Freshwater Mussels
and the
Connecticut River Watershed

Chapter 1: Biology and Ecology

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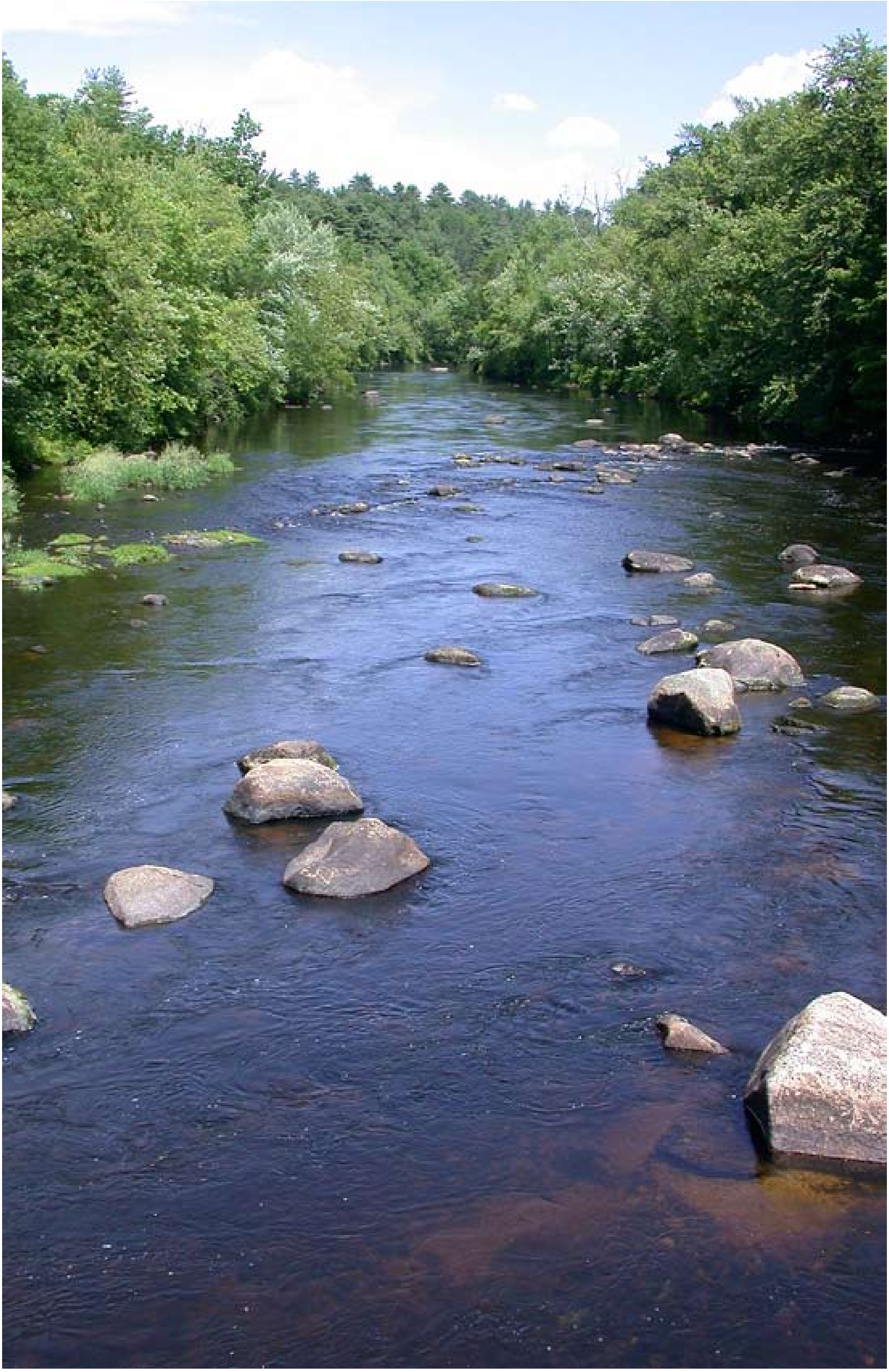

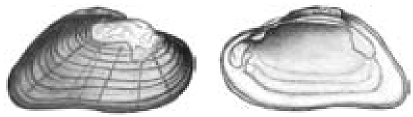

CHAPTER 1

Biology and Ecology

Learning mussel biology and ecology is the first step in learning to decipher their untold stories. The 12 species that occur in the watershed provide 12 unique perspectives on the history and health of the Connecticut River, its tributaries, and its lakes. Aspects of their reproduction, growth, survival, behavior, and habitat determine their sensitivity to variable environmental conditions and human-caused threats. Likewise, the condition of individuals, populations, and communities may provide insight into the health of aquatic ecosystems. It is important to become well versed in the biology and ecology of each species—especially imperiled species—to appreciate efforts to protect and restore freshwater mussels in the Connecticut River watershed.

