# Freshwater Mussels
*of the*
# Pacific Northwest

*This edition is dedicated to the memory of Dr. Terry Frest (1949-2008), dean of Northwest malacologists and mentor to many novices.*

# Freshwater Mussels *of the* Pacific Northwest

SECOND EDITION

Ethan Jay Nedeau, Allan K. Smith, Jen Stone, and Sarina Jepsen

THE XERCES SOCIETY
FOR INVERTEBRATE CONSERVATION

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Front cover photos: Columbia River, Dennis Frates (top); western pearlshells, Marie Fernandez, USFWS (bottom)

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Marie Fernandez, USFWS

# Introduction to Freshwater Mussels

To a casual observer, a freshwater mussel may look no different than a stone. Mussels do not move very far during their adult lives; they may inch their way along the bottom of a river or slowly bury themselves if the need arises, but the unobtrusive animals seem to not do anything that some might consider…dramatic. But these humble creatures can ascend waterfalls! Their young attach to unwitting fish that carry them to new places in a watershed—over waterfalls, across lakes, up and down rivers from headwaters to tidewaters, and even across the Continental Divide. This is one of the many wonders of freshwater mussels, and sadly, we are losing many species without ever learning their amazing secrets.

Some species of freshwater mussels can outlive most animal species on Earth; one species in the West can live longer than a century. But their longevity may depend on stability—they seem to be finicky about where they live, and some species are sensitive to changes in their environment. Mussels rely on fish to reproduce and replenish populations; and therefore changes in the West's fish fauna have threatened the region's mussel fauna. By studying mussel populations we can observe and measure the long-term degradation—or recovery—of aquatic ecosystems. The "canary in a coalmine" analogy is apt for freshwater mussels in rivers throughout North America.

Nearly three-quarters of all 297 native freshwater mussel species in North America are imperiled and 35 are thought to have gone extinct in the last century[91]. Freshwater mussels are one of the most endangered groups of animals on Earth, yet surprisingly little is known about the life history and habitat needs of many species, or even how to distinguish among species in the West.

This book provides an introduction to freshwater mussels in western North America, focusing primarily on the Pacific Northwest. This second edition benefits from recent and ongoing research on the region's mussel fauna. Like the first edition that was published in 2005, this book is intended to help raise awareness about freshwater mussels and spotlight the importance of freshwater mussels in protection and restoration of our freshwater ecosystems. A more extensive bibliography, research highlights, and taxonomic updates also will make this new edition more relevant to resource managers and others interested in the science upon which this publication is based.

## Basic Anatomy

Freshwater mussels are mollusks that produce a bivalved shell. The two valves are mirror images of each other and are connected by an elastic-like ligament along the dorsal hinge. The outside of each valve is covered with material called periostracum that gives the shell its color, and the inside of each valve is lined with a smooth mother-of-pearl material called nacre. The raised rounded area along the dorsal margin is called the beak; shells grow outward from the beak in a concentric pattern. Mussels may possess "teeth" on the hinge that create a strong and sturdy connection between the valves. There are two types of teeth—lateral teeth are thin elongate structures parallel to the hinge, and pseudocardinal teeth are short stout structures below and slightly in front of the beak. No native mussel species west of the Continental Divide have lateral teeth and only two species—*Margaritifera falcata* and *Gonidea angulata*—have pseudocardinal teeth (although the pseudocardinal teeth in

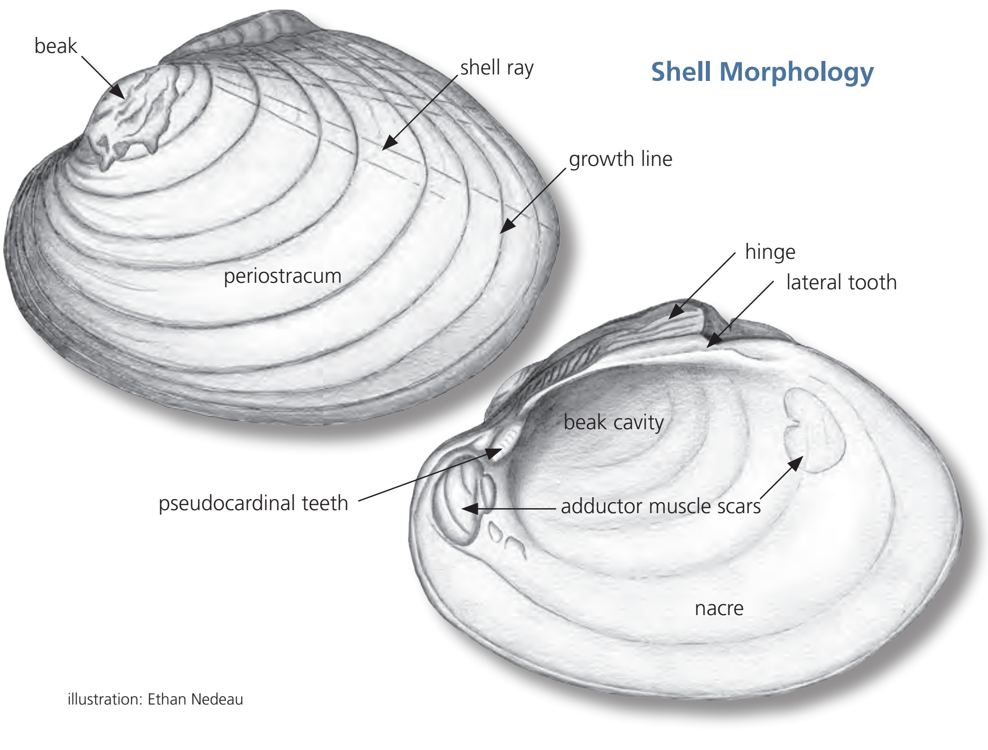
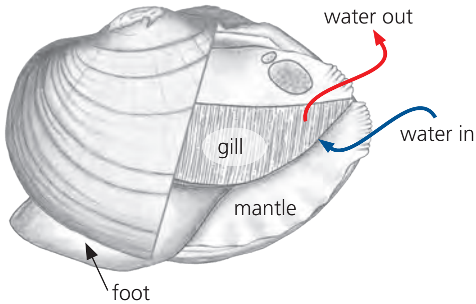



illustration: Ethan Nedeau




### Filter Feeding

Mussels draw water and food into the inhalent aperture, use their gills to filter food and other materials from the water, and then expel filtered water and waste out the exhalent aperture.

illustration: Ethan Nedeau

*Gonidea* are very small). The species in the genus *Anodonta* have no teeth at all; the Latin word *anodonta* means "without teeth".

The living mussel occupies the cavity between the two valves. The only body parts that are visible outside of the shell are the foot that is used for locomotion and feeding, and the mantle edges that are modified into inhalent and exhalent apertures. The mantle is a thin sheet of tissue that lines the shell and envelops the body of the mussel. When disturbed, mussels will withdraw the mantle edges and foot into the shell and pull the two valves tightly together using their strong adductor muscles. This affords mussels some defense against predators and harsh environmental conditions. Mussels draw water and food into the body through the inhalent aperture and expel filtered water, waste, and larvae out the exhalent aperture.

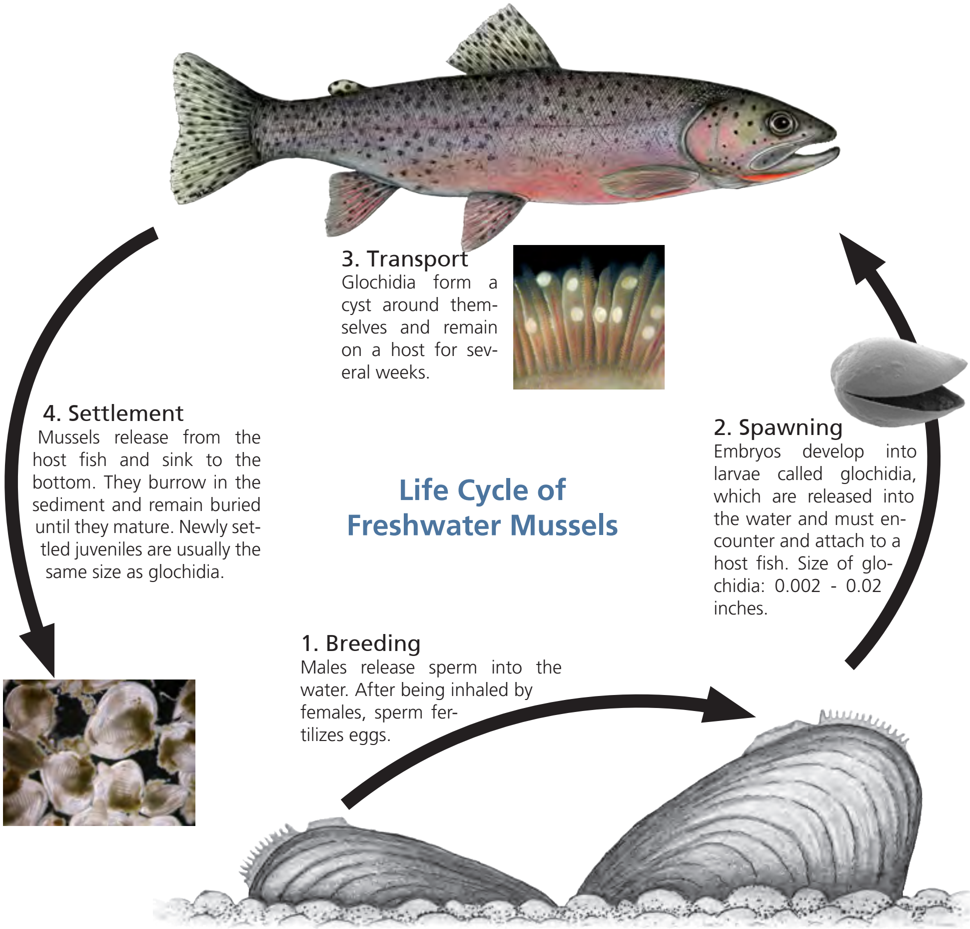
Typically, adult mussels in the West range in size from three to eight inches. Though sometimes mistaken for juvenile native mussels, fingernail clams and pea clams (Family Sphaeriidae), and non-native Asian clams (*Corbicula fluminea*) are much smaller than native mussels (less than one inch). Aside from obvious size differences, clams have thinner shells, different teeth morphology, mantles fused to form true siphons, and different reproductive strategies than mussels[61].

