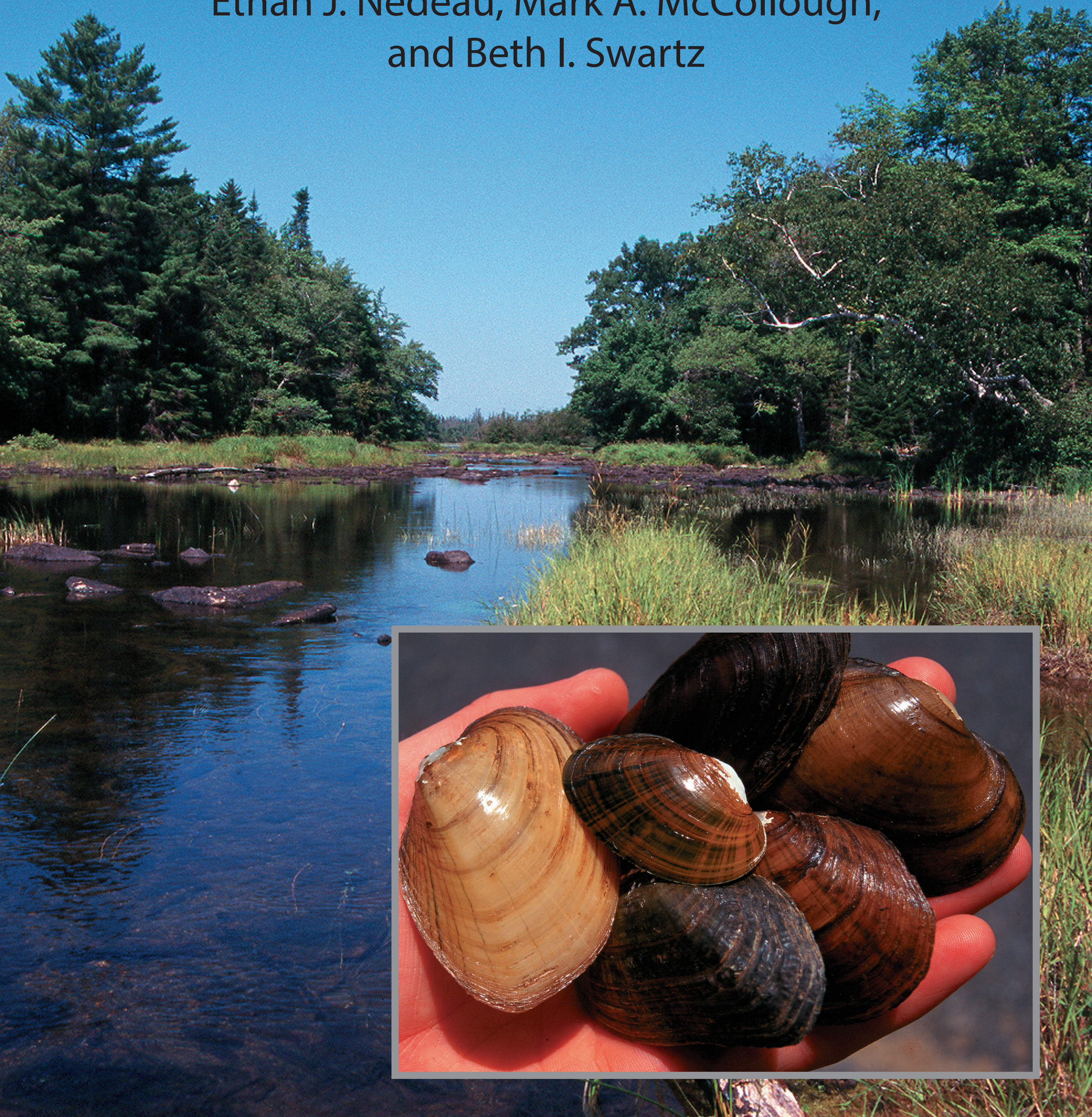
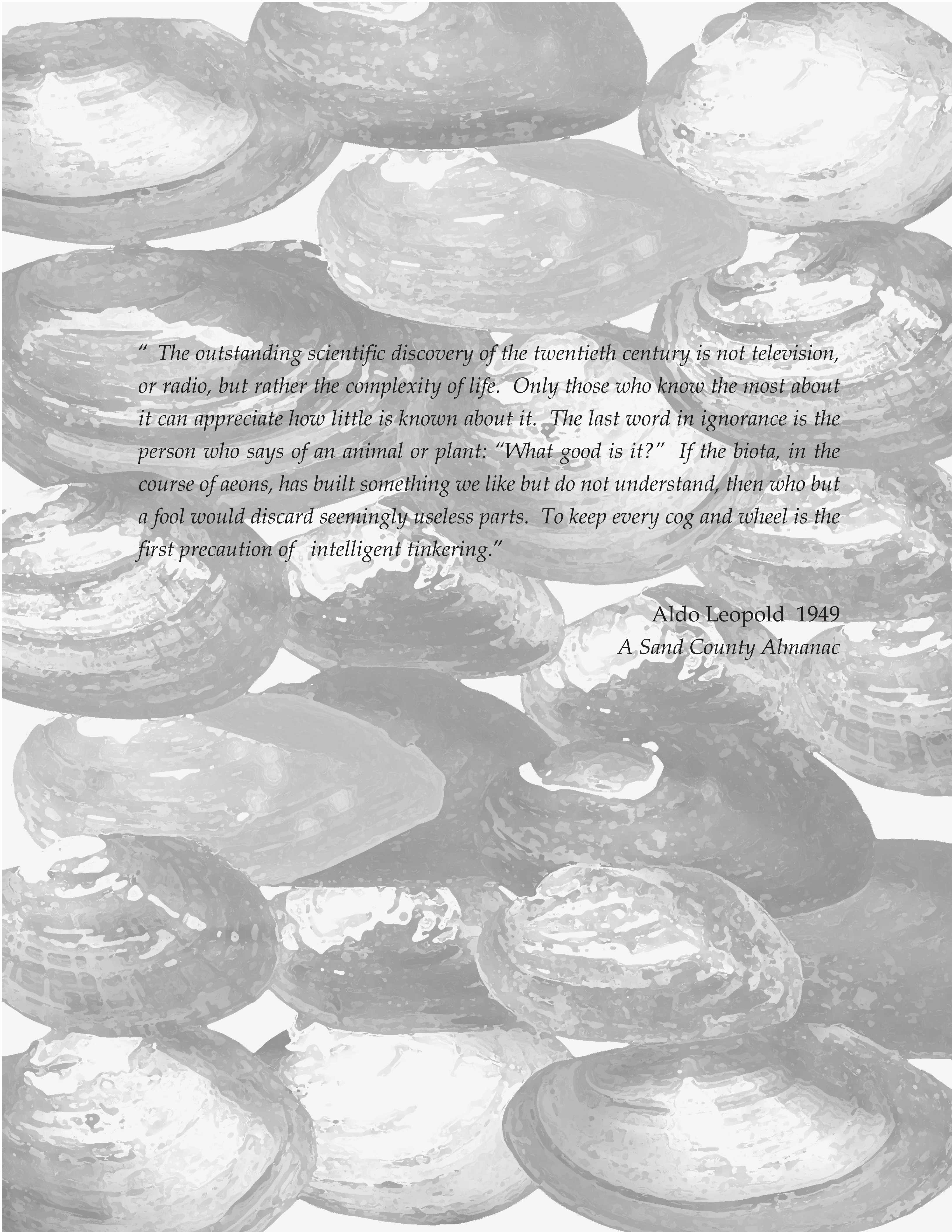
The Freshwater Mussels of Maine

Ethan J. Nedeau, Mark A. McCollough,
and Beth I. Swartz





" The outstanding scientific discovery of the twentieth century is not television, or radio, but rather the complexity of life. Only those who know the most about it can appreciate how little is known about it. The last word in ignorance is the person who says of an animal or plant: "What good is it?" If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts. To keep every cog and wheel is the first precaution of intelligent tinkering."

Aldo Leopold 1949

A Sand County Almanac

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Illustrations, Design, and Layout
Ethan Nedeau
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Contents

Foreward

My first exposure to freshwater mussels came as a youth growing up in western Pennsylvania. About 1969, our Boy Scout troop embarked on a weeklong adventure canoeing the upper Allegheny River. Euell Gibbons' book *Stalking the Wild Asparagus* was in vogue, and we foraged for frogs, smallmouth bass, and crayfish along the way. At a campsite near the mouth of French Creek, we happened upon a large and conspicuous bed of freshwater mussels. "Let's have a meal of clams!" Hundreds of mussels were promptly gathered, and we all stood around a steaming cauldron in anticipation of the feast. However, the aroma of the simmering mussels soon smelled more like the mud in the bottom of the Allegheny, and when they were dished out, no one ate more than a bite of the unpalatable, rubbery bivalves. The bushel of mussels was tossed back into the river. Little did I know (or did anyone at the time?) that French Creek had the highest diversity of freshwater mussels in Pennsylvania, with 26 different species! How many rare and endangered species did we "do in" that evening?

Few of my college classmates in the late 1970s would have guessed that 20 years later we would be applying our hard-learned principles of wildlife management to the conservation of freshwater mussels, frogs, dragonflies, butterflies, and crayfish. But times have changed, and there is growing public interest in conserving the diversity of all wildlife — with or without a backbone. Starting in the early 1990s, the United States Fish and Wildlife Service (USFWS) provided endangered species funding to northeastern states to conduct an inventory of freshwater mussels. By this time, it was apparent that this neglected group of animals was in real trouble. Dams and deteriorating water quality took their toll in the last two centuries, and currently many mussel populations face an equally formidable foe in the zebra mussel.

Encouraged by federal support, the Maine Department of Inland Fisheries and Wildlife (MDIFW) began a systematic statewide survey of freshwater mussels. Maine, being the size of all the other New England states combined, took six years to complete its survey. The exploration of most of Maine's rivers and lakes made for real adventure, as we were the first to catalog the mussel species present in many of the state's waters. We found that although the number of species is not nearly as great as in the Southeast, Maine has perhaps the most significant remaining populations of nationally rare species such as the brook floater, yellow lampmussel and tidewater mucket. Maine's relatively clean, free-flowing rivers are an asset to be proud of, and we are now finding that in addition to a diverse mussel fauna, the Penobscot, upper Saco, St. George, and Union River watersheds host a suite of rare aquatic invertebrates. If we can dodge the invasion of the zebra mussel and other exotics and continue to work diligently to enhance water quality, Maine's aquatic resources will be among the greatest legacies that we can leave to future generations.

One purpose of writing this book was to provide the results of the statewide survey of freshwater mussels undertaken by MDIFW between 1992 and 1997. Another goal was to write a book that would be understandable to lay naturalists and professionals alike. It took us several years to fully understand the complex keys and scientific nomenclature needed to gain competence in identifying mussels. In this book we attempted to develop a non-technical approach to identification, although use of some technical terms was unavoidable. Only ten species are currently known in the state (although one or two more could potentially exist), and most foresters, boaters, fisheries biologists, anglers, and natural historians can probably learn to identify most of them in a season or two. Some species (tidewater mucket and yellow lampmussel) are classified as threatened in the Maine Endangered Species Act, and taking of live animals is strictly prohibited. Therefore, it is important that people are able to recognize these species before they begin activities that could threaten their existence. Finally, we hope to convey the amazing diversity and distribution of freshwater mussels, their fascinating biology and ecology, their importance to naturally functioning ecosystems and humans, and the conservation needs of this often-overlooked group of animals.

We would like to thank Susi von Oettingen, endangered species biologist with the USFWS in Concord, New Hampshire, who initiated and guided conservation initiatives for mussels in New England. Susi's enthusiasm and encouragement greatly enhanced our efforts and established a tight-knit network of mussel researchers in the Northeast. Doug Smith, University of Massachusetts at Amherst, was our mentor and provided technical assistance throughout the survey. Keel Kemper, a regional wildlife biologist with MDIFW, provided many years of support and has been a champion of mussel conservation. Financial support for the statewide survey and production of this book came from the USFWS Office of Endangered Species, Maine Nongame and Endangered Wildlife Fund (your Loon Plate and Chickadee Check-off dollars at work!), Environmental Protection Agency State Wetland Protection Development Grants, and the Maine Outdoor Heritage Fund.

We especially thank Jaime Haskins, of Thomaston, Maine, who led the survey crew from 1993 to 1997. Jaime's ability to endure long days immersed in Maine rivers and lakes and his keen natural history skills contributed to securing most of the data for the field survey. We also thank Kris Higgins and Rick Seekins (1992), Anne Perillo (1993), Marcia Siebenmann (1994), Ethan Nedeau (1995), Shane Hanlon (1996), and Jamie Welch (1997), who each worked for a summer surveying Maine freshwater mussels. It was a pleasure working with each of them, and their contributions and support of the survey project are greatly appreciated. Northrup, Devine, and Tarbell provided additional data for mussel surveys in 1997 and 1998 associated with the Maritimes & Northeast natural gas pipeline. Voucher specimens were collected from each of 1650 sites surveyed in Maine. A collection of nearly 3500 labeled specimens resides at the Maine Department of Inland Fisheries and Wildlife in Bangor.

David Strayer (Institute of Ecosystem Studies), Douglas Smith (University of Massachusetts Amherst), Barry Wicklow (Saint Anselm College), and Susi von Oettingen (USFWS) reviewed portions of the manuscript. Norma Roche provided proofreading and editorial services. Thanks also to the Canadian Museum of Nature in Ottawa for loaning us a specimen of *Pyganodon fragilis* for illustrative purposes, and to Barry Wicklow, Susi von Oettingen, Richard Neves, and Maine Natural Areas Program (MNAP) for loaning us photographs. Jeffrey Hepinstall at the University of Maine Wildlife Ecology Lab provided the lake and river basemap used to create range maps for each species.

Mark McCollough
Endangered Species Group Leader
Maine Department of Inland Fisheries and Wildlife
June 2000

Looking west toward Mount Katahdin, with Katahdin Lake in the foreground. MNAP PHOTO

INTRODUCTION

Nearly everybody that has spent time on a river or lake knows that freshwater mussels exist, but few appreciate the importance of these animals to aquatic ecosystems, their remarkable life history and ecology, or the dramatic decline that they have experienced throughout the world. Few know that North America holds the greatest diversity of freshwater mussels on the planet, with nearly 300 species. Few know that freshwater mussels are one of the most endangered groups of animals in the world — just in the last century we have witnessed the extinction of nearly 35 species in North America (Bogan 1996). Many other populations are no longer capable of reproducing and will likely become extirpated in coming years. Seventy-five percent of North America's freshwater mussel species are considered endangered, threatened, or special concern throughout all or parts of their range (Williams et al. 1992). Only 70 species are considered stable range-wide. Despite the fact that Maine has some of the most unspoiled aquatic ecosystems in eastern North America, one-half of our species are currently state-listed as threatened or special concern.

Conservation biologists are attempting to understand the causes of widespread declines in freshwater mussel populations and develop strategies to reverse these trends. In some instances causes are easy to identify — such as the dramatic changes that result from converting a free-flowing river to a large reservoir. In other instances the causes behind declining populations may not be so obvious, and may involve a variety of factors such as pollution, habitat degradation, or introduced species. Scientists may not always know why populations are in decline, yet they still face the task of trying to conserve or manage these species.

One important conservation strategy is to educate people about freshwater mussels. After reading this book, we hope the next time you pick up a mussel shell from a muskrat's midden or stream bottom, you will know what species you are holding in your hand, why it is important to its ecosystem, and how it is distributed throughout Maine and North America. Understanding mussels may start you thinking about how the construction of a dam that impedes migration of anadromous

Freshwater mussel enthusiasts wading in shallow water, looking for mussels through glass-bottom buckets. MARK McCOL-LOUGH.

fish might affect mussel populations, or what might happen to Maine's mussels if the exotic zebra mussel were introduced. We want you to understand how land use (both historical and current) in the watershed might affect freshwater mussels in your lake or river, and how the relative health of aquatic ecosystems can be assessed by studying the population structure of freshwater mussels. By fostering an understanding and appreciation of freshwater mussels, we hope to increase support for conservation programs designed to protect mussels and the aquatic ecosystems in which they live.

Systematics and Diversity

Freshwater mussels belong to the phylum Mollusca, a diverse group containing many familiar organisms such as snails, slugs, oysters, and squid. With almost 110,000 described species, this phylum is second only to the phylum Arthropoda (insects, spiders, crustaceans) in terms of worldwide diversity. Molluscs exhibit a remarkable array of shapes, sizes, colors, and lifestyles. They range in size from snails smaller than a pinhead to the giant squid, which can attain lengths of 50 - 60 feet. Many molluscs produce exquisite shells, whereas others produce no shells at all. The greatest diversity of molluscs is found in shallow marine environments, though thousands of species have adapted to life in freshwater and terrestrial environments. They can be found in a wide variety of habitats, including deep ocean thermal vents, high mountain lakes, temporary woodland pools, and in leaf piles and rotting logs.

Scientific Nomenclature

Using the yellow lampmussel as an example, the scientific nomenclature for a freshwater mussel is outlined below. The approximate number of species in each taxonomic level is indicated in parentheses.

Phylum: Mollusca (110,000)
Class: Bivalvia (25,000)
Order: Unionoida (1,000)
Family: Unionidae (950)
Genus: *Lampsilis* (30-35)
Species: *Lampsilis cariosa*
Full Name: *Lampsilis cariosa* (Say, 1817)

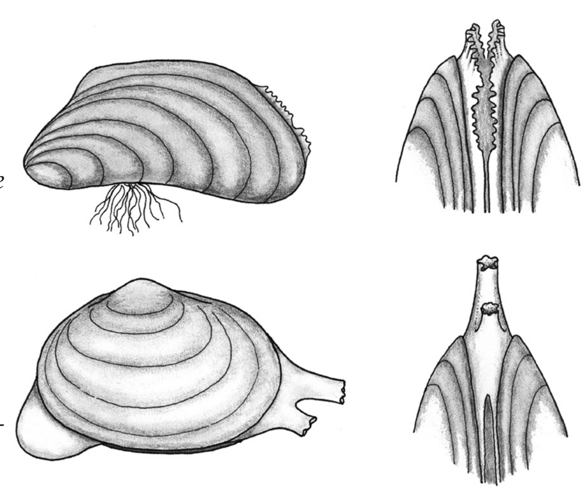
The final part indicates that Thomas Say first described this species in 1817.

All freshwater mussels belong to a single subgroup (class) called the Bivalvia (sometimes called the Pelecypoda). This is a fairly large group of molluscs, with almost 25,000 described species — all characterized by having a pair of hinged shells. Most bivalves live in oceans and estuaries, though a number of families are found almost entirely in freshwater environments. All freshwater bivalves evolved from marine forms. Based on fossil evidence, scientists think that mussels began inhabiting freshwater environments about 200 million years ago, approximately the same time that dinosaurs were beginning to roam the land (Taylor 1988).

Two basic types of freshwater bivalves occur in North America: the fingernail or pea clams and the mussels. Fingernail clams belong to the order Veneroida; these are small (0.1 - 0.8 inch) bivalves that are found in a broad range of permanent and temporary aquatic habitats. Freshwater mussels all belong to the order Unionoida; these are large (up to 10 inches) bivalves that are usually confined to large permanent water bodies. Although the words "clam" and "mussel" are often used interchangeably, there are distinct differences between the two kinds of bivalves.

Clams vs. Mussels

True mussels (top) attach to objects with byssal threads, and their mantle margins are not fused. True clams (bottom) do not produce byssal threads, and their mantle margins are fused into siphons. Unlike their marine counterparts, North American freshwater mussels do not produce byssal threads as adults, but often do as juveniles. Though sometimes called clams, freshwater bivalves in the order Unionoida are more correctly referred to as mussels.



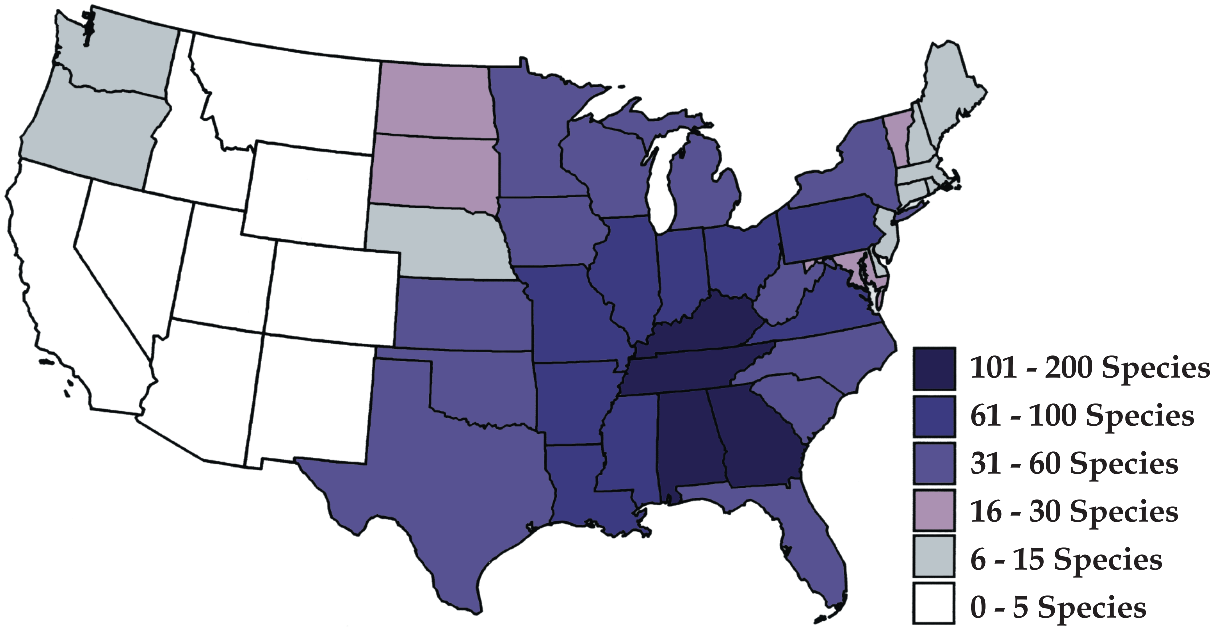


Figure 1. State Diversity of North American Freshwater Mussels
(**Source data**: Williams et al. 1992)

There are nearly 1000 species of fresh water mussels worldwide. North America supports the greatest diversity on the planet, with nearly 300 species. Over half of these are found in the Ohio and Tennessee Rivers and their tributaries, where dozens of species can be found at a single location. In contrast, New England (outside of Vermont's Champlain Basin) has a very low diversity of freshwater mussels, with only 12 species. The state-by-state distribution of freshwater mussels is shown in Figure 1.

Muscle Shoals

There is a place on the Tennessee River known as Muscle Shoals. The spelling of its name is unfortunate, since it is the most famous site for freshwater mussels in the world because of the tremendous diversity it once supported, and the drastic loss of species it has experienced. In 1834, Conrad wrote:

"The bivalves are…particularly abundant in those rivers of North Alabama and Tennessee, which have cut their channels in the carboniferous limestone, and where generally a long grass affords them a secure hold against the rapid current of these mountain streams. The expansion of the river, known by the name of Muscle Shoals, is of the character I described; it is shallow, ornamented with a number of small islands, and its bed is full of the long grass which abounds in various species of Naiades. The lover of the beautiful in scenery, as well as the student in science, will here find abundant sources of interest…" (Conrad 1834, as cited in Ortmann 1924).

In the early 1900s over 70 species of freshwater mussels were found at this location, representing nearly 30 genera (Ortmann 1924). By 1924, habitat degradation resulting from dams and pollution had taken its toll on this once magnificent assemblage of freshwater mussels. Today less than 30 species can be found at Muscle Shoals. Ortmann wrote:

" The beautiful islands, and the general features of the river itself are gone, as well as a large portion of the fauna, chiefly that of the mussels…for a dam has been built."

Biology and Ecology

Morphology

The morphology (shape and structure) of fresh-water mussel shells is illustrated in Figure 2, and the anatomy is illustrated in Figure 3. You should refer to these figures as you read this chapter to become familiar with the scientific terms used throughout this book. Words in bold print are also defined in the glossary.

Like all bivalves, mussels possess a pair of shells, or **valves**, that protect the animal from the surrounding environment. Freshwater mussel shells range in size from 1.5 to ten inches long, though rarely exceed six inches in Maine. The shell is the non-living portion of the animal, much like our hair or fingernails. It is mostly calcium carbonate and protein, and is secreted by the animal as it grows. The outside of each shell is covered with a protein-rich material called **periostracum** that is relatively impermeable to water. Without the protection of the periostra-cum, the shell would dissolve faster in acidic water than the animal could produce it. Damage to the periostracum by physical abrasion will quickly lead to loss of underlying shell material, and if a hole wears through the shell, the animal will die. The periostracum exhibits a broad range of colors and patterns among different species. Internally, the shell is lined with a pearly material called **nacre**. When a foreign object such as a sand grain gets between the shell and tissue of a living mussel, the mussel will often deposit nacre around the grain and create a pearl.

The two shells of a mussel are essentially mirror images of each other, and are connected along the **hinge** by an elastic-like **ligament**. Two large, powerful **adductor muscles** located toward the **anterior** and **posterior** ends of the mussel are used to pull the two shells together. The attachment sites of these muscles can be seen on the shells as large muscle scars. The adductor muscles and

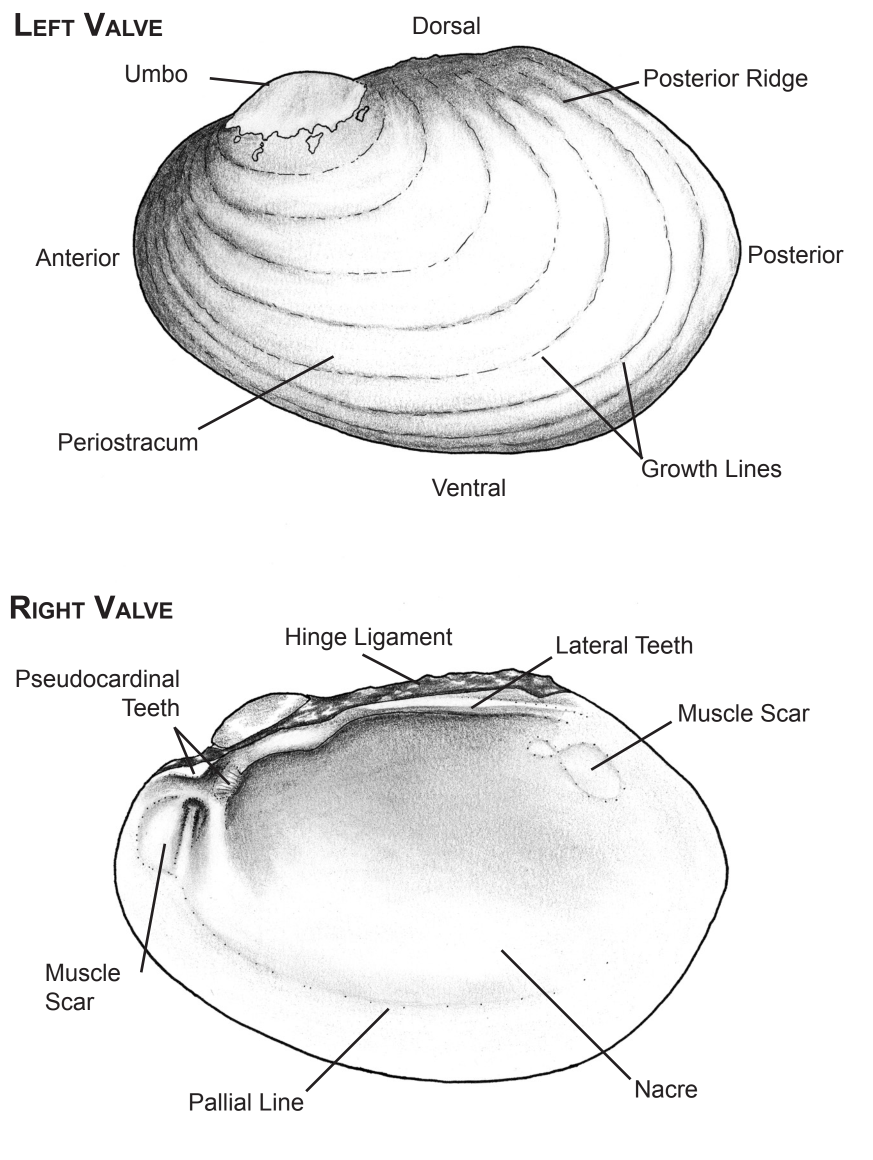


Figure 2. Shell Morphology of a Typical Freshwater Mussel

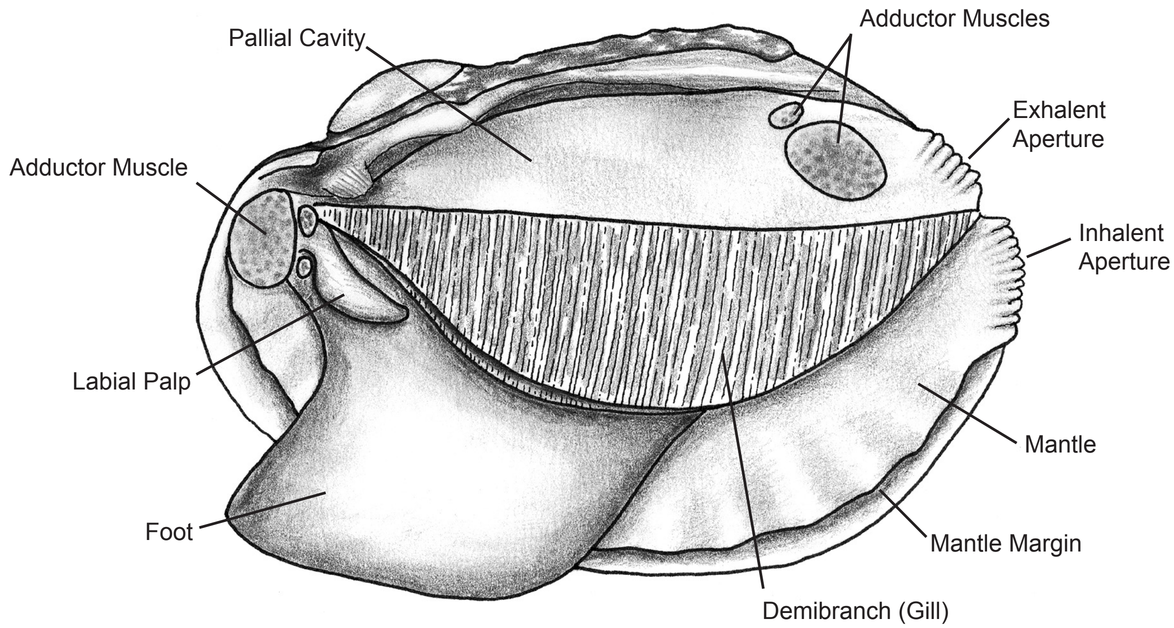
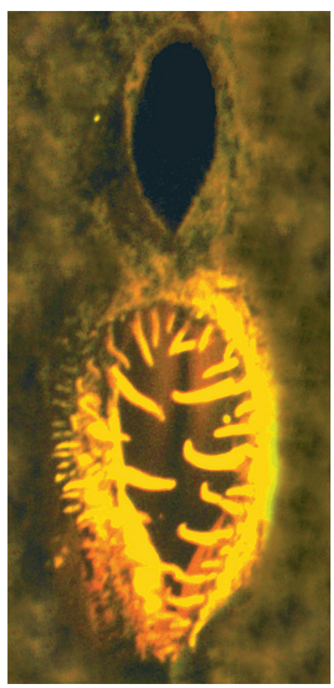


Figure 3. Gross Anatomy of a Typical Freshwater Mussel *(internal organ anatomy not illustrated)*

hinge ligament act in opposition to each other: when the adductor muscles are relaxed the ligament causes the shells to gape or open.