I. MORPHOLOGY

The most prominent feature of a freshwater mussel is its pair of shells, or valves, that protect the animal (Figure 1). The two shells are mirror images and are connected by an elastic-like ligament along a portion of the dorsal surface of the shell called the hinge. The raised and rounded area on each shell is called the beak; shells grow outward from the beak in a concentric pattern. Many species have one or two types of structures along the hinge, called teeth. The teeth interlock and help to create a solid connection between the two shells. Lateral teeth are long, thin structures that lie parallel to the hinge. Pseudocardinal teeth are more tooth-like structures located toward the anterior end of the shell, usually below the beak. Different species may have obvious teeth, inconspicuous teeth, or no teeth at all.

Mussel shells are comprised largely of calcium carbonate. On the outside, shells are covered with a material called periostracum that give shells their characteristic color, and in some species, colored rays that radiate outward from the beak. The hard and durable periostracum protects underlying shell material from physical abrasion and from being dissolved by acidic water. On the inside, shells are lined with nacre, which is a strong and iridescent material commonly known as "mother of pearl." Pearls are comprised of nacre.

The shell is the non-living portion of the animal; the living mussel occupies the space in between the two shells. Two strong adductor muscles control whether the shells are gaped

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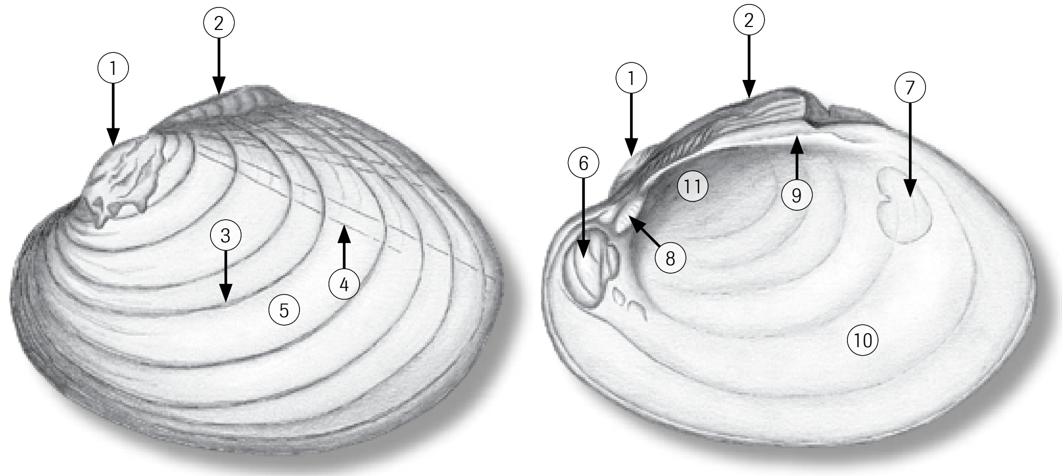
Photo: The Ashuelot River near Winchester, New Hampshire. This river supports a higher diversity than any of New Hampshire's Connecticut River tributaries. Ethan Nedeau



1. **Beak:** rounded or raised area along the dorsal side of a shell valve
2. **Hinge:** portion of the dorsal margin where two valves connect
3. **Growth line:** concentric ring on the shell that indicates a period of slow growth
4. **Shell ray:** lines radiating from the beak that are perpendicular to growth lines
5. **Periostracum:** the colored outer lining of a mussel shell
6. **Adductor muscle scar:** attachment site of the anterior adductor muscle
7. **Adductor muscle scar:** attachment site of the posterior adductor muscle
8. **Pseudocardinal teeth:** thick and often stout teeth located under the beak
9. **Lateral teeth:** long thin teeth that are parallel to the hinge
10. **Nacre:** mother-of-pearl inner lining of a mussel shell
11. **Beak cavity:** deep recessed portion of the inner shell, located under the beak

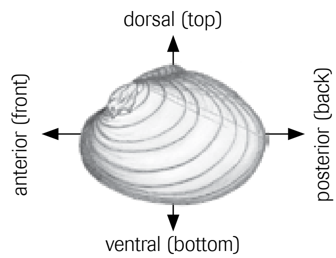


Figure 1. Typical shell morphology of a freshwater mussel. The species shown here is the yellow lampmussel.
Illustrations by Ethan Nedeau.