## Life Cycle

People who take the time to learn about freshwater mussels are amazed at the complex life cycle and reproductive traits that freshwater mussels possess. Freshwater mussels have separate sexes, although hermaphrodites (individuals with male and female traits that are capable of self-fertilization) have been documented for some North American species, including the western pearlshell[43,44]. During breeding, males release sperm into the water and females must filter it from the water for fertilization to occur. Fertilization occurs in a special portion of the female gill called the marsu-



illustration: Ethan Nedeau

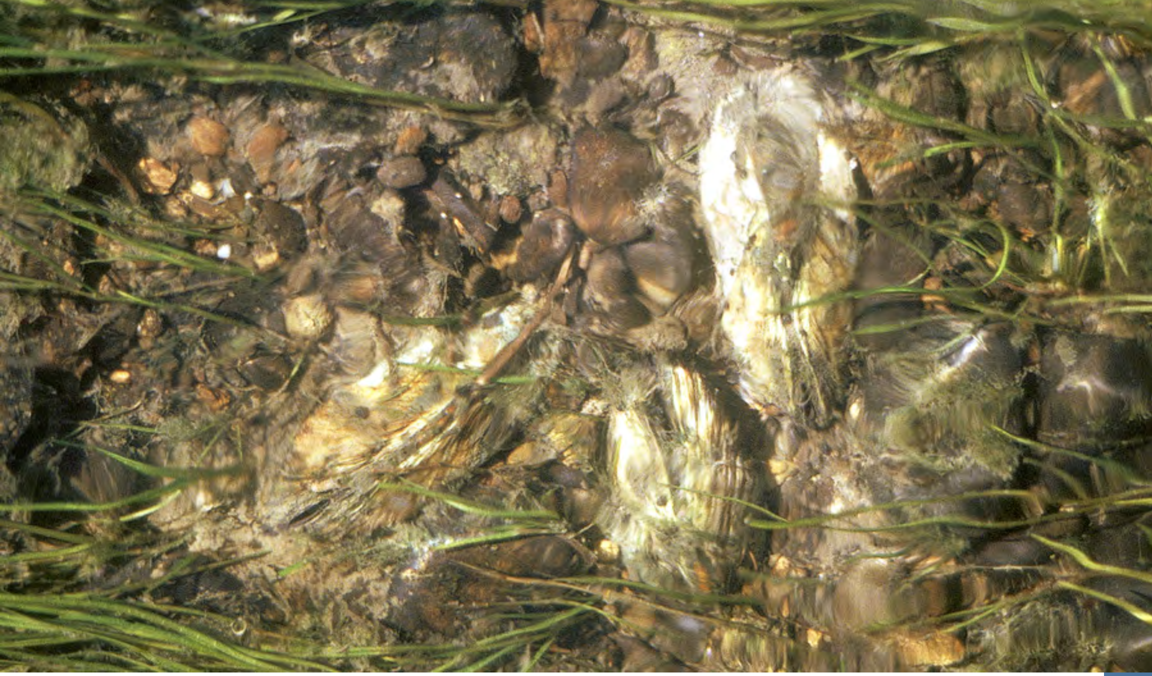



illustrations: Ethan Nedeau; glochidia image: U.S. Geological Survey; encysted glochidia and juveniles: Chris Barnhart

pium, and newly formed embryos develop within the marsupium into larvae called glochidia. Microscopic glochidia, which look like miniature mussels, range in size from 0.002 to 0.02 inches when they are discharged into the water[5,7], usually several weeks to months after fertilization.

The release of glochidia varies by species, environmental conditions such as water temperature, and triggers such as hydrologic disturbance or presence of fish. Glochidia are external parasites of fish that clamp onto fins or gill filaments. Strategies used by different species for releasing glochidia are adaptations that increase the likelihood of glochidia reaching their preferred host fish species[5,37,56].

The small light specks on this trout's gills are mussel glochidia.
photo: Michelle Steg-Geltner, The Nature Conservancy



Underwater view of western ridged mussels situated in a gravel bed. photo: Allan Smith

Some species simply expel thousands of individual glochidia with the expectation that some will encounter a host; this simple strategy is thought to be prevalent among the mussel species of western North America[5]. Some species release aggregates of glochidia, called conglutinates, that are bound by mucus. These conglutinates take on a remarkable variety of shapes and colors among North American species, including some that mimic the natural prey of their host fish, such as worms, insect larvae, or small fish[5,34,37]. When fish attack, conglutinates rupture and the fish get a mouthful of glochidia. Both the western pearlshell and western ridged mussel may release loosely bound conglutinates that quickly disintegrate and leave free glochidia to find a host on their own[5].

Females of some North American species have mantle margins that are modified to attract fish, with either bright colors or fleshy lobes that undulate to look like prey[5,35,36,37]. Using photoreceptive spots, female mussels can usually sense when fish approach and will discharge at just the right moment to give the fooled fish a mouthful of glochidia. The mussel species that occur in western North America are not known to attract host fish in this way[5].

Glochidia must encounter and attach to a suitable host fish soon after being released into the water. They form a cyst around themselves and may remain attached for several days or months, depending on the water temperature and mussel species[5]. During this period, fish (particularly migratory species) may swim many miles from where they encountered glochidia and thereby help mussels disperse within a waterbody. When ready, the glochidia release from the fish, burrow into the sediment, and begin their free-living



Mussels can inhabit both pristine and urban rivers and lakes, provided that water and habitat quality are suitable. photos: Allan Smith

existence. Mussels may spend the early part of their lives buried in the sediment[61,73]. During this time, they grow quickly to protect themselves against predators and the crushing and erosive force of rocks and water. Once mature, they spend most of their lives with their posterior end sticking above the surface of the sediment during warmer months of the year, and usually completely buried during colder months[61,110], but this varies widely among and within species, habitats, and geographic regions. The chances of glochidia finding a host, attaching, landing in a suitable environment, and reaching adulthood are incredibly slim. For example, in a population of the eastern pearlshell (*Margaritifera margaritifera*), which has among the highest fecundity of all mussel species, it was estimated that only one in every 100,000,000 shed glochidia became a juvenile[114].

Some species of freshwater mussels can live longer than 100 years[6,118]. *Margaritifera falcata* and the closely related *M. margaritifera* are the longest-lived freshwater mussel species and also among the longest-lived animal species on Earth. *M. margaritifera* living in stable northern rivers have life expectancies approaching 200 years[118]. During their lives, they may move less than a few yards from the spot where they first landed after dropping from their host fish. Other species in western North America, such as *Anodonta*, may live only ten to fifteen years[44].

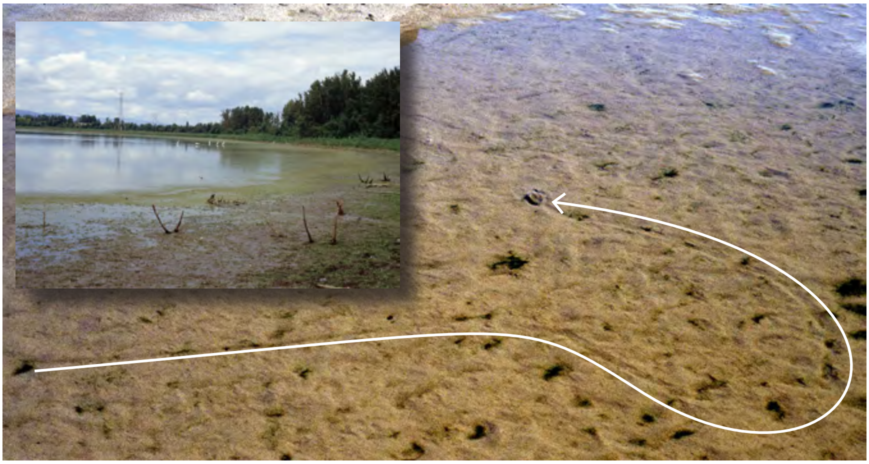
## Habitat

Freshwater mussels are confined to permanent bodies of water, including creeks, rivers, ponds, and lakes. Mussels tend to concentrate in areas of streams with consistent flows and stable substrate conditions[51,75,92,93,105]. They are often absent or sparse in high-gradient, rocky rivers where the erosive forces of rocks and water may be too strong for juveniles to become established or for mussels to live long lives. Mussels are frequently encountered in low-gradient creeks and rivers, perhaps because they provide a variety of habitat conditions, reliable flow, good water quality, and diverse fish communities. Species that live in flowing water may inhabit a variety of substrate types, but require flow velocities adequate to keep the water and sediment well oxygenated, and depths that are not prone to dewatering during dry periods.

Some species can be found in lake and pond habitats that have muddy substrates, lower levels of dissolved oxygen, and warmer water temperatures. Mussels also can be found in freshwater tidal habitats such as the lower Columbia River and Kalama River. Brief exposure during low tides does not seem to affect their populations[122]. Although many mussel species are sensitive to pollution and habitat disturbance, some appear to be able to tolerate moderate human disturbance and persist near the densely populated areas of Seattle and Portland.

## Role in Ecosystems

Mussels are important to food webs, water quality, nutrient cycling, and habitat quality in freshwater ecosystems[52,108]. Mussels greatly influence food webs by filtering tiny suspended materials such as algae, bacteria, zooplankton, and sediment from the water column. Some of the material they ingest is bound and released as larger particles that sink to the bottom and become important food for other benthic (bottom-dwelling) animals, especially aquatic macroinvertebrates[108]. Mussels can filter a substantial volume of water each year and may help reduce turbidity and control nutrient levels[55,70,98]. Mussels sometimes comprise the greatest proportion of animal biomass (the sum total of living tissue and shells) in a waterbody[71]. Because mussels are so long-lived, they retain nutrients and minerals for a very long time.



