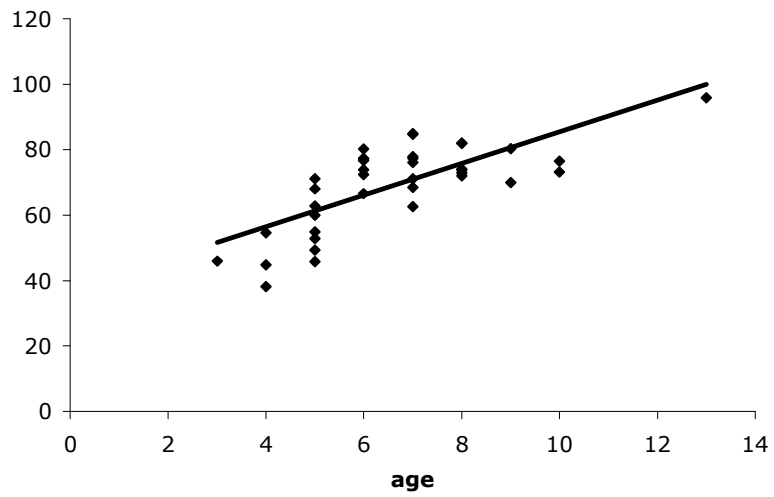


Fig 3: Mussel length as predicted by recorded age of shell samples.

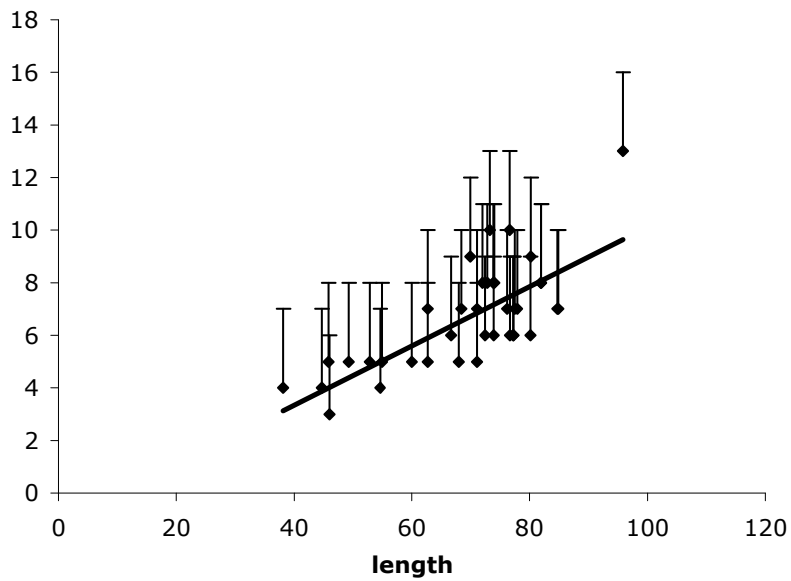


Fig 4: relationship between measured mussel shell length in millimeters and age determined by shell thin sections. Age is predicted from length because length is what was observed in the field. Error bars represent approximate three year age discrepancy due to shell erosion.

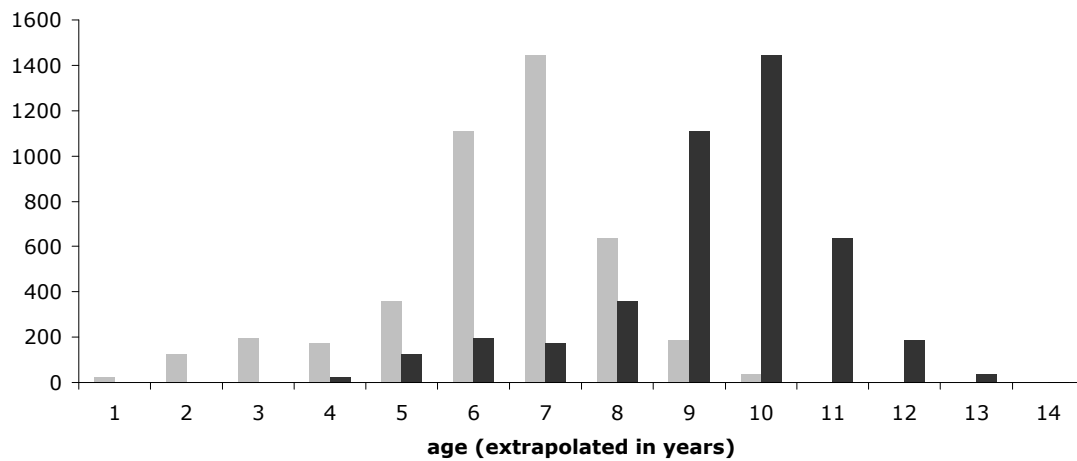


Fig 5: Frequency of mussels per age category under two conditions. Young estimation: pure shell analysis data (light grey). Adjusted estimation: assumes three shell layers lost to erosion (dark grey).