(muscles relaxed) or tightly closed (muscles contracted); the attachment sites of these mussels are evident on the shells. The attachment site of the anterior adductor muscle is always more prominent than the posterior adductor muscle. The ability of an animal to survive predators, desiccation, and other challenging environmental conditions depends, in part, on the strength of its adductor muscles and the strength of its shell.

The foot is a large and prominent muscle that is used for locomotion and feeding. Mussels extend their foot between the shells along the antero-ventral margin. By relaxing and contracting the foot, mussels can move vertically or horizontally in the substrate, sometimes at surprising speeds and distances…for a mussel! A determined mussel might match the speed of a garden slug and move ten to perhaps 100 meters if compelled to do so; the primary reasons for such movement are to seek more favorable habitat conditions. Juveniles, which generally remain fully buried in the substrate, use their foot to pull food into their body. The foot is usually visible when live animals are first removed from the substrate, but it is quickly drawn into the shell cavity.

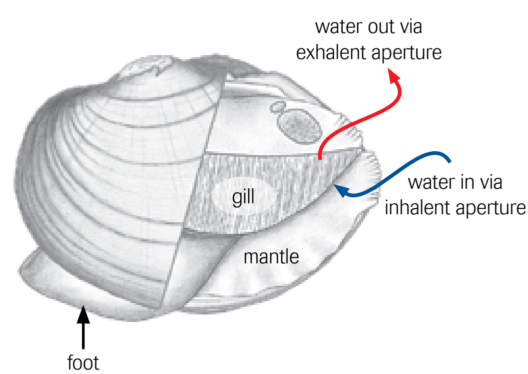
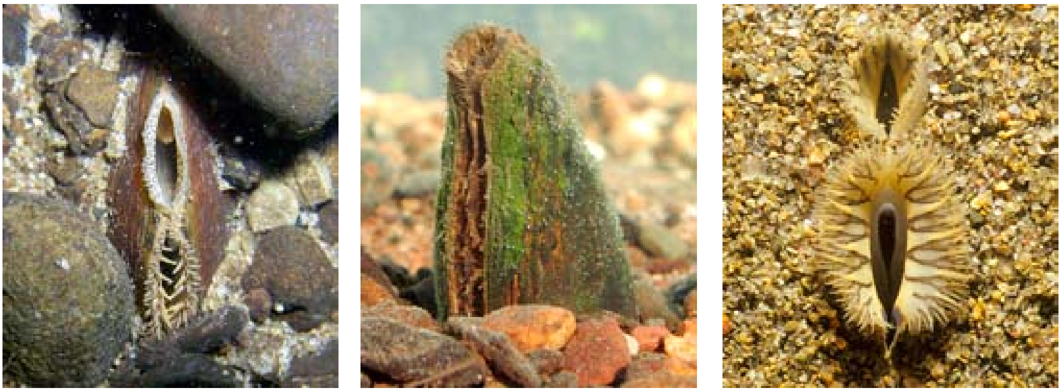


Figure 2. Major internal features and filter-feeding apparati of freshwater mussels.
Illustration by Ethan Nedeau; figure adapted from Nedeau *et al.* 2005.



Three mussel species undisturbed on the stream bottom, including the creeper (left), eastern pondmussel (middle), and tidewater mucket (right). This is how live mussels are typically seen—partially buried in the substrate with their posterior end pointing up and inhalent and exhalent apertures visible from above. Jeff Grabarkiewicz (left), Don Pugh (middle), and André Martel, reproduced with permission of the Canadian Museum of Nature, Ottawa, Canada (right).

The mantle is a thin sheet of living tissue that lines the shell and envelops the body of the mussel. The margins of the mantle are modified at the posterior end to form inhalent and exhalent apertures. Mussels are filter feeders; they draw water (along with food and sperm) into the inhalent aperture, and expel filtered water, waste, and larvae through the exhalent aperture (Figure 2). The other prominent feature of a mussel is its large gills, or demibranchs, that serve three important functions. These functions include respiration (similar to gills in other aquatic animals) and filter feeding in both sexes, and female gills have pouches called marsupia where eggs are fertilized and embryos develop.

II. LIFE CYCLE

For a group of animals that lead somewhat sedentary adult lives, freshwater mussels have an amazing life cycle (Figure 3) and exhibit fascinating behaviors. Many of the interesting behavioral traits of mussels are associated with reproduction. Although mussels have been studied for centuries, biologists are only now uncovering some of the more unusual aspects of their lives and behaviors. Many basic questions about their biology are still not known, even for some of the most imperiled species in North America.