The **beak**, or **umbo**, is the swollen area along the **dorsal** slope from which all growth lines begin and shell rays (if present) radiate. Most freshwater mussels possess grooves and structures along the internal part of the hinge, called teeth, which create a solid connection between the two valves and prevent front to rear slipping. Freshwater mussels possess two types of teeth: the **pseudocardinals** and the **laterals**. Pseudocardinals are short heavy teeth located immediately below the beak, toward the front of the hinge. Laterals are long thin teeth that extend from the pseudocardinals back along the hinge toward the rear of the animal. The size and shape of the hinge teeth are highly variable among species. The most important characteristics used to identify freshwater mussels are the nature of the periostracum and nacre and the hinge tooth morphology.

The **mantle** is a flap-like sheet of tissue that lines the interior of the shell and envelops the body of the mussel. It secretes the shell material and periostracum, and also protects the animal. It is attached to the shell by the dorsal muscles and at the **pallial line**. The pallial line parallels the shell's interior margin and can be seen on most shells. Mantle margins are modified to form **inhalent** and **exhalent apertures** at the posterior end of the body. Water and food are drawn in through the inhalent aperture, and filtered water and waste are expelled through the exhalent aperture. While mantle margins are fused in true clams to form tubes or siphons, in mussels they are not fused, and are more aptly called apertures (see "Clams vs. Mussels," page 8).



Exhalent (top) and inhalent (bottom) apertures of a yellow lampmussel. ETHAN NEDEAU

The **pallial cavity** is the space within the mantle. Most of the major organs are situated within this cavity. There is a pair of large gills, or **demibranchs**, located on each side of the body and extending across the entire pallial cavity. The gills serve three essential functions. They are sites of gas exchange — much like the gills of other aquatic animals. They are also used to filter material (water, food, and sperm) that enters through the inhalent aperture. Finally, there are specialized portions of

A mussel with its foot extended. RICHARD NEVES

the female gills called **marsupia** that are designed to hold unfertilized eggs and developing embryos.

Internally, mussels have a digestive system similar to that of other animals, with a mouth, esophagus, stomach, intestine, rectum, and anus. Their food consists primarily of bacteria, algae, plant and animal debris suspended in the water column, and some protozoans. The gills trap food particles and transport them to the **labial palps**, where they are sorted and pulled into the mouth. Food is digested in the stomach and intestines, and exits through the anus, which is located near the exhalent aperture. Mussels also have a circulatory system complete with heart and blood vessels.

Like all bivalves, freshwater mussels possess a large muscular **foot** that is primarily used for locomotion, but has been shown to be an important food-gathering organ, especially for juvenile mussels (Yeager et al. 1994). The foot extends from the shell along the anteroventral margin, and can be pulled into the shell by a pair of muscles. By probing and digging with its foot, a mussel can pull itself deeper into the substrate or move horizontally along the bottom (Lewis and Riebel 1984).

Since shells can be used to identify most species, and because they are easy to collect and store, the actual living organism has long been neglected by scientists. The living portion of the animal is probably quite variable among species, though there have been few efforts to differentiate species based on soft-part anatomy. Such studies might help resolve taxonomic confusion between species with similar or highly variable shell shapes. More detailed treatment of the anatomy of freshwater bivalves is provided by McMahon (1991) and a number of general invertebrate biology textbooks.

Life History

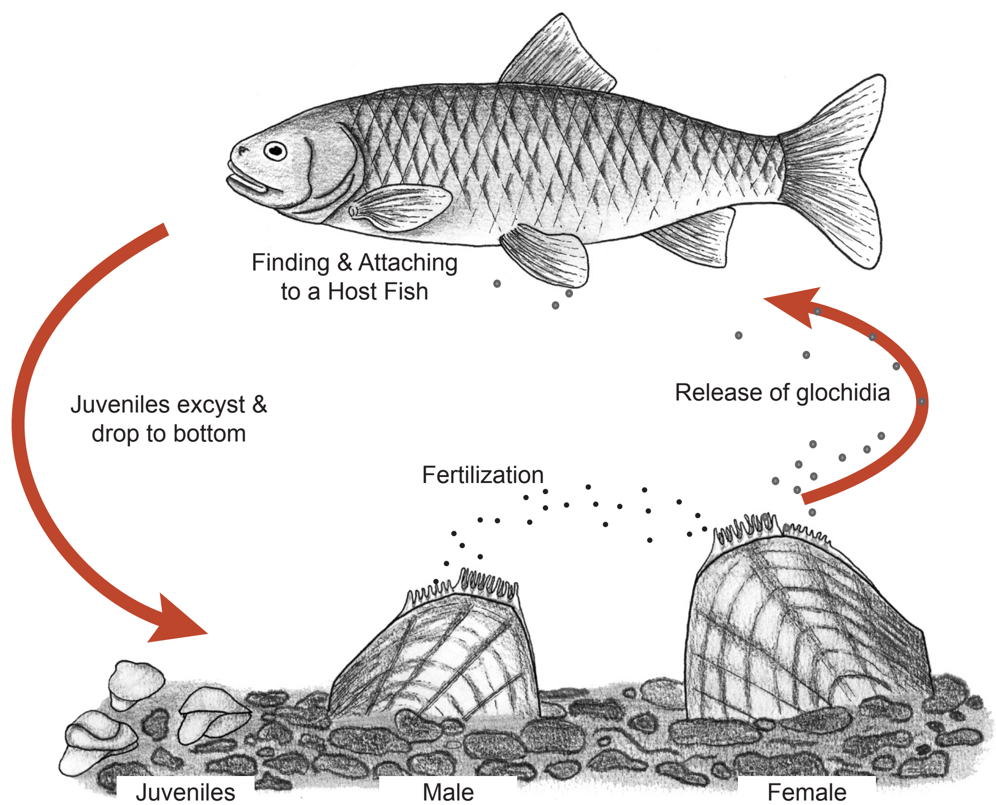
Freshwater mussels have a fascinating life history that has captured the interest of biologists and naturalists for over two centuries. While amateur naturalists and historians made many early observations, scientists have recently taken a more systematic and rigorous approach to describing the life history of these animals. This is largely because of growing concern about the conservation status of freshwater mussels and the need for basic life history data to make in-formed decisions regarding conservation and management. As with any wildlife species, a thorough knowledge of the factors that influence reproduction, recruitment, growth, and survival is critical to understanding conservation needs. The population and community structure of freshwater mussels may also yield a great deal of insight into the long-term health of aquatic ecosystems and the effects of environmental disturbances such as habitat degradation.

Freshwater mussels are usually **dioecious**, meaning there are both male and female individuals. Males release sperm into the water through the exhalent aperture, and females filter sperm out of the water with their gills. Eggs are fertilized in a specialized region of the female gills called the marsupia. The prospects of successful fertilization can be quite low, especially if population density is very low. Yet Neves (1997) asserts that our understanding of fertilization success at low population densities is inadequate, and is skeptical about the importance of low population density to fertilization success. Some species may become **hermaphrodites** and capable of self-fertilization under conditions of low population density (van der Schalie 1970, Kat 1984, Bauer 1987, Downing et al. 1993). Though only four North American species are known to be hermaphrodites, Neves (1997) suggests that many, and perhaps most, females are facultative hermaphrodites — meaning they usually rely on fertilization by males but can switch to self-fertilization when population density is low, or there is a large proportion of females in the population, or other conditions exist that favor hermaphroditism. Though this would help explain how recruitment can continue to occur under conditions of extremely low population density, there is little experimental evidence to support this assertion. Freshwater mussels can increase the chance of successful fertilization by moving closer together during the spawning season (Amyot and Downing 1998).

After fertilization, embryos develop into larvae called **glochidia**. The glochidia of nearly all freshwater mussels require a vertebrate host — typically a fish — to complete larval development and reach the juvenile stage. Glochidia are held within the marsupium for a variable amount of time. In some species, fertilization occurs in the summer or early fall, and the glochidia are held until the following spring; these species are called long-term brooders (or **bradytictic**). In other species, fertilization occurs in the spring and glochidia are released later the same summer; these species are called short-term brooders (or **tachytictic**). Of the ten species of freshwater mussels known to occur in Maine, eight are long-term brooders and two are short-term brooders.

Toward the end of embryonic development, glochidia look like miniature mussels with a bivalved shell and a single adductor muscle. The size of glochidia is highly variable among different species, ranging from approximately 0.002 to 0.02 inches (0.05 to 0.45 mm) (Bauer 1994). The basic shape is analogous to a lever in which the valves are the arms and the adductor muscle applies the force. This design allows them to clamp onto their host (Arey 1924, Hoggarth and Gaunt 1988). Glochidia of some species possess sensory cilia that are thought to aid in detection of or attachment to a host (Kat 1984). Some glochidia have hooks on the valve margins that allow them to penetrate the scales or fins of hosts (Kat 1984, Pekkarinen 1996), whereas others have rounded margins and are more specialized for attaching to gill filaments (Kat 1984).

When environmental conditions are right, females release glochidia into the water column through the exhalent aperture. The timing of glochidial release is not random — successful reproduction depends on the ability of glochidia to find suitable hosts. Some of the factors that are thought to govern the timing of glochidial release include the presence of migratory or nesting fish (Davenport and Warmuth 1965), tactile stimulation (often by foraging fish), temperature (Matteson 1955, Parker et al. 1984, Lellis and Johnson 1996), and **photoperiod** (Lellis and Johnson 1996). Glochidia can survive

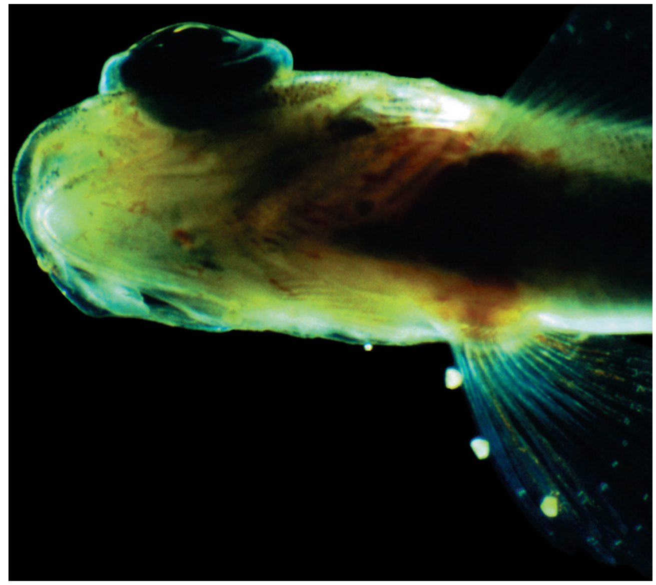


Life Cycle of a Typical Freshwater Mussel

Table 1. Hosts for the Freshwater Mussels of New England

Fish that have been identified as hosts but are not found in New England are not included in this table. Mussel species confined to the Champlain Basin of Vermont are excluded. An asterisk (*) indicates a suspected host.

Mussel species	Hosts	Source
Eastern Pearlshell *Margaritifera margaritifera*	Atlantic Salmon, Landlocked Salmon, Brook Trout, Brown Trout	Smith 1976, Cunjak and McGladdery 1991
Triangle Floater *Alasmidonta undulata*	Common Shiner, Blacknose Dace, Longnose Dace, Pumpkinseed Sunfish, Fallfish, Largemouth Bass, Slimy Sculpin, White Sucker	Barry Wicklow, *personal communication,* Watters et al. 1999
Brook Floater *Alasmidonta varicosa*	Longnose Dace, Blacknose Dace, Golden Shiner, Pumpkinseed Sunfish, Slimy Sculpin, Yellow Perch, Margined Madtom	Barry Wicklow, *personal communication,* Wicklow and Richards 1995
Dwarf Wedgemussel *Alasmidonta heterodon*	Tesselated Darter, Johnny Darter, Slimy Sculpin, Mottled Sculpin, Atlantic Salmon	Michaelson and Neves 1995, Wicklow 1999, Barry Wicklow, *personal communication*
Creeper *Strophitus undulatus*	Largemouth Bass, Creek Chub, Fathead Minnow, Bluegill, Longnose Dace, Fallfish, Golden Shiner, Common Shiner, Yellow Perch, Slimy Sculpin, Two-Lined Salamander, Atlantic Salmon	Watters et al. 1999, Hoggarth 1992, Wicklow and Beisheim 1998, Gray et al. 1999, Barry Wicklow, *personal communication*
Eastern Floater *Pyganodon cataracta*	White Sucker, Pumpkinseed Sunfish, Threespine Stickleback, Carp, Bluegill	Hoggarth 1992, Watters 1994, Gray et al. 1999, Wiles 1975
Alewife Floater *Anodonta implicata*	Alewife, American Shad*, Blueback Herring*	Davenport and Warmuth 1965
Eastern Elliptio *Elliptio complanata*	Yellow Perch, Banded Killifish, Largemouth Bass	Watters 1994, Wiles 1975
Yellow Lampmussel *Lampsilis cariosa*	Unknown	
Eastern Lampmussel *Lampsilis radiata radiata*	Yellow Perch, Largemouth Bass, Smallmouth Bass, Black Crappie, Pumpkinseed Sunfish	Watters 1994
Tidewater Mucket *Leptodea ochracea*	Unknown	
Eastern Pondmussel *Ligumia nasuta*	Unknown	

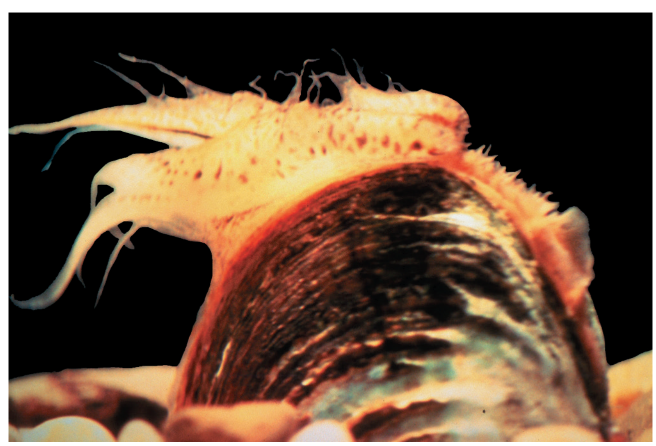


A dwarf wedgemussel glochidium photographed through a scanning electron microscope (left), and three glochidia attached to the pectoral fin of a young Atlantic salmon (right). BARRY WICKLOW.

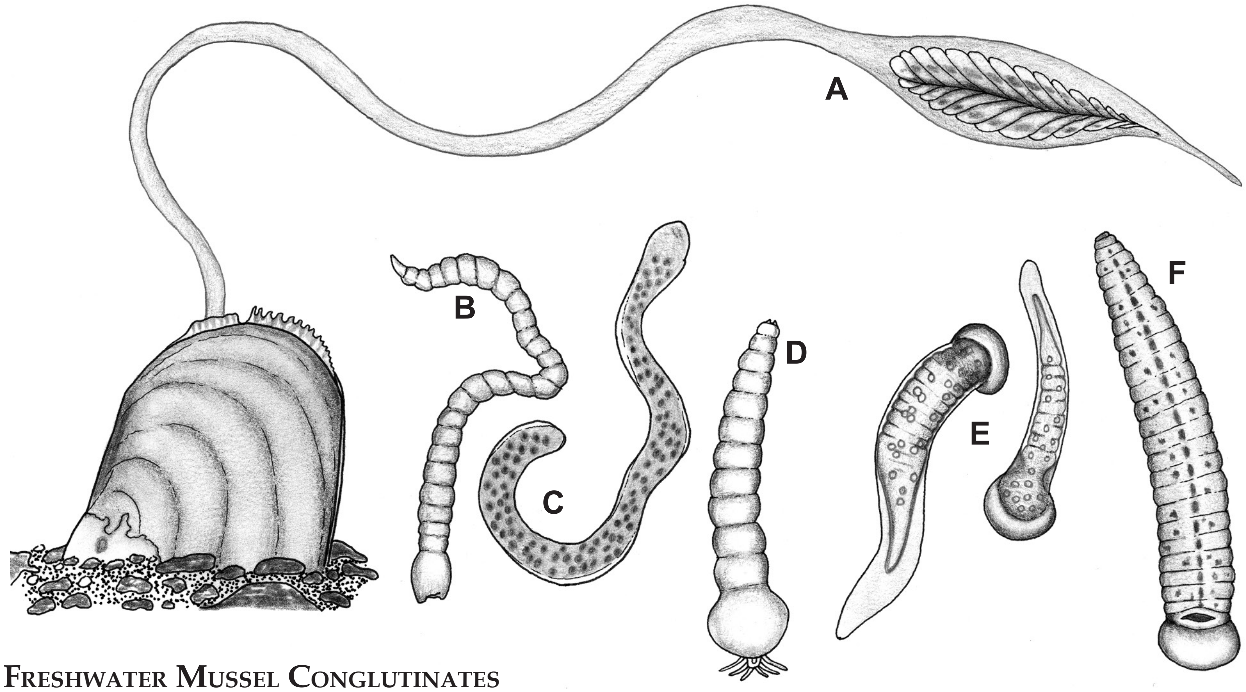
only a short period of time on their own, so they must quickly find and attach to a suitable host. The majority of freshwater mussels use fish as hosts (Kat 1984), though some species can also use amphibians (Watters 1997, Watters and O'Dee 1998, Wicklow and Beisheim 1998). Although the host fish relationships for most freshwater mussels in North America are poorly understood, we know that many mussels can successfully parasitize just a few fish species — often only a small fraction of the total fish available in a river or lake. Table 1 lists the known hosts for New England's freshwater mussels.

The chance of a glochidium successfully finding and attaching to a suitable host is very slim. Freshwater mussels compensate for this uncertainty by producing very large numbers of glochidia, ranging from 200,000 to 17,000,000 per growing season (Kat 1984, Bauer 1994). They also display a remarkable array of adaptations to ensure that glochidia come in contact with a host (Kat 1984). Many species release glochidia in a matrix of mucus, called a **conglutinate**, that remains intact in the water column. It is thought that a tangled mass of glochidia has a greater chance of encountering a host than randomly dispersed glochidia. These conglutinates often resemble food items of fish in both color and shape (Kat 1984, Hartfield and Hartfield 1996, Hartfield and Butler 1997). At least two species in the genus *Lampsilis* release a conglutinate that resembles a small minnow and remains tethered to the female by a long strand of mucus. This lure disintegrates when attacked by a predatory fish, causing glochidia to come in contact with the fish's gill filaments (Haag et al. 1995). Several species in the genus *Lampsilis* also have brightly pigmented mantle margins that resemble minnows, complete with eyespots. The female pulsates her mantle flaps to mimic an active fish, and when attacked by a predatory fish, discharges glochidia into the fish's mouth (Kraemer 1970).

The glochidium becomes encysted in the host tissue soon after attachment (Arey 1932a, Kat 1984) and receives nutrients from the host as it develops within the cyst (Arey 1932b). This parasitic stage lasts from six to 160 days, depending on the species and environmental conditions, especially water temperature (MacMahon 1991). Deleterious effects of the glochidia on the host



This species has a bright and attractive mantle margin that it uses to attract potential host fish. RICHARD NEVES



Freshwater Mussel Conglutinates

Can you tell which of these are conglutinates and which are actual organisms? A, C, and E are conglutinates. B is an aquatic worm, D is an aquatic fly larvae, and F is a leech. Notice the similarity between the conglutinates and other aquatic life!

fish are rarely observed, mainly because infection rates are low. Mortality of host fish has been observed under laboratory conditions, where hundreds or thousands of glochidia may attach to the fish's gills and interfere with respiration (Smith 1976).

Toward the end of the parasitic phase, the glochidium metamorphoses into a juvenile mussel, drops from the host, burrows into the sediments, and begins its bottom-dwelling (**benthic**) existence. For species with strict habitat requirements, the location where a juvenile settles is an important factor in its survival. For instance, the brook floater and eastern pearlshell are stream dwellers and relatively intolerant of silt, so juveniles would probably not survive to adulthood in soft mud or standing water. Like saltwater clams, juvenile freshwater mussels are interstitial —meaning they live entirely buried in the substrate (Neves and Widlak 1987, Yeager et al. 1994). Unlike the filter-feeding adults, they are thought to feed on organic detritus in the sediments (Yeager et al. 1994). Little is known about the habitat ecology or post-settlement movement of juvenile mussels.

With the many hazards that larvae and juveniles face during the parasitic phase, one may wonder why mussels have evolved such a unique relationship with a vertebrate host. Scientists believe the most important reason is dispersal. Adult mussels are virtually sedentary — they presumably move only a few meters during their lifetimes, and cannot move very far within a river or watershed. The parasitic phase is the only time that significant dispersal can take place. The only way mussels can disperse into new habitats, or depleted populations can be replenished with new individuals, is through the movement of infected host fish. Dispersal is especially important for genetic exchange between populations.

Growth

Freshwater mussels undergo their greatest shell growth in the first four to six years of life (Coker et al. 1921, Payne and Miller 1989, McMahon 1991). It is important that the shell grow quickly because it is the protective barrier between the animal and the environment. Juvenile mussels can be crushed by shifting sediments or eaten by predators, so it is advantageous to grow quickly to escape these risks. The rate of shell growth is much lower in adults. Once shell growth slows down, soft tissue growth, and especially reproductive development, occurs at a proportionately higher rate (McMahon 1991).

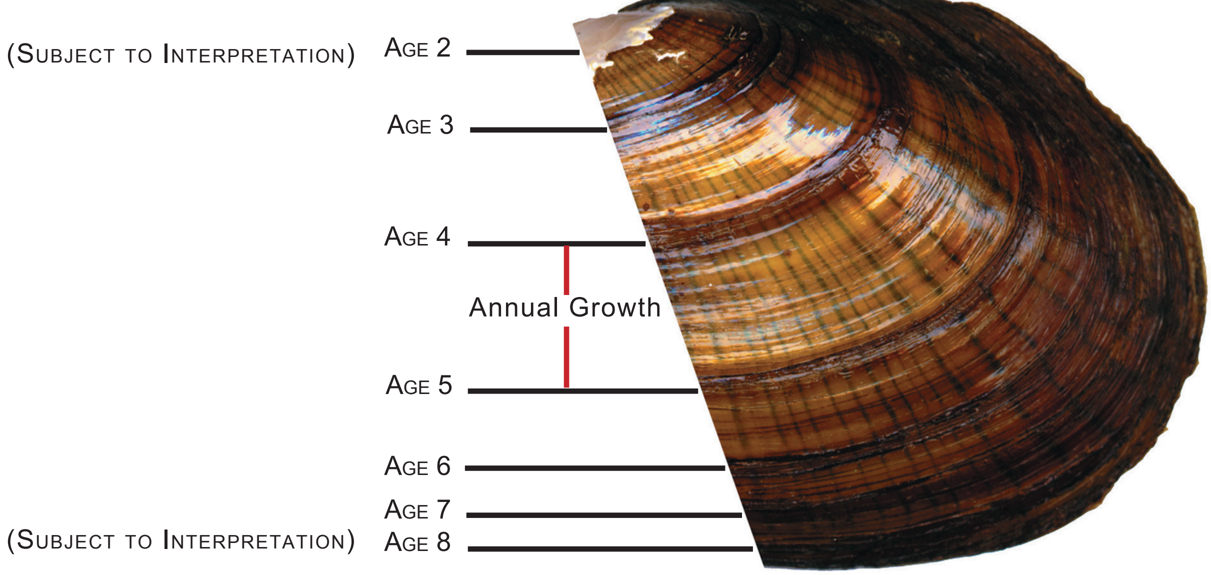


Figure 4. Age and Growth of Freshwater Mussels
Each dark band on the shell usually indicates the end of a growing season, and the number of dark bands indicates an approximate age of the animal. The distance between two consecutive bands is the amount of growth accrued during a single growing season.

The average age at sexual maturity in freshwater mussels is generally greater than six years but is highly variable across species (McMahon 1991).

The growth rate of mussels depends on age and physiological condition of the animal, food and calcium availability, water temperature, and environmental stressors (McMahon 1991). Freshwater mussels grow faster in summer than in winter. The winter ecology of freshwater mussels has not been well studied, especially across a broad latitudinal gradient. Many species burrow into the sediment in winter and enter a dormant period (Balfour and Smock 1995, Amyot and Downing 1997). During these periods they produce a dark band of periostracum along the shell margin, called an interruption ring or **growth annulus**. Since the annuli are laid down annually, they can be used to determine the age of a shell (Neves and Moyer 1988) (Figure 4). The spacing of annuli is also used to infer growth rates and to determine the productivity of mussel populations (Negus 1966, Strayer et al. 1981, Bauer 1983, Muller and Patzner 1996). Since mussels living in an environment with abundant resources and few environmental stressors should have a higher growth rate than mussels living in an inhospitable environment, researchers have used growth rates to assess the long-term health of aquatic ecosystems (McCuaig and Green 1983, Metcalfe-Smith and Green 1992). Scientists also use the age structure, size structure, and growth rates of freshwater mussel populations to determine if a population is declining, increasing, or remaining stable (Figure 5).

Once mature, freshwater mussels may survive for a very long time. Life spans are highly variable among species, but generally range from six to over 100 years (McMahon 1991). The eastern pearlshell, which is found in Maine, is perhaps the longest-living invertebrate in the animal kingdom, with average life spans of 73 years reported for some populations in Germany, and maximum life spans upward of 150 years (Bauer 1987). Most other freshwater mussels in Maine live eight to 20 years.

Drawbacks of Techniques to Determine Age or Growth

There are several drawbacks to the different techniques used to age freshwater mussels. The application of these techniques is described in McCuaig and Green (1983), Neves and Moyer (1988), Downing et al. (1992), and Kesler and Downing (1997).

Technique: Counting External Annuli
It is often difficult to count annuli accurately because the shell is eroded, or annuli are too close together (especially near the shell margin). Also, dark bands are often obscured on dark individuals, and it is difficult to distinguish between true annuli and dark bands forming as a result of environmental stress.

Technique: Counting Internal Annuli
Age is estimated carefully by cross-sectioning the shell and counting annuli under a microscope. Though more reliable than counting external annuli, the true annuli may be confused with false annuli that form in response to environmental stress. This technique requires that an animal be killed. It is also fairly labor-intensive because thin sections must be cut from shells, polished, mounted on glass slides, and examined under high magnification.

Technique: Mark-Recapture
This technique is labor-intensive, because a large number of animals must be marked and relocated for several years. This is the only way to determine annual growth without having to interpret shell annuli. To get accurate growth rates for a population, you need to follow annual growth for several (>15) individuals for at least 3-5 years.

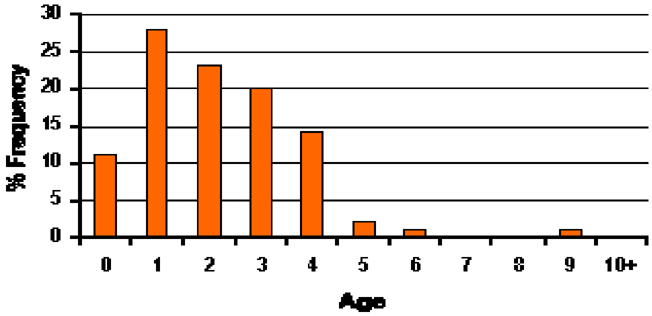
Habitat

Freshwater mussels are found in a wide range of permanent aquatic habitats, including flowing and standing water. They are usually not found in swamps, marshes, bogs, or streams and ponds that dry annually. They are rarely found in high-gradient mountain streams because of extremes in hydrology (especially spring floods) and geology (extensive bedrock substrate), or in ponds smaller than a few acres in size, unless the pond is an impounded section of a stream or mussels have been stocked by humans.

Despite their rather broad environmental tolerance, freshwater mussels reach their greatest diversity in flowing waters. Rivers offer a diversity of habitat types along their lengths, from high-gradient sections with fast-flowing water and rocky substrate to slow-moving water with silt or sand substrate. These habitat extremes intergrade in a sequence of riffles, runs, and pools along the length of most rivers, creating different combinations of habitat conditions that support different types of aquatic organisms. Biologists have just begun to understand the habitat preferences of many mussels — an important step in conserving their habitat.