Mussels that sense receding water levels will often move to avoid exposure, but they are vulnerable to predators during these events (line drawn for emphasis). photos: Allan Smith

Muskrats (right) and many other animals eat freshwater mussels. Muskrats leave shells in piles called middens (left). photo: Christine Humphreys, Painet Inc. (right), Ethan Nedeau (left)

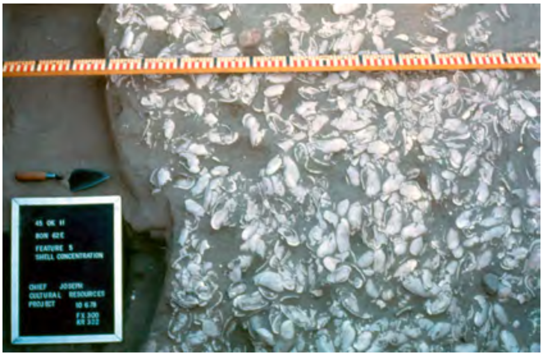
Mussels may also improve habitat quality and promote higher diversity of other benthic macroinvertebrates[52,89,106]. Their vertical and horizontal movements help stir sediments and increase the exchange of oxygen and nutrients between the sediment and water[108]. They serve a function similar to earthworms in your garden by allowing sediment to retain more organic matter and by increasing sediment porosity. Mussel shells also provide an attachment surface for algae and animals such as sponges and insect larvae[108].

Mussels are an important source of food for river otters and muskrats. Non-aquatic mammals, including raccoons and skunks, may eat mussels accessible in shallow water, or when water levels drop during droughts or reservoir drawdowns. Raccoon tracks are common in the mud and silt of the lowland waters of western Oregon and Washington, as they are on a ceaseless patrol for mussel meals. Gulls and shorebirds also scavenge dead mussels when water levels are low. Some fishes, including native sturgeon and nonnative sunfish, eat mollusks[113]. Muskrats, which are efficient mussel predators, may affect native mussel communities[74,104,115]. Healthy mussel populations can withstand normal levels of natural predation, but mussel populations that are low in density, fragmented, and exposed to excessive predation might be at risk of local extirpation.

## Diversity and Distribution

Eight currently recognized native freshwater mussel species occur west of the Continental Divide[103], although the taxonomy of the genus *Anodonta*, which includes six of those species, is undergoing revision (see Part II of the guide). The West has a very low diversity compared to the 290 species that occur in the eastern two-thirds of North America. Some rivers in the southeastern United States historically supported more then seventy species. In contrast, it is rare to find more than two mussel species together in a single waterbody in the Pacific Northwest.

The low diversity of mussels west of the Continental Divide is the result of glaciers, dispersal barriers, climate, and geology[100]. The Cordilleran Ice Sheet covered northern parts of the landscape up to about 13,000 years ago, destroying aquatic habitats and pushing mussels into southern refugia. The Continental Divide was an insurmountable dispersal barrier for most aquatic animals, keeping the rich diversity of eastern species from colonizing western rivers. The arid climate throughout parts of the West made conditions difficult for mussels to disperse and proliferate. Many streams and rivers were rocky, high-gradient environments with tremendous erosive force that inhibited these long-lived, fragile, and sedentary animals from becoming established[30,50,100].

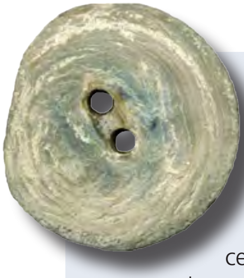



Native American shell midden excavated from the Chief Joseph Dam Project. photo: Chief Joseph Dam Project

Species composition in Native American shell middens (piles of shells left by animals or humans) provides information on mussel communities and perhaps environmental conditions before European settlement[23,24,80]. For example, mussel shells found in middens of prehistoric Native Americans on the main Owyhee River of eastern Oregon included shells of *Margaritifera falcata* and *Gonidea angulata*, indicating that both species were present and accessible for harvest 1,000-9,500 years ago[124]. However, only *Gonidea angulata* is widespread today. Shell middens in the mid-Columbia River watershed contain *Margaritifera* as the most common species but a recent survey in the same region found only *Anodonta*[46]. Absence of western pearlshells could be the result of changes in water quality, or may be related to historic extirpation of their anadromous salmon hosts and the subsequent introduction of unsuitable fish hosts, such as nonnative bass.

## Mussels as Biomonitors

Freshwater mussels have several traits that make them excellent indicators of the long-term health of aquatic ecosystems, as they are easy to observe, identify (at least to genus), and measure. Since individuals live from ten to more than one hundred years and adults have such limited mobility, their populations can reflect the cumulative effects of environmental conditions and extreme events over time. Mussels cannot respond quickly to escape adverse conditions (as a fish can), and if they disappear from an area, they may be slow to recolonize. If conditions become unsuitable for mussels, they stop



### Use by Humans

Humans have exploited freshwater mussels for millennia, beginning with Native Americans that fashioned tools and implements from shells and ate mussels when there was a scarcity of more palatable food[79]. Large, heavy-shelled species of the central United States were commercially harvested for buttons throughout the 1800s and early 1900s until the advent of plastic ended the shell button industry[1,72]. The economic value of mussel shells grew when it was discovered that mussel shells could be used in the cultured pearl industry. When shell nuclei cut from thick-shelled North American species were slipped under the mantle of marine oysters, the oysters would create a pearl around it. Supplying Asia's cultured pearl industry became a multi-million dollar fishery in the United States[1,72]. However, none of the species occurring west of the Continental Divide were commercially exploited for the cultured pearl industry because their shells were too thin. Freshwater mussels were harvested in Oregon in the early 1990s to provide specimens for biological supply companies. While western freshwater mussels are not directly sold for profit, the ecological services they provide to humans and other animals are tremendous.

reproducing, stop growing, or die. Thus, mussel recruitment, growth, age, and mortality provides insight into population health and environmental conditions[41,53,77]. Shells can be tagged so that growth, movement, or survival of animals can be tracked over time[58]. Methods exist for estimating population sizes and studying long-term trends in abundance[95].

Mussels are sensitive to changes in water quality, habitat, and fish communities. Low dissolved oxygen, chemical contamination, and sedimentation are just three of the myriad stressors that may affect mussels. Due to their reliance on fish to reproduce, loss of host fish will eventually eliminate mussel communities even if other physical and chemical conditions remain suitable for mussels. Mussels accumulate chemical contaminants in their bodies and shells. Tissue concentrations of contaminants such as mercury, lead, dioxin, polychlorinated biphenyls, and polycyclic aromatic hydrocarbons may indicate exposure risk for the entire aquatic community and provide insight into ecosystem health[20,29].

## Conservation and Management

Freshwater mussels are one of the most endangered groups of animals on Earth[9,112]. Of the nearly 300 North American species, 35 have gone extinct in the last 100 years. Nearly 25 percent are listed as endangered or threatened under the United States Endangered Species Act and 75 percent are listed as endangered, threatened, or of special concern by individual states[91,112]. The

Freshwater mussels have been greatly affected by river management and the Grand Coulee Dam is a symbol of man's effort to tame the West's rivers.

conservation crisis of freshwater mussels is a result of continent-wide degradation of aquatic ecosystems and is mirrored by declines of other native freshwater fauna[26,83].

Western freshwater ecosystems have suffered increased levels of alteration and exploitation since settlers first arrived more than 150 years ago. Mussels have been eliminated from portions of rivers and even entire watersheds through the combined effects of habitat loss, pollution, blockage of anadromous fish, and introduced species[13,30,50]. The factors that seem to have had the greatest effect on western freshwater mussels include water availability, dams, introduced species, loss of host fish species, and the chronic effects of urbanization, agriculture, and logging on habitat quality. Global climate change will exacerbate the effects of many of these stressors on western ecosystems (see www.epa.gov/climatechange).

There is a critical need for greater research into freshwater mussel biology, distribution, status, and threats. This information is vital for effective conservation of western mussels. Specifically, there is a need to better understand the distribution, habitat, host fish species, life history, population structure, recruitment, and population trends of all western freshwater mussel species. More information is needed to understand the taxonomy of what is currently called the western *Anodonta*, and whether these animals can be identified by shell morphology. In addition, there is a need to understand how western freshwater mussels are affected by threats to water quality, habitat fragmentation, hydrologic alteration, global climate change, altered water levels, and loss or reduction of host fish. Increasing public and government awareness of

Healthy rivers and healthy salmon runs are vital to freshwater mussels, and in turn, mussels contribute to riverine ecosystems for the benefit of all species. photo: Thomas P. Quinn

the importance of freshwater mussels will contribute to effective conservation of these species in the West.

Freshwater mussels have come into the spotlight in recent years because of a growing awareness of aquatic ecosystem health and a public desire to protect and restore native ecosystems and wildlife. Pacific salmon have been the symbol of this movement in the Northwest, but people are learning that the fate of mussels and salmon are intertwined. Some western mussels use native salmon to complete their life cycle, and benefit from the increased productivity (from nutrient-rich salmon carcasses) and diversity that healthy salmon runs provide[33,69,84]. In turn, salmon and other aquatic species benefit from the ecosystem services provided by freshwater mussels[117].

## Searching for Mussels

Searching for freshwater mussels can be an enjoyable experience, and spending time by a river or lake, looking carefully and moving deliberately, can foster a strong appreciation for aquatic environments. The information you collect can be important for mussel conservation and management. The discovery of rare mussels in new places, or in places where people thought mussels had been eliminated, will help scientists and managers protect them. If you find freshwater mussels, report your sighting to your state Fish and Wildlife Agency but **do not collect live animals**.

People who spend a lot of time near the water, such as boaters, anglers, landowners, and naturalists, can be trained to identify mussels and ultimately serve as an army of "mussel watchers." The three basic methods for surveying mussels are described below. When using these methods, please be aware of potential hazards, such as slippery banks and rocks, stinging or biting insects,

### Warning about collecting mussels!

Scientists and managers want new information on mussel distribution, but they discourage people from killing and collecting live animals to prove that they found them. State or federal law protects some species, and it is a punishable crime to kill them or possess their shells. People are encouraged to submit observations of mussels and habitat conditions to state and federal fish and wildlife offices, including photographs of shells and habitat. Experts can then verify the information.

snakes, deep mud, broken glass, pollution, dangerous flow conditions, underwater hazards such as drowned trees or debris, and boat traffic.