Freshwater mussels have separate sexes. During the breeding season (usually early summer through early fall for northeastern species), males release sperm into the water and females must filter it from the water, where it then fertilizes eggs in the marsupium. Breeding success is more likely in populations with a high density of males and females, and at times when environmental conditions (e.g., flow and temperature) favor the survival of sperm and increase the encounter rates with females. Low-density populations are often plagued by chronic failure to breed due to a low number of breeding animals and vulnerability to stochastic events during the breeding season, such as floods. Individuals of some species can become hermaphroditic (having male and female reproductive traits) and capable of self-fertilization under conditions of low population density (Kat 1984, Bauer 1987), but it is not clear how common and effective this strategy is for mussels in the Northeast. Lake populations of eastern elliptio have been shown to move closer together during the breeding season to increase chances of fertilization (Amyot and Downing 1998).

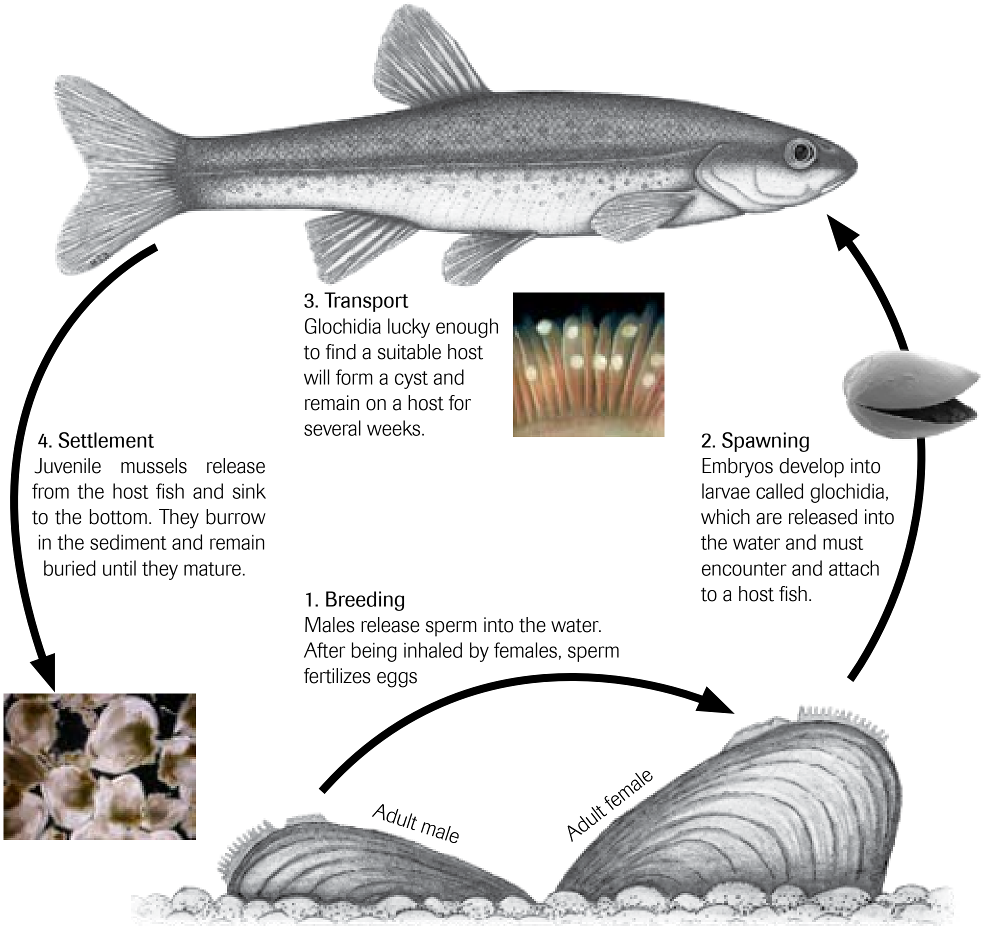


Figure 3. Life cycle of a typical freshwater mussel.

Illustrations: Ethan Nedeau; glochidia image: U.S. Geological Survey; encysted glochidia and juveniles: Chris Barnhart. Figure adapted from Nedeau *et al.* 2005.

Freshwater mussel larvae are called glochidia. Glochidia develop into what look like miniature mussels that range in size from 0.002 to 0.02 inches (0.05 to 0.45 millimeters) (Bauer 1994). To complete larval development and metamorphose into juveniles, larvae typically attach to an aquatic vertebrate—usually a fish—for a period of a few days to a few months. When environmental conditions are favorable, usually in early spring to late summer for northeastern species, females begin to release glochidia into the water where they must find a suitable host. They attach to the fins or gills of fish, but the glochidia of the creeper may also attach to two-lined salamanders and eastern newts (Gray *et al.* 2002).