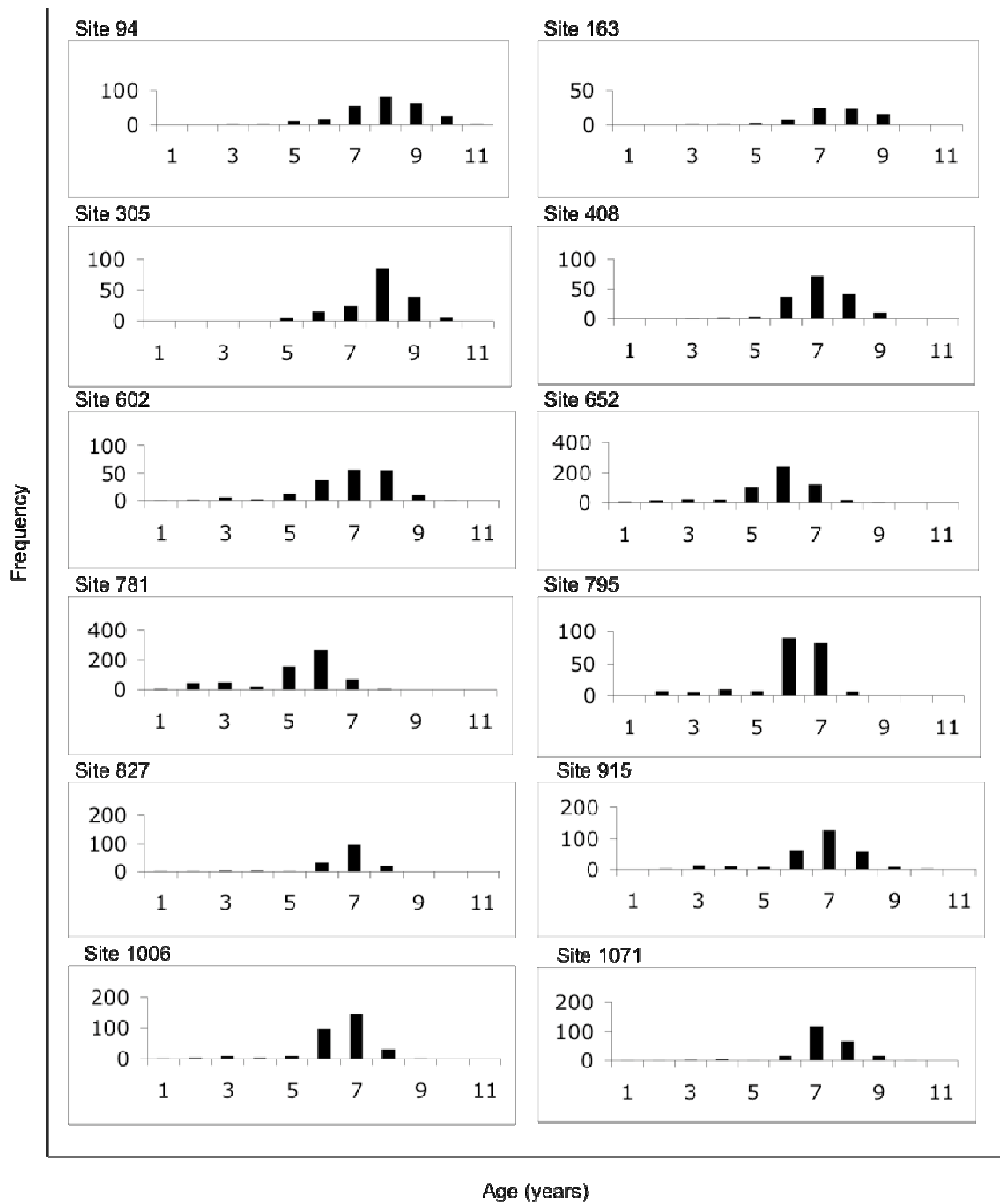


Fig 6: frequency of mussels by age at each of 16 survey sites. Note that frequency axes vary.