**Shoreline Searches:** Walk along the shoreline and look for shells discarded by predators or from mussels that died when water levels dropped. This is a safe and easy way to look for mussels without having to get wet. Shoreline searches can be particularly effective when water levels are low, and provide information on mortality that the low-flow event may have caused. Lowland freshwater tidal areas are good places to look for mussels during low tide. Shoreline searches may be suitable for determining which species occur in a waterbody. Unfortunately, shells found near the shore may not always represent the mussel community in the water. Predators may target certain species (especially large common species) and some species may be more abundant in deep water.

**Bucket Surveys:** Surveyors commonly use aquascopes or buckets fitted with a clear plastic bottom. This method enables you to search for live mussels in shallow water while staying on your feet. Because swimming for mussels can sometimes be difficult or unsafe, bucket surveys or shoreline searches are used instead. Use of aquascopes or buckets is a more favorable method than shoreline searches because you can find live animals in the water, but searches are limited to shallow areas less than two or three feet deep and water with sufficient clarity to see the mussels.

**Snorkeling and Diving:** Searching for mussels while swimming, using a mask and snorkel or SCUBA gear, can be an enjoyable experience as long as conditions are suitable. This allows you to survey large areas, search in deeper water, and see live animals up-close. These methods are more enjoyable in warm water with good water quality and an environment free of hazards. Wetsuits or drysuits—and weights to counter the buoyant effect of these suits—are often required in cold water.

photo: Dennis Frates

# Field Guide

## Identification

The purpose of these descriptions is to help the user identify adult mussel shells or live animals to genus. Descriptions, photographs, and illustrations are provided in the species, clade, and family accounts that follow.

Outline of shell triangular or round. Beak inflated and centrally located along dorsal edge. Well-developed concentric sculpture lines, absent on other genera (introduced)...Asian clam, *Corbicula* (page 40)

Very small (0.08 to 0.60 inches long). Adult shell round, oval or quadrate, fragile, with one or two cardinal teeth in one valve. Shell sculpture, if present, very fine with no color pattern...Fingernail clams, Sphaeriidae (page 40)

Well-developed pseudocardinal teeth. Ventral margin slightly concave. Nacre purple on fresh specimens. Arborescent papillae surrounding the incurrent opening...western pearlshell, *Margaritifera* (page 31)

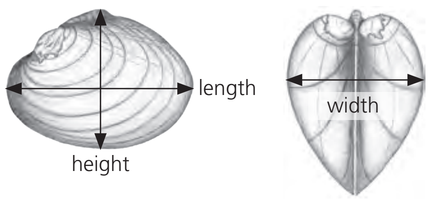
Distinct heavy ridge running at an angle from beak to posterior ventral surface. Shell thick, heavy, sturdy. Divided, purplish incurrent aperture papillae...western ridged mussel, *Gonidea* (page 36)

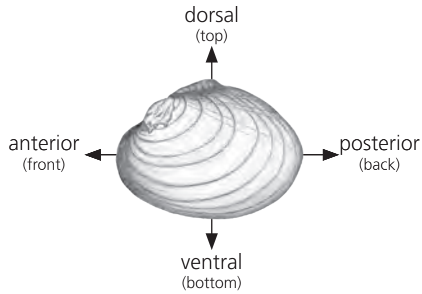
Pseudocardinal and lateral teeth and heavy ridge absent. Shell thin, light, and fragile. Single, whitish incurrent aperture papillae...Floaters, *Anodonta* (page 17)

## Key Terms

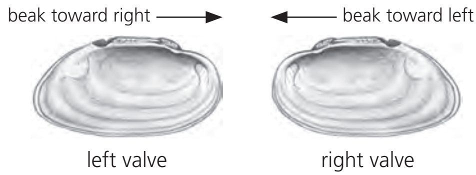
It can be daunting to learn all of the words used to describe the shape and appearance of mussels. Species identification is a visual process, so we try to minimize the technical words and illustrate the ones that we use. Please also refer to the general morphology diagrams on pages 2-3.

### Directions and Dimensions



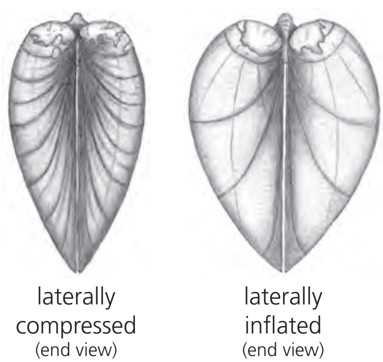



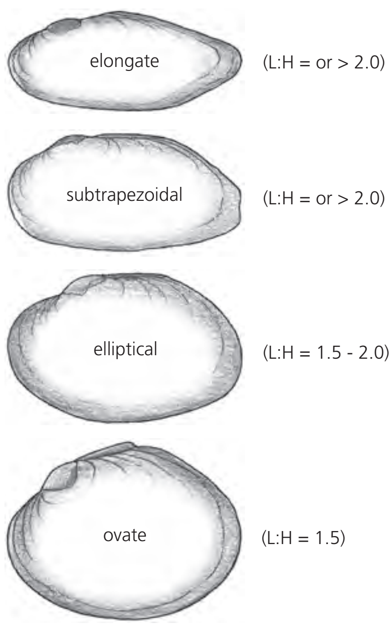

**Left versus right valve:** Place the shell in your palm with the nacre toward you and the beak up. If the beak is toward the right, it is the left valve. If the beak is toward the left, it is the right valve.




### Shell Shape

L:H = ratio of length to height



## *Anodonta* Taxonomy

It would be misleading to publish a field guide to western mussels without explaining how little we know about the genus *Anodonta*. This genus has challenged taxonomists since 1838 when Isaac Lea first described shells from one location in the lower Willamette River as three different *Anodonta* species: *nuttalliana* (winged floater), *oregonensis* (Oregon floater), and *wahlametensis* (Willamette floater). Subsequently, taxonomists described four more species of *Anodonta* west of the Continental Divide: *beringiana* (Yukon floater), *californiensis* (California floater), *kennerlyi* (western floater), and *dejecta* (woebegone floater). The species *A. wahlametensis* is no longer recognized[103], and the existence of *A. dejecta* is uncertain. *A. dejecta* was considered to be the same species as *A. californiensis* in Arizona by some researchers[8], but more recently was validated as its own species[103]. It is unknown whether this species is alive today, and since *A. dejecta* lacks an accepted type locality[8], there is the added complication of having no source population with which to compare current *Anodonta* in the region.

Taxonomy of *Anodonta* based on shell characteristics is difficult because this genus lacks some of the morphological features—especially hinge teeth—that are used to distinguish other mussel genera. As a rule, *Anodonta* species have no teeth (the Latin word *anodonta* means "without teeth") and therefore identification of *Anodonta* in the past has relied almost solely on shell shape, which unfortunately is quite variable. Age, sex, environmental conditions, and individual variation influence shell shape. Animals that live in lakes may appear different than the same species that live in rivers. Shell erosion—the intensity of which depends on water chemistry, sediment types, and flow conditions—will often obscure shell features such as shape, beak sculpture, and rays.

Species with broad geographic ranges and poor dispersal abilities, such as freshwater mussels, often exhibit a high degree of genetic variation across their range[11,12]. Differences in the genetic make-up of isolated populations might affect their appearance, but not be sufficient to affect their ability to interbreed. In other words, they might look different, but still be the same species. Conversely, they may look similar and yet be different species. Scientists are trying to understand if the currently recognized "species" are genetically distinct throughout their range, and recent advances in genetic research may help resolve the uncertain *Anodonta* taxonomy in the West[10,17,64,116].

The first edition of this publication generally followed currently accepted classification[103], which considered six species of *Anodonta* west of the Continental Divide: *californiensis, dejecta, nuttalliana*, *oregonensis*, *kennerlyi*, and *beringiana*. The first edition departed from this standard reference by not including the southwestern species *A. dejecta* in the guide for the reasons described above and because the species does not occur in the Pacific Northwest. An issue raised by leading scientists regarding the taxonomy presented in the first edition was that there was no reliable way to distinguish some of these "species" in the field. They felt it was misleading to present a key to each species when it was possible that further research might combine or subdivide two or more of the species. Therefore, this guide does not contain a key to the *Anodonta* species.

Advanced phylogenetic analyses published in the last few years have shed some light on the taxonomic uncertainty of western *Anodonta*. Rather than confirming the validity of western species, researchers have found three distinct clades (defined as a group of species that share features inherited from a common ancestor) within which there is considerable variation[17]. The species *kennerlyi* and *oregonensis* comprise a separate clade and are genetically similar enough to possibly warrant being combined into a single species. The species *californiensis* and *nuttalliana* comprise the second distinct clade[17], which shows considerable genetic and morphological variation across the West, and may eventually be subdivided into different species. *Anodonta beringiana* was found to be genetically most similar to *Anodonta woodiana* of Asia[17].

What does this new information mean for a practical user-friendly guide to freshwater mussels of the West? The taxonomic names from the currently accepted standard names[103] are recognized, since that standard reference has not been revised, although information on *Anodonta dejecta* is not presented. Based on new information[17], this second edition presents two species (*Margaritifera falcata* and *Gonidea angulata*) and three distinct clades of *Anodonta* that may contain one, two or more species. Unlike the first edition, this edition does not try to distinguish between any of the *Anodonta* species, but rather presents the three clades identified in recent research[17]. This guide still presents some of the historical descriptions of *Anodonta* species, but those descriptions are likely to change as new research unfolds.

It can be discouraging to be unable to put a precise name to a shell that you find. It can also be difficult for resource managers to develop specific conservation and management plans for "species" that they cannot identify in the field. In spite of the taxonomic uncertainty surrounding western *Anodonta*, there is still a need for the conservation of western mussel fauna and their aquatic habitats. Resource managers should consider the three genetically distinct clades of *Anodonta* in conservation and monitoring programs[17]. These taxonomic issues highlight the need for increased research into western freshwater mussels.

Variation in the shape and color of western *Anodonta*.