Dwarf wedgemussel glochidium. Barry Wicklow

Host fish for mussels of the Connecticut River watershed are not entirely known but have been researched in recent years (Table 1).

Table 1. Host fish for freshwater mussels of the Connecticut River watershed.

Species	Host Fish	References
Dwarf Wedgemussel *Alasmidonta heterodon*	Tessellated darter, slimy sculpin, mottled sculpin*, Atlantic salmon (parr), striped bass, banded killifish	Michaelson and Neves 1995, White 2008, Barry Wicklow, Saint Anselm College
Triangle Floater *Alasmidonta undulata*	Common shiner, blacknose dace, longnose dace, pumpkinseed sunfish, fallfish, slimy sculpin, white perch, white sucker, largemouth bass*	Watters *et al.* 1999, Barry Wicklow, Saint Anselm College, Kneeland and Rhymer 2008
Brook Floater *Alasmidonta varicosa*	Longnose dace, blacknose dace, slimy sculpin, golden shiner, pumpkinseed sunfish, yellow perch, margined madtom, tessellated darter	Barry Wicklow, Saint Anselm College
Alewife Floater *Anodonta implicata*	American shad, alewife, blueback herring. Possibly striped bass	Davenport and Warmuth 1965, Knneland and Rhymer 2008
Eastern Elliptio *Elliptio complanata*	White perch, yellow perch, American eel, alewife, blueback herring, threespine stickleback, banded killifish, white sucker, pumpkinseed sunfish, redbreast sunfish, black crappie*, largemouth bass*, smallmouth bass*, brook trout, lake trout, mottled sculpin*	Wiles 1975, Watters 1994, Lellis *et al.* 2001, Kneeland and Rhymer 2008
Yellow Lampmussel *Lampsilis cariosa*	White perch, yellow perch. Striped bass possible but not tested**. Potential species: banded killifish, chain pickerel, white sucker, smallmouth bass, largemouth bass.	Wick 2003, Kneeland 2006, Kneeland and Rhymer 2008
Eastern Lampmussel *Lampsilis radiata*	Generalist. Yellow perch, largemouth bass*, smallmouth bass*, black crappie*, pumpkinseed sunfish	Watters 1994, Kneeland and Rhymer 2008
Tidewater Mucket *Leptodea ochracea*	White perch, banded killifish. Striped bass possible but not tested**.	Wick 2003, Kneeland 2006, Kneeland and Rhymer 2008
Eastern Pondmussel *Ligumia nasuta*	Unknown: anadromous or coastal.	
Eastern Pearlshell *Margaritifera margaritifera*	Atlantic salmon, brook trout, brown trout, rainbow trout	Smith 1976, Cunjak and McGladdery 1991
Eastern Floater *Pyganodon cataracta*	Generalist: Warmwater species. Published examples include white sucker, carp*, threespine stickleback, pumpkinseed sunfish, bluegill*	Wiles 1975, Watters 1994, Gray *et al.* 1999
Creeper *Strophitus undulatus*	Generalist: Creek chub, longnose dace, blacknose dace, fallfish, golden shiner, common shiner, white sucker, pumpkinseed sunfish, bluegill*, largemouth bass*, rock bass*, yellow perch, tessellated darter, slimy sculpin, yellow bullhead, Atlantic sturgeon, Atlantic salmon, two-lined salamander, red-spotted newt	Watters *et al.* 1999, Gray *et al.* 2002, Barry Wicklow, Saint Anselm College

* Species not native to the Connecticut River watershed

** White perch and striped bass are in the same genus (*Morone americana* and *Morone saxatilis*) and striped bass are prevalent in many of the large coastal rivers within the current range of the tidewater mucket and yellow lampmussel. This is particularly evident for the mainstem Connecticut River. Striped bass have not been tested as hosts for yellow lampmussels or tidewater muckets.