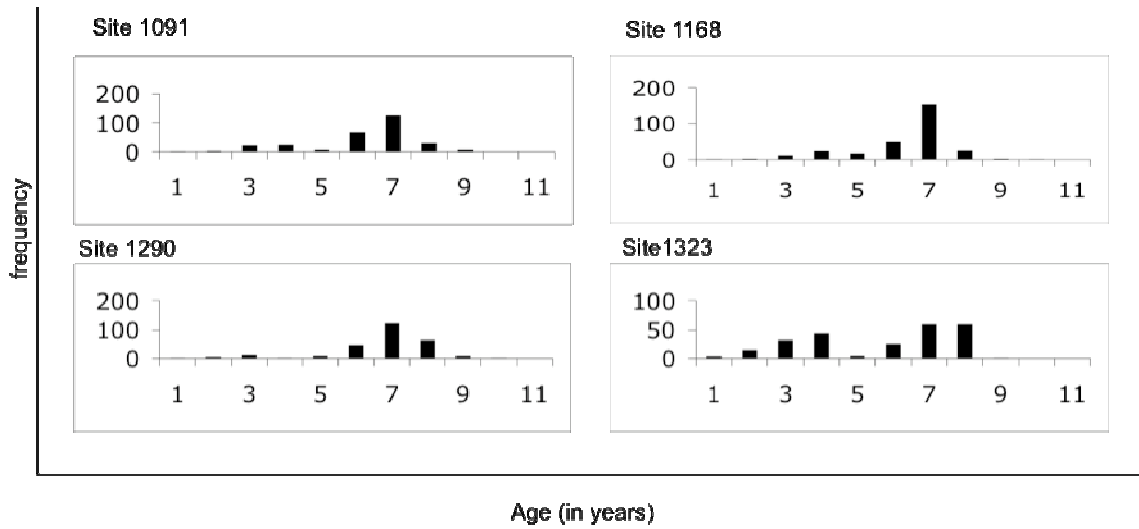


Fig 6 (continued): frequency of mussels by age at each of 16 survey sites. Note that frequency axes vary.

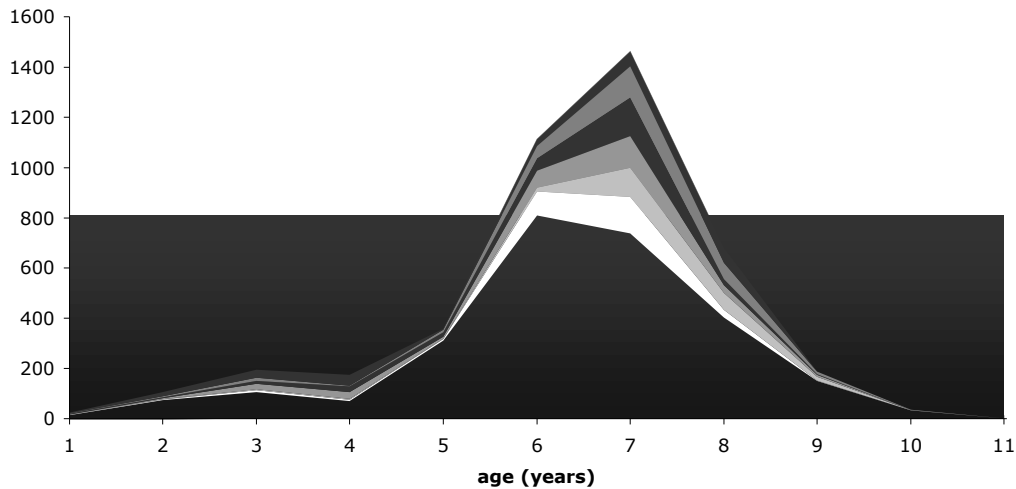


Fig 7: Frequency of mussels per age category per research site; bottom layer is upriver, top layer is downriver. More upriver sites had fewer younger age classes, while sites from the middle of our research area had younger beds on average.