## *Anodonta*
## General Account

### Description[15,18]

*Size:* Up to eight inches, but more commonly four to five inches.
*Shape:* Elliptical or ovate; length to height (L:H) ratio ranges from about 1.5 (ovate) to 2.0 (elliptical). Valves thin and fragile. Laterally inflated. Commonly, valves are slightly compressed toward the posterior dorsal margin and raised to form a "wing", the height of which varies among species.
*Beaks:* Small; may be elevated above the hinge line, but usually is not at all.
*Periostracum:* Color usually includes some combination of yellow, green, brown, or black. Young animals are usually lighter and shinier than adults; most shells become brownish or black with age. May have greenish rays on the posterior slope. Growth lines are usually prominent, except in old dark shells.
*Hinge Teeth:* None
*Nacre:* Usually white, though sometimes with a pinkish or bluish tint toward the posterior end.

*Anodonta* hinge that lacks lateral or pseudocardinal teeth

## Range

In western North America, *Anodonta* are widely distributed from Baja California to the Yukon Territory and Alaska[15,18]. Most of the species in this guide occur west of the Continental Divide, though *A. kennerlyi* is found east of the divide in northern Saskatchewan and Alberta. *A. beringiana* is found on the Aleutian Islands and into Kamchatka in eastern Asia.

## Life History and Habitat

Compared to most other North American mussel genera, *Anodonta* are short-lived and fast-growing[44]. They are considered generalists in terms of their reproductive requirements, and though they usually have separate sexes, some species have been shown to be hermaphroditic[44]. Fertilization presumably occurs in the summer; females are gravid from late summer through the following spring, and glochidia are released from late fall to spring[44]. For example, in lake populations of *A. kennerlyi*, gravid females were observed from late summer to the following spring, and glochidia were found on fish from fall through the spring but peaked in the spring[60]. Timing of breeding and spawning varies by species and habitat but more research is needed to understand this variability.

Glochidia are relatively large, with ventral hook-like projections on each valve that enables them to attach firmly to the fins or gills of host fish[5,49]. *Anodonta* in eastern North America are usually not highly host specific[101,109], but less is known about the biology of western *Anodonta*. In lakes on Vancouver Island, British Columbia, glochidia of *A. kennerlyi* were found on all fish species examined (four species) but prickly sculpin and threespine stickleback were more important hosts than the two trout species, possibly because the sculpin and stickleback were more prevalent in areas of the lakes where mussels were concentrated[60]. Preliminary results from a host fish study in the middle fork of Oregon's John Day River suggest that *Anodonta* found in that water body may use speckled dace as fish hosts[14]. In general, the length of time that glochidia remain on fish varies by species and may be strongly influenced by water temperature, with a shorter duration in warm water and longer encystment periods in cold water[7].

*Anodonta* grow rapidly, often reaching sexual maturity within four to five years[44]. Although data on growth of western *Anodonta* is lacking, studies on other species and in other regions suggest that growth rate varies according to factors such as physical habitat, productivity of their environment, and water temperature[2,4,67,97]. *Anodonta* may grow quickly and attain large sizes in stable, nutrient-rich water bodies such as lakes. *Anodonta* have one of the shortest life spans of all freshwater mussels, often only living ten to fifteen years[44]. They have thin shells compared to most freshwater mussels, making them vulnerable to damage from erosion and predators. Because their shells are easy to crush and pry open, predators—such as muskrats, otters, and raccoons—may prefer them to other mussels[115]. During droughts or low tides in freshwater tidal areas, predators often consume *Anodonta* in shallow sloughs.

*Anodonta* inhabit natural lakes, reservoirs, and downstream, low-gradient reaches of rivers in depositional (pool) habitats; they are more common in lentic (lake-like) habitats than either *Margaritifera falcata* or *Gonidea angulata*. Some *Anodonta* seem to be more tolerant of low oxygen than the other two western genera and can be found in small nutrient-rich waterbodies such as permanently flooded marshes, oxbow lakes, and even farm ponds[122]. Their thin shells and inflated shape allows them to inhabit silt found in the deeper areas of lakes and reservoirs. They can also occur in rivers with strong flows, especially in areas of streams where they are protected from shear stress, such as near banks, behind boulders, and in pools and eddies. Higher gradient rocky streams, favored by other western species such as western pearlshells and western ridged mussels, are more difficult environments for *Anodonta* because their thin shells are prone to damage, but *Anodonta* can still be found in these habitats. Sandbars near the mouths of tributary streams or below riffles are important habitats.

The common name "floater" has been given to all North American species of *Anodonta*. All species have thin fragile shells compared to most other native mussels, enabling them to inhabit silt because they can "float" on semiliquid substrates. A second origin of the descriptor "floater" is more morbid: mussel die-offs can occur during stressful periods in small nutrient-rich waterbodies that are subject to oxygen and temperature stress in the summer, and the build-up of gases in the shell cavity of decaying animals may "float" the light shells to the water's surface[122].

*Anodonta* are particularly vulnerable to water-level fluctuations. Dry periods and reservoir drawdowns usually expose these animals. As water levels recede, you can often see trails that *Anodonta* create in the sediment as they move toward deeper water. Few make it to deeper water—most will burrow into the sediment and die if water levels do not quickly return to normal before the mussels desiccate and overheat[122]. Marauding birds and mammals eat many that remain exposed.

## Conservation

It is difficult to assess the rarity of individual species because the taxonomy of the western *Anodonta* is still unresolved and the historical abundance of *Anodonta* populations is largely unknown. *Anodonta* populations have likely been extirpated from some historic sites in Arizona[8], California[99], Utah[76] and Nevada[50]. Populations seem to be more stable in northern areas where human influence is less severe; for example, the authors are not aware of any evidence of *A. beringiana* declining in Canada and Alaska.

One major threat to western *Anodonta* is water diversion for irrigation, water supply, and power generation. Water extractions to supply expanding human populations and agricultural demands lower groundwater tables and cause chronic low flows in many rivers. Dams have greatly altered natural habitat and fish communities in most rivers. Although some *Anodonta* may be able to tolerate impoundments and thrive in reservoirs, many reservoirs have severe annual drawdowns that lead to the extirpation of mussel populations[50]. For example, a drawdown of the Lower Granite Reservoir on the lower Snake River in 1992 killed many mussels[30].

*Anodonta* can be found in depositional habitats in downstream reaches of watersheds, where chemical and organic pollution from the watershed accumulates. In urban environments, industrial wastes, oil and chemical spills, and urban runoff can deliver enormous amounts of harmful materials into the water. Excessive turbidity, low dissolved oxygen levels, and toxic contaminants likely have a strong negative effect on mussel health. Dredging, shipping, and gravel removal also likely affect mussels.

Nonnative species are prevalent throughout the West. Many nonnative fish exist in western watersheds[66,82]; these fish may affect the distribution or abundance of native fish hosts, or consume mussels directly (such as common carp[78]). Unfortunately, the host fish of most western *Anodonta* are unknown, yet this information is vital to our ability to conserve them. Introduced bivalves, including the Asian clam (*Corbicula fluminea*), zebra mussel (*Dreissena polymorpha*), and quagga mussel (*Dreissena rostriformis bugensis*) are found in several areas west of the Continental Divide and are expected to spread even further. These species will compete with native bivalves for food or space[94,96,107].

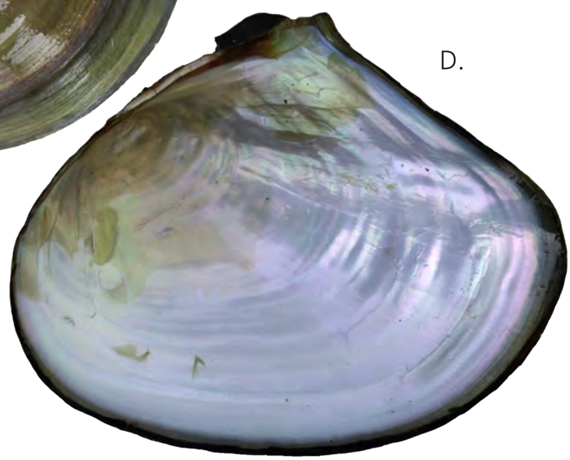
The John Day River. photo: Dennis Frates

## *Anodonta* Clade 1

### California Floater *Anodonta californiensis* Lea, 1852
### Winged Floater *Anodonta nuttalliana* Lea, 1838

### Description[15,18]

*Size:* Up to five inches.
*Shape:* Elliptical or ovate; L:H ratio usually less than 1.5. Valves laterally inflated but this trait is variable. Valves slightly to moderately compressed toward the posterior dorsal margin, broad, and raised to form a "wing". The prominence of the wing is variable. Valves are thin and fragile.
*Beaks:* Small; scarcely elevated above the hinge line.
*Periostracum:* Color is variable, with individuals appearing yellowish-green, yellowish-brown, olive, pale brown, reddish brown, or black. There are greenish rays on the posterior slope. The periostracum is smooth and growth lines are prominent.
*Hinge Teeth:* None
*Nacre:* Usually white, but sometimes with a flesh-colored, purplish, or bluish tint.


Internal and external valves of two "species" that comprise clade 1, including *A. californiensis* (A & B) and *A. nuttalliana* (C & D).

## Range

Given the recent taxonomic work suggesting that *A. californiensis* and *A. nuttalliana* belong to a single clade[17], it is difficult to denote the range of these "species" in western North America. The range map on page 25 combines ranges of these two "species". The native range of what has been called *A. californiensis* extended from Baja California to southern British Columbia, and east to western Wyoming, eastern Arizona, and Chihuahua (Mexico)[3,15]. It was originally widespread in California, but its distribution is now greatly reduced[99]. It was once distributed throughout six major drainages in Arizona, but today only remnant populations are thought to exist in portions of the Black River drainage and Little Colorado River[3]. In Washington, recent records are mainly from the Columbia River drainage[120]. *A. nuttalliana* had been considered the least common western *Anodonta*. Even before the recent genetic work was published, people had difficulty identifying this species and historical data are difficult to assess because *A. nuttalliana* was often called by other names. One reason for the confusion is that specimens of *A. nuttalliana* with a low dorsal wing are nearly indistinguishable from *A. californiensis*.

Range of *Anodonta* Clade 1 in western North America

## Life History and Habitat

More research is needed to understand the life history of this clade. Like other *Anodonta*, they are thought to be fast-growing species that reach sexual maturity in four to five years and live only ten to 15 years[44]. Host fish are unknown. Preferred habitats include shallow muddy or sandy habitats in slow rivers and lakes[30], though they are also known from some reservoirs. They can inhabit streams and rivers but usually are found in stable areas with fine sediments and little shear stress.