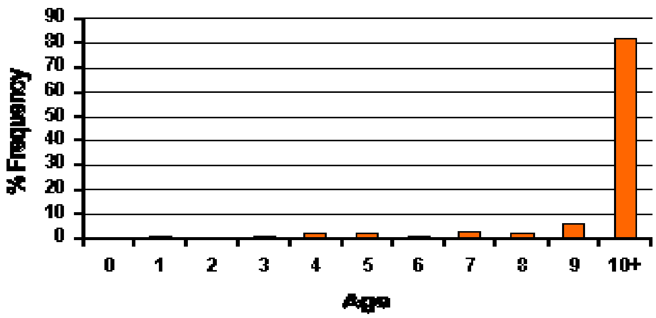
Scientists have studied the habitat preferences of freshwater mussels at different spatial scales. **Microhabitat** refers to conditions in the immediate vicinity of an animal (< 30 feet), and includes variables such as water depth, flow velocity, substrate type, and presence of aquatic plants (Salmon and Green 1983, Strayer and Ralley 1993). **Macrohabitat** refers to conditions at larger spatial scales, such as a long river segment, an entire river, or even a watershed. It includes variables such as stream size and gradient, flow patterns, soil types, topography, surrounding land use, tidal influence, and water chemistry (Strayer 1993).

It is difficult to generalize the microhabitat preferences of freshwater mussels. Some species occupy a variety of habitats, while others are much more specialized. Species living in lakes and ponds (e.g., eastern floater, eastern elliptio, and eastern lampmussel in Maine) typically do not show a strong habitat preference. In general, they are numerous in sand, gravel, and cobble substrates in shallow waters (< 30 feet), and tend to avoid deep water and soft silt (Cvancara 1972, Ghent et al. 1978, Nalepa and Gauvin 1988). Some species, such as the eastern floater, have thin shells and can inhabit soft silt. Species living in streams and rivers (e.g., east



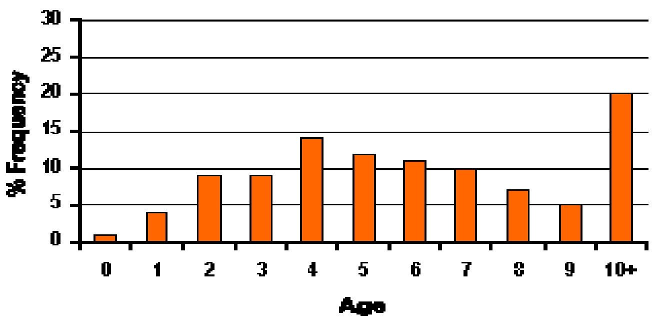
Population A

A large proportion of individuals are juveniles and adolescents. Reproductive success is high, and the population may be increasing. However, some factor is limiting the survival of older reproductive individuals, such as size-selective predation.



Population B

There are a disproportionate number of older individuals, reproductive success is low, and this population may be decreasing in size. This type of age structure is typical for many threatened mussel populations throughout North America.



Population C

In this population, there is a fairly even distribution of young age classes, as well as a large number of reproductively mature individuals. Both recruitment and adult survival is high. This type of age structure indicates a healthy population of freshwater mussels.

Figure 5. Age Structure and Health of Mussel Populations

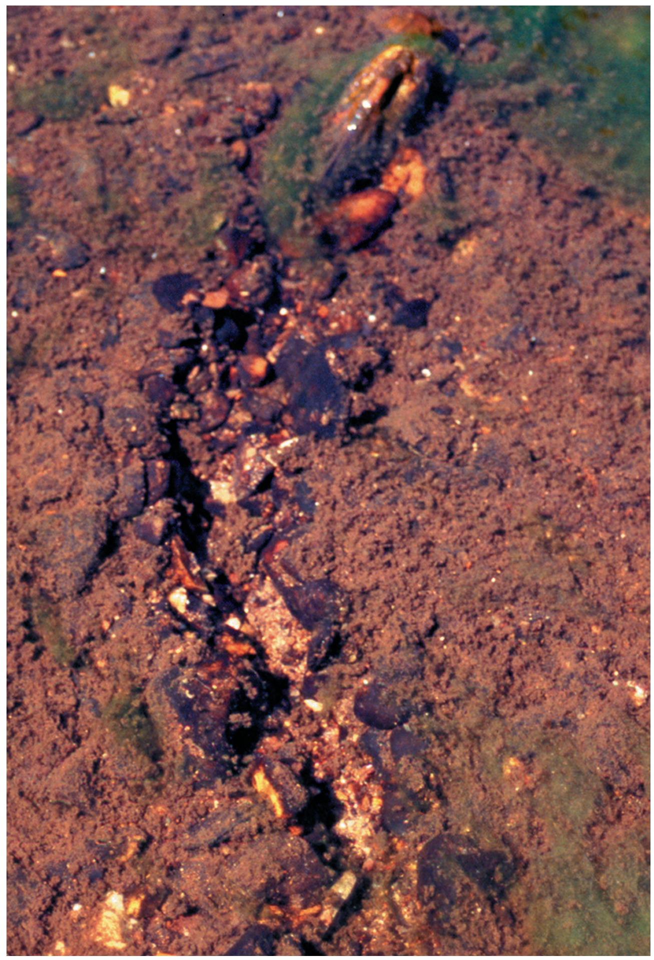
ern pearlshell and brook floater in Maine) have more specialized microhabitat requirements. Many cannot tolerate standing water or small amounts of silt. The most important microhabitat variables for riverine mussels are water depth, current speed, proportion of fine sediment, and patchiness of fine sediment (Strayer and Ralley 1993). Riverine mussels prefer coarse sand and gravel substrates, in slow to moderate current velocity, at depths ranging from one to 30 feet. Although mussels will not move around much if they are in a suitable location, they do have the ability to move several feet per month in order to seek out suitable habitat conditions (Johnson 1999). Recent evidence suggests that mussels may be more common in "flow refugia" in streams – areas where flow patterns remain stable even during high-water events, and the substrate does not shift (Strayer 1999).

Recent research has focused on macrohabitat parameters to explain the distribution and abundance of mussels in a watershed or region. Physical geography, which in New England is strongly influenced by glacial history, plays a very important role. This includes variables such as soil types, drainage patterns, and topography. Waterfalls act as natural constraints on fish dispersal and may explain distribution patterns of mussels (Smith 1982, 1985). For instance, mussel diversity in the North Branch, South Branch, upper East Branch, and upper West Branch of the Penobscot River is significantly lower than in the mainstem. We think this is because of a series of waterfalls that block the upstream movement of some fish species. The Mattawamkeag and Passadumkeag Rivers, two large tributaries of the Penobscot, lack natural falls and have a higher diversity of mussels than any of the upper branches of the Penobscot.

Physical geography and climate strongly influence water chemistry and flow patterns in a watershed or region. These factors exert considerable influence on the distribution patterns of mussels (Strayer 1983, 1993, Di Maio and Corkum 1995). Proximity to the ocean is important for mussels that use **anadromous** fish hosts, or prefer large rivers. The alewife floater is restricted to coastal rivers or lakes because its hosts are anadromous clupeids (alewife, shad, blueback herring). The eastern pearlshell is restricted to coldwater rivers and streams that support trout and salmon populations. Often this species will be found in small coolwater tributaries of a large river (such as Sunkhaze Stream, a tributary of the Penobscot River), but not in the main river itself.

There is a close correlation between diversity of fish and diversity of freshwater mussels in North American watersheds (Watters 1992). On average, rivers with a high diversity of fish will also have a high diversity of mussels. There is some evidence to suggest that the distribution of fish and the reproductive strategy used by the mussels may explain distribution patterns of mussels better than traditional microhabitat descriptors (Haag and Warren 1998). For instance, species such as the yellow lampmussel that use a lure to attract a host may have a better chance of reproducing when fish densities are low than a species without such an attracting mechanism.

In river systems of interior North America, there is a gradual increase in mussel species richness with an increase in the size of the water body, with large rivers supporting a much greater diversity of mussels than small streams (van der Schalie 1938, Strayer 1983). This pattern is not evident for most Atlantic coastal drainages, where diversity is usually higher in the middle reaches of a river system than it is toward the mouth or the headwaters (Strayer 1987). One explanation is that mussels of the Atlantic slope are either small-river species (such as the brook floater, creeper, or eastern pearlshell) or habitat generalists (such as the eastern elliptio, triangle floater, or eastern lampmussel). There are few large-river species in Atlantic coastal drainages, primarily because most of the large-river species of the interior drainages were not able to disperse across the Appalachian divide (Strayer 1987).



This eastern elliptio found itself in shallow water and decided to move. Its trail stretched for over eight feet along the mostly gravel streambed. ETHAN NEDEAU

Importance to Aquatic Ecosystems and Humans

Importance to Aquatic Ecosystems

During the past 25 years, freshwater mussels have become a conservation priority for both state and federal agencies throughout the United States. With many populations declining or nearing extinction, scientists are becoming more aware of their importance to the structure and function of natural ecosystems. Freshwater mussels play an important role in aquatic food webs, nutrient cycling, water quality, and the structure of the benthic environment (Strayer et al. 1994, Strayer et al. 1999).

Compared to the volume of a lake, an individual mussel filters a tiny amount of water annually. However, the cumulative filtering capacity of an entire mussel community can be quite remarkable. The mussels' **filter feeding** removes a large quantity of suspended material from the water column — including plankton, organic material, and inorganic material — and reduces **turbidity** in some situations (Strayer et al. 1999). Most of these nutrients are quickly released back to the aquatic environment by **biodeposition** and **excretion**. Biodeposition is the release of feces or **pseudofeces** (material released before it is digested), whereas excretion is the release of dissolved inorganic nutrients such as ammonia. Freshwater mussels can have a significant influence on nutrient cycling in aquatic systems by converting food resources into forms readily assimilated by other animals and plants (Figure 6).

Freshwater mussels often make up the largest proportion of the total **biomass** of aquatic animals in a lake or river. Negus (1966) reported that in the Thames River (England), freshwater mussels constituted 90% of the total animal biomass — twice the biomass of the fish population. The high biomass and longevity of freshwater mussel populations make them particularly important for long-term storage and release of important elements, such as calcium, phosphorus, nitrogen, and

Filtering Capacity of Freshwater Bivalves

Filtration rates of individual bivalves depend on a number of factors, including species, size, physiological condition, and environmental conditions. The most important environmental conditions are 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).

- An estimated three million mussels inhabiting a Polish lake could collectively filter 79% of the lake's volume during the growing season. This removed approximately 11.5 tons of material from the water column (Kasprzak 1986).
- Freshwater mussels in the tidal Hudson River (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).
- The native mussel community in Lake St. Clair (a minor Great Lake) filtered 1.4–5.3% of the total lake volume per day, depending on the season (Vanderploeg et al. 1995). After the exotic zebra mussel reached maximum densities of over 5000 individuals per square meter, it was estimated that the entire volume of the lake was filtered 1 to 2 times daily (Hebert et al. 1991)!

carbon. They have the capacity to retain energy and nutrients for years or even decades, whereas the turnover of nutrients and energy is much faster in other aquatic organisms (such as insects and plants).

The movements of freshwater mussels may have an important effect on the benthic environment of aquatic ecosystems. By moving horizontally and vertically through the sediment, they "stir up" the sediment and enhance the exchange of important elements (e.g., oxygen and nutrients) between the water column and the substrate (McCall et al. 1979, Nalepa et al. 1991). Freshwater mussels also affect other qualities of the substrate, including retention of organic material, substrate heterogeneity, and sediment porosity (McCall et al. 1979). In this regard, mussels perform a function similar to that of earthworms in your garden — just as earthworms contribute to the quality of the garden soil, mussels contribute to the quality of the substrate on the bottom of a river or lake. Some scientists have found that freshwater mussels actually promote the diversity and abundance of other aquatic organisms by improving local conditions (Sephton et al. 1980).

Mussel shells provide a good colonization surface for other invertebrates. In lakes or rivers dominated by sand or silt substrates, mussel shells can be one of the few solid and stable surfaces that animals can attach to (Strayer et al. 1994, Beckett et al. 1996). Many invertebrates are parasites of freshwater mussels, including protozoans, flatworms, aquatic earthworms, leeches, midges, and water mites that live within the mantle or pallial cavity. In fact, one family of water mites is named the Unionicolidae, in reference to its close relationship

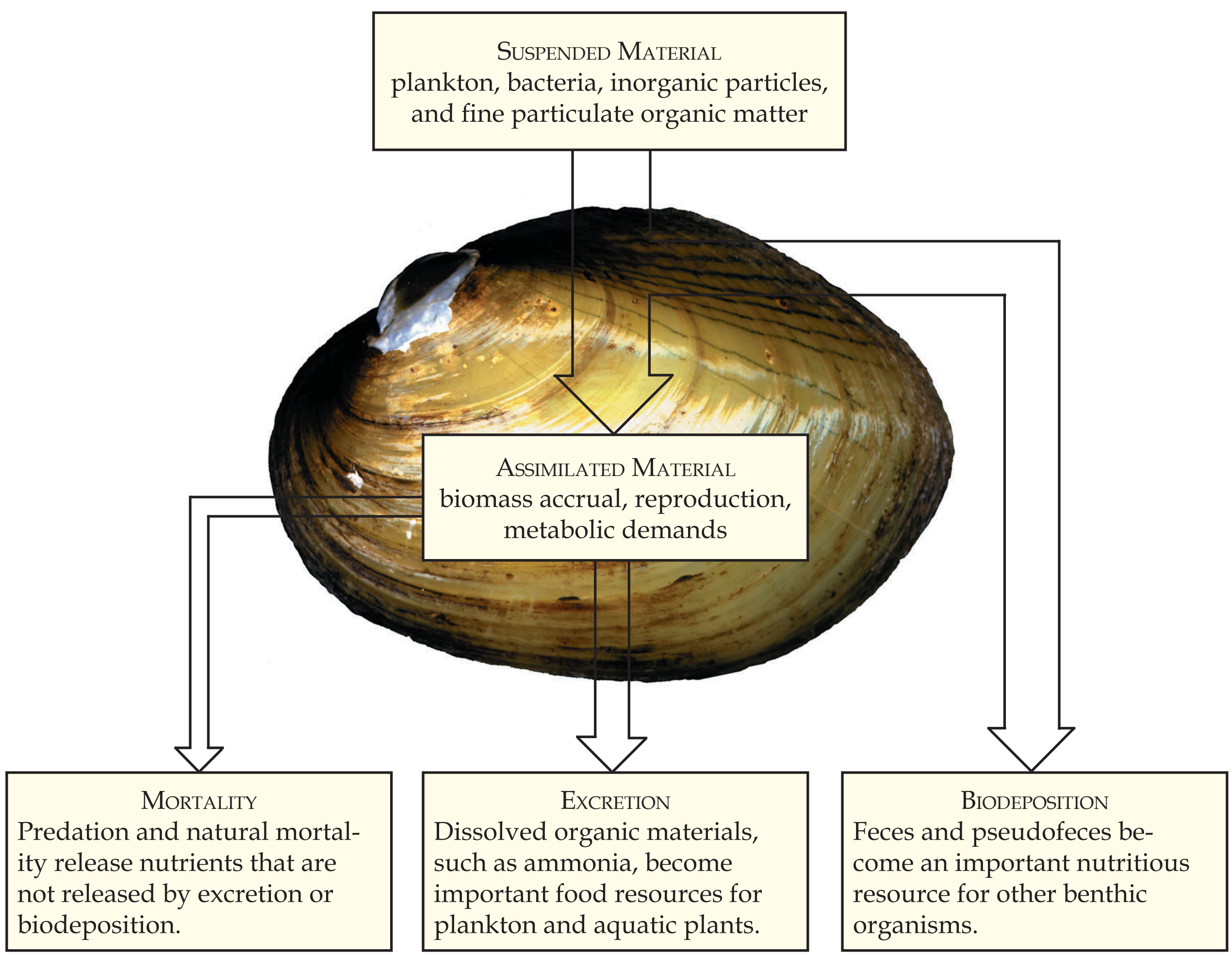


FIGURE 6. ROLE OF FRESHWATER MUSSELS IN NUTRIENT CYCLING

The thickness of the arrows indicates the relative importance of each pathway of energy flow.

The Importance of Freshwater Mussels to Energy Flow

Freshwater mussels play an important role in nutrient cycles and energy flow through aquatic ecosystems. The uptake of nutrients from the water column depends on ambient concentrations of suspended material, the composition of suspended material, filtration rate, time spent filtering, and population density. Though reliant on a number of assumptions, estimates of filtration rate and nutrient removal give us a crude idea of the importance of bivalves to energy flow.

- James (1987) estimated that the population of 10.9 million mussels in a small New Zealand lake had a profound effect on nutrient cycling. The population removed an estimated 1200 pounds of particulate nitrogen, 170 pounds of particulate phosphorus, and generated nearly 300 pounds of ammonia-nitrogen annually — in a lake with a surface area of only 0.5 square kilometer!

- In Lake St. Clair (a minor Great Lake), native mussels filtered approximately 210 metric tons of phosphorus per year, roughly 13.5% of the total load of phosphorus into the lake (Nalepa et al. 1991). The mussels assimilated only 36% of what they filtered — the remainder was deposited as feces or pseudofeces. Of the assimilated material, 42% was excreted. The remainder went toward growth and reproduction or was lost through mortality.

- There is often a greater abundance of benthic animals (such as insect larvae, crustaceans, and a variety of other detritus feeders) in the vicinity of mussels. This has been attributed in part to a behavioral response of these species to the high-quality food resource deposited by the mussels (Sephton et al. 1980, Stewart and Haynes 1994). Biodeposition by bivalves has been shown to enhance the growth of rooted aquatic plants by increasing nutrient levels in the sediment (Bertness 1984).

with freshwater mussels. Some parasites live within the body tissue itself, including trematodes (flukes), nematodes (roundworms), and some protozoans (Fuller 1974).

Freshwater mussels are eaten by a number of invertebrate and vertebrate predators (Fuller 1974). Flatworms, leeches, and crayfish are able to eat small juveniles. There are some fish that are predators of freshwater mussels, including carp, sturgeon, shad, freshwater drum, catfishes, sunfishes, and suckers (McMahon 1991). Most fish cannot eat mussels larger than a half-inch long. Mammalian predators include otters, mink, muskrats, raccoons, and sometimes skunks (Neves and Odum 1989, Jokela and Mutikainen 1995). Muskrats are probably the most effective predators of freshwater mussels, leaving shells in piles called **middens** along the shoreline.

Importance to Humans

In addition to their importance to aquatic ecosystems, freshwater mussels have long been important to humans. Indigenous tribes in North America used their shells and pearls for decorations (jewelry, pendants, etc.) and implements (spoons, hide scrapers, hoes, dippers, etc.). Mussels also served as an important food source for some native tribes (Parmalee and Klippel 1974). In some areas of the country, native peoples relied so heavily on mussels that villages were often located where mussels were especially plentiful; some mussel middens on the Tennessee River accumulated to a depth of several hundred feet and covered acres of ground.

Freshwater mussels have also had considerable economic importance to modern societies. Beginning in the 1800s, people found that the nacre was an ideal material for making buttons, and a commercial fishery arose to supply the button manufacturing industry. This industry reached its peak in the early 1900s, when over 40 million gross of buttons were produced, representing a 12.5 million dollar industry (Fassler 1997). Button manufacturing was never an important industry in New England, where mussels tend to be small and thin-shelled. The best shells came from midwest-ern rivers where some species grow ten inches long and have very

A muskrat left this large shell midden along the shore of Baskahegan Lake in northern Washington County. Over 99% of the shells were eastern elliptio; a single yellow lampmussel was found in the pile. ETHAN NEDEAU

thick shells. The use of mussel shells to make buttons ceased in the mid-20th century because of the invention and widespread use of plastic.

In the early 1900s, the Japanese discovered that beads cut from freshwater mussel shells could be inserted beneath the mantle of marine oysters, causing the oyster to secrete nacreous material over the bead and produce a pearl. A cultured pearl industry arose shortly thereafter, and has since been dominated by the Japanese. However, Japan did not have enough heavy-shelled mussel species to meet its demands, and a fishery developed in the United States to supply Japan with beads cut from North American mussel shells (Fassler 1997). In 1988, Japan produced 71.6 tons of cultured pearls, valued at $482 million. Other countries have also developed cultured pearl industries, including Australia, Indonesia, French Polynesia, and China. In the late 1980s the United States exported over 25,000 tons of shells, but recently exports have declined to less than 10,000 tons due to declining stocks and harvest restrictions. Today, the shell export industry is valued at approximately $50 million, and large mussels from the Midwest can be worth as much as $7 per pound. New England's mussels have been spared this commercial harvest pressure because their shells are generally small and thin.

Occasionally individuals inquire about eating freshwater mussels in Maine. Although edible, they are much tougher than their marine cousins, and tend to acquire the taste of their surroundings — lake and river bottoms. Because of their unpleasant taste, they are infrequently collected for food. Also, many long-lived species in Maine could have high concentrations of contaminants, such as mercury and PCBs (synthetic organic toxicants).

Humans benefit from freshwater mussels because of their ability to serve as monitors of ecosystem health. Many species are sensitive to different forms of pollution and changes in habitat. Unlike fish, which can swim away to avoid potential threats, mussels are sedentary animals that cannot escape polluted or disturbed habitats. If they cannot tolerate local conditions, they will perish. Mussels are easier to collect than other benthic invertebrates, and less expensive to monitor than water chemistry. Also, because they are so long-lived, individual mussels can be marked and their growth rates and survival can be monitored from year to year. Scientists are beginning to use freshwater mussels as indicators of heavy metal (mercury, lead) or chemical (organochlorines such as dioxin) pollution (for a review see Keller and Lydy 1997). These contaminants often have long-term consequences for aquatic ecosystems that are difficult to detect over short time scales.

A Conservation Crisis

Current Conservation Status

There are 297 species or subspecies of freshwater mussels recognized in North America. Only 25% of these are thought to be maintaining stable populations. Thirty-five species (12%) are believed to be extinct (Bogan 1996), and 69 (23%) are listed as endangered or threatened under the federal Endangered Species Act (updated January 31, 2000). Most states have their own endangered species lists, and over 75% of North American freshwater mussel species are listed as endangered, threatened, or special concern at the state level.

Endangered, Threatened, and Special Concern

Endangered, **threatened**, and **special concern** are terms designated to species listed under endangered species regulations at the state level. For a listed species, these different categories imply an increasing probability of extinction and need for management attention. Definitions of these terms established in Maine regulation are as follows:

Endangered: Any species in danger of extinction throughout all or a significant portion of its range.

Threatened: Any species likely to become endangered in the near future throughout all or a significant portion of its range.

Special Concern: Any species that does not meet the criteria as endangered or threatened but is particularly vulnerable and could easily become a threatened, endangered, or extirpated species because of restricted distribution, low or declining numbers, specialized habitat needs or limits, or other factors, or is a species expected to be endangered or threatened or likely to become so but for which insufficient data are available. This term has no legal status in Maine.

Most endangered mussel species are found in rivers of Alabama, Georgia, Tennessee, and Virginia. These rivers support a rich diversity of **endemic** species — species with a very restricted geographical distribution. Only one federally endangered species occurs in New England — the dwarf wedgemussel, which is found in Connecticut, Massachusetts, New Hampshire, and Vermont. Table 2 summarizes the conservation status of New England's freshwater mussels.

Reasons for Declines

There are a wide variety of threats to the health and integrity of aquatic ecosystems (Wilcove and Bean 1994, Richter et al. 1997, Master et al. 1998). Because it is beyond the scope of this publication to deal with all threats to aquatic systems, we will focus on the factors of greatest importance to freshwater mussels, or which may become important in the future. These factors fall into the following categories:

- Habitat degradation (dams, channelization, flow diversion, wetland destruction, watershed disturbance, etc.)
- Inorganic and organic pollution from point and nonpoint sources
- Introduction of exotic species
- Climate change
- Overharvest by humans

Dams and Impoundments

Habitat degradation resulting from dam construction has had a great influence on freshwater mussels worldwide (Bogan 1993). Dams have been constructed for irrigation, flood control, water supply, and generation of energy (Dynesius and Nilsson 1994). They cause changes in flow patterns, water temperature, water chemistry, sediment transport, and nutrient cycling. Scientists can predict the upstream and downstream ecological effects of dams on mussels by knowing the habitat and life-history requirements of species present (Baxter 1977, Yeager 1993, Ligon et al. 1995). Converting a river to a lake causes many riverine species to perish.

TABLE 2. CONSERVATION STATUS OF NEW ENGLAND'S FRESHWATER MUSSELS

*This information was derived from individual states' Natural Heritage Programs, and was current as of February 2000. This table excludes species restricted to Vermont's Champlain Basin. Abbreviations: S = Stable, SC = Special Concern, T = Threatened, E = Endangered, NP = Not present in the state, EXT = Extirpated. * Presumed extirpated.*

MUSSEL SPECIES	ME	NH	VT	MA	CT	RI
Eastern Pearlshell *Margaritifera margaritifera*	S	S	T	S	SC	S
Triangle Floater *Alasmidonta undulata*	SC	S	S	SC	S	S
Brook Floater *Alasmidonta varicosa*	SC	E	T	E	E	EXT
Dwarf Wedgemussel *Alasmidonta heterodon*	NP	E	E	E	E	EXT
Creeper *Strophitus undulatus*	SC	S	S	SC	S	S
Eastern Floater *Pyganodon cataracta*	S	S	S	S	S	S
Alewife Floater *Anodonta implicata*	S	S	NP	S	S	S
Eastern Elliptio *Elliptio complanata*	S	S	S	S	S	S
Yellow Lampmussel *Lampsilis cariosa*	T	NP	NP	E	SC*	NP
Eastern Lampmussel *Lampsilis radiata radiata*	S	S	S	S	S	S
Tidewater Mucket *Leptodea ochracea*	T	NP	NP	SC	T	NP
Eastern Pond Mussel *Ligumia nasuta*	NP	S	NP	SC	SC	S

Many studies have documented drastic declines in diverse mussel communities following the construction of dams. Blalock and Sickel (1996) documented an 84% decline in original species richness of freshwater mussels on the Cumberland River (Tennessee and Alabama) since 1911, caused mostly by impoundments. Many riverine species cannot tolerate the deep, cold water of reservoirs, nor can they tolerate the sediment that accumulates upstream of the dam. Even a small amount of fine sediment (< 0.5 inch) can eliminate sensitive species because it interferes with feeding and respiration. In one Kentucky reservoir, three to ten feet of fine silt accumulated upstream of the dam (Blalock and Sickel 1996)!

Dams often have devastating effects on freshwater mussels downstream as well. Strayer and Ralley (1993) and others have found that patches of fine sediments are preferred habitats for many riverine mussels, such as the brook floater and dwarf wedgemussel. Since virtually all of a river's sediment load is trapped upstream of a dam, downstream reaches no longer receive an influx of sediments, and eventually the substrate becomes dominated by large particles (cobble, boulder). Layzer et al. (1993) found no live mussels for nearly eight miles below a large hydropower dam, largely because of the loss of fine particle substrates.

Ripogenus Dam, on the West Branch of the Penobscot River, blocks the upstream migration of salmonids and has a profound influence on the upstream and downstream environment of the river. ETHAN NEDEAU

A dam that releases water from the surface of the reservoir can also have a large effect on the downstream environment (Stroud and Martin 1973). Surface water in the reservoir gets warm in the summer, and may exceed the thermal tolerance of cold-water fish in downstream areas. Thus, surface-release dams may negatively affect the reproduction and survival of mussels that parasitize cold-water and coolwater fishes (such as the eastern pearlshell and brook floater). Surface release dams may also promote the establishment of warm-water fish communities downstream, which may have im-portant consequences for the mussel community.

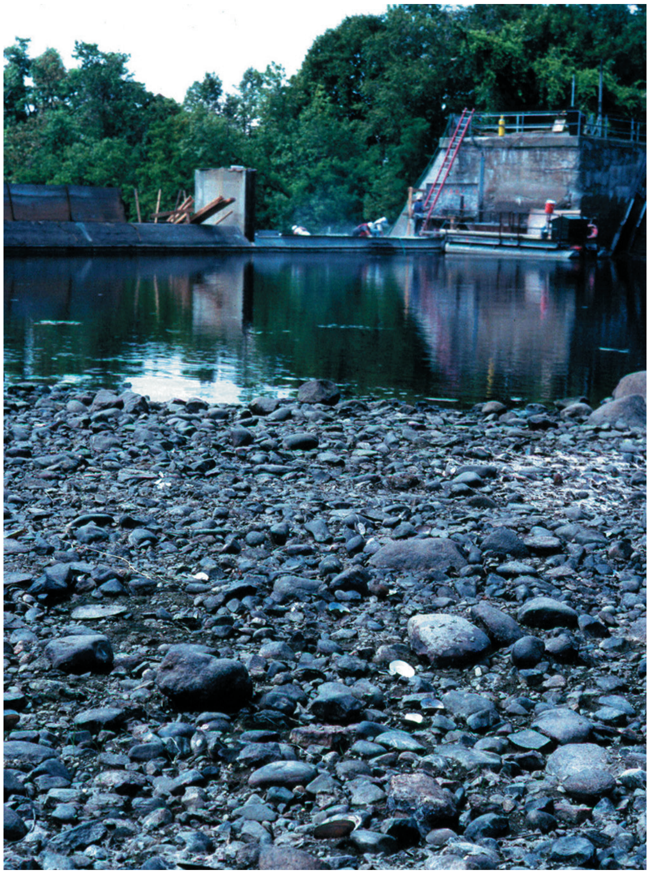
Dams also block the upstream and downstream migration of fish, which in turn affects mussels that may use these fish as hosts (Watters 1996). Beginning as far back as the late 1600s, runs of anadromous fish such as Atlantic salmon, and freshwater fish such as landlocked smelt, were halted in many of Maine's rivers because of dam construction.

Dams may also change the thermal regime of a river, which may have important consequences for species that use water temperature as a cue for growth or reproduction. This effect is largely dependent on the size of the dam, the residence time of water in the reservoir, and the type of dam. Deep-release dams release water from the base of the dam, and since this water is coming from the bottom of the reservoir, it tends to be at a fairly constant, cold temperature (Ward 1974, 1976). Discharges below a deep-release dam on the Cumberland River in Tennessee remained below 55°F throughout the year, which was well below the optimal temperature for many warm-water fish that served as hosts for the freshwater mussels in the river (Layzer et al. 1993). Chronically low temperatures may also directly affect freshwater mussels by slowing metabolism or delaying reproductive cycles (Matteson 1948, 1955, Parker et al. 1984, Lellis and Johnson 1996).