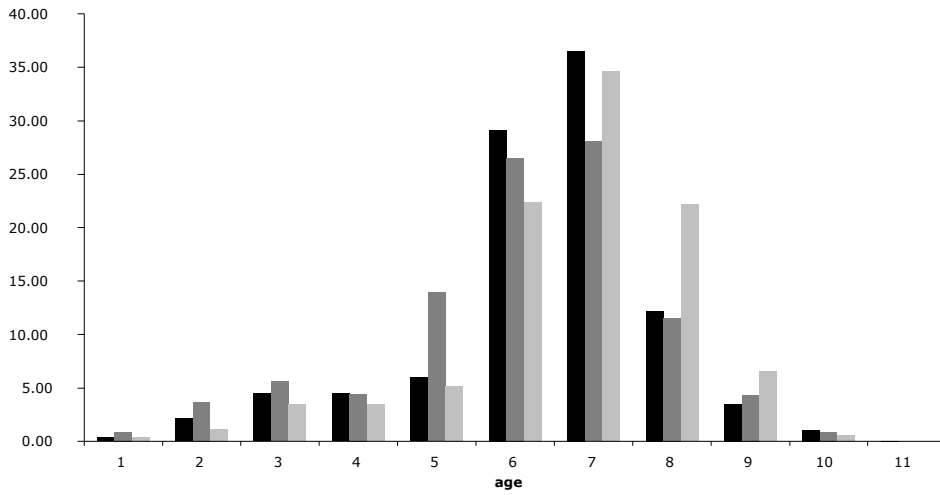


Fig. 8: Percent of population in each age class for each of three bed placement categories: bank edge (black), middle (dark grey), and thalweg edge (light grey).

Acknowledgements:

This thesis research had been very much a group effort. Funding came from a Tribal Fish and Wildlife Grant. The Freshwater Mussels Project would not have been possible without the never-ending support and leadership of Principle Investigator Kari Norgaard, whose tireless efforts have truly been a gift. Field Supervisors Emily Davis and Aaron David also deserve continual gratitude for the dedication, encouragement, compassion, and sense of humor that they brought every day into the field. Endless thanks to Cultural Biologist Ron Reed for providing the original direction to focus on freshwater mussels, ongoing cultural knowledge and field assistance, and Toz Soto and the Karuk Tribe DNR Fisheries Crew, especially Binx, JJ and Alex for their contributions of time, energy, and wisdom. Many thanks to Whitman College Professors Tim Parker for his diligent statistical guidance and tolerance as I fumbled with data analysis, Kirsten Nicolaysen for teaching lab techniques, and Don Snow for leading me to develop the craft of nature writing. Thanks also to Brett Blundon of Oregon State University for generously sharing his knowledge of cross sectional techniques, and Kara McKay for her enthusiasm and helping hand in the laboratory. Finally, thank you to field partners Marie Westover and Michelle Krall for waking me up every morning and reminding me of why we were working so hard to protect and learn from the place we came to love; I could not have asked for better research partners or friends.

Sources Cited:

- . 2010. "Klamath Water Wars Settled With Agreements to Remove Four Dams." Environmental News Service. <<http://www.ens-newswire.com/ens/feb2010/2010-02-18-092.html>>
- Bauer G. 1992. Variation in the life span and size of the freshwater pearl mussel. *Journal of Animal Ecology*. 61: 425-236.
- Bauer G. 1987. Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *Journal of Animal Ecology*. 56: 691-704.
- Berg D, Levine T, Stoeckel J, Lang B. 2008. A conceptual model linking demography and population genetics of freshwater mussels. *Journal of the North American Benthological Society*. 27: 395-408.
- Black B. 2009. Climate driven synchrony across tree, bivalve, and rockfish growth-increment chronologies of the northwest Pacific. *Marine Ecology*. 378: 37-46.
- Black B, Copenheaver C, Frank D, Stuckeu M, Kormanyos, R. 2009. Multiproxy reconstructions of northeastern Pacific sea surface temperature data from trees and pacific geoduck. *Paleogeography, Paleoclimatology, Paleoecology*. 278: 40-47.
- Bright B, Gehr S. 2008. Karuk Online Dictionary. <http://corpus.linguistics.berkeley.edu/~karuk/karuk-lexicon.html>. Karuk Tribe of California.
- COSEWIC. 2003. COSEWIC assessment and status report on the Rocky Mountain ridged mussel *Gonidea angulata* in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada. 29 p.
- David A. 2008. A Population and Distribution Survey of Freshwater Mussels (Bivalvia: Unionoidea) in the Klamath and Salmon Rivers of Northern California. B.A. Thesis, Department of Biology and Environmental Studies, Whitman College, Walla Walla, WA.
- Davis E. 2008. Freshwater Mussel Abundance, Distribution, and Habitat Preference In Two Northern California Rivers Within Karuk Ancestral Territory. B.A. Thesis, Department of Biology and Environmental Studies, Whitman College, Walla Walla, WA.
- Dunca E, Schone B, Mutvei H. 2005. Freshwater bivalves tell of past climates: But how clearly do shells from polluted rivers speak? *Paleogeography, Paleoclimatology, Paleoecology*. 288: 43-57.
- Frest T, Johannes E. 1995. Interior Columbia Basin mollusk species of special concern. Final Report to Interior Columbia Basin Ecosystem Management Project. Deixis Consultants. Seattle, WA.