## Conservation

Most natural populations of *A. californiensis* in California have been extirpated, particularly in southern California and most of the Central Valley[99]. It may be nearly extirpated from Arizona[8], and is a candidate for protection in Washington. These species have historically been affected by water diversion for irrigation, water supply, and power generation. They have been found in reservoirs, but many reservoirs experience severe annual water level fluctuations that decimate the standing crop of mussels during low-water periods[50]. Nonnative fish may compete with a mussel's host fish, or eat young mussels (e.g., common carp), and nonnative mollusks can compete with mussels for food and space (e.g., Asian clams, zebra mussels, and quagga mussels).

Upper Klamath Lake. photo: Dennis Frates

## *Anodonta* Clade 2

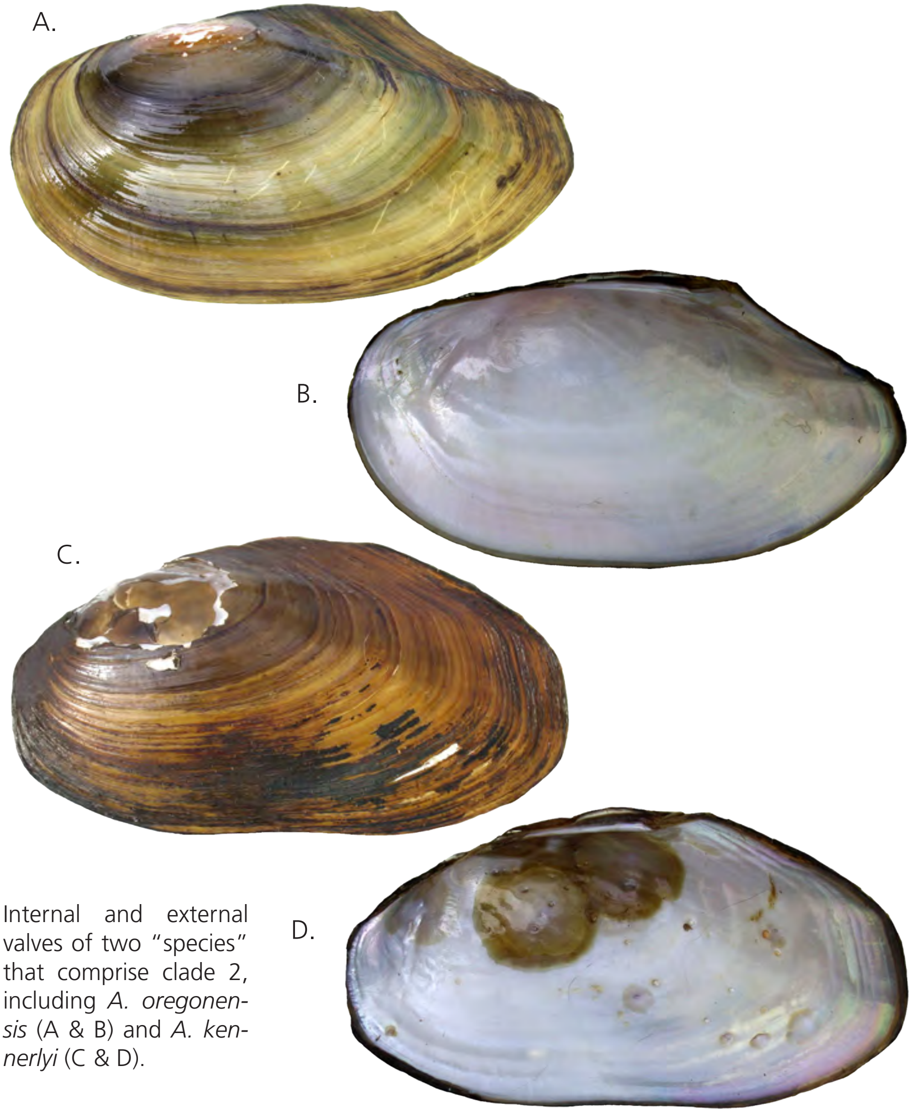
### Oregon Floater *Anodonta oregonensis* Lea, 1838
### Western Floater *Anodonta kennerlyi* Lea, 1860

### Description[15,18]

*Size:* Adult size from 4.75 to 7.25 inches.
*Shape:* Elliptical; L:H ratio close to, or exceeding, 2.0. Dorsal posterior margin may be compressed and formed into slight wing, but this trait is variable. Valves laterally inflated, thin, and fragile.
*Beaks:* Low; rarely project above the hinge line.
*Periostracum:* Yellowish, yellowish-brown, brown, or black. Some specimens may have a tinge of green. Periostracum is usually shiny, and growth lines are usually evident.
*Hinge Teeth:* None
*Nacre:* White or bluish-white, sometimes pinkish toward the central portion of the nacre and iridescent toward the posterior end.

### Range

The geographic range of this clade is in question because of the taxonomic uncertainty that has plagued these "species." *A. oregonensis* were confused with *A. beringiana* in the northern part of their range and confused with *A.*




Internal and external valves of two "species" that comprise clade 2, including *A. oregonensis* (A & B) and *A. kennerlyi* (C & D).

*californiensis* in the southern part of their range. Currently, *A. oregonensis* and *A. kennerlyi* are thought to belong to a lineage that is distinct from the other western *Anodonta*[17]. *A. oregonensis* is thought to range as far north as southern British Columbia. *A. kennerlyi* has been considered a more northern species found in watersheds of Oregon, Washington, Alaska, British Columbia, Alberta, and northern Saskatchewan[18,88]. It is found in the Peace River in British Columbia, which is part of the Arctic watershed, and also on coastal islands in British Columbia[60].

## Life History and Habitat

Range of *Anodonta* Clade 2 in western North America

*A. oregonensis* and *A. kennerlyi* inhabit low gradient rivers, lakes, and reservoirs. They often share habitat with *A. californiensis* where their ranges overlap. Like other *Anodonta*, they are likely long-term brooders that breed in the summer and spawn in the fall or spring. In lake populations of *A. kennerlyi*, gravid females were observed from late summer to the following spring, and glochidia were found on fish from fall through the spring but peaked in the spring[60]. Very little is known about host fish relationships. Coho salmon have been identified as hosts for the Oregon floater[65]. In lakes on Vancouver Island, British Columbia, glochidia of *A. kennerlyi* were found on all fish species examined (four species) but prickly sculpin and three-spine stickleback were more important hosts than the two trout species (Dolly Varden trout and cutthroat trout), possibly because the sculpin and stickleback were more prevalent in areas of the lakes were mussels were concentrated[60].

## Conservation

This clade is likely affected by the same factors that affect other western *Anodonta*, including water diversion, dams, loss of host fish species, pollution, and invasive species. Since *A. kennerlyi* is distributed in less-disturbed northern areas, it has probably not experienced the full range of stressors experienced by more southern and coastal *Anodonta*. Thorough surveys are needed to determine the current distribution of this clade, although the authors are not aware of any evidence that suggests this clade is in decline.

The Yukon floater is found in lakes and rivers of northwestern Canada and Alaska.

## Yukon Floater

*Anodonta beringiana* Middendorff, 1851

### Description[15,18]

*Size:* Up to 8.25 inches.
*Shape:* Elliptical or elongate; L:H ratio near 2. Posterior narrowly rounded. Laterally inflated over the anterior half of the shell. Valves thin but relatively strong. No wings on the dorsal posterior slope.
*Beaks:* Inflated and raised above the hinge line. Beak sculpture consists of a series of straight, irregular bars parallel to the hinge line.
*Periostracum:* Olive-green in juveniles to nearly black in older individuals. Surface roughened by growth lines.
*Hinge Teeth:* None
*Nacre:* Lead-color to dull blue.

### Range

*A. beringiana* is a northern species of the Yukon Territory, Alaska, Aleutian Islands, and Kamchatka in eastern Asia[15,18]. It was historically thought to occur in the Fraser and Columbia River systems of British Columbia[39], but recent records have not confirmed this. There are historical museum specimens of *A. beringiana* from Oregon and Washington[47], but the problems associated with identifying western *Anodonta* based on shell morphology alone makes it


Internal and external valve of *A. beringiana*.

difficult to validate the identity of these records[121].

## Life History and Habitat

*A. beringiana* inhabits lakes and rivers in sand and gravel substrates. It is often very abundant, providing a staple food source for otter and muskrat. Host fish include sockeye salmon, Chinook salmon, and threespine stickleback[19].

Range of *Anodonta beringiana* in western North America

## Conservation

*A. beringiana* may be the most stable of western *Anodonta* because of its northern distribution, with little human disturbance in its range. More research is needed into the taxonomy, historical and current distribution, life history and threats to this species.

Small wooded creeks often have abundant populations of western pearlshells. photo: Danielle Warner

## Western Pearlshell

*Margaritifera falcata* (Gould, 1850)

### Description[15,18]

*Size:* Up to five inches

*Shape:* Elongate, with a broadly curved dorsal margin and slightly concave ventral margin.

*Periostracum:* Light brown (juveniles) to dark brown or black. No shell rays, but growth lines are prominent and heavy.