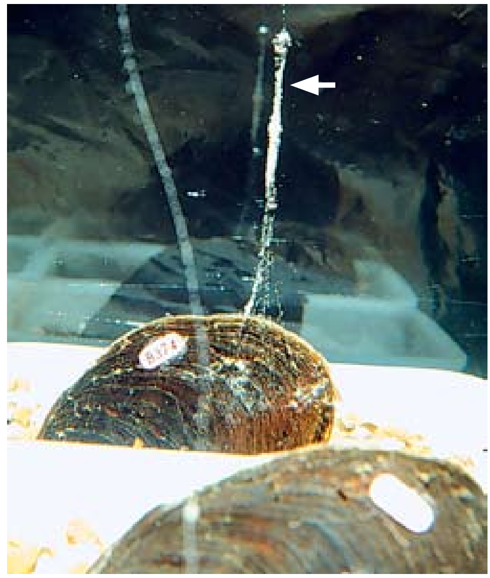
Mussels are often labeled as "generalists" or "specialists" with regard to the variety of fish they will use as hosts. Reproduction among host specialists tends to rely on the distribution and dynamics of its host fish, adding uncertainty to an already tenuous reproductive strategy. For example, the alewife floater relies on three species of anadromous fish: American shad, alewife, and blueback herring. Loss of these species in areas upstream of impassable dams will eliminate the alewife floater; likewise, restoring these species by removing dams or providing fish passage will restore the alewife floater (Smith 1985). Declining stocks of river herring in the mainstem Connecticut River and its tributaries may be mirrored by the dynamics of alewife floater populations. Widespread stocking of brook trout, brown trout, and rainbow trout in rivers throughout the Connecticut River watershed may help to sustain populations of the eastern pearlshell in streams that have become too warm and degraded to support self-sustaining populations

When gravid and ready to release glochidia, female yellow lampmussels display colorful mantle margins that are intended to lure host fish. The mantle has extensions that resemble the tail of a small fish and a dark eyespot on the other end; females undulate, or "wiggle" this lure to draw fish closer. Chip Wick

of salmonids. Some species are thought to have a large number of hosts (i.e., host generalists). This understanding is either based on actual host suitability studies (e.g., creeper and triangle floater) or is inferred from the wide distribution and high abundance of a species in habitats with different fish communities (e.g., eastern elliptio and eastern lampmussel).

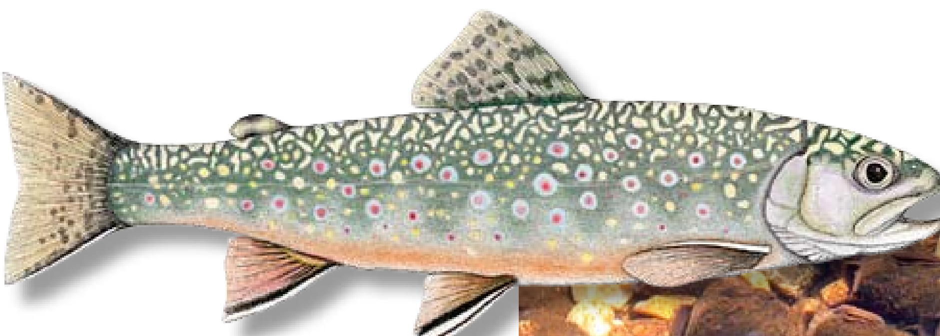
The odds of a single glochidium finding and attaching to a host are very slim, but females have very high fecundity and exhibit behaviors that help to increase the odds (Kat 1984). The eastern pearlshell will expel millions of glochidia each spawning season. Several species release glochidia with stringy mucous webs that may ensnare a fish's fins. Species such as the creeper and eastern lampmussel bind glochidia in packets called conglutinates, with shapes or colors that mimic the natural prey of their host fish, such as worms, insect larvae, or small fish. When fish attack, conglutinates rupture and the fish get a mouthful of glochidia. The yellow lampmussel and eastern lampmussel have mantle margins modified with bright colors and fleshy lobes (complete with eyespots!) that they undulate to look like prey of predatory fish. During spawning, females of the yellow lampmussel, eastern lampmussel, and eastern pondmussel (and perhaps others) often move up in the substrate to "stand on their tippy toes" and expose their mantle margins to make themselves more visible to fish. Female mussels will often discharge their glochidia at just the right moment to give the fooled fish a mouthful of glochidia.

The parasitic phase of a mussel's life represents the only potential for long-distance dispersal within a waterbody or watershed. Glochidia may remain attached for several days to several months, during which time fish may swim great distances (particularly migratory species). A shad infected with alewife floater glochidia in southern Connecticut could swim all the way to southern Vermont before glochidia release from the fish. Once the parasitic stage is complete, the glochidia metamorphose into juvenile mussels, release from the fish, burrow into the sediment, and spend the rest of their lives as free-living animals.



The eastern elliptio binds its glochidia to long strands of mucous that ensnare fish (arrow). Swimming among a high-density patch of elliptio during the spawning season, when the water is teeming with these strands, helps one gain an appreciation for why elliptio exhibits such high reproductive success. William Lellis/U.S. Geological Survey.