Reservoirs are occasionally drained to maintain and repair dams. This often leaves mussels stranded for a few days to weeks, usually resulting in mortality. In 1998, thousands of mussels, including four state-listed species, were killed when the Halifax Dam on the Sebasticook River was opened for repairs. Such large-scale losses of mussels can be avoided with foresight and planning. Locational information on Maine's freshwater mussels is available and can be used for screening dam repair projects to avoid accidental dewatering and mortality of listed species. Pre-project surveys in high-probability areas can determine the potential for conflict with rare mussels. When listed species do occur in an impoundment where dam repairs are necessary, several alternatives are available to mini-mize or eliminate the loss of mussels, including relocation of stranded individuals and construction of temporary coffer dams.

Point-source Pollution

A point-source pollutant is one for which we can determine an exact source. Examples include industrial effluent pipes, releases from wastewater treatment plants, and chemical spills. Historically, release of raw human sewage into Maine's rivers caused severe reductions in water quality and eliminated most aquatic life in some rivers. Today, treatment of wastewater also causes problems for aquatic systems. Chlorine, which



Halifax Dam on the Sebasticook River, shortly after it was opened for repairs in the summer of 1998. The mussels in the foreground died when left stranded by the receding water. MARK McCOLLOUGH

is used in the wastewater treatment process, is toxic to plants and animals. Goudreau et al. (1993) found freshwater mussels to be absent below water treatment plants, and laboratory bioassays indicated that a form of chlorine resulting from the treatment process was the likely cause.

There are a number of other elements and compounds that have a toxic effect on freshwater mussels, including heavy metals. Among the responses to such toxicants are decreased metabolism and respiratory rate, disruption of ionic balance, disruption of enzyme function, decreased glycogen content (the main energy reserve for mussels), cellular destruction in various body tissues, reduced growth rate, and death (Walker and Peterson 1994, Keller and Lydy 1997).

The response of an individual mussel to a toxicant will depend on a suite of physiological and environmental factors, such as the life stage and physiological condition of the animal. What may seem relatively harmless to an adult may be very toxic to glochidia or to a physiologically stressed reproductive female. If death is the only endpoint considered in toxicology studies, the chronic effects of pollutants on the health and reproduction of mussels may be overlooked. Many toxicants have sub-lethal effects on freshwater mussels, such as disruption of hormonal cycles, behavioral modifications, or reduced metabolic rates. In the long term, these sub-lethal effects may have profound implications for the survival and growth of freshwater mussels. It is also important to consider the additive or synergistic effects of different toxicants or stressors on freshwater mussels.

Nonpoint-source Pollution

Nonpoint-source pollutants come from a variety of sources in a landscape, and are transported to aquatic systems either overland, underground, or through the atmosphere. They include sediment, nutrients, acid rain, heavy metals such as mercury and lead, and gasoline additives such as MTBE. Control of nonpoint-source pollution usually involves regulating the types or intensity of land use in a watershed, or controlling the types and amounts of material released to the atmosphere. Nonpoint-source pollution resulting from land management practices is considered the greatest threat to aquatic systems nationwide and is thought to have made the greatest single contribution to the imperiled status of freshwater animals (Richter et al. 1997). However, Box and Mossa (1999) discuss the difficulty in ascribing cause and effect when considering the effects of land use and sedimentation on freshwater mussel populations.

Sedimentation can change the physical nature of the aquatic environment, including the types and spatial distribution of stream sediments, depth and flow conditions, habitat diversity, streambank stability, and aquatic vegetation (Karr and Schlosser 1978, Karr 1991). Freshwater mussels may be negatively affected by such changes depending on their specific habitat requirements and the degree of disturbance (Obermeyer et al. 1997, Brown and Curole 1997, Box and Mossa 1999). Aquatic habitats in Maine have been affected by sedimentation for centuries because of forestry practices, agriculture, and manufacturing of paper and lumber.

Another form of nonpoint-source pollution is nutrients. Smith (1998) provides an excellent review of nutrient additions to freshwater and coastal marine environments. Nonpoint sources of nutrients include

Mats of blue-green bacteria and algae are commonly seen in rivers draining agricultural watersheds because of excess nutrient loading. ETHAN NEDEAU

Consequences of Eutrophication

Nutrients (especially nitrogen and phosphorus) are essential to the health and integrity of ecosystems, yet too much can cause a number of problems. The negative consequences freshwater eutrophication include:

- Increased biomass of phytoplankton, especially those species that form harmful algal blooms
- Changes in the biomass or species composition of aquatic **macrophytes**
- Increased turbidity
- Oxygen depletion due to high biological and chemical oxygen demand
- Reduction in sensitive fish species, and increase in tolerant (and usually undesirable) fish species
- Overall reduction in biological diversity
- Reduction in the aesthetic, recreational, and commercial value of the water body.

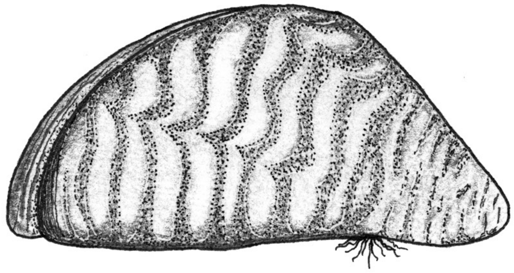
atmospheric deposition and runoff from agricultural lands, pastures and feedlots, septic fields, and urban areas (Carpenter et al. 1998, Fenn et al. 1998, Smith 1998). The process of nutrient addition is called **eutrophication** and has had a number of adverse effects on aquatic ecosystems (Carpenter et al. 1998). Little is known about how freshwater mussels respond to eutrophication. Some authors have suggested that certain stream-dwelling species respond negatively (Bauer 1988, Strayer 1993, Buddensiek 1995). Included among these are three species that occur in Maine: the eastern pearlshell, triangle floater, and brook floater. Further research is needed to establish strong causal links. Such research might encourage the incorporation of landscape ecology and land-use planning into conservation and management plans for freshwater mussels.

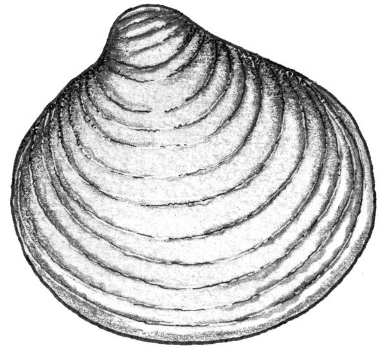
Finally, scientists are concerned about some toxicants because they affect the health of both wildlife and humans. In the 1970s, the United States switched to unleaded gasoline because lead was having negative effects on aquatic and terrestrial ecosystems. More recently, there is concern about the gasoline additive MTBE, which has been found in groundwater and presumably enters lakes and rivers. Its effect on mussels is currently unknown. Mercury (especially methyl-mercury) is one of the most toxic heavy metals, and comes from a variety of sources, including coal burning, industrial discharges, and natural sources. There is a statewide fish consumption advisory in Maine because of mercury contamination and toxic organic pollution. We know that heavy metals and many organic chemicals accumulate in the tissue of freshwater animals (Elder and Collins 1991, Metcalfe-Smith 1994, Walker and Peterson 1994, Metcalfe-Smith et al. 1996, Keller and Lydy 1997, Anderson et al. 1999), yet we do not know what the long-term consequences are for freshwater mussel communities.

Introduced Species

The introduction and spread of non-native species is one of the greatest concerns for freshwater ecosystems in North America (Moyle and Light 1996, Richter et al. 1997). There are hundreds of species of freshwater plants and animals that have been accidentally or purposefully introduced to North America from other parts of the world or have spread beyond their native ranges within North America. Many of these are fish that were deliberately introduced to enhance sport- fishing opportunities (such as brown trout) or to control other species (such as mosquitofish and grass carp). Most introductions of invertebrates have been accidental. There are a variety of introduced species that pose a threat to freshwater mussel populations (Strayer 1999).

In terms of the welfare of native freshwater mussels,





EXOTIC BIVALVES OF NEW ENGLAND
The zebra mussel (left) and Asian clam (right) are two freshwater bivalves that have been accidentally introduced into waterways of North America, including New England.

the most important introduced species are the zebra mussel (*Dreissena polymorpha*) and the closely related quagga mussel (*Dreissena bugensis*). The zebra mussel was introduced into North America in the 1980s by cargo ships carrying freshwater ballast water from eastern Europe to the Great Lakes shipping lanes. In a decade, this invasive species quickly spread east to Vermont and Connecticut, south to New Orleans, and west to Oklahoma and Minnesota. During that time a second dreissenid mussel, the quagga mussel, was accidentally introduced into the Great Lakes in the same manner (Mills et al. 1996). The effects of these exotic bivalves on native freshwater mussels have been disastrous (Mackie 1991, MacIsaac 1996, Strayer and Smith 1996, Schloesser et al. 1996, Schloesser and Masteller 1999). Like blue or ribbed mussels in marine environments, these introduced bivalves attach to solid objects — including the shells of native freshwater mussels. Densities of over 10,000 individuals have been reported on a single native mussel! This severely restricts the ability of the mussel to reproduce, feed, and move.

Neither the zebra mussel nor the quagga mussel requires internal fertilization or a vertebrate host. Thus, they are extraordinarily effective at reproducing and dispersing into new habitats (for a review of the biology of dreissenid mussels, see Hebert et al. 1991, Mills et al. 1996). Native freshwater mussels have declined precipitously in portions of the Great Lakes and the Mississippi River basin where zebra mussel densities are the highest, and the continued existence of these native species is uncertain.

By 1999, the only areas in New England that supported zebra mussels were Lake Champlain in Vermont and East Twin Lake in southwestern Connecticut. Whittier et al. (1995) provided a regional assessment of the potential for the spread of zebra mussels in northeastern lakes based on knowledge of their alkalinity and calcium requirements. Based on water chemistry, he concluded that only a small number of lakes in Maine are vulnerable to zebra mussels. These lakes are in the central interior (portions of the Kennebec, Sebasticook, Penobscot, and Piscataquis River drainages) and northeastern regions of Maine, where the soil is considerably

Over 500 zebra mussels are attached to this native mussel. ETHAN NEDEAU

Keep Zebra Mussels Out of Maine!

If you have been boating or fishing in waters that are infested with zebra mussels (such as Lake Champlain, the Hudson River, or lakes in southwestern Connecticut), please:

- Remove any vegetation attached to your boat or trailer before moving to another lake or river.
- Flush the engine cooling system, bilge areas, and live wells with tap water.
- Leave unused bait behind and discard bait bucket water.
- Leave the boat out of water to dry for at least 48 hours. If it is visibly fouled, leave it out until the exterior is completely dry or you've washed it at a car wash. Hot water (140º F) or drying for several days will kill zebra mussels.
- Importation of baitfish into Maine is illegal. In addition to the introduction of exotic species, baitfish imports could easily carry zebra mussel larvae.

more calcareous (Whittier et al. 1995). Zebra mussels can enter Maine only if humans tranport them; the most likely means include bait buckets, bilge water, boat hulls, livewells, and trailers with aquatic vegetation (and mussels) attached. Efforts are under way throughout North America to prevent the spread of the zebra mussel into uninfested areas by controlling these means of transport.

The Asian clam (*Corbicula fluminea*) is a third freshwater bivalve that was introduced into North America (Isom 1986, Counts 1986). It arrived sometime in the early 1900s from Southeast Asia, and though it has become abundant in some localities, it has not affected native fauna as severely as the zebra mussel. It may compete with native mussels for food, or consume larval and juvenile mussels (Leff et al. 1990). The lower lethal temperature for the Asian clam is 35º–37ºF, and thus it has been unable to spread far into northern North America (Graney et al. 1980). It is found in Connecticut below the nuclear power plant in Haddam, where warm water is discharged into the Connecticut River.

There are some introduced species that may have already caused declines of freshwater mussels in the Northeast. Aquatic systems in this region have a naturally low diversity of fish compared to the Southeast or Midwest, and considerable effort has been made to increase sportfishing opportunities by stocking (Stroud 1955, Simmons and Tisa 1994, Whittier et al. 1999). Nearly one-half of all fish species found in Massachusetts are introduced (Simmons and Tisa 1994), where even an occasional piranha can be caught in the Connecticut River! Largemouth bass, smallmouth bass, black crappie, bluegill, rainbow trout, brown trout, Pacific coho salmon, northern pike, walleye, and carp were all deliberately introduced into Maine to enhance sportfishing opportunities, either by state biologists or private individuals. Additionally, many species were introduced outside of their native ranges in the state, including chain pickerel and white perch (Whittier et al. 1999). Many of these species are fish-eaters, or "**piscivores**."

The most notable exotic fish species in streams and rivers of the Northeast is the smallmouth bass, which was widely introduced beginning in 1869 (Everhart 1976). Bass are now found in over 0.5 million acres of Maine's rivers and lakes (MDIFW 1998). This and other introduced predators may have had a substantial

An Early Warning

"He (black bass) would feed to a great extent on other fishes, and would not confine himself to devouring worthless species, but would prey upon young trout, salmon, smelts, white perch, shad, alewives, and any other that he could catch…We advise that legislation should forbid the introduction of pickerel into any waters where they do not now exist. The same prohibition should rest against sunfish and yellow perch, and the indiscriminate introduction of black bass should not be permitted."

Report of Commission of Fisheries
State of Maine, 1867

influence on native fish communities throughout Maine and New England, especially the native cyprinids (dace and minnows), through predation and competitive displacement (Whittier et al. 1997). Garman and Nielson (1982) provided evidence that the biomass of non-game fish was reduced following the introduction of piscivorous brown trout. These studies suggest potentially serious implications for mussels that rely on native fish as hosts. Displacement or loss of native fish by an introduced predator could have an indirect effect on mussels by reducing their ability to reproduce (Figure 7). Unfortunately, we do not yet have a complete understanding of the host fish relationships for mussels in Maine, or the critical abundance of host fish needed to ensure successful recruitment. Further investigation of these factors would give us insight into the current distributions and population and community structure of freshwater mussels in Maine.

Climate Change

Global temperatures are expected to increase in the coming decades because of increases in greenhouse gases such as carbon dioxide (Vitousek 1994). Temperature increases are expected to cause a melting of glacial ice, which will raise sea levels by nearly 15–20 inches, in addition to the 4–10 inch rise already experienced in the last century (IPCC 1995). Obviously, these predictions are quite serious, and a vast amount of literature has been published on the potential effects on aquatic and terrestrial ecosystems (IPCC 1997, Peters and Lovejoy 1992, Kareiva et al. 1993).

One very important prediction in terms of the long-term health and sustainability of freshwater mussel populations is that global warming will affect the diversity and distribution of freshwater fish because of its effect on surface water temperatures (Meisner 1990, Schuter and Post 1990, Eaton and Scheller 1996). Tempera-

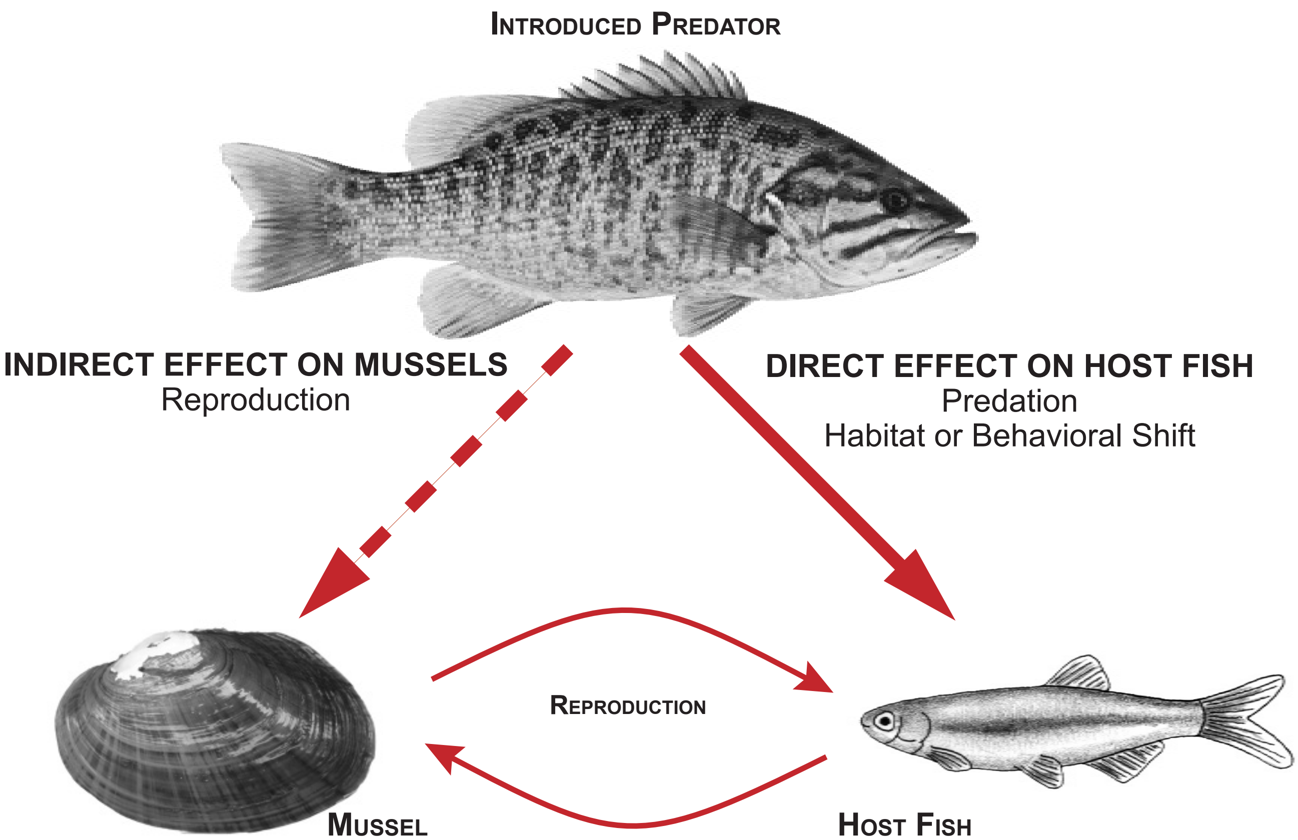


FIGURE 7. HOW MIGHT A FISH PREDATOR AFFECT FRESHWATER MUSSELS?
Introduced predators (such as the smallmouth bass) could directly affect the distribution and abundance of their fish prey, thereby indirectly affecting the reproduction of mussels that rely on the prey items as hosts. (Smallmouth bass photo from Everhart 1976).

Climate Change and Fish Thermal Habitat

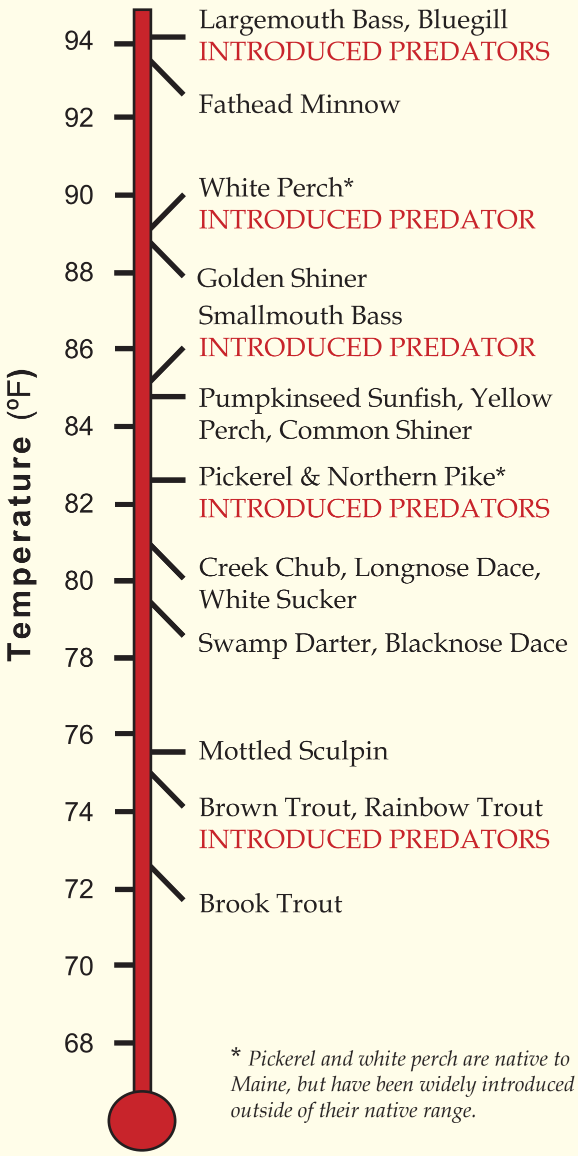
- Average annual temperatures in the northeastern United States have increased 2ºF over the last century.
- Global climate models predict a 4–8ºF (range 2–10ºF) increase in average air temperature in the Northeast over the next century. This would result in water temperature increases of 3.5–6.5ºF, based on Stefan and Preud'homme (1993).
- Eaton and Scheller (1996) predict an average range reduction of approximately 50% for coldwater and coolwater fish in streams of the United States because of climate warming, and a 30% increase in suitable habitat for the largemouth bass.
- Climate change is expected to result in substantial (> 50%) range reductions for several of Maine's native fish, including brook trout, blacknose dace, white sucker, and creek chub.
- For Dolly Varden trout in the Japanese archipelago, Nakano et al. (1996) predicted a 28%, 67%, 80%, and 90% range reduction, respectively, for a 1.8º, 3.6º, 5.4º, and 7.2ºF increase in annual mean stream temperature.

ture-induced changes in fish community structure could have a profound influence on freshwater mussels that require a host for development. Global warming may also affect native fish communities indirectly, because the competitive interactions among species in a community are largely mediated by temperature. Though more research is needed to understand these predictions, it is evident that any changes to the structure of native fish assemblages may have consequences for mussels. The results of this research could be used to develop and prioritize conservation or management programs for freshwater mussel species.

Overharvest

Although humans have harvested freshwater mussels for food or commodities since prehistoric times, only in the last century has harvest pressure been intense enough to require harvest regulations and enforcement. The eastern pearlshell was harvested in Europe and northeastern North America for pearls as early as the 1800s, and this may have caused some populations to become nearly extirpated (Young and Williams 1983). The manufacture of pearl buttons was a vibrant industry in the early 1900s, and mussel harvest went on entirely unrestricted for decades, resulting in population declines for many species. The invention and widespread use of plastic may have saved some species of freshwater mussels from extirpation, especially the large midwestern species such as the washboard, three-ridge, and maple leaf. Resurgence in the commercial harvest of freshwater mussels for the cultured pearl industry in the latter half of the 20th century came when scientists and regulators were better versed in ideas of sustainable harvest and conservation. Harvest regulations have been imposed in most states that have commercially valuable species, and harvest of mussels for the cultured pearl industry is considered a sustainable fishery. However, there is still concern about the effect of illegal poaching (Luoma 1997); the economic incentive to poach mussels in some areas is high because legal-sized mussels are becoming increasingly scarce in areas that allow commercial harvest.

Maine has never had to impose harvest regulations on freshwater mussels because there has never been a strong commercial interest in our species. However, there has been some interest in harvesting freshwater mussels from Maine for scientific purposes (i.e., biological supply companies that supply schools and universities with dissection specimens) and as bait for eels. Traditionally, horseshoe crabs were used in "eel-pots," but recent declines in horseshoe crab populations along the Atlantic coast have caused fishermen to look for alternative baits. Recently, some individuals have also expressed an interest in commercially harvesting freshwater mussels for human consumption. Apparently they have never sat down to a plate of cooked freshwater mussels — they are stringy, rubbery, and have an



* *Pickerel and white perch are native to Maine, but have been widely introduced outside of their native range.*

Competition and Temperature

Freshwater fish exhibit a range of temperature tolerances (see left). Near the upper limit of a species' temperature tolerance, its ability to meet its energetic demands decreases — think about how lethargic you feel on a hot July afternoon! The ability of a species to compete against other fish for food or space will depend on whether the species is within its optimal temperature range. For example, Taniguchi et al. (1998) showed that at temperatures below 68ºF, brook trout and brown trout were superior competitors over creek chub, but by 78ºF, the creek chub outcompeted both of the trout species.

The figure on the left shows the *maximum* temperature tolerance for many fish commonly found in New England (Eaton et al. 1995, Eaton and Scheller 1996). Note that many of the species with higher temperature tolerances are non-native predators that were introduced to enhance sportfishing. Our native freshwater fish face a double whammy — they must contend with both introduced predators and water temperatures slowly exceeding their thermal optimum.

This may have important consequences for freshwater mussels that rely on native fish as hosts. Mussels, such as the eastern pearlshell, that use only coldwater fish as hosts would not be able to reproduce if their hosts were eliminated by rising temperatures and competition.

unpleasant smell and flavor. On a more serious note, they are also likely to have fairly high concentrations of heavy metals or organic chemicals in their tissues.

Freshwater mussels in Maine would not be able to withstand intensive commercial exploitation, even of the most common species. Recovery from harvest could take decades because of their low recruitment success, delayed maturation, and limited dispersal ability. These attributes make freshwater mussels particularly sensitive to overharvest, unlike marine mussels, which have more efficient reproduction, do not require a host fish, and have higher rates of growth than their freshwater relatives. Currently, only those species listed as endangered or threatened under the Maine Endangered Species Act are protected from take or possession. However, should commercial harvest pressures become an issue for Maine's freshwater mussel populations, developing harvest regulations would be an important conservation tool.

Conservation and Management

Scientists and managers are beginning to develop conservation and management programs for freshwater mussels based on growing knowledge of their biology, ecology, and threats to their survival. The National Native Mussel Conservation Committee (NNMCC) has drafted a national strategy for the conservation of native freshwater mussels that identifies specific problems, goals, and objectives that need to be addressed to achieve long-term conservation of freshwater mussels in North America (NNMCC 1998). Currently the most common conservation and management programs include protection and restoration of natural habitats, surveying and monitoring, reintroduction and relocation, artificial propagation, and harvest regulations.

Key Issues for Freshwater Mussel Conservation

In 1998, the National Native Mussel Conservation Committee published the "National Strategy for the Conservation of Freshwater Mussels" (NNMCC 1998). The specific purposes of the document were the following: (1) *identify the research, management, and conservation actions necessary to maintain and recover the mussel fauna*; (2) *increase government and public awareness of the plight of these animals and their essential ecosystems, and garner support for species and habitat protection programs*; and (3) *foster creative partnerships (working and funding) among federal, state, tribal, and local governments and the private sector to restore the mussel fauna and environmental quality to our rivers*. Ten problems were identified as being critically important to the long-term success of this national conservation strategy (from Neves 1997, NNMCC 1998):

- A coordinated national conservation strategy for mussels does not exist.
- Quality mussel habitat continues to be lost.
- Insufficient information is available on basic mussel biology.
- Insufficient information is available on current and historic mussel populations.
- Insufficient information is available as to how habitat alterations affect mussels.
- Invasion of zebra mussels threatens native mussel species and populations.
- The public has a lack of understanding of the plight and value of mussels.
- Mussel propagation technology is not fully developed.
- Mussel captive holding and reintroduction technology is not fully developed.
- Insufficient funds are available for mussel conservation and recovery.

Protecting or Restoring Natural Habitats And Fish Communities

Successful conservation of freshwater mussels will depend on maintaining or restoring the healthy, diverse ecosystems upon which they depend. Maine has an impressive freshwater resource, with over 32,000 miles of rivers and streams and over 5000 lakes and ponds. Although Maine has the greatest amount of free-flowing riverine habitat in the northeastern United States, a large number of our rivers have suffered from centuries of habitat degradation and pollution. Logging debris, domestic sewage, industrial waste, agricultural and urban runoff, dams, and other forms of habitat degradation have affected all of Maine's rivers.

Environmental legislation has been an important means of protecting or restoring natural habitats in Maine. Legislation was passed as early as 1834, but it was not until the late 1960s that widespread public support existed for strict and enforceable laws to protect the health of our aquatic ecosystems. Many Maine communities were discharging domestic sewage into rivers or coastal areas as recently as the 1980s. Thus, many of our rivers are still in early or intermediate stages of recovery.

One important component of water quality restoration and stream management is the protection or restoration of riparian habitats (Karr and Schlosser 1978, Moring et al. 1985, Osborne and Kovacic 1993). **Riparian**

zones are transitional zones between aquatic and terrestrial ecosystems and are very important in moderating stream temperatures, intercepting runoff (including sediment and nutrients), stabilizing streambanks, and providing the energy base for many aquatic systems (Gregory et al. 1991). One tool that has been used to protect riparian zones is zoning laws, which establish land-use restrictions in an area. By preventing certain types of human disturbance in riparian zones, shoreline zoning laws provide protection for aquatic systems (Venno 1991). Industrial paper companies often utilize riparian zone management plans to protect the quality of aquatic ecosystems.

Another stream protection tool is an effort to keep livestock out of streams. Livestock reduce the stability of streambanks, increase sedimentation, and cause eutrophication problems by defecating in the water (Strand and Merritt 1999). They can also crush mussels by stepping on them. One livestock exclusion program

Legislation that Protects Freshwater Mussels and Their Habitat

Below is a partial list of state and federal legislation that protects endangered and threatened species and/or aquatic ecosystems in Maine. All of Maine's legislative statutes can be viewed online at: www.janus.state.me.us/legis/statutes. Legislation that deals specifically with natural resources is found under Title 12 (Conservation) and Title 38 (Waters and Navigation).

Clean Water Act (Pub. L. No. 95-217): Federal legislation whose primary objective is to attain water quality standards considered necessary for fish, shellfish, and wildlife to maintain healthy populations.

Maine Endangered Species Act (Title 12 M.R.S.A. Sections 7751-7756): This act provides a process for listing species as endangered or threatened, and protects them from take and harassment. It also prohibits municipal and state governments from permitting, licensing, funding, or carrying out any project that would significantly harm an area that has been designated as "Essential Habitat" for an endangered or threatened species.

Maine Rivers Act (Title 12 M.R.S.A. Sections 401-407): This broad-sweeping legislation seeks a balance between competing uses on Maine's rivers while trying to restore or maintain ecosystem health. This act also provides special protection for many of Maine's outstanding rivers, as identified by the Maine Rivers Study of 1982.

Natural Resources Protection Act (Title 38 M.R.S.A. Section 480): This Act provides the primary legislation protecting the state's freshwater resources (wetlands, streams, rivers, and great ponds) and other wildlife habitats. It also regulates potentially harmful activities (dredging, bulldozing, removal of soil or vegetation, draining, filling, or repair or alteration of permanent structures) in areas designated as Significant Wildlife Habitat.