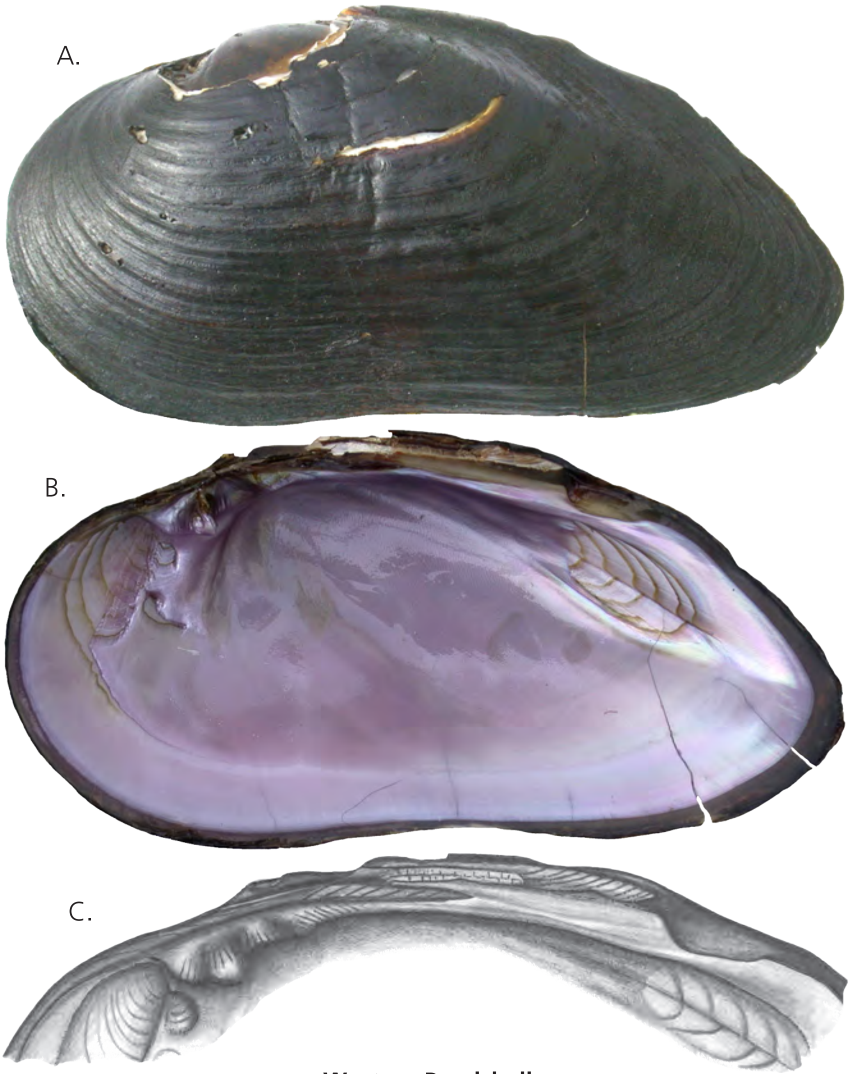
*Lateral Teeth:* One poorly defined lateral tooth on each valve, though these are sometimes hard to distinguish.

*Pseudocardinal Teeth:* Right valve has one triangular-shaped tooth that is slightly down-turned. Left valve has two triangular-shaped teeth; the posterior tooth is larger with a ragged edge, and the anterior tooth is smaller and sometimes indistinguishable.

*Nacre:* Usually purple, salmon-colored, or pink (sometimes white). Nacre color fades to white over time. Anterior adductor muscle scar is sharply defined, whereas the posterior adductor muscle scar is less defined. Tiny faint pits are sometimes evident on the central part of the nacre.

### Range

*M. falcata* is found in Pacific drainages from California to British Colum-




**Western Pearlshell**

A. External shell (left valve) B. Internal shell (right valve) C. Hinge (right valve)

bia and southern Alaska[18,30,50]. Some scientists consider some of the coastal and large-river populations extirpated, nearly extirpated, or declining rapidly[13,30,41,99]. This species is still common throughout parts of the northern Rockies[18,105], although some populations in Montana may be declining[90]. It is also found east of the Continental Divide in the headwaters of the Missouri River. Originally, these populations were thought to be the eastern species *M. margaritifera* but recently scientists have confirmed that the populations are *M. falcata* and that the species crossed the divide[32]. The most likely explanation for this distribution is headwater capture, where pre-glacial watersheds were cut and reconfigured by glacial advance or retreat. West-slope cutthroat trout are thought to have crossed the Continental Divide from the West into the headwaters of the present-day Missouri River during the Pleistocene glaciation, more than 20,000 years ago[102]. Since cutthroat trout are an important host for *M. falcata*, it is likely that mussels hitched a ride on the trout.

Range of *Margaritifera falcata* in western North America

## Life History and Habitat

*M. falcata* is one of four North American species that may be hermaphroditic[43], meaning that individuals may have both male and female reproductive traits. However, this condition is rare in *M. falcata* populations, and most populations have separate sexes. Precise timing of breeding and release of glochidia is not known. Fertilization is thought to occur in the spring and gravid females may be found from late summer to early spring. In *M. margaritifera*, the timing of glochidia release and the amount of time spent attached to host fish are strongly influenced by temperature[42,87,119]. Glochidia of *M. falcata* were released from mid-June to early July in the Truckee River of California, when water temperatures increased from 10 degrees to 15 degrees Celsius[68]. For the closely related *M. margaritifera*, release of glochidia may occur over a period of several months beginning in late summer, and glochidia may overwinter on the gills of host fish. Host fish for *M. falcata* are thought to include native and non-native trout and salmon, including cutthroat trout, rainbow trout, Chinook salmon, coho salmon, redband trout, sockeye salmon, steelhead trout, brook trout, and brown trout[31,54,62,68,123]. Non-salmonid hosts have been suggested based on limited laboratory tests[68]. Average life spans of *Margaritifera* are sixty to seventy years, with some living more than one hundred years, making them among longest-lived animal species on Earth[6,118].

*M. falcata* seem to prefer cold clean creeks and rivers that support salmonid populations. They can inhabit headwater streams less than a few feet wide, but are more common in larger rivers. Less commonly, this species can be found in more degraded habitats such as irrigation ditches in Washington and Oregon. Sand, gravel, and cobble are preferred substrates, especially in stable areas of the streambed. Large boulders help create these stable environments by anchoring the substrate and creating a refuge from strong currents[105]. Banks and pools are often favorable habitats because the currents are weaker, shear stress is lower, and the substrates are more stable[51,92]. *M. falcata* does not tolerate sedimentation. In Idaho's Salmon River, *M. falcata* covered with a substantial amount of sand and gravel were unable to move to the surface and perished[105]. In environments where host fish are abundant, physical habitat is ideal, and human threats are minimal, *M. falcata* can attain very high densities (>300 per square yard), often carpeting the stream bottom. In 1981, Clarke wrote, "In favourable localities in British Columbia the mussels may be so abundant and closely packed that they completely obscure the stream bottom."[18]

## Conservation

Recent conservation concerns about *M. falcata* closely mirror well-known stories of the decline of Pacific salmon fisheries. Both need clean cold streams and rivers, and *M. falcata* reproduction requires salmon and trout hosts. The greatest threats to western pearlshells come from loss of host fish species and water diversion projects for irrigation, power generation, and water supply, particularly in Washington, Oregon, Idaho, and California. Dams destroy many miles of free-flowing rivers, disrupt native fish communities, and may have contributed to the demise of many populations of western pearlshells. Agriculture and rapid urbanization are affecting aquatic ecosystems throughout the West through nutrient enrichment, siltation, and chemical pollution, all of which may negatively impact western pearlshells. Climate change has been implicated in the decline of the closely related *M. Margaritifera* in North America and Europe[40] and it is likely that *M. falcata* will be affected in similar ways.

Invasive species that compete with native fish may affect *M. falcata*. In some locations where western pearlshells are still abundant, native cutthroat trout are being replaced by nonnative rainbow, brown, and brook trout[27,28,48,81]. The long-term effects of increasing nonnative fish populations on native mussels, albeit with fish species that may also serve as hosts, are

illustration: Ethan Nedeau

The cutthroat trout is an important host species for *Margaritifera falcata* unknown. Native hosts with which mussels have coevolved might be superior to nonnative hosts because their populations may be more stable in the long-term. Also, the mussel may be specifically adapted to traits unique to its native host, such as habitat use, behavior, and lack of immune responses to glochidial parasitism[5].

*M. falcata* has been extirpated throughout much of the mainstem Snake River and Columbia River of Oregon and Washington[13,30] and has dramatically declined in abundance in one area of the Truckee River of California[111]. This species historically existed in northern Utah, but has probably been extirpated from the state[76]. The range of *M. falcata* is also contracting in Montana; historical populations from some larger rivers such as the Blackfoot, Big Hole, Bitterroot, and Clark Fork have been extirpated from the entire drainage, or are only present in low numbers[90]. Many historic sites have been lost and some populations show little evidence of recruitment[41,52]. The fate of this species throughout much of its native range remains uncertain.

The Crooked River is home to populations of western ridged mussels. photo: Dennis Frates

## Western Ridged Mussel

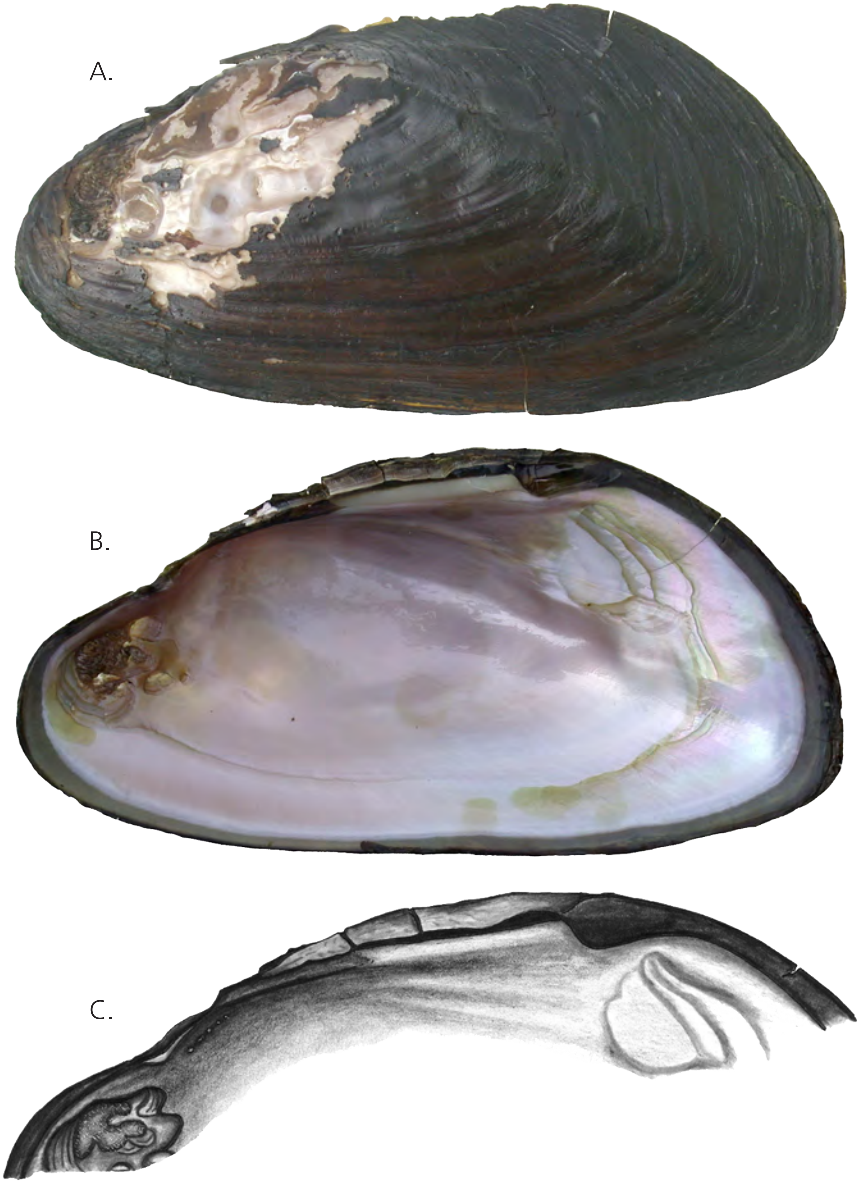
*Gonidea angulata* (Lea, 1838)