Mussels spend their early years completely buried in the sediment. During this time, they grow fast to overcome predation risks and to resist the crushing and erosive force of rocks and water. Growth rate depends on a variety of factors, including the age and condition of the animal, availability of essential nutrients, and water temperature. Growth rates slow as mussels mature and begin to put more energy into sexual development. Most northeastern species are sexually mature by five to six years of age. Once mature, they spend most of their lives partially buried, with their posterior end extended above the surface of the sediment. In the winter, most mussels burrow into the sediment and become dormant until spring arrives. Life spans vary widely but generally range from eight to more than 100 years; most northeastern species likely do not live longer than 30-40 years. However, the eastern pearlshell, which is common in coldwater streams of the Connecticut River watershed, is one of the longest-lived invertebrates in the animal kingdom; Bauer (1987) reported average life spans of 73 years and maximum life spans of 150 years for the same species in Germany.



Despite living in some of the most physically challenging environments in the watershed—small coldwater streams—the eastern pearlshell is the longest-lived freshwater mussel on Earth and among the longest-lived animals in the entire animal kingdom. It relies on salmonids to reproduce, notably brook trout and Atlantic salmon.

Ethan Nedeau photo and illustration.

ASSESSING FRESHWATER MUSSEL POPULATIONS

Many types of information can be gathered when studying freshwater mussels. The simplest is the presence of species at a particular location, but this basic information provides little or no information about the health of a population. The information below should be gathered because it tells a much more complete story, and because it can often be done quickly and inexpensively (see Strayer and Smith 2003).

- **Age or size data** can reveal phenomena such as poor reproduction (if no young or small animals are present), low adult survival (if no older animals are present), or a population dominated by individuals of a certain age. They may also reveal healthy populations with strong recruitment and high adult survival. Age can be difficult to determine (methods reviewed in Nedeau *et al*. 2000) but the size distribution of animals, determined by measuring each animal that is encountered, can provide a suitable alternative to age data (see figure below).
- **Population density** is the number of individuals within a defined area. High population density may indicate a healthy and stable population whereas low population density may be cause for concern. Combined with age or size data, population density can be used to qualitatively (and subjectively) assess likelihood of spawning success.
- **The condition of individual animals**, such as the degree of shell erosion, shell deformities, and staining on the periostracum can provide insight into longevity of individuals and the severity of environmental conditions.
- **The amount, distribution, and continuity of habitat** at multiple spatial scales (portions of rivers, entire rivers, and entire watersheds) can provide important context when assessing the health of populations. Habitat is discussed in Chapter 2.

This information is particularly valuable when gathered in the same location over a long period (i.e., long-term monitoring), or used to compare populations in different portions of rivers, entire rivers, or entire watersheds. Detailed studies like these in high-priority rivers will greatly benefit freshwater mussel conservation.

Figure: This is an example of a size-frequency histogram. It is used to illustrate the size range of individuals in a population, which is important for assessing population health. Population A exhibits a range of sizes, with evidence of reproduction and longevity. Population B is comprised of older animals and there is no evidence of reproduction; this population may be of concern. Population density, shell condition, availability of fish hosts, and habitat would provide supporting information for this simple analysis.

Hundreds of eastern elliptio are seen here in an area less than one square meter. This mussel bed in the Holyoke Canals was exposed when water was emptied for routine mainenance. Ethan Nedeau

III. ECOSYSTEM ROLE

Mussels are important to food webs, water quality, nutrient cycling, and habitat quality in freshwater ecosystems. They filter suspended algae, bacteria, zooplankton, and sediment from the water. Much of the ingested material is released as feces or large undigested particles that sink to the bottom. Essentially, mussels filter small particles whose energy and nutrients are unavailable to most animals and convert them into larger particles that can be consumed by a large number of animals. Filtration rates depend on species, size, physiology, temperature, season, and food availability. Typically, individual filtration rates range from 0.5 to 1.25 gallons of water per hour (Kryger and Riisgard 1988); this may not sound like a lot until you consider how many mussels inhabit a particular waterbody. Collectively, mussels can filter an enormous volume of water each year and may help reduce turbidity in some waterbodies. Three examples illustrate the profound importance of mussels in aquatic environments:

- In a one-half mile portion of the Ashuelot River downstream of a flood control dam, Nedeau (2006a) estimated that even if only 50 percent of the estimated population size of eastern elliptio were actively feeding, they would filter more than 1.5 million cubic feet of water each day. At typical summer flows of 50 cubic feet per second, this represented 35 percent of the total daily discharge that mussels filtered within one-half mile of the dam.
- Freshwater mussels in the tidal Hudson River in New York filtered nearly 5.3 million gallons of water per day, approximately equal to the daily freshwater discharge of the Hudson River during the summer (Strayer *et al.* 1994).

- An estimated three million mussels inhabiting a lake in Poland collectively filtered 79 percent of the lake's volume during the growing season and removed approximately 11.5 million tons of material from the water column, such as particulate nitrogen and phosphorus (Kasprzak 1986).