- Gustafson RG, Iwamoto EM. 2005. A DNA-based identification key to Pacific Northwest freshwater mussel glochidia: importance to salmonid and mussel conservation. *Northwest Science*. 79: 233-245.
- Hastie LC, Cosgrove PJ, Ellis N, Gaywood MJ. 2003. The threat of climate change to freshwater pearl mussel populations. *Ambio*. 32: 40-46.
- Harling A. 2006. Summary of factors affecting the Karuk Tribe's access to Klamath River freshwater mussels as a traditional dietary and material resource. Internal Karuk Tribal document. 5p.
- Helama S, Valorvirta I. 2007. Shell morphometry, pre-mortal taphonomy and ontogeny related growth characteristics of freshwater pearl mussel in northern Finland. *Annales Zoologici Fennici*. 44: 285-302.
- Helmstetler H, Cowles, D. 2008. Population characteristics of native freshwater mussels in the mid-Columbia and Clearwater Rivers, Washington State. *Northwest Science*. 82: 211-221.
- Helmstetler H. 2006. Population structure and pollutant levels of freshwater mussels in the mid-Columbia river. M.S. Thesis, Department of Biology, Walla Walla College, College Place, WA
- Howard JK, Cuffey KM. 2006. The functional of native freshwater mussels in the fluvial benthic environment. *Freshwater Biology*. 31: 460-474.
- Heizer, R. 1949. Curved Single-Piece Fish Hooks of Shell and Bone in California. *American Antiquity*. 15: 89-97.
- Hruska J. 1992. The freshwater pearl mussel in South Bohemia: Evaluation of the effect of temperature on reproduction, growth, and age structure of the population. *Arch. Hydrobiol*. 126: 181-191.
- Kann J. 2008. Technical memorandum: Microcystin bioaccumulation in Klamath River fish and freshwater mussel tissue: Preliminary 2007 results. Karuk Tribe of California.
- Karna D, Milleman R. 1978. Glochidiosis of salmonid fishes. III. Comparative susceptibility to natural infection with *Margaritifera margaritifera* (L.) (*Pelecypoda: Margaritanidae*) and associated histopathology. *Journal of Parasitology*. 64: 528-537.
- Nedeau E, Smith AK, Stone J. 2005. Freshwater Mussels of the Pacific Northwest. Pacific Northwest Mussel Work Group and the United States Fish and Wildlife Service. 45 p.
- Osterling E, Greenberg L, Arvidson B. 2008. Relationship of biotic and abiotic factors to

- recruitment patterns in *Margaratifera margaratifera*. *Biological Conservation*. 141: 1365-1370.
- Parmalee, P, Klippel W. Freshwater mussels as a prehistoric food source. *American Antiquity*. 39: 421-434.
- San Miguel E, Monserrat S, Fernandez C, Amaro R, Hermida M, Ondina P, Altaba C. 2004. Growth models and longevity of freshwater pearl mussels (*Margaratifera margaratifera*) in Spain. *Canadian Journal of Zoology*. 82: 1370-1379.
- Strayer, D. Challenges for freshwater invertebrate conservation. *Journal of the North American Benthological Society*. 25: 271-287.
- Taylor D. 1981. Freshwater mollusks of California: A distributional checklist. *California Fish and Game*. 67: 140-163.
- Williams JD, Warren ML Jr., Cummings KS, Harris JL, Neves RJ. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries*. 18: 5-22.
- Westover ML. 2010. Freshwater mussel distribution, abundance, and habitat preference in the middle Klamath River, Northern California. B.A.Thesis, Department of Biology, Whitman College, Walla Walla, WA.