### Description[15,18]

*Size:* Up to five inches
*Shape:* Obovate to trapezoidal. Slightly laterally compressed. The shell has an angular ridge that runs from the beak to the basal part of the posterior margin; this ridge may be less angular in specimens living in slow-moving water. The ventral margin is usually straight. The shell is heavier than that of all other native species.
*Periostracum:* Color yellowish-brown to brown or black. No shell rays or sculpturing on the shell.
*Lateral Teeth:* Absent.
*Pseudocardinal Teeth:* The right valve has one small tooth and the left valve has either one small tooth or none at all. The teeth are small and compressed, sometimes hard to distinguish.
*Nacre:* Usually white, but sometimes salmon-colored in fresh specimens and pale blue toward the posterior margin and beak cavity.

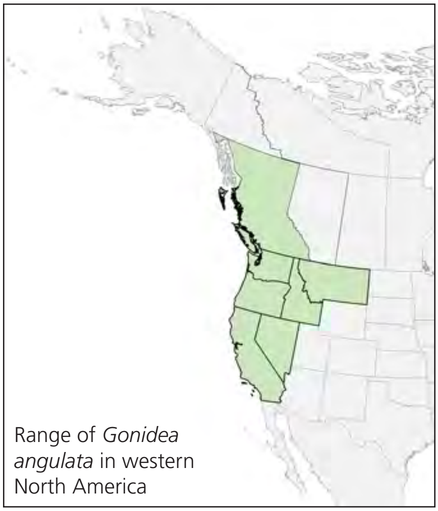
### Range

Also known as the Rocky Mountain ridged mussel, this species is widely distributed west of the Continental Divide from California to British Colum-




**Western Ridged Mussel**
A. External shell (left valve), B. Internal shell (right valve), C. Hinge (right valve)

bia[21,30,99]. It is found east to Idaho and Nevada, and in the northern part of its range it is mainly distributed east of the Cascades but also occurs on the west side[30]. There is a historical record from the Columbia River in western Montana, although this record is problematic because the Columbia River is not in Montana. Some researchers reason that the record was probably from the Clark Fork River or Kootenai River in the Columbia River headwaters, but these species are not now known to occur in these waters and they may have been extirpated following the construction of two impoundments or due to metal contamination[32]. Its strongholds are in large tributaries of the Snake River and Columbia River in Washington, Idaho, and Oregon[30].



Range of *Gonidea angulata* in western North America

## Life History and Habitat

Little is known about the life history of this species. Gravid females have been found during the months of April through July[21]. Glochidia are released individually in watery mucous, or within light-colored leaf-like conglutinates[5]. Fish host species are unknown. It is a relatively slow-growing, long-lived species; some authors have suggested a lifespan of 20-30 years[21,105] based on counting its growth rings, but this method can be an unreliable way to age mussels[25].

Habitat descriptions are provided in survey reports[21,30]. *G. angulata* occur in streams of all sizes and less frequently in lakes. They are found mainly in low to mid-elevation watersheds. They often share habitat with *M. falcata* throughout much of the Pacific Northwest, but their range rarely extends into high elevation headwater streams where *M. falcata* may occur. Like other stream-dwelling species, they are more common in stable stream reaches and tend to avoid areas with shifting sediments or areas prone to scour or frequent dewatering. However, *G. angulata* seem to be more tolerant of fine sediments than *M. falcata* and may occupy depositional habitats and banks. For example, in the Salmon River, Idaho, where both species co-occur, *G. angulata* dominated in sand and gravel bars, comprising 97.1 percent of overall mussel density, but in more stable, boulder-dominated reaches nearby, *M. falcata* comprised 94.9 percent of overall mussel density[105]. Thus, distinct habitat preferences allow for habitat partitioning in streams where *M. falcata* and *G. angulata* co-occur. Unlike *M. falcata*, *G. angulata* also occurs in impoundments and natural lakes, including nutrient-rich waterbodies and in soft substrates to water depths of ten feet[21].

## Conservation

*G. angulata* have disappeared from their original range in California, particularly in southern California and the Central Valley[99], as well as from many sites in the Snake and Columbia River basins, presumably due to environmental degradation[13,21,30]. However, the magnitude and geographic extent of the declines are not fully known. There is a critical need to understand the life history, reproduction, distribution and ecology of *G. angulata* in order to effectively conserve and manage them. In the absence of further research, it is prudent to take measures to protect the aquatic ecosystems where they currently exist.

## Other Freshwater Bivalves

### Native Clams: Family Sphaeriidae

The Family Sphaeriidae contains three genera and at least 20 species native to western North America, including *Pisidium*, *Sphaerium*, and *Musculium*[16,61]. Commonly known as fingernail clams and pea clams, they are much smaller than native mussels (less than one inch long) but are sometimes mistaken for juvenile mussels. Aside from obvious size differences, fingernail and pea clams have thinner shells, different teeth morphology and life histories than mussels, and their mantles are fused to form true siphons (as opposed to the unfused "apertures" of mussels). One of the more interesting aspects of their reproduction is that although they are the smallest aquatic bivalves in North America, they have the largest young and have the lowest fecundity. They occupy a wide range of habitats, including those where mussels are not present, such as intermittent streams, vernal pools, and other wetlands. The clams tend to be more tolerant of harsh environmental conditions than mussels, including low dissolved oxygen and warm water temperatures, and some even tolerate periodic drying[61].

### Asian Clam (non-native)
*Corbicula fluminea* (Müller, 1774)

The Asian clam is a small bivalve, usually less than one inch long, which resembles a small marine clam. The beak is centrally located on the dorsal margin and there are lateral teeth on both sides of the beak[61]. The beak is high, giving Asian clams a triangular or acutely oval shape. The serrated lateral teeth are a distinct identifying character. Asian clams are usually yellowish, light to dark brown, or black, depending on age and environmental conditions, and have prominent growth ridges on the outer shell.

The Asian clam is native to Southeast Asia and was introduced to North America in the early 1900s[22]. It spread throughout southern parts of North America and became very abundant in some locations. In the Pacific Northwest, Asian clams are often the most numerous bivalve in some waterbodies, especially in shallow water. Along the lower Columbia River, hundreds of thousands of Asian clam shells litter the shoreline[122]. This species is tolerant of a variety of environmental conditions, and seems to prefer medium to large rivers in sand or gravel substrates. The species was recently discovered in Lake Tahoe in a sandy area near a residential development at the south end of the lake[38]. Water temperatures below 35-37°F were once considered lethal[86], and its presence in cold northern waters was often the result of thermal pollution, such as cooling water from nuclear power plants and other industries. However, the species now occurs in colder waters throughout northern North America, suggesting it may have adapted to colder conditions. They compete with native mussels for food, consume larval or juvenile mussels, and affect nutrient cycling[57,94,107]. Asian clams do not require a host fish for larval survival and dispersal, giving them a reproductive advantage over native freshwater mussels.

## Zebra Mussel and Quagga Mussel (non-native)

*Dreissena polymorpha* (Pallas, 1771) and
*Dreissena rostriformis bugensis* Andrusov, 1897

Zebra mussels and quagga mussels are native to the Caspian and Black Sea region of Eastern Europe. Both were accidentally introduced to the Great Lakes and St. Lawrence River in North America in the late 1980s, arriving in ballast water of trans-Atlantic freighter ships. These species quickly spread throughout the Great Lakes and Mississippi River drainage, and within a decade their ranges spanned much of the eastern two-thirds of the United States[45,63,94].

Zebra and quagga mussels are among the most destructive nonnative aquatic invertebrate species ever to reach the North American continent. They have economic consequences for water-dependent industries, boating, and fishing. They clog intake pipes and cover boat hulls, docks, piers, and virtually any other underwater structure. They have great reproductive and colonization capabilities over native mussels, as they have free-swimming larvae and do not require host fish to complete their life cycle. Densities as high as 750,000 per square yard have been reported, and the cumulative filtering capacity of billions of zebra mussels has profound effects on water clarity, nutrient cycling, and food webs. In Lake St. Clair in the Great Lakes region, once zebra mussels reached densities greater than 5,000 per square yard, they filtered the entire volume of the lake one to two times daily[45]. Native freshwater mussels are particularly vulnerable because zebra mussels attach to their shells, thereby inhibiting feeding and restricting mobility[59,85,94,96]. Zebra mussels and quagga mussels may ultimately be responsible for the extirpation of dozens of native mussel species throughout eastern and midwestern North America.

Zebra mussels
photo: U.S. Geological Survey

Humans are the main vectors for spreading zebra and quagga mussels. Adults and juvenile mussels attach to boat hulls or to vegetation that gets entwined in boat propellers or trailers. Boats transported from infected waterbodies spread the mussels into new waters if the boats and trailers are not properly cleaned. Bilge water, live wells, and bait buckets are other means of introduction. *Dreissena* had not been found west of the Continental Divide until January 2007 when it was discovered in Lake Mead, and currently (May 2009), zebra and quagga mussels have been found in 33 waterbodies in Nevada, Arizona, California, Colorado, and Utah.

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