Site Location of Development Act (Title 38 M.R.S.A. Section 481-490): This law includes provisions to regulate the location and extent of development projects to prevent degradation of the natural environment, including wildlife and fisheries habitat.

Mandatory Shoreland Zoning Act (Title 38 M.R.S.A. Section 435-448): Institutes land-use restrictions adjacent to lakes, ponds, rivers, streams, and coastal wetlands that are designed to prevent water pollution, protect fish and wildlife habitat, and protect economic and ecological resources from the effects of flooding and erosion.

Various acts concerning fishways in inland and coastal waterways (Title 12 M.R.S.A. Sections 6121-6125): Grants the state's fishery agencies the power to require fish passage facilities in dams where they are needed to restore and maintain commercial or sport fisheries.

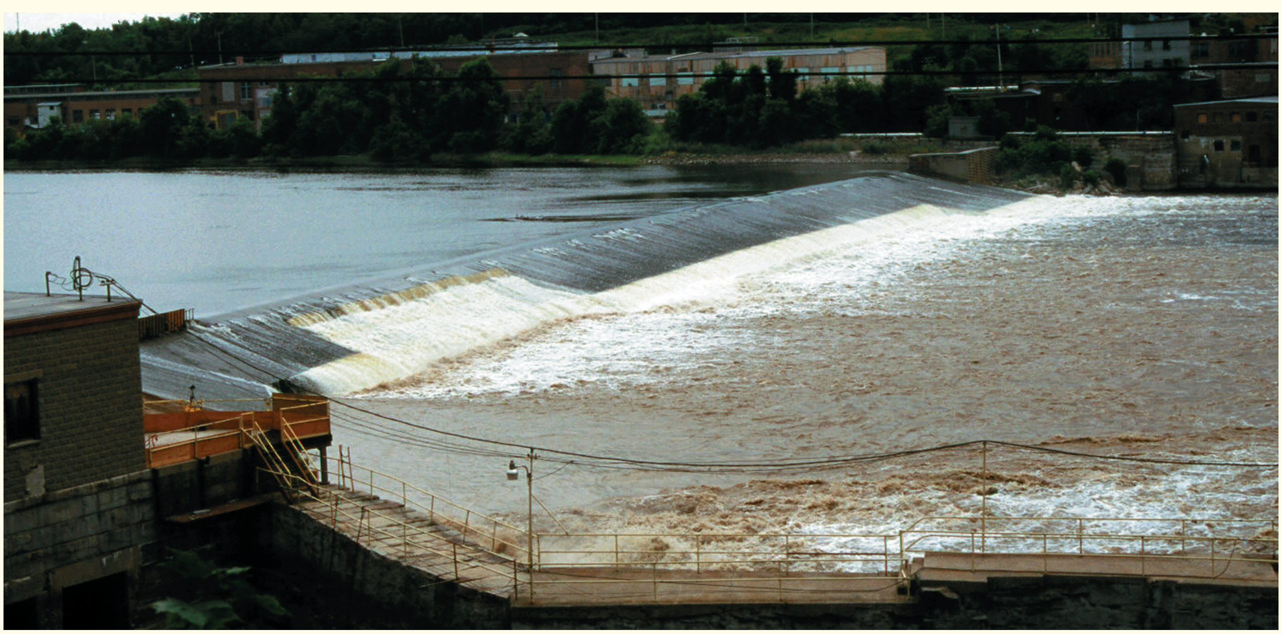
was recently implemented by The Nature Conservancy in a critical stretch of mussel habitat on the Clinch River in Virginia. With cooperation from the USFWS and local farmers, they promoted a riparian restoration program intended to restore degraded streambanks by keeping cattle out. In exchange for a commitment from farmers to keep their cattle out of the river, The Nature Conservancy and USFWS provided fencing material (Kuznik 1993). Similar programs have been attempted on some of Maine's rivers, including the Sheepscot River and Kenduskeag Stream.

Cows contribute to the sedimentation and eutrophication of aquatic ecosystems and should be kept away from streambanks. ETHAN NEDEAU

Most of the dams constructed in the past three centuries did not include facilities to accommodate migratory fish. In recent decades there has been considerable effort to install fish passages in new and existing dams. In some cases, this has allowed mussels to re-disperse into previously occupied habitats. Smith (1985) showed that the alewife floater was able to rapidly expand its

Edwards Dam Removal

Do you know where to find Bacon's Rapid, Babcock's Rapid, or Coon's Rapid? On July 1, 1999, these and other features reappeared for the first time in 160 years when the Edwards Dam in Augusta was removed. Dam removal dropped the water level upstream ten feet and restored habitats that had been inundated since 1837. Edwards Dam once provided power for a textile mill, and never produced more than 1/10 of 1% of Maine's electricity needs. In 1997 the Federal Energy Regulatory Commission decided not to renew the license for the dam and advocated its removal. They recognized that the ecological benefits of removing the dam outweighed any costs. This project restored 18 miles of habitat for ten species of anadromous fish, including Atlantic sturgeon, shortnose sturgeon, Atlantic salmon, and alewife.



ETHAN NEDEAU

range nearly 125 miles in the Connecticut River once fish passage facilities were constructed to allow its hosts (alewife, shad, blueback herring) to migrate up the river. An alternative to fish passage facilities is to remove unused or inefficient dams altogether. Many small dams due for relicensing by the Federal Energy Regulatory Commission are receiving increasing scrutiny of their economic value versus their ecological costs.

Surveying and Monitoring

Since the 1980s, freshwater mussel surveys have been a priority of state and federal agencies and private conservation groups. Many states, including Maine, needed information on the status and distribution of species in order to initiate conservation programs. The surveys that were conducted in Maine from 1992 to 1997 marked the first time in history that biologists conducted a systematic survey of freshwater mussels in the state, and allowed us to obtain important information on the distribution and relative abundances of our species. Surveys have also allowed states to identify species, habitats, or watersheds of particular concern. They have provided insight into species-habitat relationships, as well as historical and contemporary causes of mussel declines. Another important benefit of surveying and monitoring is developing and refining sampling protocols.

The completion of a state survey and publication of an atlas does not mark the end of conservation efforts, but only the beginning. Survey information presented in this book will be used to notify landowners, land trusts, lake and watershed coalitions, municipalities, and other conservation interests of unique resources. These data will also be used to evaluate proposed projects that may affect aquatic habitats, including dam construction or removal, road and bridge construction, water diversion, or changes in land use. Continued monitoring allows scientists to judge whether populations are increasing or decreasing.

Reintroduction and Relocation

Catastrophic events (e.g., toxic spills or severe non-point-source pollution) can potentially eliminate all of the mussels in a stretch of river. Rivers may be quite resilient and return to their previous state within a few years (Niemi et al. 1990). However, freshwater mussels may take a much longer time to recolonize because of their limited dispersal ability. In such instances, it may be appropriate to reintroduce mussels to sites where they previously existed, presumably after habitat and host fish populations have recovered (Neves 1997, Dunn and Sietman 1997). Several reintroduction programs have been attempted in North America, and the results are somewhat variable. Common problems associated

Successes and Failures of Relocation and Reintroduction Programs

It is difficult to judge the success or failure of relocation or reintroduction programs without long-term, post-relocation monitoring. Several researchers have attempted to determine the success of these efforts.

Survival can be quite high... Over 8000 mussels were moved prior to the demolition of bridge piers on the Wolf River in Wisconsin. After three years, there was nearly 98% survival of the relocated mussels (Havlik 1997).

Survival can also be quite low... Over 5000 mussels were relocated prior to the construction of a barge fleeting area and coal unloading facility on the Ohio River. In the first two years after relocation, mean survival was estimated at 50%; this dropped to 35% by the third and fourth years. Survival of individual species ranged from 11% to 50% by the fourth year (Dunn 1993).

Sometimes it's hard to tell... Over 1200 mussels were reintroduced into a section of the Upper Duck River in Tennessee where they had been previously extirpated. Initial survival was estimated to be quite high — over 92% — yet between one and three years after reintroduction nearly 80% of the mussels had disappeared. The fate of these mussels was not determined — they may have died, or they may have been washed downstream by high flows (Layzer and Gordon 1993).

with **reintroduction programs** include handling stress, choice of relocation sites, lack of host fish, and lack of continued monitoring (Waller et al. 1995, Dunn and Sietman 1997).

Relocation programs involve moving mussels out of an area because of proposed habitat alteration or other threats. For instance, bridge construction or removal usually results in mortality of mussels within the project area. The drawdown of reservoirs for dam maintenance may result in losses of individuals around the margin of the reservoir. Relocation of threatened or endangered species would be appropriate in these situations (Havlik 1997). When the Edwards Dam in Augusta was removed during the summer of 1999, a large team of state biologists and volunteers gathered to comb the newly exposed shoreline for two threatened species: the tidewater mucket and yellow lampmussel. A total of 607 tidewater muckets and 16 yellow lampmussels were moved into deeper water, along with thousands of common species. It is difficult to judge the success of these efforts, since long-term post-relocation monitoring is rarely conducted (Cope and Waller 1995).

Time of year is an important consideration in relocation projects. Long-term brooders should not be moved from April 15 to June 15 (due to release of glochidia) or from August 15 to September 30 (due to spawning); short-term brooders should not be moved from May 15 to July 31. Admittedly, we do not know the precise reproductive periods of Maine's freshwater mussels, though it is likely that the best time to relocate mussels is midsummer.

Mussels are sometimes moved out of harm's way and temporarily placed in "safe havens," such as small ponds. This technique has been attempted for rare species facing threats from zebra mussel invasion. The duration of such programs depends on how long the threats exist in the native habitat. Survival in these refugia depends on a variety of conditions, but is usually quite high. Dunn and Layzer (1997) reported 85–100% survival of captive mussels in three of four holding facilities, but no survival in the fourth, after over a year in captivity.

Artificial Propagation

Some species are on the verge of extinction, and extreme efforts are required to maintain remnant populations or individuals. **Artificial propagation**, or captive breeding, involves techniques to maintain individuals in a laboratory setting to ensure successful fertilization and glochidial development (Keller and Zam 1990). The goal is to produce a large number of juveniles for eventual distribution back into the wild. This is a controversial and "last-ditch" means of recovering a species. One problem with artificial propagation is that it serves only as a stopgap measure; if the factors endangering a species in the wild cannot be identified or remedied, then there is little chance that reintroduced juveniles will succeed in reestablishing a population. On the other hand, it would be a tragedy to lose species while we search for causes and solutions, when artificial propagation could temporarily help ensure their survival (Neves 1997). Artificial propagation of freshwater mussels is a relatively new science, and so the methods and protocols are still being developed (Keller and Zam 1990, Buddensiek 1995). Although several artificial propagation programs have been initiated, there is no data regarding the long-term success of such attempts. The time period needed to judge the success of these programs is probably greater than five years.

Harvest Regulations

Some states have protected commercially valuable mussels from overharvest by setting harvest regulations. These include restrictions on the type of harvest gear, fishing seasons, minimum length requirements, and daily catch limits. In some instances, a permit is required to harvest mussels. Some states have also established "aquatic ecological reserves" to protect sites from harvesting. Since none of Maine's freshwater mussels are currently commercially valuable, there are no harvest regulations for them. However, if new markets for freshwater mussels were to develop in Maine, the Department of Inland Fisheries and Wildlife would have to consider appropriate harvest regulations. It is also important to remember that absolutely no harvest or possession is allowed of species listed as endangered or threatened under the Maine Endangered Species Act.

The Distribution of Maine's Mussels

Some intriguing questions have emerged from our knowledge of the distribution patterns of freshwater mussels in Maine and the Northeast. Where did Maine's freshwater mussels seek refuge during the last glaciation, and by what route did they disperse back into Maine? Why does Maine have only ten species of mussels, when New York has 50 species and the southeastern states have over 150? Why haven't we found the rare dwarf wedgemussel in Maine, when it occurs to the east (New Brunswick) and west (New Hampshire)? How important is recent (350 years) environmental history to the patterns we see today? Why does the central portion of Maine, extending from the lower Kennebec River to the upper Mattawamkeag River, have a much higher diversity than the rest of the state?

Zoogeography

Answers to many of these questions lie in New England's glacial history and the natural history of freshwater mussels. Most of New England's mussel species are believed to have migrated around the northern end of the Appalachian Mountains prior to the last glaciation (over 50,000 years ago) from locations in the present-day Great Lakes and Mississippi River drainages, and then spread southward along the Atlantic coast (Johnson 1970). The most recent glacial period began 50,000 to 70,000 years ago, subsequent to the arrival of freshwater mussels. Ice covered nearly all of northern North America during this period and destroyed nearly all of the freshwater and terrestrial ecosystems in the region (Figure 8). The glaciers began receding about 18,000 years ago; by 12,000 years ago all but northern Maine was deglaciated, and by 11,000 years ago the glacial ice was virtually gone (Hughes et al. 1985, Bonnichsen et al. 1985). The plants and animals that originally inhabited New England are thought to have survived in four important refugia during the glacial period (Figure 8), though the location of these refugia, and the species that inhabited them, have long been debated among zoologists. Zoologists have speculated for decades how freshwater mussels returned to New England after the glaciation. This question is particularly intriguing because virtually the only way that freshwater mussels can disperse is during the parasitic larval stage, when glochidia are attached to their hosts.

During the last glaciation, the maximum extent of glacial ice was well offshore of Maine's present-day coastline. The glacier's terminal moraine was located near present-day Nantucket Island, Martha's Vineyard, Georges Bank, the Grand Banks, and the Sable Islands. At that time, the sea level was about 300-400 feet lower than it is today, and a considerable amount of the continental shelf beyond the glacial maximum was dry land. Pollen grains, mastodon and mammoth teeth, diatoms (freshwater algae), and freshwater peat deposits have been found in ocean depths of 360 feet off the coast of northeastern North America, indicating that this area contained a terrestrial/freshwater ecosystem 25,000 years ago (Whitmore et al. 1967, Emery et al. 1967). This area was an important refugium for freshwater fish and mussels during the last glaciation (Schmidt 1986). The glaciers terminated at the ocean over the deep channel extending from the Gulf of Maine into the Atlantic Ocean, splitting the northeastern coastal plain refugium into two refugia: one over Georges Bank, and the other over the Grand Banks and Sable Islands. This is important because plants and animals in these two refugia likely took different dispersal routes back into New England. A third refugium was located farther south along the Atlantic coastal plain, extending from Pennsylvania and New Jersey south to North Carolina (Schmidt 1986). Unglaciated areas of the Mississippi Valley were also an important refugium for some species now found in New England.

Did freshwater fish (and mussels) disperse back into New England by swimming up freshwater rivers and following the retreating glaciers? One problem with this simple explanation is that nearly all of the present-day rivers in the Atlantic coastal region flow in an easterly or southeasterly direction, directly into the sea. To disperse in a northeasterly direction from a refugium in the mid-Atlantic region, a freshwater fish would have to cross many drainage divides, or move along coastal estuaries. This is especially difficult for

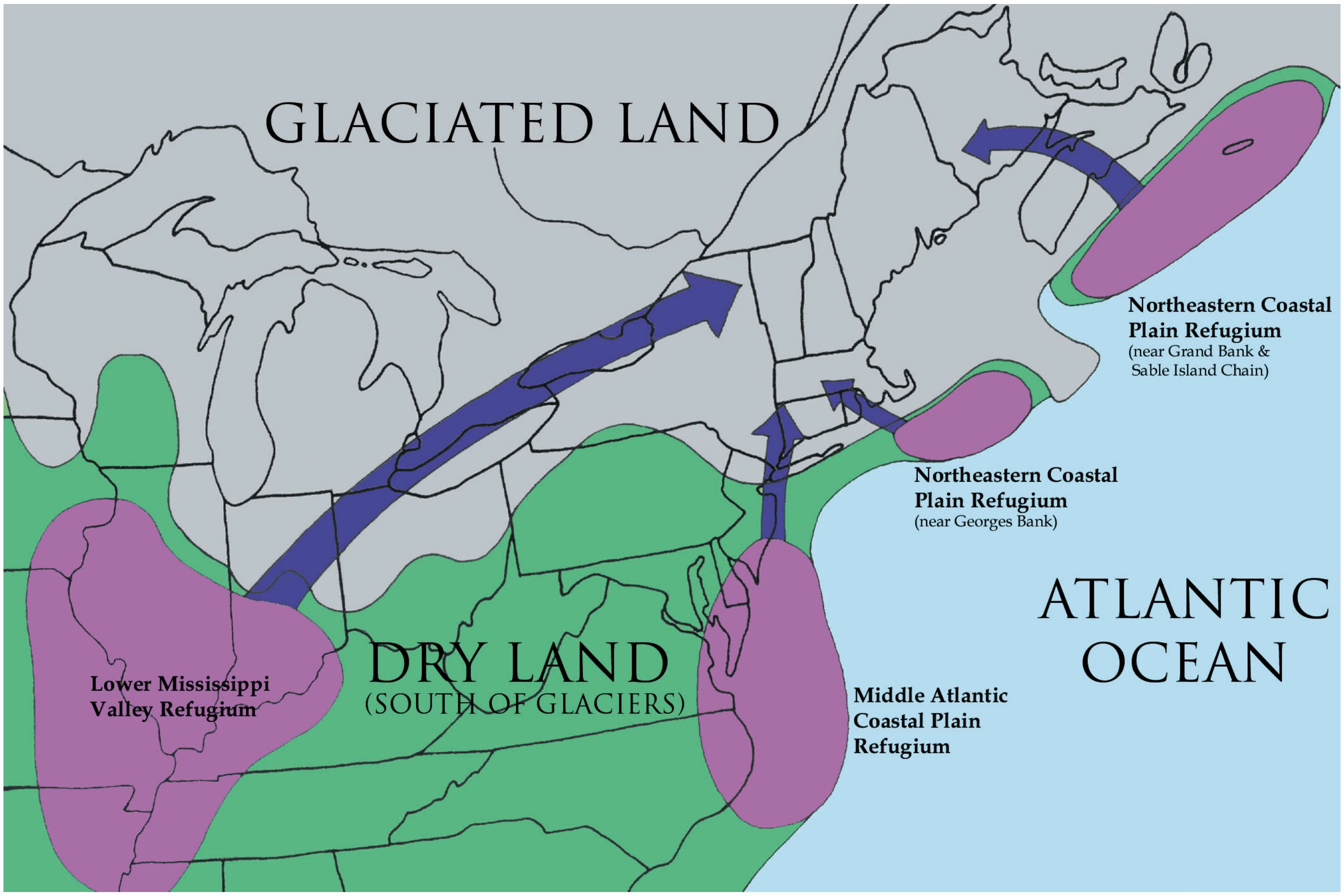


FIGURE 8. GLACIATION, GLACIAL REFUGIA, AND POST-GLACIAL DISPERSAL
The map shows the locations of four refugia south and east of advancing glaciers and the likely dispersal routes of plants and animals back into the Northeast. (Derived in part from Schmidt (1986), Pielou (1991), and Strayer (1987))

species such as suckers and chubs that cannot tolerate salinity. Species with some tolerance for salinity, such as sticklebacks and smelt, would have had an easier time dispersing northward.

One explanation is that modern-day lakes and river drainages are configured significantly different than when the glaciers retreated. There may have been freshwater connections between drainage basins at the mouths of developing rivers, permitting the dispersal of host fish across drainage divides. There may have also been large lakes that spanned two or more modern drainage basins, allowing species to "leapfrog" from basin to basin. Caldwell et al. (1985) reconstructed the pattern of Maine's streams and rivers using inferences from glacial meltwater deposits, and the patterns are strikingly different than what we see now. Even today, the Piscataquis River (a large tributary of the Penobscot River) begins at the foot of Indian Hill at the southern tip of Moosehead Lake, yet Moosehead Lake is entirely within the Kennebec River drainage. It is not difficult to see how Moosehead Lake may have once been part of the Penobscot River drainage. In 1841, engineers were able to add 286 square miles to the Penobscot drainage by damming the northern end of Lake Telos and cutting through a natural ravine between Lake Telos and Lake Chamberlain. This effectively diverted some of the flow of the Allagash River (part of the St. John River watershed) into the Penobscot River watershed (Coolidge 1963). This event was important to Maine history (the controversy it sparked among loggers was known as the "Telos War"), but it also illustrates how interconnected the modern watersheds of Maine could have been during the retreat of the glaciers. Our lack of knowledge of historical freshwater lake and river drainage patterns probably represents the greatest obstacle to understanding the details of how freshwater fish and mussels dispersed into New England.

How quickly could freshwater fish and mussels disperse from glacial refugia back to New England? The immense weight of the glaciers compressed the land, and though the land eventually rebounded, the lag time between glacial retreat and **isostatic rebound** meant that seawater flooded much of northern New England. Seawater flooded Maine all the way north to southern Piscataquis and northern Penobscot counties. If freshwater fish and mussels did occupy a refugium off the coast of northeastern North America, and migrated directly into Maine, they would have had to disperse quickly enough so that they would not be inundated by seawater, and far enough inland to avoid encroaching

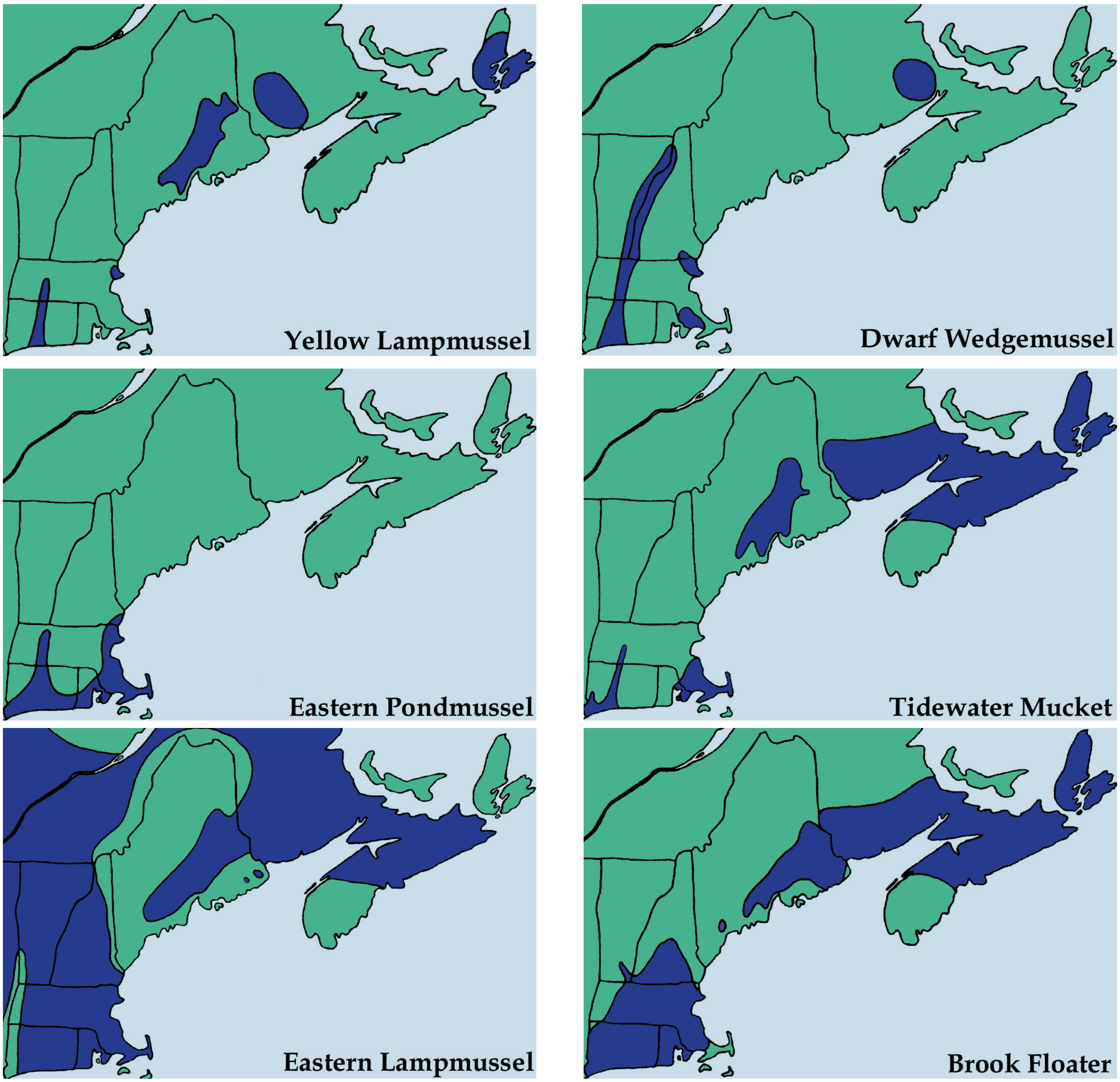


Figure 9. Distribution of Six Species in the Northeast
The historical distribution of these species in the Northeast suggests that a glacial refugium existed off the coast of modern-day Nova Scotia, and dispersal into Maine was from the east. The distribution gap in southern Maine suggests these species were unable to disperse northeastward from New Hampshire and Massachusetts, or that something caused these species to be extirpated from Maine's southern coastal plain. (**Source data**: Johnson (1947), Clarke (1981b), Smith (1995), Fichtel and Smith (1995), and MDIFW Database).

seawater. In this scenario, dispersal into modern-day coastal watersheds may have been from areas north of the maximum extent of seawater encroachment. A more plausible explanation is that plants and animals followed a dispersal route into southern New England (from Georges Bank) and the highlands of the Canadian Maritime Provinces (from the Grand Banks and Sable Islands). Once the land rebounded and the shoreline reached its present-day location, these species spread into Maine from the west and east. Distribution patterns of many mussels in northern New England suggest that the latter route — dispersal from the Canadian Maritime provinces — is more important for Maine's mussels (Figure 9). The state's greatest diversity of freshwater mussels exists in central and eastern Maine, so it seems unlikely that these mussels would have dispersed from southern Maine, where they do not even exist today. The eastern pondmussel and dwarf wedgemussel, as well as a number of fish species, are found in the Merrimac River watershed in eastern Massachusetts and New Hampshire, but are not found in Maine. Their inability to disperse into Maine's southern coastal watersheds suggests that other species may have also had the same difficulty. If Maine's fish and mussel species had dispersed from the southwest, it is likely these other species would be found here as well.

One of the most perplexing questions is why the dwarf wedgemussel is found in the Concord River in New Hampshire and the Petitcodiac River in New Brunswick but has never been found at points in between (Figure 9). Three of its suspected host fish — the slimy sculpin, swamp darter, and Atlantic salmon — occur in the state. The most logical answer is that the dwarf wedgemussel does exist in Maine, but has not yet been discovered. This seems unlikely, especially since thousands of hours have been spent surveying well over 1600 locations. Where did this species take refuge during the glacial period, and what was its dispersal route back into southern New England and the Canadian Maritimes? Is recent environmental history responsible for its absence in Maine? These questions continue to puzzle zoologists and zoogeographers.

Recent Environmental History

In the last 400 years, Maine's aquatic ecosystems have been subjected to an extraordinary amount of abuse. Settlers relied on aquatic ecosystems as sources of food, energy, transportation, and waste disposal. It is difficult to look at a clean, flowing river today and comprehend how different it may have looked 100, 200, 300, or even 400 years ago. It is especially difficult to understand the current diversity and distribution of aquatic animals — such as fish or freshwater mussels — without knowing how their populations responded to nearly four centuries of intensive human use. With what we know about post-glacial dispersal of freshwater animals into northern New England, we are perplexed about some of the distribution patterns we see for freshwater mussels — such as the absence of the dwarf wedgemussel in Maine, the low diversity of mussels in southern Maine, and why some species are found only in the central part of the state. Since we do not know pre-disturbance distribution patterns, any discussion is purely conjecture. However, it is worth reviewing the recent environmental history of Maine's aquatic ecosystems, if only to promote an appreciation and awareness of the injury and insult that these ecosystems have faced.

Maine's rivers once supported remarkable runs of anadromous fish, notably Atlantic salmon, alewife, American shad, river herring, striped bass, and sturgeon. The first water-powered sawmill was built in 1634 on Great Works Stream in South Berwick, and during the following 250 years over 1600 dams would be built on Maine's rivers for industrial, commercial, or domestic purposes. Dams were considered critically important to early communities, and legislation was passed to protect dam builders from any lawsuits (Hasbrouck 1984). The effect of these dams on anadromous fish was immediate and profound. Salmon were gone from the Piscataqua River by 1750, and from the upper Salmon Falls River by 1800 (Cronon 1983). The Mousam River flows only a short distance from Mousam Lake to the ocean, yet by the 1860s there were 19 dams built along its length, none of which had fish passage facilities (Report of Commission on Fisheries 1867). The Saco River salmon runs ceased by the early 1800s, and in 1867 the Fish Commissioner's report stated "*We could obtain no estimate of their numbers in former times, as they had ceased to be plenty beyond the recollection in the present generation.*" The first sawmill in the Penobscot Bay area was built in 1720 on a tributary of the St. George River, but was soon destroyed by native peoples who were outraged that the dam interfered with fish runs (Coolidge 1963). Alewife, salmon, and shad once migrated up the Penobscot River nearly 200 miles from the ocean, but were barely able to get past Bangor once dams were constructed.

Mill dams constructed in the 18th and 19th century, such as this one, blocked fish migration and may have extirpated mussel species upstream. ETHAN NEDEAU

The alewife floater is conspicuously absent from the Saco River and other coastal rivers of southern Maine. Blockage of its host fish — alewife, shad, and river herring — undoubtedly caused it to be extirpated from these rivers. Is it possible that the dwarf wedgemussel, which is known to use the Atlantic salmon as a host, existed in these rivers prior to European colonization? Yes, but we may never know. Darters, dace, and minnows may have also been affected by dams because of habitat degradation, and were probably further threatened by the introduction of predatory gamefish beginning in the mid-1800s.

Throughout the 18th and 19th centuries, settlers were clearing forests and replacing them with pastures and cultivated land. More fields and pastures existed in the 1800s than exist today — well over a million acres were cleared in Maine for agriculture, or as a result of lumbering activity (Coolidge 1963). This was done with little regard for the protection of riparian zones, curbing erosion and sedimentation, or reducing the inputs of nutrients to rivers and lakes. Rivers must have been degraded immeasurably during this time. Rivers and streams were also the unfortunate recipients of nearly all the waste from communities along their banks, including domestic sewage and industrial waste. Unfortunately, the prevailing belief at the time was that "*dilution is the solution to pollution*" — that the harmful effects of pollutants would be dissipated once they were released into a river, lake, ocean, or the atmosphere.