Muskrats are one of the most important predators of freshwater mussels. They often leave shells in piles called middens.
Alan D. Wilson, www.naturespicsonline.com

Mussels often comprise the greatest proportion of animal biomass (the sum of living tissue, including shells) in a waterbody. Negus (1966) reported that mussels comprised more than 90 percent of the total animal biomass in a river in England—twice the biomass of the fish population. This is typical of many waterbodies in the Connecticut River watershed. In stable river segments in the Connecticut River watershed, densities of all mussels combined can often exceed 100 animals per square meter; in some locations, densities have even exceeded 400 per square meter. In the Ashuelot River, Nedeau (2006a) quantitatively estimated a population of 1.12 million eastern elliptio within one-half mile of a flood control dam! Areas with such high densities of mussels are usually dominated by a single species, the eastern elliptio. The high biomass and longevity of freshwater mussel populations make them important for long-term storage and release of calcium, phosphorus, nitrogen, and carbon.

Mussels are an important source of food for aquatic predators and land-based scavengers, including river otters, muskrats, raccoons, and skunks. Flatworms, leeches, and crayfish eat small juveniles. Carp, sturgeon, catfishes, sunfishes, and suckers will eat juvenile mussels up to about an inch long. Gulls and shorebirds scavenge live or dead mussels when water levels are low and some waterfowl may consume juvenile mussels while feeding in shallow water. Of all the predators, muskrats are probably the most effective. They often leave behind large piles of shells, called middens, along the shoreline, especially under comfortable "feeding stations" such as overhanging banks, root wads, or docks. Protozoans, flatworms, aquatic earthworms, leeches, midges, and water mites may live within the mantle or pallial cavity of mussels, and some parasites live within the body tissue itself, including trematodes (flukes), nematodes (roundworms), and some protozoans (Thorp and Covich 1991).

A striking example of the role that predators play in the ecology of mussels was observed in Sandy Brook, a tributary of the West Branch Farmington River (Nedeau and Low 2008a). A large population of the eastern pearlshell was observed in June of 2007; several hundred mussels were largely confined to small isolated pools at densities greater than 100 per square meter. A summer drought caused historically low water levels for several weeks during the summer, and when the site was revisited in early September, more than 90 percent of mussels observed several weeks earlier had been eaten. The opportunistic predator (whose identity was never discovered) found this vulnerable mussel population at a time when water levels were low and feasted until the mussels were nearly gone. The predator cracked the posterior end of each shell and pried open the valves. This observation illustrates the importance of mussels as

This pile of eastern pearlshell was found alongside a small shallow pool in Sandy Brook, a tributary of the West Branch Farmington River. The predator ate far more mussels than it left behind; more than 90 percent of the mussels that were observed prior to the arrival of the predator had been eaten just a few weeks later. Ethan Nedeau

a food source for other animals, but also that even seemingly large mussel populations can be at risk if they occur in habitats that expose them to danger.

Mussels influence habitat and diversity of other benthic macroinvertebrates (Vaughn and Hakenkamp 2001, Howard and Cuffey 2006, Spooner and Vaughn 2006). Their movement helps stir sediments and increase the exchange of oxygen and nutrients between the sediment and water. They serve a similar function as earthworms in your garden by increasing the retention of organic matter in the sediment and increasing sediment porosity. Mussel shells provide a surface for algae and animals (such as sponges and insect larvae) to attach.

IV. SUMMARY

- Freshwater mussels are bivalved mollusks whose durable non-living shells protect the animal from the environment and provide characteristics used to identify species.
- Mussels spend their lives fully or partially buried in the substrate and use a muscular foot to move vertically or horizontally in the substrate. Movement is primarily to seek favorable conditions for feeding and survival, and the presence and movement of mussels also enhances the benthic environment.
- As filter feeders, mussels can filter materials such as algae, bacteria, and detritus from the water and convert that energy into a form that other aquatic animals (including mussel predators) can consume. Filter-feeding can have a positive effect on water quality.
- Mussels rely on fish to reproduce and disperse into new areas, and thus the viability of mussel populations is intimately linked to the availability and health of their fish hosts.
- Life spans can range from eight to more than 75 years, during which time mussels may move less than a few meters from where they first landed as juveniles.
- The longevity, sedentary nature, and sensitivity of mussels to environmental changes makes them uniquely suited for long-term monitoring and for assessing the stability and health of waterbodies.
- Conservation of freshwater mussels will benefit from a better understanding of the biology of each species, and from population studies that determine age and size distribution, population density, condition, and habitat at multiple spatial scales.