Industrial waste was by far the most serious source of pollutants to Maine's rivers. The cutting and transport of logs downriver to sawmills, and the normal operations of the sawmills, caused excessive sedimentation with logs, bark, and sawdust. Wood (1961) recounted stories of a log jam on the Kennebec River in Norridgewock in 1854 that covered an area of 40–50 acres at a depth of two to ten feet — an estimated 25,000 logs! As far back as colonial times, there were ordinances that forbade activities detrimental to alewives, and laws stating that streams must be kept clear of debris. Yet log drives continued in Maine until the 1970s. The last log drive in Maine was on the Kennebec River in 1976.

The pulp and paper industry had a profound influence on the quality of Maine's rivers. The first

Types and Sources of Pollution

The plants and animals that live in our rivers have had to deal with…

raw sewage, sawdust, wood pulp, logs and bark, lime, tar, coal oils, ammonia, dyes, soaps, free sulphuric acid, sulphite liquors, black ash, white water, lead, mercury, chlorine, polychlorinated biphenyls (PCBs, among which are dioxins), polycyclic aromatic hydrocarbons (PAHs), nitrogen, phosphorus, arsenic, pesticides, sediment, and more…

from a variety of sources, including…

municipalities, forestry operations, sawmills, paper mills, dye houses, cotton and woolen mills, tanneries, industrial wastes, agricultural activities, atmospheric pollution, and more…

commercial pulp mill was built at Topsham in 1868. In 1930, eight pulp and paper mills discharged waste into the Penobscot River between Millinocket and Brewer (Walker 1931), and there were another six on the lower Kennebec. The Androscoggin River was probably the most polluted river in Maine during this time, especially near the communities of Lewiston and Auburn, where a number of paper and textile mills lined the river, along with a human population of 54,000. During a particularly hot and dry summer in 1941, the entire Androscoggin River smelled of rotten eggs, and paint peeled from houses in the Lewiston area (Hasbrouck 1984).

Throughout the 1800s, many communities were dumping their industrial and domestic waste into rivers and using the same rivers as a source of drinking water. It wasn't until a typhoid outbreak in the lower Kennebec River valley in 1902–1903 that people began to create municipal water systems and make provisions for protecting the health of rivers (Campbell 1958). Yet the health of the Kennebec continued to decline. In the 1950s the Kennebec River from Madison to the ocean was referred to as an open sewer and barely supported aquatic life. Many communities continued to pump raw sewage directly into rivers or coastal areas well into the 1970s (Maine Water Resources Plan 1969) — even by 1984 over 50 of Maine's communities were without sewage treatment plants (Hasbrouck 1984).

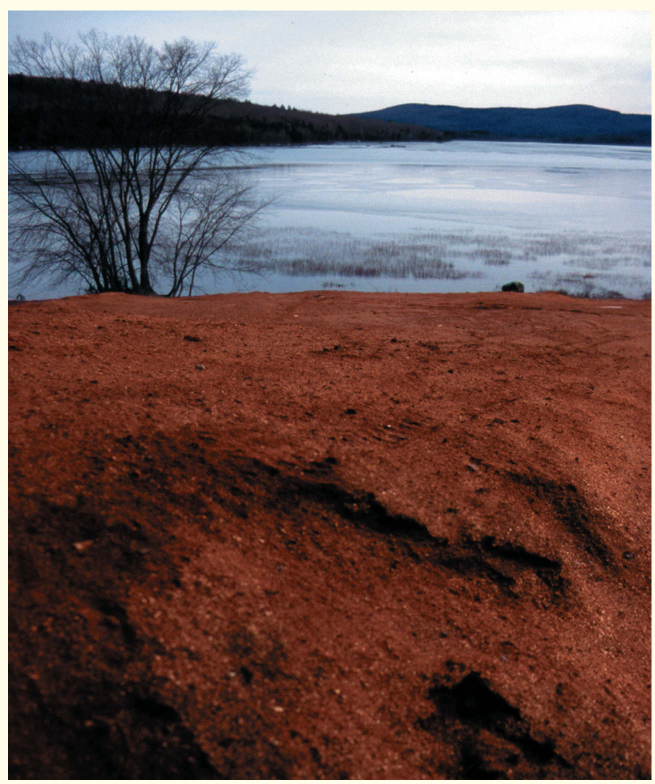
The hydropower industry also has had a significant impact on Maine's aquatic ecosystems. The first hydropower dams were built around the same time that the pulp and paper industry was getting started. Today, there are nearly 100 hydroelectric dams in Maine, with a combined generating capacity of 547 megawatts — less than 20% of the electric power consumed in Maine (Hasbrouck 1984). These dams are certainly important from an economic standpoint, but they came at substantial ecological costs. They reduced the quality of water and habitat, as well as the natural and recreational values of the rivers.

Because of environmental legislation and other conservation programs, the quality of Maine's aquatic ecosystems has improved over the last three decades. Communities are targeting obvious sources of pollution, modern waste treatment plants are operating in many communities, and some communities are beginning to recognize the value of wise land-use planning to protect aquatic systems from sedimentation and runoff. Anad-

Forestry Operations and Sedimentation

At the peak of Maine's lumbering operations, there were nearly 1300 sawmills on Maine's lakes and rivers, which collectively produced 600 million to over 1 billion board feet of lumber per year (Wood 1961). You can imagine the volume of waste that these operations generated — including sawdust, bark, and logs. Much of this material was dumped directly into rivers and lakes, despite early legislation that prohibited such activity (Coolidge 1963). Since these materials are slow to decompose in aquatic systems, deposits of sawmill refuse are still evident — and continue to have an effect on the environment — in many locations throughout the state.

In 1914, Olaf Nylander remarked: "*Many of the tributaries of the St. John's River are in the forest … Sawmills large and small are to be found nearly everywhere. The sawdust and other waste is thrown in the water, and is forming extensive deposits in the river and its tributaries. It is very destructive to molluscan and other animal life*" (Nylander 1914).



Looking over a mountain of sawdust on the shore of Saponac Pond, near Burlington, Maine. ETHAN NEDEAU romous fish are returning to many rivers to spawn, and the diversity of other aquatic animals is slowly increasing in response to clean-up efforts.

Freshwater mussels are slow to respond to environmental change, and especially to disperse back into areas where they were previously extirpated. Maine did not begin to systematically survey freshwater mussels until 1992 — well after environmental legislation was enacted and water quality dramatically improved. The diversity, distribution, and abundance of freshwater mussels have undoubtedly changed since pre-settlement times, and the patterns that we see today should be viewed in the context of 400 years of dams, pollution, introduced species, and recent efforts to correct abuses to the environment.

Diversity And Distribution

Ten species of freshwater mussels have been documented in Maine. An eleventh species, the Newfoundland floater, had been reported in Maine, but these historical records are thought to be misidentifications (Hanlon and Smith 1999). All of the freshwater mussels of Maine are part of the Northern Atlantic Slope fauna, which is a group of 16 species (Table 3). Johnson (1970) defined the Northern Atlantic Slope as the region extending from the York River, Virginia, to the lower St. Lawrence River, Canada, and including Labrador and Newfoundland. The Northern Atlantic Slope fauna is a subset of a larger group known as the Atlantic Slope fauna, which includes 37 species occupying rivers as far south as the Altamaha River system, Georgia (Johnson 1970). Some of the Northern Atlantic Slope species have a broad geographical distribution, such as the creeper, which is found throughout the Mississippi River basin, and the eastern pearlshell, which is found throughout the Northern Hemisphere, including Europe. Seven of the Northern Atlantic Slope species are not found in Maine. The federally endangered dwarf wedgemussel has not been documented in Maine, though it exists in all other New England states except Rhode Island, and was known to exist in the Petitcodiac River in New Brunswick as recently as 1963 (this disjunct population is now thought to be extirpated). The eastern pondmussel is found in southeastern Massachusetts and New Hampshire, and though it could have occurred in coastal plain ponds of southern Maine, it is more likely that it never dispersed into Maine. Four other species of the Northern Atlantic Slope — green floater, yellow lance, northern lance, and elktoe — are not found in Maine or New England.

Table 3. North Atlantic Slope Fauna

These 16 species exist in Atlantic coastal drainages from Virginia to Newfoundland, but only ten are known from Maine. Species with an asterisk (*) are not found in New England or eastern Canada. (**Source**: Johnson, 1970)

Scientific Name	Common Name
Margaritifera margaritifera	Eastern Pearlshell
Elliptio complanata	Eastern Elliptio
*Elliptio lanceolata**	Yellow Lance
*Elliptio fisheriana**	Northern Lance
*Lasmigona subviridis**	Green Floater
Alasmidonta undulata	Triangle Floater
*Alasmidonta marginata**	Elktoe
Alasmidonta varicosa	Brook Floater
Alasmidonta heterodon	Dwarf Wedgemussel
Pyganodon cataracta	Eastern Floater
Pyganodon fragilis	Newfoundland Floater
Anodonta implicata	Alewife Floater
Strophitus undulatus	Creeper
Ligumia nasuta	Eastern Pondmussel
Lampsilis cariosa	Yellow Lampmussel
Leptodea ochracea	Tidewater Mucket
Lampsilis radiata radiata	Eastern Lampmussel

The seventh member of the Northern Atlantic Slope fauna that is not found in Maine is the Newfoundland floater (*Pyganodon fragilis*). This species has a northerly distribution, occupying rivers and lakes in Newfoundland, northern Quebec, and perhaps parts of New Brunswick. It has been reported to exist in northern Maine, though the validity of these reports remains questionable. It is thought to hybridize with other species in its genus, especially the eastern floater (*Pyganodon cataracta*), which is common and widespread in Maine. In fact, these two "species" were considered subspecies until recently (Kat 1983). Despite the fact that *P. fragilis* and *P. cataracta* are thought to hybridize, Hoeh (1990) used molecular markers to determine that these should be recognized as distinct species. Hanlon and Smith (1999) carefully analyzed the anatomy and beak sculpture of *Pyganodon* collected from Maine, as well as historic information and museum collections. They concluded that early workers in Maine mis- identified the eastern floater as the Newfoundland floater, and that the Newfoundland floater has yet to be reported from the state. Some authors have recognized two subspecies within the species *Pyganodon cataracta*: *P. cataracta cataracta*, and *P. cataracta marginata* (Turgeon et al. 1988). Further, Hoeh and Burch (1989) suggested that these two subspecies should be elevated to the rank of species, and proposed that they be named *Pyganodon cataracta* and *Pyganodon lacustris*. The net result of all of this research is that three species in the genus *Pyganodon* could potentially exist in Maine: *Pyganodon cataracta*, *Pyganodon lacustris*, and *Pyganodon fragilis*. Until further research clarifies these taxonomic differences, and demonstrates valid reports of the Newfoundland floater in Maine, our stance is that the Newfoundland floater has not yet been documented in Maine. We hope that researchers will continue to examine this genus in closer detail — especially genetic or molecular markers across a broad latitudinal gradient.

The greatest diversity of freshwater mussels in Maine is found in the Penobscot and Kennebec River drainages of midcoast and central Maine. Lakes generally support a lower diversity of freshwater mussels, though six species are found in Pushaw Lake in southern Penobscot County. Rivers of southern Maine are less diverse than rivers of central Maine — there are seven species in York and Cumberland counties combined. The Royal River has the greatest diversity in southern Maine, with four species present. The low diversity in southern Maine may be explained in terms of zoogeography, but may also be a reflection of the recent (400 year) environmental history of these watersheds. Also, few coldwater or coolwater fish survive and reproduce in the warm rivers and streams of southern Maine, which may help explain the absence of some mussels.

Rivers east of the Penobscot drainage contain five to seven species each, though neighboring tributaries of the Penobscot support eight to ten. In some locations of Hancock and Washington counties, there is only a single ridge or mountain separating the Penobscot drainage from several Down East rivers, yet their mussel faunas are distinctly different. The tidewater mucket and yellow lampmussel are found throughout the Penobscot drainage, but are not found in neighboring eastern coastal drainages.

Lakes and rivers in northwestern and northern Maine contain the lowest diversity of mussels, with only two species found consistently, and a maximum of five species found at a single location. The eastern lampmussel, yellow lampmussel, tidewater mucket, brook floater, and alewife floater are absent from the major drainages of the north (St. John River, Aroostook River, Fish River, and Allagash River). However, these species are found in the lower St. John River in New Brunswick (Clark 1981b). The low diversity in the north is likely a result of zoogeography — especially constraints on post-glacial dispersal into the region. Diversity generally decreases as one moves north away from a glacial refugium, and the species found are those with good dispersal ability and tolerance for a broad range of ecological conditions (Strayer 1987).

Maine's Freshwater Mussel Atlas Project

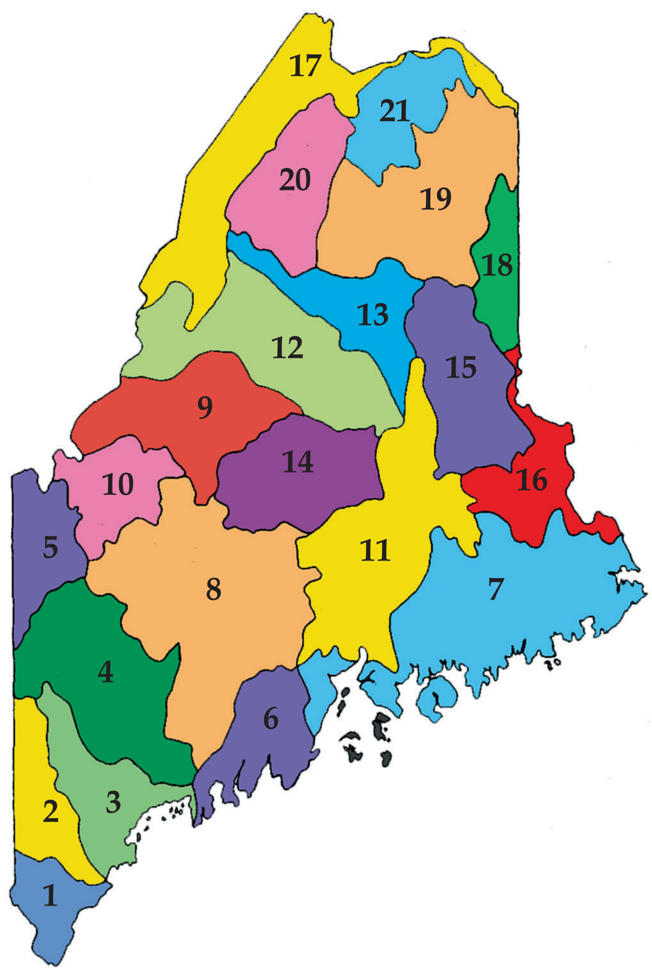
Prior to the 1990s, the state of Maine had little information about the distribution and abundance of its freshwater mussels. Naturalists had collected shells from Maine's waters since the beginning of the 19th century, and we owe a debt of gratitude to these people for their efforts. However, the historical data was scant, scattered, and often lacked important information needed for verification. By the 1980s, many state and federal agencies and private organizations were documenting startling declines in species diversity throughout North America and had long since included freshwater mussels on their endangered species lists. In 1991, nearly 72% of North America's freshwater mussel species had been listed as endangered, threatened, or special concern. Some of the species known to occur in Maine were recognized by other states as needing protection, yet their status in Maine was still uncertain. A systematic, statewide survey of freshwater mussels became a priority conservation need for the state.

In 1991, the Maine Department of Inland Fisheries and Wildlife began seeking funds to conduct surveys of rare mussel species, especially the yellow lamp- mussel and brook floater, which at the time were candidates for federal listing. These early surveys, facilitated by the U.S. Fish and Wildlife Service, blossomed into a comprehensive, systematic survey of all freshwater mussel species throughout the state. The primary goals of this work were to document species occurrence and obtain critical baseline data on the current distribution, relative abundance, and conservation status of all of Maine's freshwater mussels. These efforts continued from 1992 to 1997 at over 1600 survey locations throughout Maine. The valuable information obtained from these surveys has enabled MDIFW to identify those species needing special protection in Maine, and ensured that their habitat is conserved. In addition, our knowledge and understanding of freshwater mussels in general has increased tremendously. Although many unanswered questions remain, such as host fish species, population trends, and specific conservation needs, the results of this statewide survey effort have provided MDIFW with a solid foundation on which to begin building a long-term freshwater mussel conservation program for Maine.

Diversity by Watersheds

Below is a list of Maine's major watersheds, and the number of mussel species found within each. The numbers on the map correspond to the watershed divisions listed below. Major tributaries of each watershed are also listed.

Watershed	# Species
1. Southern Coastal Rivers Piscataqua, Salmon Falls, Mousam	4
2. Saco River Ossippee, Little Ossippee, Kezar	4
3. South-Central Coastal Rivers Presumpscot, Royal	7
4. Lower Androscoggin River Little Androscoggin, Nezinscot, Ellis	8
5. Upper Androscoggin River Magalloway, Cupsuptic, Kennebago	4
6. Central Coastal Rivers Sheepscot, St. George, Medomak	10
7. Eastern Coastal Rivers Union, Narraguagus, Machias	9
8. Lower Kennebec River Sebasticook, Sandy, Carrabassett	10
9. Upper Kennebec River Moose, Roach	5
10. Dead River	3
11. Lower Penobscot River Passadumkeag, Pushaw	10
12. West Branch Penobscot River North Branch, South Branch	6
13. East Branch Penobscot River Seboeis, Wassatoquoik	7
14. Piscataquis River Pleasant	8
15. Mattawamkeag River Baskahegan, Molunkus	8
16. Saint Croix River	6
17. St. John River	5
18. Meduxnekeag River	5
19. Aroostook River	4
20. Allagash River	2
21. Fish River	3



Notable Figures in the Early Malacological History of Maine

The freshwater, terrestrial, and marine molluscs of Maine have been described and catalogued since the early 1800s. Martin (1995) provided a short biography of several malacologists who made important contributions to our knowledge of Maine's molluscs; here we provide highlights of this excellent account, and include two more recent malacologists who have made notable contributions.

Thomas Say (1787–1834): Thomas Say is known as the "Father of American Malacology." He was the first to describe hundreds of molluscs from North America, including seven of the freshwater mussels found in northern New England. His descriptions were published in the *American Edition of the British Encyclopedia or Dictionary of Arts and Sciences*, 1817.

Dr. Jesse Wedgwood Mighels (1795–1861): This Maine native catalogued 174 species of marine, terrestrial, and freshwater molluscs in his 1843 publication in the *Boston Journal of Natural History*. He was also one of the founders of the Portland Society of Natural History.

Edward Sylvester Morse (1838–1925): This Maine native became an accomplished scientist and illustrator at the Peabody Academy of Science and Essex Institute in Massachusetts. He made important contributions to our knowledge of terrestrial and freshwater gastropods with his 1864 publication entitled "Observations on the Terrestrial Pulmonifera of Maine, Including a Catalogue of All the Species of Terrestrial and Fluviatile Mollusca Known to Inhabit the State," which appeared in the *Journal of the Portland Society of Natural History*.

Norman Wallace Lermond (1861–1944): This Maine native published *Shells of Maine: A Catalogue of the Land, Fresh-Water and Marine Mollusca of Maine* in 1908. He began the scientific journal *The Maine Naturalist* in 1921. He co-published "A Bibliography of the Recent Mollusca of Maine — 1605–1930," which appeared in *The Maine Naturalist*. He was also the co-founder of the American Malacological Union, which remains one of the premier malacological organizations in the world today.

Olaf Olsson Nylander (1864–1943): This Swedish immigrant made his home near Caribou, Maine, where he spent much of his life documenting the natural history of northern and eastern Maine. He collected, identified, and helped decribe freshwater and terrestrial molluscs from this region. Several of these species bear his name, such as the snail *Vertigo nylanderi*. Today you can visit the Nylander Museum in Caribou to learn of the contributions he made to our knowledge of the natural history of Maine.

Dr. Arthur H. Clarke: Arthur Clarke has made a number of important contributions to malacology in northeastern North America, especially regarding systematics and distribution. These include a monograph on the systematics of the Tribe Alasmidontini (which includes the genus *Alasmidonta*) (Clarke 1981a), a publication on the freshwater mussels of New York (Clarke and Berg 1959), and a book on the freshwater molluscs of Canada (Clarke 1981b).

Dr. Richard I. Johnson: Richard Johnson has been one of the most influential malacologists of the 20th century because of his outstanding work on systematics and zoogeography of freshwater mussels, especially the Atlantic Slope fauna. His two most important monographs are "The Systematics and Zoogeography of the Unionidae (Mollusca: Bivalvia) of the Southern Atlantic Slope Region" (Johnson 1970) and "Zoogeography of North American Unionacea (Mollusca: Bivalvia) North of the Maximum Pleistocene Glaciation" (Johnson 1980).

Finding and Documenting Freshwater Mussels

There are several important considerations to take into account when deciding how to go about searching for freshwater mussels. These include the survey location, survey method, and types of information that should be recorded. There are also some important considerations in regard to safety and etiquette. The following guidelines were used by the Maine Freshwater Mussel Atlas Project, and should make finding and learning about freshwater mussels safe and enjoyable.

Where to Look

Freshwater mussels are found in nearly every permanent water body in the state. In rivers, surveys are often conducted upstream and downstream of bridge crossings because of ease of access. However, it is often desirable to survey less accessible sites because bridge construction often changes local conditions (substrate, depth, and flow) and may affect the local distribution of mussels. When determining the species composition of an entire river, numerous sites should be surveyed along its length. This is because habitat conditions change along the length of a river from its headwaters toward the mouth, and species with different habitat preferences will not be distributed uniformly throughout the river. Habitat conditions in lakes are less variable and it is not necessary to survey as many sites to determine which species exist there. Surveys should be done at different depths, and in different substrate types. Boat launches or public beaches are often the most accessible, but may also be the most disturbed in terms of habitat quality.

Methods

There are three survey methods that have been used by the Maine Freshwater Mussel Atlas Project. Each method is suited for different conditions, and usually a thorough survey will include some combination of the three.

Shoreline Search: An easy way to determine whether mussels are present is to walk along the shoreline and search for shells. Muskrats prey upon mussels and leave shells in piles called "middens." Middens can be found on the bank, in shallow water, or under structures such as docks and bridge abutments. During periods of low water (midsummer droughts, low tide), mussel shells are often exposed along the shoreline. An advantage of searching the shoreline for shells is that nice specimens can be collected without having to sacrifice live animals. Also, wading or swimming in waters that may be particularly dangerous or unpleasant can be avoided. The disadvantage of this method is that it provides little information about the species composition and abundance of live animals, or the quality and availability of instream habitat. Since muskrats often prey on species that are easy to pry open, the species composition of a shell midden may not always accurately represent what exists in the water.

Glass-Bottom Buckets: A five-gallon bucket fitted with a clear Plexiglas or plate glass bottom is an important tool for surveying freshwater mussels in shallow water. It allows the surveyor to walk in the water and search for live animals in the substrate. This method is usually

Things to Remember When Surveying for Freshwater Mussels

- Be aware of potential hazards, including strong currents, slippery rocks, poor visibility, submerged trees, or heavy boating activity.
- Wear adequate footwear when wading as protection from broken glass, other trash, or sharp rocks.
- Always be respectful of the rights of private landowners, boaters, and fishermen.

Two methods commonly used to search for mussels include peering through a clear bottom bucket (left) and snorkeling (right). MARK McCOLLOUGH

useful only in water depths up to three feet, and is the most common method used to survey small streams, rivers, and shallow portions of lakes. Usually hip boots or chest waders are worn. This is a good method to use when the water is too cold for swimming, or if there are concerns about water quality or broken glass. One drawback of this method is that the substrate may be disturbed, making viewing difficult. When in flowing water, the surveyor should walk upstream so that sediments will be flushed behind them. Another drawback to this method is the risk of stepping on live mussels, or damaging fragile plants and animals living on the bottom (such as liverworts, sponges, snails, crayfish, or aquatic insects).

Snorkeling: For those with snorkel gear and experience, snorkeling is perhaps the most enjoyable way to survey freshwater mussels. This method allows large portions of a lake or river to be surveyed, permitting a better understanding of the species composition and abundance of mussels. Snorkeling is necessary in depths greater than three feet, and is recommended in shallower water because there is less chance of disturbing the substrate and trampling live mussels. A wet-suit is recommended for extended periods in the water or snorkeling in cool streams and rivers. Snorkelers must be especially mindful of the many hazards that may exist in a lake or river, including boat traffic, dangerous current, and poor visibility. Snorkeling is also an excellent way to explore and appreciate under- water life — there are many interesting creatures besides freshwater mussels that can be found.

A final survey method that is sometimes used is SCUBA diving. Diving has been used in some of Maine's larger rivers where it is impractical to snorkel. Professional certification is required to use SCUBA gear — otherwise dive shops will not fill oxygen tanks. Large rivers are sometimes dangerous due to deceptively strong current, low visibility, and hazards such as submerged trees. It is strongly recommended that sufficient dive experience, preferably in flowing water, should be acquired before attempting to dive in Maine's larger rivers. Observe safety rules and never SCUBA dive alone.

Collecting, Preserving, and Reporting Specimens

Collecting Etiquette: Always attempt to find shells before killing a live animal. Since the Maine Endangered Species Act protects some of Maine's freshwater mussels, purposefully killing a listed species or possessing their shells is a violation of state law. A MDIFW biologist should verify the identity of any suspected rare species. It is likely that the biologist is already aware of the occurrence and there is no need to kill any individuals for voucher specimens. If shells are present (in middens or otherwise), collect those of the rare species and submit them to a biologist. The size range and condition of shells are important types of information that biologists use to evaluate the health of a population.

Killing and Preserving Specimens: The easiest way to kill live specimens humanely is to place them in boiling water for a few minutes until the shells gape. Inserting a knife between the two valves along the top-front and top-rear margins, and slicing the front and rear adductor muscles is a second way to open the shell and remove the soft parts. After removing the animal, the shell should be scrubbed with a soft toothbrush in warm soapy water to remove dirt or debris. Once dry, shells can be labeled, coated with lacquer, and placed in permanent storage. Shells in MDIFW's voucher collection are labeled with a catalog number, species name, water body, town, and date collected.

This yellow lampmussel shell is part of the extensive voucher collection that MDIFW has compiled in the last decade.
ETHAN NEDEAU

Reporting Specimens: Maine has 31,673 miles of rivers and streams, and 5782 lakes over an acre in size, making a statewide survey of freshwater mussels a formidable task. Thus, state biologists depend in part on private agencies, environmental consultants, and interested citizens to provide data on the distribution of freshwater mussels. It is important that collectors record certain types of information when finding and reporting a specimen. The following information is absolutely critical: name of water body where found, exact location where the survey was conducted, date collected, and name of collector. Without these, a shell has virtually no value to any scientific study. In addition, information related to survey methods, site location, site description, habitat conditions, and attributes of the mussel population are usually recorded. An example datasheet is provided on the facing page.

Contact Numbers for MDIFW Regional Wildlife Biologists and Endangered Species Group

MDIFW
Regional Wildlife Office
RR1, 358 Shaker Road
Gray, Maine 04039
(207) 657-2345

MDIFW
Regional Wildlife Office
270 Lyons Road
Sidney, Maine 04330
(207) 547-5318

MDIFW
Regional Wildlife Office
68 Water Street
Machias, Maine 04654
(207) 255-4715

MDIFW
Regional Wildlife Office
689 Farmington Road
Strong, Maine 04983
(207) 778-3324

MDIFW
Regional Wildlife Office
P.O. Box 551
Greenville, Maine 04441
(207) 695-3756

MDIFW
Regional Wildlife Office
HCR 67, Box 1066
Enfield, Maine 04493
(207) 732-4132

MDIFW
Regional Wildlife Office
P.O. Box 447
Ashland, Maine 04732-0447
(207) 435-3231

MDIFW
Endangered Species Group
650 State Street
Bangor, Maine 04401
(207) 941-4466

Facing Page: *Example datasheet used during freshwater mussel surveys. A datasheet such as this is critically important to a good survey.*

Mussel Survey Data Form

Observer: ____ **Date:**____________________

Water Type: _________ L = Lake, Pond W = All others **Site Number:**____________

Water Name: ____

Town: ____ **County:**________________

Survey Type: _________________________ **Duration of Survey:**______________________

Directions: (landmarks, include sketch if necessary):

Description of Local Habitat (Land Use, Depth/Flow/Substrate, etc)

Species Found and Relative Abundance: X = Live Individuals, S = Shells Only

MM EC AU AV PC AI SU LO LC LR

Specimens Collected:

Notes on Mortality, Reproduction, Shell Erosion, etc:

Additional Comments:

Species Accounts

Introduction

The Maine Freshwater Mussel Atlas Project led biologists to lakes and streams in every corner of the state, where inquisitive fishermen, boaters, and landowners would almost invariably ask, "What are you looking for." When told we were looking for freshwater mussels, one of the most common responses was, "Are there more than one kind?"

Unfortunately, many wildlife and fisheries biologists, environmental regulators, consultants, and other conservation professionals whose decisions affect aquatic ecosystem health know little more than the public about freshwater mussels. One of the primary goals of this book is to teach people how to identify the freshwater mussels they encounter in New England's lakes and rivers. This sounds like a simple enough task, especially since there are only 12 species that occur in the region (outside of Vermont's Champlain Basin). Yet virtually all freshwater mussel identification manuals are difficult to use because they require readers to be familiar with complex scientific terms, rely on a complicated **dichotomous key**, and are usually poorly illustrated.

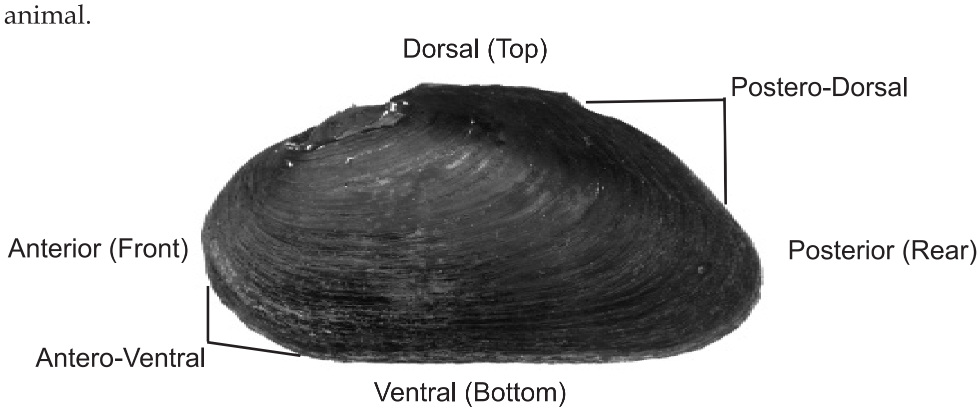
In this book, we try a simpler, friendlier approach to identifying freshwater mussels. There is no dichotomous key; instead we rely heavily on illustrations and photographs similar to what most naturalists are used to in popular field guides. The scientific jargon is kept to a minimum, and most of the terms used throughout the species accounts are illustrated. Each species description references corresponding photographs and illustrations, and species that are easily confused with each other are compared and contrasted. In addition, information on range, habitat, reproductive characteristics, and conservation status is provided in each species account. Every water body in Maine where each species is currently known to exist is listed and a range map is provided.

In addition to the ten species known to occur in Maine, species accounts are also provided for the dwarf wedgemussel, eastern pondmussel, Newfoundland floater, zebra mussel, and quagga mussel. Thus, this manual includes all species found in Maine, New Hampshire, Massachusetts, Connecticut, Rhode Island, and the Canadian Maritime Provinces. The zebra mussel is included because it exists in New England and could possibly spread into Maine in the future, and the quagga mussel is included because it might spread into New England in the future.

Hints for Identifying Freshwater Mussels

I. Orientation

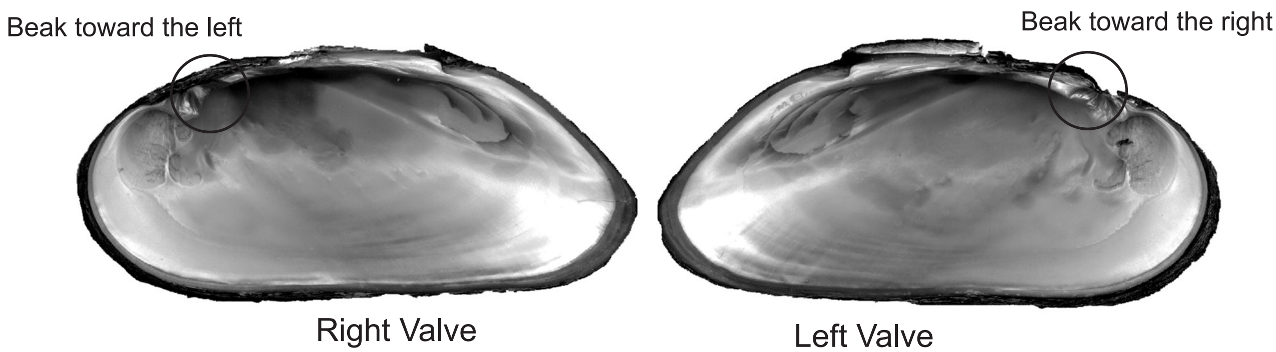
There are six directional terms used when describing species, denoting the top, bottom, front, or back of the animal. The beak and foot are toward the anterior (front) of the animal, and the apertures are towards the posterior (rear) of the animal.



II. Left versus Right Valve

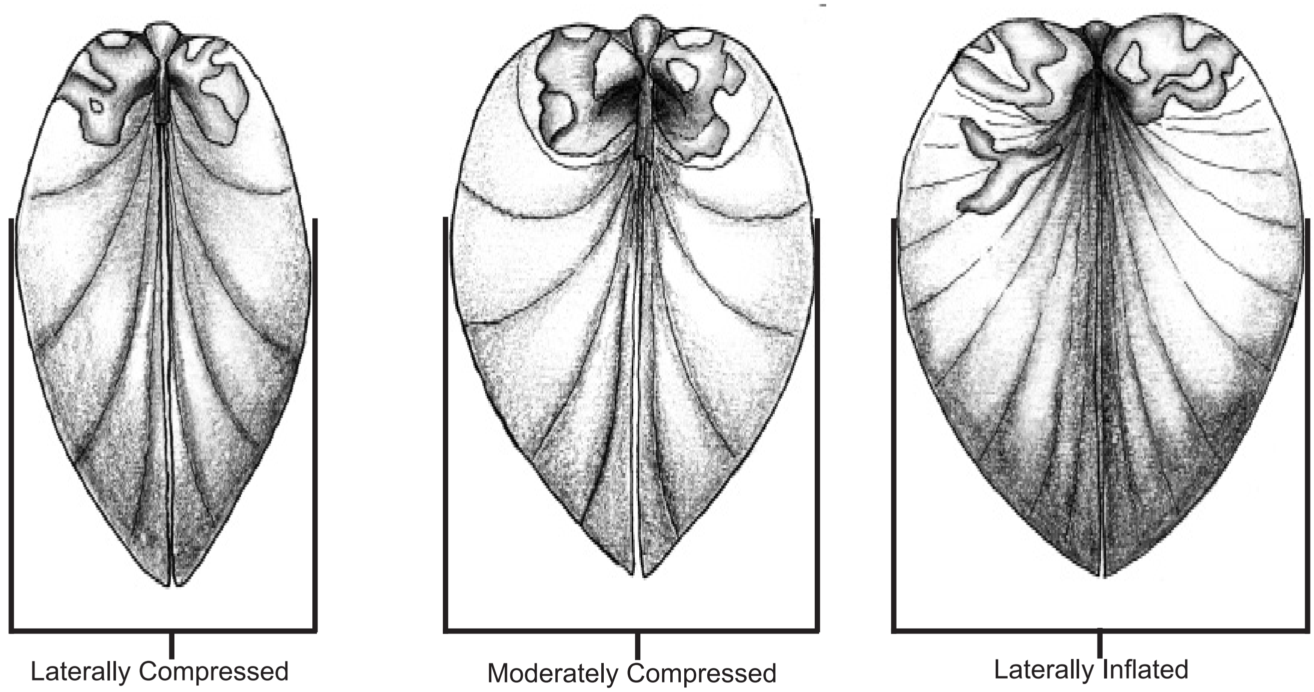
It is important to know the difference between the left and right valve, because hinge teeth morphology is different on each. Throughout the species accounts, the right valve is illustrated. This is easy to determine:

1. Position the valve with the nacre facing you and the beak pointing upwards (as shown).
2. If the beak is toward the left, it is the right valve.
3. If the beak is toward the right, it is the left valve.



III. Shell Width

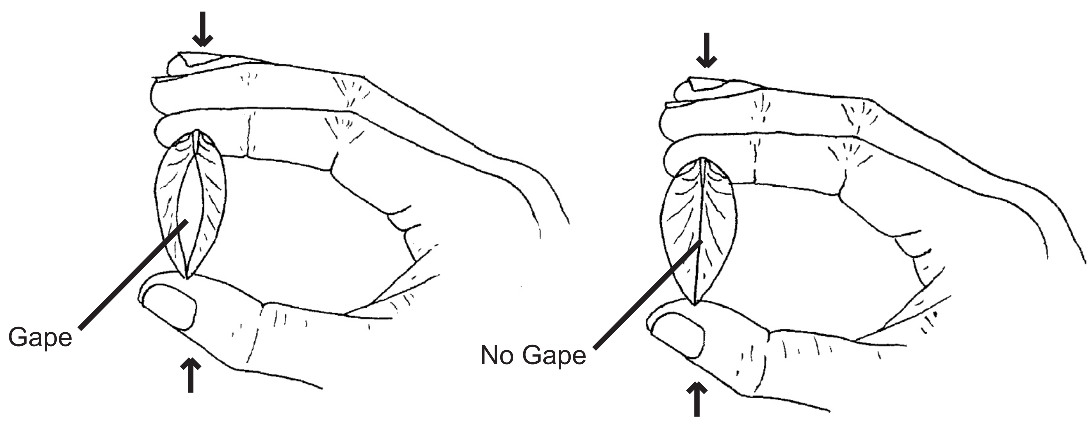
Each species is characterized as being either laterally compressed, laterally inflated, or somewhere in between. Hold the valves together and look at the anterior end. Some shells will appear swollen or "inflated", whereas others will appear skinny or "compressed".



IV. The "Squeeze Test"

Some mussels have thin shells that are relatively weak, and application of slight pressure on the dorsal and ventral margins will cause the shells to gape at the posterior end. Other species have very strong shells, and virtually no amount of pressure will cause the shells to gape. The "squeeze test" is a reliable way of differentiating certain species WITHOUT having to kill the animal to examine internal shell morphology. This test is especially important for distinguishing the creeper (state-listed special concern) from the eastern elliptio (a common species).

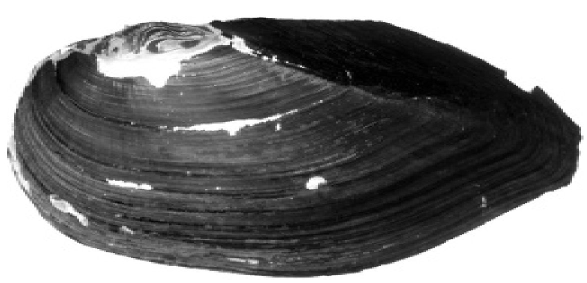
The eastern floater and Newfoundland floater gape wide when moderate pressure is applied. The creeper and alewife floater have slightly more durable shells, and more pressure must be applied to force them to gape. The other species generally will not gape at all, unless the animal is very young or you apply a tremendous amount of force.



CAUTION: Do not squeeze too hard! You may break the shell and kill the animal.

V. Shape

Several terms are used to describe the shape of each species. These terms refer to the shape in profile - that is, with the shell placed on its side as shown below. Two commonly used terms are rounded (oval) and elongate. Rounded means that the shell is almost as high as it is long, and elongate means the shell is much longer that it is high.



Elongate

Rounded (Oval)

A Word of Caution

As more time is spent collecting and studying freshwater mussels, the degree of variability that exists for each species in terms of color, shape, and appearance of the shell will become apparent. People who have surveyed freshwater mussels for more than a few months can often identify a species with their eyes closed, just by the way it "feels", and knowing the environment that it came from. There are also times when even the most experienced mussel biologists emerge from the water shaking their heads in disbelief at the unique shape or color of an individual. Often environmental conditions in a river or lake will cause mussels to be darkly stained, making it difficult to use color or shell rays to distinguish species. There are many populations of the eastern elliptio in Maine that have green rays on the periostracum, and sometimes an eastern lampmussel without shell rays will be found. Individuals living in flowing water are often more stunted in growth (appearing shorter and fatter) than those living in lakes. While variability in shell appearance certainly does pose an additional challenge to learning to identify freshwater mussels, it also forces the use of several different pieces of "evidence" rather than relying on one or two features. Once familiar with the freshwater mussels of Maine, it will become easier to learn to correctly identify a species DESPITE the fact that one or more shell features are not *typical* for that species. The best strategy for learning to identify freshwater mussels is to always weigh several pieces of evidence (including habitat and location) and keep an open mind!

Abbreviations Used in the Species Accounts

In the tables listing specific waterbodies where each species is known to occur, the following abbreviations are used:

R = River
S = Stream
B = Brook
L = Lake
P = Pond
WB = West Branch
MB = Main Branch
EB = East Branch
MidB = Middle Branch
SB = South Branch

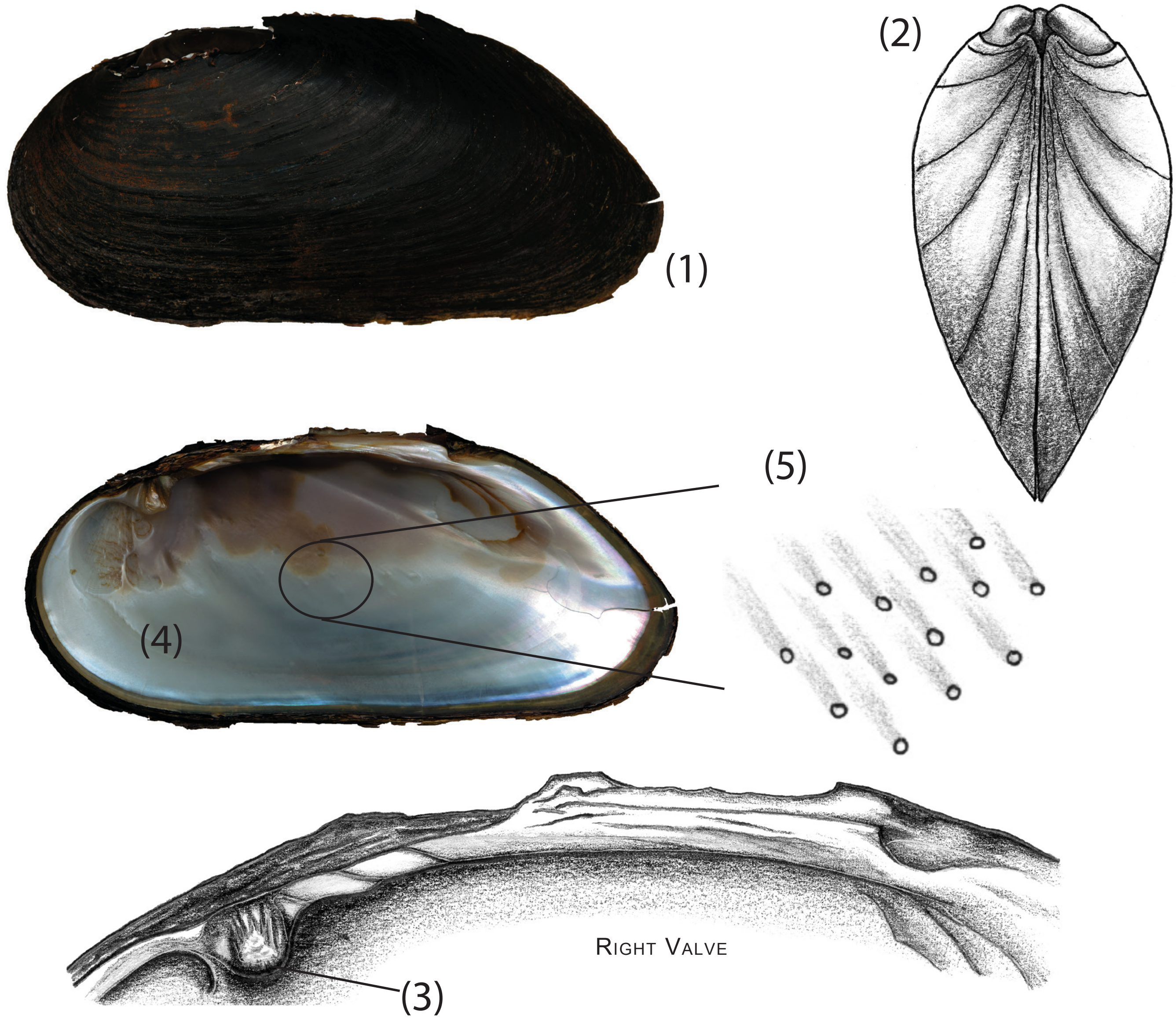
Eastern pearlshells, along with good trout fishing, can be found in the headwaters of the Aroostook River. BILLIE BRADEEN

Eastern Pearlshell
Margaritifera margaritifera (Linnaeus, 1758)

Description: This is a medium-sized to large (5 inches) mussel with a thick, elongate shell. Older individuals have a slight to pronounced ventral curvature, almost appearing "banana-shaped" (1). The valves are usually laterally compressed (2), with low umbos. The shell is smooth, brown to golden-brown in juveniles and nearly black in adults. There are rarely rays on the periostracum. The periostracum is thick and durable, and even older individuals tend not to be very eroded. Pseudocardinal teeth are well developed — the left valve has two and the right valve has one (3). Lateral teeth are absent. The nacre is usually white (4). The central portion of the nacre has distinctive "pits", each with a faint "tail" pointing toward the beak cavity (5), though this feature is sometimes obscured in very young or very old individuals. These pits and tails are diagnostic for all members of the family Margaritiferidae. Key distinguishing features in live undisturbed animals are the lack of separation between the inhalent and exhalent apertures, and dark gray or black mantle margins.

Confusing Species: The shape, hinge tooth morphology, and "pits" on the nacre make shells of the eastern pearlshell easily distinguishable from all other species. Live specimens, especially juveniles, are often confused with the eastern elliptio. The eastern pearlshell is usually more elongate than the eastern elliptio. Habitat can also be an important way to help distinguish these two species, since the eastern pearlshell occurs only in small or medium-sized streams that support trout populations. The eastern pearlshell has an interesting habit of "sputtering and wheezing" soon after being removed from the water — this trait is unique among Maine's mussels. Without sacrificing the animal to examine internal shell structure, the only other reliable way to distinguish between the two species is to observe them in an undisturbed state and check the morphology of the inhalent and exhalent apertures.

Range: The eastern pearlshell is primarily a northern species. In North America it is found as far south and west as Pennsylvania and New York. It is widespread in New England and the Canadian Maritime Provinces. Its range



also extends across the Atlantic Ocean to Scandinavia and northern Europe. It is North America's only native mussel whose range extends beyond the continent.

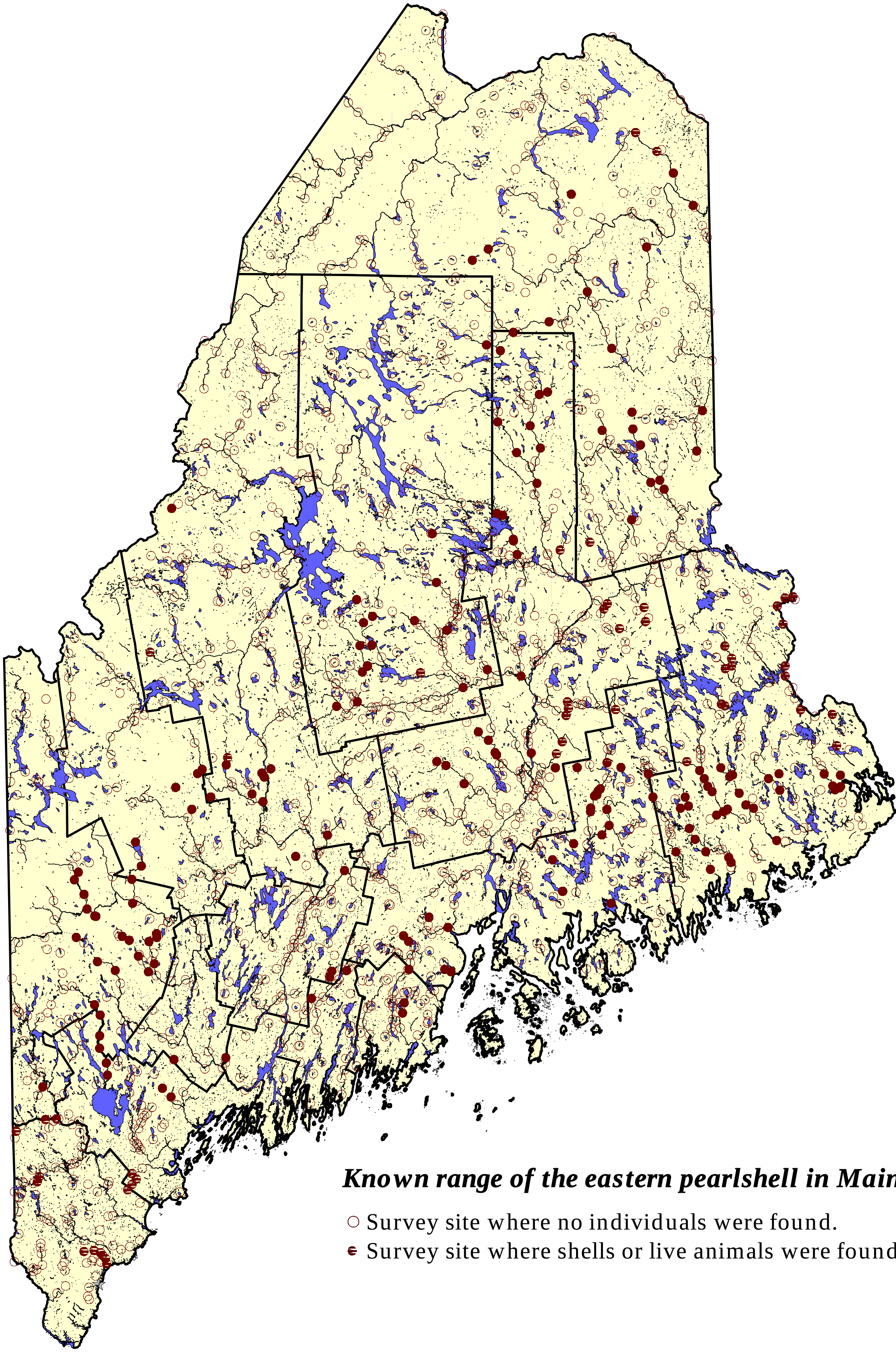
Habitat: The eastern pearlshell is found in streams and small rivers that are cool enough to support salmonids (trout, salmon). It is found in a range of flow conditions, and is remarkable in its ability to inhabit fast-flowing mountain streams. It seems to prefer firm sand, gravel, or cobble substrates, and is generally found in softwater (acidic) streams that have low levels of calcium.

Reproductive Characteristics: The eastern pearlshell has the most "primitive" reproductive characteristics of any Maine freshwater mussel species. It has the highest fecundity reported for any unionacean (upward of 17 million glochidia produced annually) and the smallest glochidia (Bauer 1987, 1994). This species has a remarkable ability to become hermaphroditic (capable of self-fertilization) when population densities become very low. Bauer (1987) reports a mean age at sexual maturity of 20 years. Individuals are known to live for over 100 years, making it the longest-living invertebrate species known on the planet. Native host fish in Maine include the brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) (Smith 1976, Cunjak and McGladdery 1991). The introduced brown trout (*Salmo trutta*) and rainbow trout (*Salmo gairdnerii*) may also serve as hosts in Maine. Smith (1976) reported that females were gravid from mid-August to late October, during which time the glochidia are released. Glochidia overwinter on the gills of their hosts and require more than five months to metamorphose into juveniles, which **excyst** in the spring.

Conservation: The eastern pearlshell is widely distributed throughout nearly every watershed in Maine, though it is not often abundant. In many streams we found only a few old individuals, and there was often little evidence of recent reproductive success. Because these animals are so long-lived, it would be difficult to detect trends in population abundance without long-term monitoring programs. Unfortunately, we do not have this type of information. The loss and degradation of clean riverine habitat in the Atlantic coastal region has undoubtedly affected this species. Several authors have provided evidence that this species is intolerant of eutrophication (Bauer 1988, Buddensiek 1995); thus landscape disturbance such as intensive agriculture and urbanization may have reduced its distribution or abundance. If predictions about global warming and stream thermal regimes are correct, then the reduction and fragmentation of salmonid populations in the Northeast will make the future of this species very uncertain. The eastern pearlshell is listed as threatened in Vermont and special concern in Connecticut.

Known Range of the Eastern Pearlshell in Maine

County	Specific Waterbodies
Androscoggin	Little R
Aroostook	Beaver B (WB), Aroostook R, Little Madawaska R, Presque Isle S, Pratt Lake S, Saint Croix S, Meduxnekeag R (MB, SB), Rocky B, Mattawamkeag R (EB, WB), Wytopitlock S, Alder B, Little Molunkus S
Cumberland	Stroudwater R, Crooked R, Collyer B, Royal R
Franklin	Webb R, Carrabassett R (MB, WB), Valley B, East B
Hancock	Union R (EB, WB, MidB), Narraguagus R, Main S, Nicatous S, Tannery B, Branch Lake S, Alligator S, Sunkhaze S, Green L
Kennebec	Sheepscot R (WB), Sebasticook R
Knox	Saint George R, Mill S, Quiggle B
Lincoln	Sheepscot R, Eastern R (WB)
Oxford	Concord R, Androscoggin R, Ellis R, Crooked R, Alder R, Tenmile R, Sparrow B, Nezinscot R (WB, EB, MB), Spears S, Little Androscoggin R
Penobscot	Mattawamkeag R (MB), Sunkhaze S, Seboeis S (MB, EB), Seboeis R, Aroostook R, Passadumkeag R, Olaman S, Mattakeunk S (MB, EB), Salmon S, Kenduskeag S, French S, Dead S (MB, WB), Birch S, Millinocket S, Penobscot R (MB, EB), Hay B, Mattagodus S, Big Mud B, Sandy S, Munsungan S
Piscataquis	Wilson S, Long Pond S, Schoodic S, Nahmakanta S, North B, Davis B, Bear B (Quarry Branch), Onawa L, Long P, Pleasant R (WB, EB), Kingsbury S, Piscataquis R, Davis B
Sagadahoc	
Somerset	Martin S, Mill S, Carrabassett S, Kennebec R, Fall B, Sandy S, Penobscot R (SB), Lemon S, Spencer S
Waldo	Ducktrap R, Passagassawakeag R, Thompson B, Wescot S, Bartlett S
Washington	Dennys R, Cathance S, Pleasant R, Moosehorn B, Wilson S, Trout B, Grand Lake S, Big Musquash S (EB, WB), Machias R (EB, WB, MB), Old S, Northern S, Mopang S, Narraguagus R, Saint Croix R, Magurrewock S (EB), Wapsaconhagan B, Black B, Chain Lakes S
York	Nonesuch R, South R, Little Ossipee R, Ossipee R, Branch B, Merriland R



Known range of the eastern pearlshell in Maine

○ Survey site where no individuals were found.
● Survey site where shells or live animals were found.

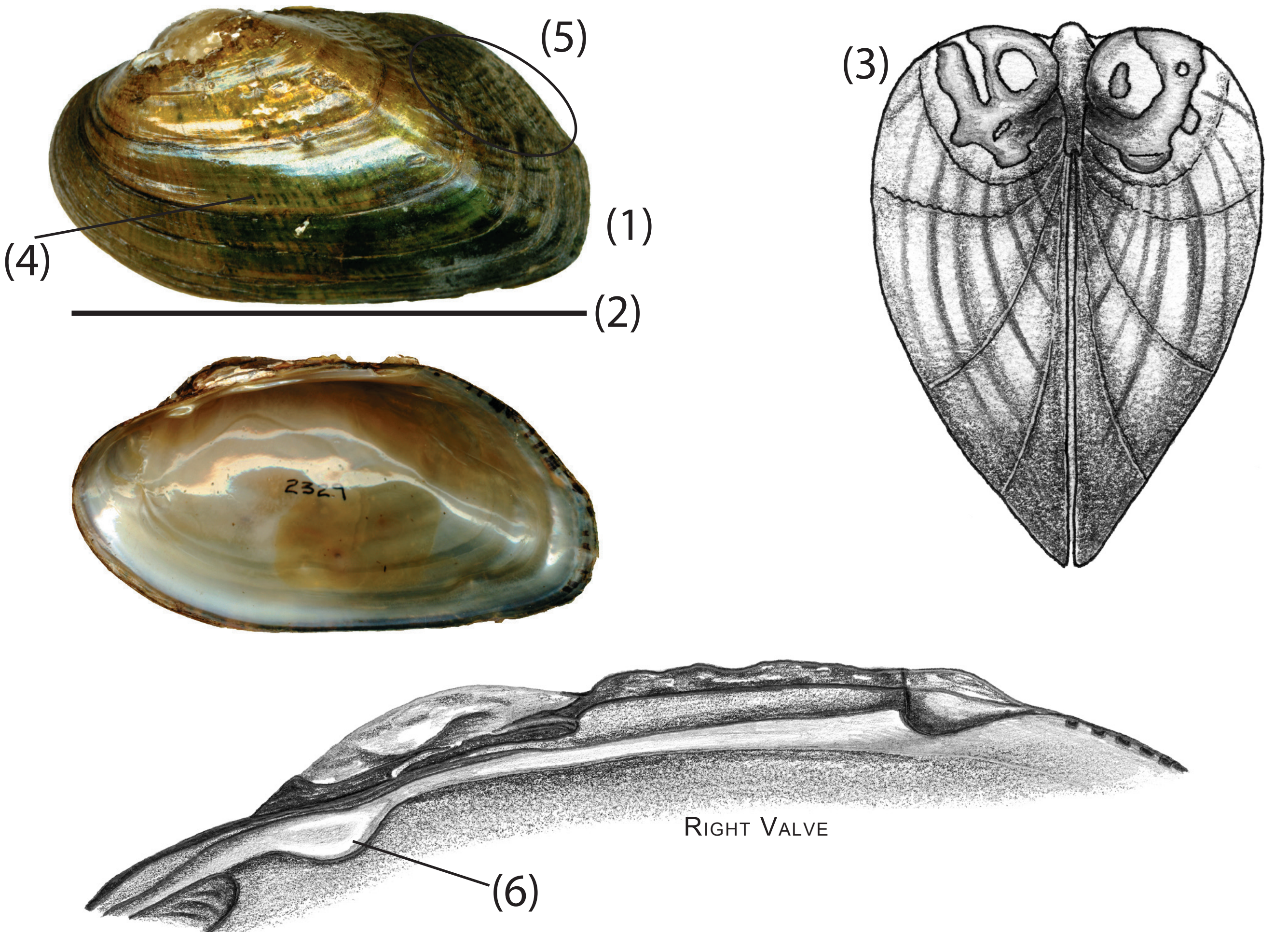
The brook floater is found throughout the Penobscot River and many of its tributaries. ETHAN NEDEAU

Brook Floater
Alasmidonta varicosa (Lamarck, 1819)

MAINE THREATENED SPECIES

Description: This is a small to medium-sized (usually ≤ 3 inches) mussel, and in profile often has a characteristic "roman nose" shape (1). The ventral margin is usually flattened or indented, so that if the bottom of the mussel were placed on a flat surface the shell would not rock forward (2). The valves are moderately inflated, giving the mussel a "swollen" appearance in cross section (3). The periostracum is yellowish-green in young animals to brownish-black in mature specimens and usually has broad, dark rays (often green) that extend from the umbo (4). The diagnostic feature for this species is a series of ridges and wrinkles along the dorso-posterior slope, perpendicular to the growth lines (5). Pseudocardinal teeth are present but poorly developed — there is just a small knob-like tooth on each valve (6). Lateral teeth are absent. The color of the nacre is variable, ranging from bluish-white to pinkish-white to a pale orange. This species has a unique habit of "gaping" (relaxing its adductor muscles and opening its valves) when removed from the water, exposing its cantaloupe-colored foot.

Confusing Species: The ridges and wrinkles on the dorso-posterior surface of the brook floater allow both shells and live animals to be easily identified. However, this feature is sometimes obscured on juvenile mussels or heavily eroded shells. In these instances, the brook floater can be confused with the dwarf wedgemussel, triangle floater, or creeper. The dwarf wedgemussel is smaller, more wedge-shaped in profile, and has lateral teeth. The triangle floater is usually shorter and more triangular in shape, and its ventral margin is more rounded so that it rocks forward evenly on a flat surface. The triangle floater also has a very well developed pseudocardinal tooth. Very infrequently, a triangle floater will also have distinct ridges perpendicular to the growth lines. The creeper is narrower in cross section than either *Alasmidonta* species, its pseudocardinal teeth are even less developed than the brook floater's, and its shell is considerably thinner and more fragile. Since all three of these species are listed as special concern in Maine, the identity of live specimens should be verified by an expert rather than sacrificing animals to examine internal shell features.



Range: The brook floater is found in streams and rivers of the Atlantic coastal region, from South Carolina to Nova Scotia and New Brunswick. Clarke (1981a) also reported that it was found in the Kanawah River system in West Virginia, part of the Ohio-Mississippi River drainage. In Maine it is known from nearly all of the rivers that historically supported runs of Atlantic salmon, including the St. George, Sheepscot, Marsh Stream, several rivers and streams in the Penobscot River watershed, and most of the Down East salmon rivers. It is found as far south as the Pleasant River in Cumberland County.

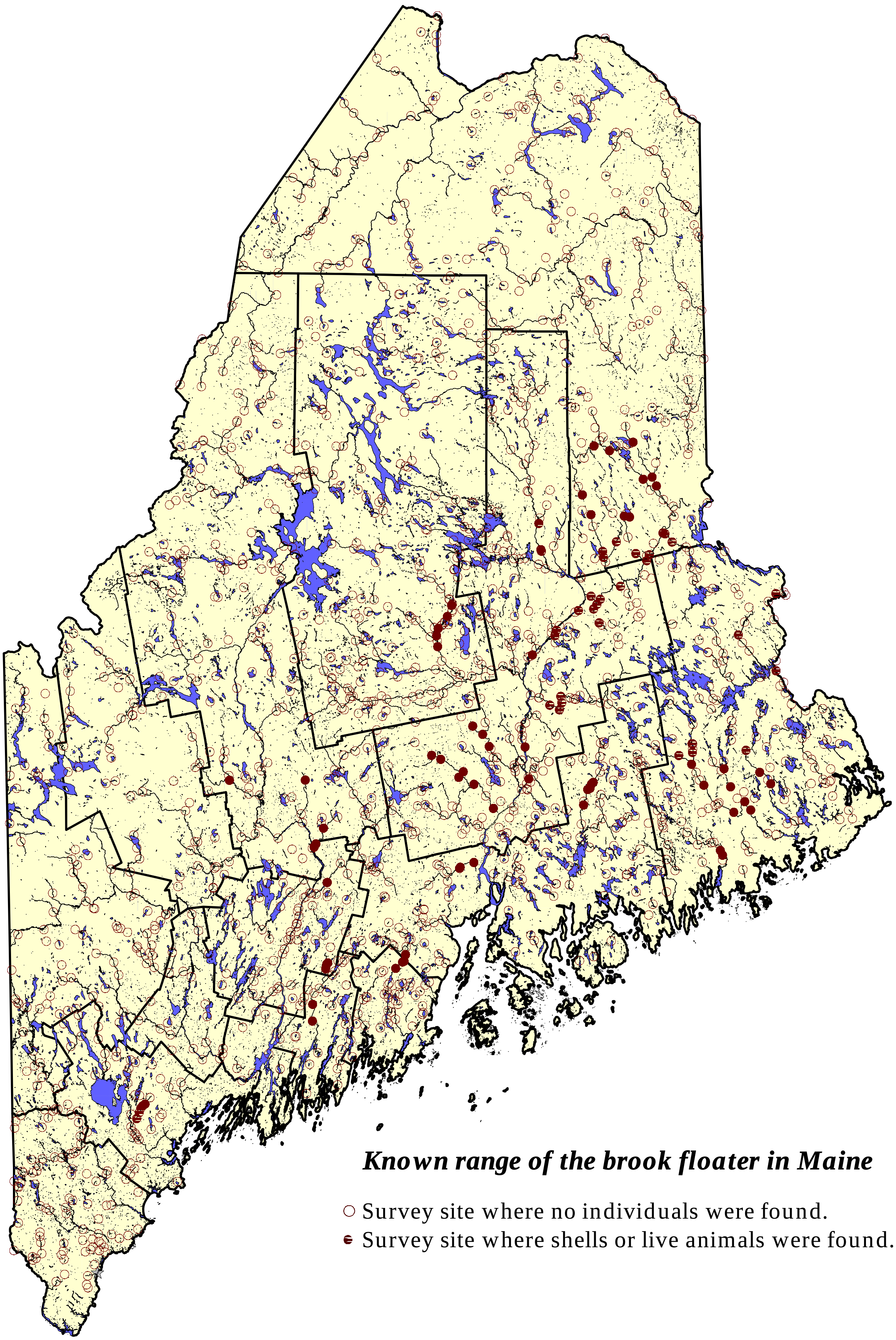
Habitat: The brook floater inhabits flowing-water habitats — from small streams to large rivers. It is found in a range of flow conditions, but does not inhabit high-gradient streams with very fast water flow and coarse substrate (cobble and boulders), nor is it usually found in slow water. Strayer and Ralley (1993) could not find a consistent substrate preference for this species, but in general it is thought to prefer stable habitats such as coarse sand and gravel. In Maine it is often found in association with rooted aquatic vegetation. It is frequently found in streams that have low calcium levels and are nutrient-poor, a trait shared with some other members of the genus *Alasmidonta* as well as the eastern pearlshell (Bauer 1988, Strayer 1993).

Reproductive Characteristics: The brook floater is a long-term brooder — fertilization presumably takes place in summer, and the gravid period is reported to last from August to May. Release of glochidia occurs in April through June, though if temperature is an important factor determining glochidial release, then a later release period would be expected in more northerly latitudes. Longnose dace (*Rhinichthys cararactae*), blacknose dace (*Rhinichthys atratulus*), golden shiners (*Notemigonas chrysoleucas*), pumpkinseed sunfish (*Lepomis gibbosus*), slimy sculpins (*Cottus cognatus*), yellow perch (*Perca flavescens*), and margined madtom (*Schilbeodes marginatus marginatus*) have been reported to serve as potential hosts for this species under laboratory conditions (Wicklow and Richards 1995, Barry Wicklow, Saint Anselm College, *personal communication*). The white sucker (*Catostomus commersoni*) is a suitable host for the closely related elktoe and triangle floater.

Conservation: The brook floater has experienced significant declines throughout its range, with many populations being extirpated. Even where it is found, the population often consists of just a small number of aging individuals, with little evidence of recruitment. Maine figures prominently in this species' conservation, having more populations than the remainder of the Northeast combined. There is some evidence that it has been locally extirpated in some of Maine's watersheds, including the Dennys River and Presumpscot River. The brook floater was considered a candidate for the federal Endangered Species List prior to 1995, when an act of Congress eliminated the candidate list. The species is currently listed as endangered in New Hampshire, Massachusetts, Connecticut, Maryland, and Virginia. It is listed as threatened in Vermont and Maine. Of all Maine's freshwater mussel species, the brook floater probably stands the greatest chance of being recognized as federally endangered.

Known Range of the Brook Floater in Maine

County	Specific Waterbodies
Androscoggin	
Aroostook	Mattawamkeag R (EB, WB, MB), Molunkus S, Fish S, Macwahoc S, Wytopitlock S, Baskahegan S
Cumberland	Pleasant R, Presumpscot R (historical, possibly extirpated)
Franklin	
Hancock	Union R (WB)
Kennebec	Sheepscot R (WB), Carrabassett S, Sebasticook R
Knox	Saint George R
Lincoln	Sheepscot R (MB)
Oxford	
Penobscot	Mattawamkeag R (MB), Dead S (WB, MB), Passadumkeag R, French S, Kenduskeag S, Penobscot R (MB, EB), Great Works S, Mattakeunk S
Piscataquis	Pleasant R (MB, EB)
Sagadahoc	
Somerset	Gilman S, Wesserunsett S, Carrabassett S
Waldo	Saint George R, Marsh S
Washington	Machias R (WB, MB), East Machias R, Pleasant R, Old S, Chain Lakes S, Tomah S, Saint Croix R, Dennys R (possibly extirpated)
York	


Known range of the brook floater in Maine
Survey site where no individuals were found.
Survey site where shells or live animals were found.

The Ossipee River in southern Maine offers excellent habitat for the triangle floater. MARK McCOLLOUGH

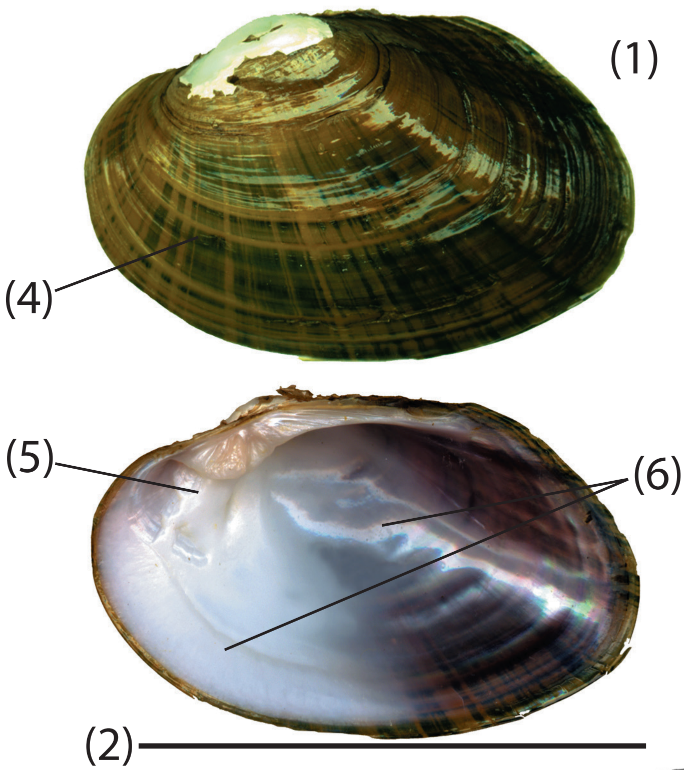
Triangle Floater
Alasmidonta undulata (Say, 1817)

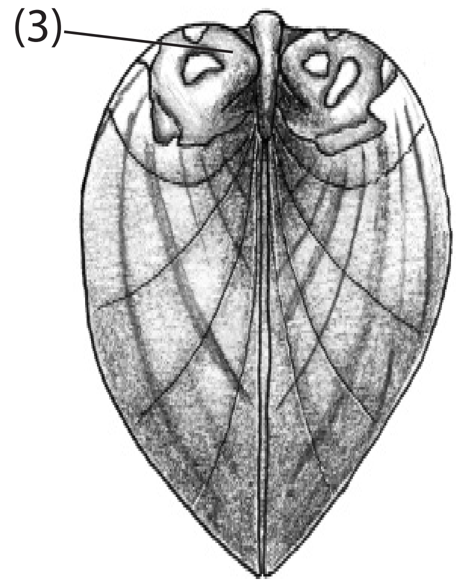
MAINE
SPECIAL CONCERN
SPECIES

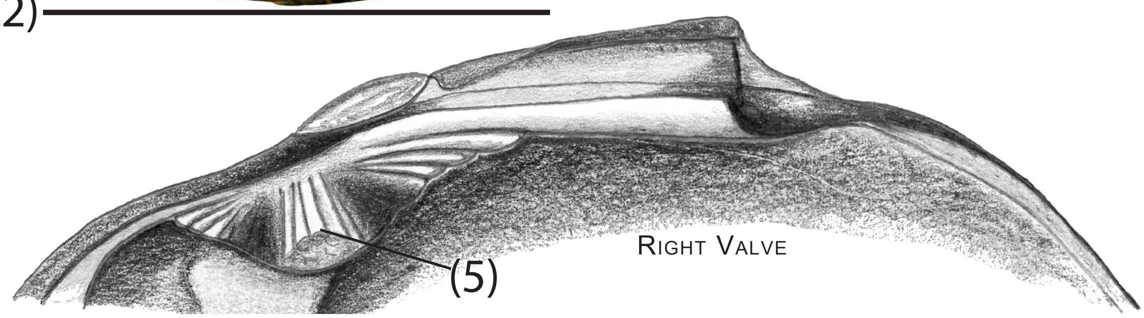
Description: This is a small to medium-sized (usually ≤ 3 inches) mussel with a somewhat "squat", triangular appearance in profile (it is short, wide, and fat) (1). The ventral margin is rounded, so that it rocks evenly when placed on a flat surface (2). The umbos are somewhat prominent and raised above the hinge line (3). The periostracum is smooth, and may range in color from yellowish-green to nearly black. The periostracum also has prominent colored rays extending from the umbos (4), though they are often obscured in older, darker individuals. Pseudocardinal teeth are very well developed and buttressed by a heavy ridge (5). Lateral teeth are absent. The nacre is distinctively bicolored: the posterior half is quite thin and iridescent bluish-pink in color, and the anterior half is substantially thicker and white or pinkish in color (6). The foot is usually white, but infrequently is cantaloupe-colored, similar to that of the brook floater.

Confusing Species: The hinge tooth morphology and distinctly bicolored appearance of the nacre make shells of the triangle floater unmistakable from other species in Maine. Without the benefit of internal shell features, live individuals can often be confused with the brook floater or creeper. However, the brook floater usually has prominent ridges and wrinkles on the dorso-posterior slope, a feature usually not found on the triangle floater and never found on the creeper. The triangle floater does not have the nearly straight ventral margin or "roman nose" shape characteristic of the brook floater. It is more laterally inflated in cross section than the creeper, and has more prominent umbos. Since all three of these species are listed as special concern in Maine, the identity of live specimens should be verified by an expert, rather than sacrificing animals to examine internal shell features. The coloration of the triangle floater may infrequently resemble that of the eastern lampmussel, but the eastern lampmussel tends to be much larger, more elliptical in outline, and has lateral teeth.

Range: The triangle floater is more widely distributed than other New England *Alasmidonta* species. Clarke (1981a) reported that its range extended south to the Apalachicola River system of Florida, Georgia, and Alabama, which flows into the Gulf of Mexico. However, Johnson (1970) asserts that the southern limit for this species is the Cooper-Santee River system in North Carolina. It is found in most Atlantic coastal drainages northward to Nova Scotia







and New Brunswick, and also westward into tributaries of the lower St. Lawrence, such as the Ottawa River. It is found in nearly every watershed in Maine.

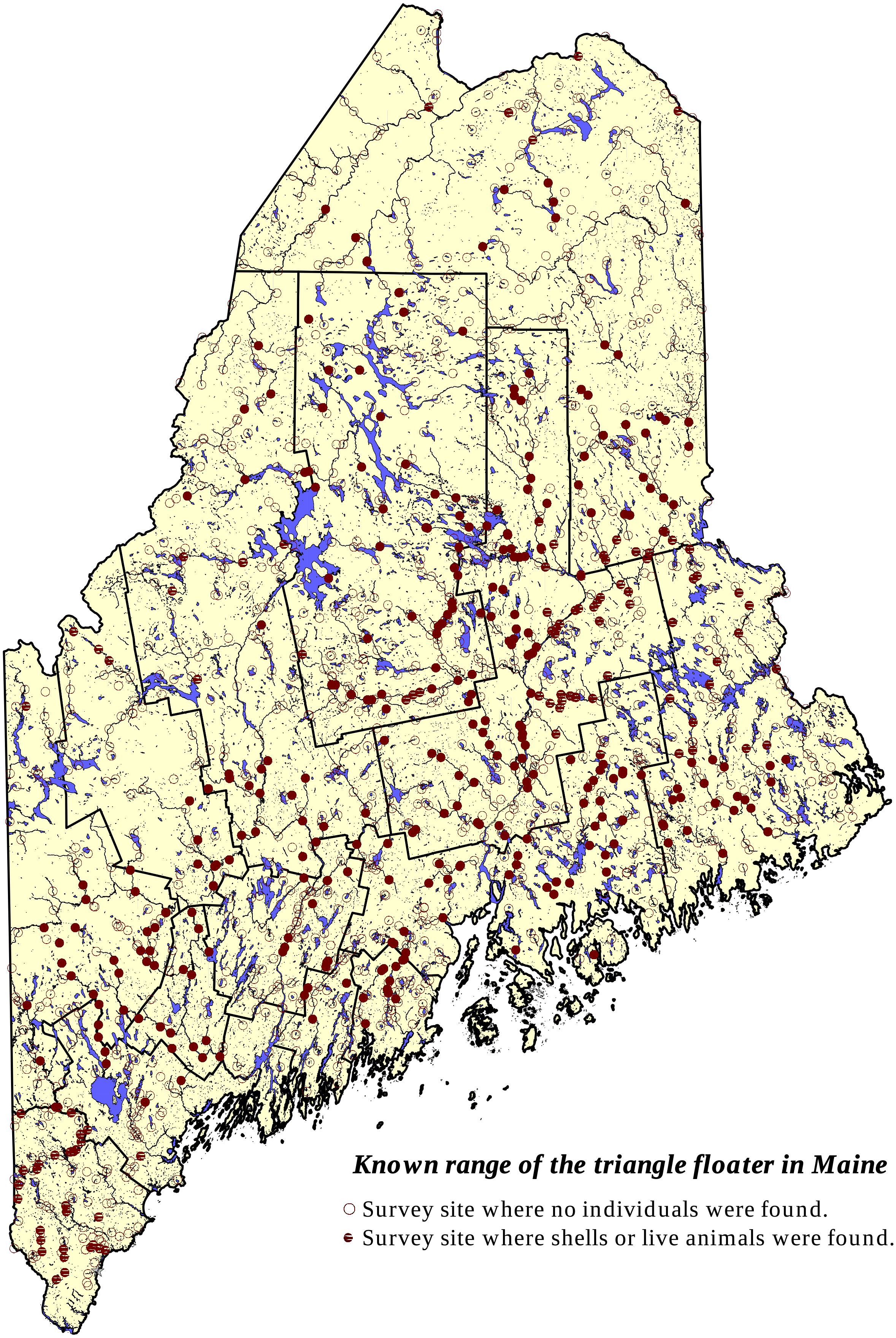
Habitat: The triangle floater is most frequently found in streams and rivers. However, it also occurs in many lakes and ponds, where it is never very abundant. It is interesting that the triangle floater can tolerate standing water, when most other species in its genus cannot. This trait makes this species less vulnerable to some of the effects of dams. It does not exhibit a particularly strong substrate preference, but is most frequently encountered in sand and gravel.

Reproductive Characteristics: The triangle floater is a long-term brooder, with fertilization taking place in summer and release of glochidia taking place the following spring. Gravid females have been found in every month of the year, though on a regional basis the reproductive cycles are probably more distinct. Confirmed hosts include the common shiner (*Luxilus cornutus*), blacknose dace (*Rhinichthys atratulus*), longnose dace (*Rhinichthys cataractae*), white sucker (*Catastomus commersoni*), pumpkinseed sunfish (*Lepomis gibbosus*), fallfish (*Semotilus corporalis*), largemouth bass (*Micropterus dolomieu*), slimy sculpin (*Cottus cognatus*), and several other fish not found in New England (Barry Wicklow, Saint Anselm College, *personal communication*, Watters et al. 1999).

Conservation: The triangle floater may be experiencing significant declines in southern parts of its range, where states are acquiring information on distribution and abundance to determine protection measures. It is widespread in Maine, but rarely abundant, and its preferred habitat (streams and small rivers) may be particularly threatened by habitat destruction and pollution. It is probably more abundant in Maine than in other states to the south, and habitats in Maine may be a particularly important refugium for this species if its populations continue to decline in southern parts of its range. It is listed as endangered in Maryland, and special concern in Maine and Massachusetts.

Known Range of the Triangle Floater in Maine

County	Specific Waterbodies
Androscoggin	Androscoggin R, Little Androscoggin R, Nezinscot R, Sabattus R, Androscoggin L
Aroostook	Fish R, Portage L, Saint Croix S, Saint Croix L, Aroostook R, Saint John R, Pratt Lake S, Umsaskis L, Drews L, Meduxnekeag R (MB, SB), Mattawamkeag R (MB, WB, EB), Little Black R, Wallagrass L, Long L, Cunliffe B, Rockabema L, Macwahoc S, Molunkus S, Fish S, Sly B, Babcock B, Mattaseunk S, Skitacook L, Skagrock B, Baskahegan S, Wytopitlock S, Mattaseunk L, Portage L
Cumberland	Crooked R, Royal R, Pleasant R, Chandler R, Stroudwater R
Franklin	Wilson S, Chain of Ponds, Valley B, Baker S, Sandy R, Little Norridgewock S, Webb R, Horseshoe S, Dead R (NB)
Hancock	Union R (MB, MidB, WB, EB), Moosehorn S, Narraguagus R, Long P, Main S, Alligator L, Sunkhaze S, Nicatous S, Webb P, Molasses P, Branch Lake S, Great P, Upper Middle Branch P, Webb B, Orland R, Patten S, Echo L, Walker P, Lower Patten P
Kennebec	Sheepscot R (WB), Eastern R (WB), Kennebec R, Sebasticook R, Fifteenmile S, Carrabassett S, Outlet S, Messalonskee S
Knox	Pettengill S, Saint George R, Seven Tree P, Sennebec P, Crawford P, Medomak R
Lincoln	Eastern R (WB), Sheepscot R (MB), Medomak R
Oxford	Little Androscoggin R, Androscoggin R, Nezinscot R (WB, EB, MB), Kezar L Outlet, Magalloway R, Ellis R, Alder R, Saco R, Songo P, Crooked R
Penobscot	Passadumkeag R, Madagascal S, Seboeis S (MB, WB), Mattawamkeag R (MB,), Piscataquis R, Penobscot R (MB, WB, EB), South Branch L, Little Mattamiscontis L, Olaman S, Hemlock S, Martin S, Blackman S, Sedgeunkedunk S, Great Works S, Wassookeag L, Kenduskeag S, Dead S (MB, WB), Pushaw S, French S, Black S, Souadabscook S, Salmon S, Mattamiscontis S, Sawtelle B, Millinocket S, Mud B, Sandbank S, Seboeis R, Hay B, Millinocket L, Rockabema S, Medunkeunk S, Big Mud B, Brewer L, Mattagodus S, Mattakeunk S
Piscataquis	Boyd L, Penobscot R (WB), Loon S, Poland P Outlet, Cuxabexis S, Duck B, Lower Jo-Mary L, Upper Jo-Mary L, Pine S, Ellis B, Dead S, Spider L, Munsungan L, Ragged S, Moosehead L, Second Roach P, Piscataquis R (MB, WB), Nahmakanta S, Harrow B, Pleasant R (EB, WB), Piper P, Kingsbury S, Whetstone P, Nahmakanta L, Salmon S, Allagash P, Cedar L, Sebec R, East Branch L, Seboeis L Outlet, Onawa L
Sagadahoc	Androscoggin R
Somerset	Kennebec R, Fall B, Sebasticook R, Turner B, Martin S, Penobscot R (SB, NB, WB), Saint John R (Baker Branch), Gilman S, Moose R, Carrabassett S, Black B, Sandy R, Lemon S, Mill S, Kincaid S, Wesserunsett S
Waldo	Saint George R, Bartlett S, Carlton S, Wescot S, Marsh S (MB, NB), Sebasticook R, Halfmoon S
Washington	Fourth Lake S, Cathance L, Machias R (MB, WB), East Machias R, Chain Lakes S, Mopang S, Pleasant R, Love L, Narraguagus R, Baskahegan S, Northern S, Old S, Tomah S, Saint Croix R, Big Musquash S (WB), West Grand L
York	Ossipee R, Little Ossipee R, Saco R, Mousam R (MidB), Great Works R, Salmon Falls R, Little R, Kennebunk R, Merriland R, Swan P



Known range of the triangle floater in Maine

○ Survey site where no individuals were found.

● Survey site where shells or live animals were found.

The creeper can be found in Baskahegan Stream, a large tributary of the Mattawamkeag River in northern Washington County. ETHAN NEDEAU

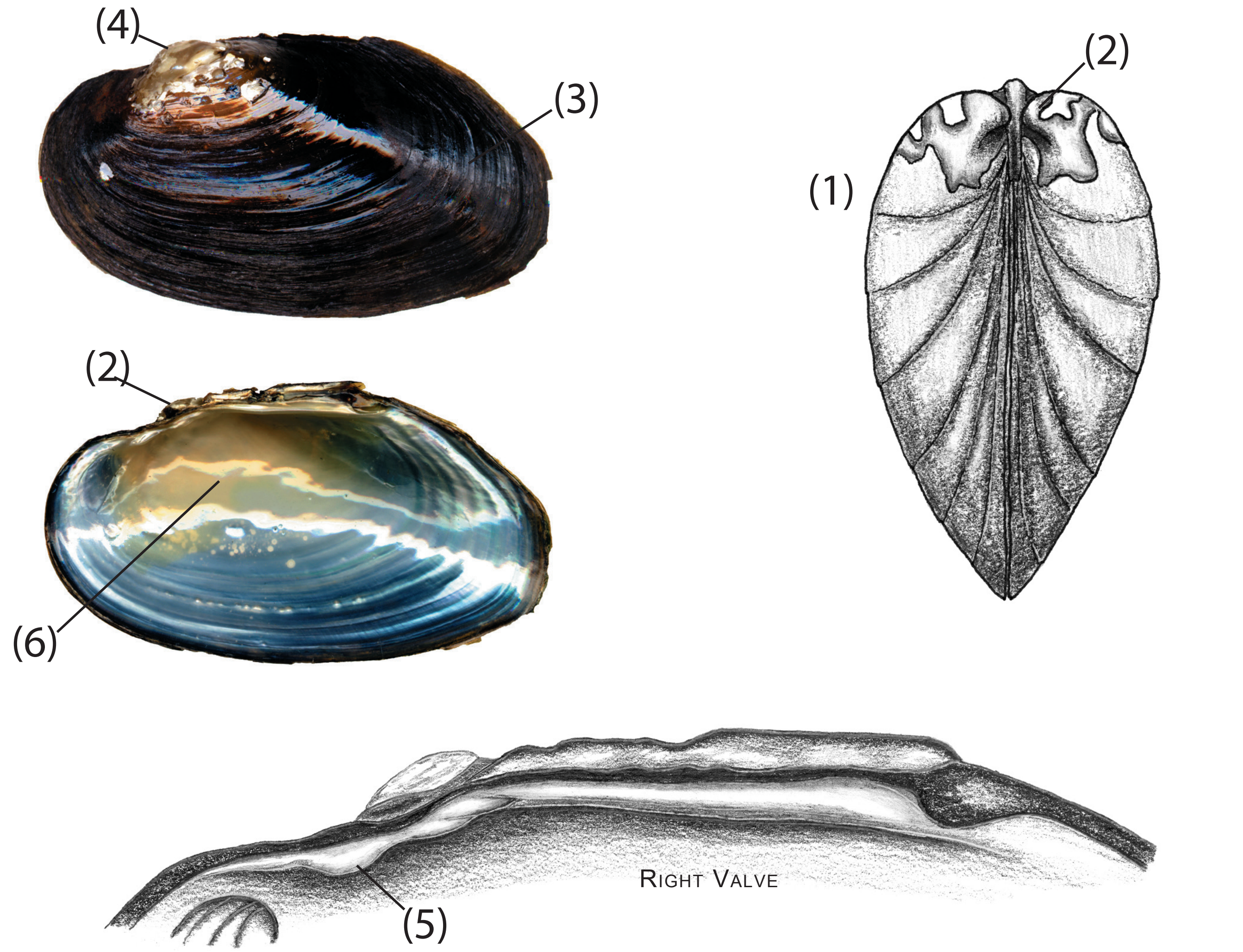
Creeper*
Strophitus undulatus (Say, 1817)

MAINE SPECIAL CONCERN SPECIES

Description: This is a small to medium-sized (usually < 3 inches) mussel. The valves are laterally compressed (1), and the umbos are not very prominent and barely raised above the hinge line (2). The shell is thin and fragile, and somewhat rough due to prominent growth lines (3). The beak sculpture is usually coarse and prominent (4), though often obscured by shell erosion. The periostracum is yellowish or greenish-brown in young individuals, and typically brown or black in older individuals. Rays on the periostracum are usually evident only in young specimens. Hinge teeth are almost entirely absent — pseudocardinals are present but consist of simple swellings that are difficult to distinguish (5). Lateral teeth are absent. The nacre is usually white or bluish-white, and is conspicuously dull yellow or greenish toward the beak cavity (6).

Confusing Species: The creeper is one of the most nondescript mussels in Maine and can be confused with a number of other species. Shells are quite easy to distinguish because of the nature of the hinge teeth and the coloration pattern of the nacre. However, without the benefit of internal shell features, the novice can sometimes confuse live individuals with the eastern elliptio, brook floater, triangle floater, alewife floater, and eastern floater. The most common error is to confuse the creeper with young individuals of the eastern elliptio. The best way to distinguish these species is by the "squeeze test" — the creeper has a very thin shell, and you can force open the two valves by applying gentle pressure on the dorsal and ventral surfaces (**see page 56**). The eastern elliptio has a very strong shell, and cannot be forcibly opened in this manner. The creeper lacks the ridges on the dorso-posterior slope that are typical of the brook floater. It is more laterally compressed than the brook floater and triangle floater and is not

* Previously known as the squawfoot, this species' common name has recently been changed to creeper (Turgeon et al. 1998)



as wide as the triangle floater. Since the creeper is listed as special concern in Maine, the identity of live specimens should be verified by an expert, rather than sacrificing animals to examine internal shell features.

Range: The creeper is one of the most widely distributed species in North America. It is found as far west as Texas and Saskatchewan and is widely distributed in the Atlantic coastal drainages, St. Lawrence River system, Great Lakes basin, and the Ohio and Mississippi River systems. It is found in most major watersheds in Maine, though it is never common.

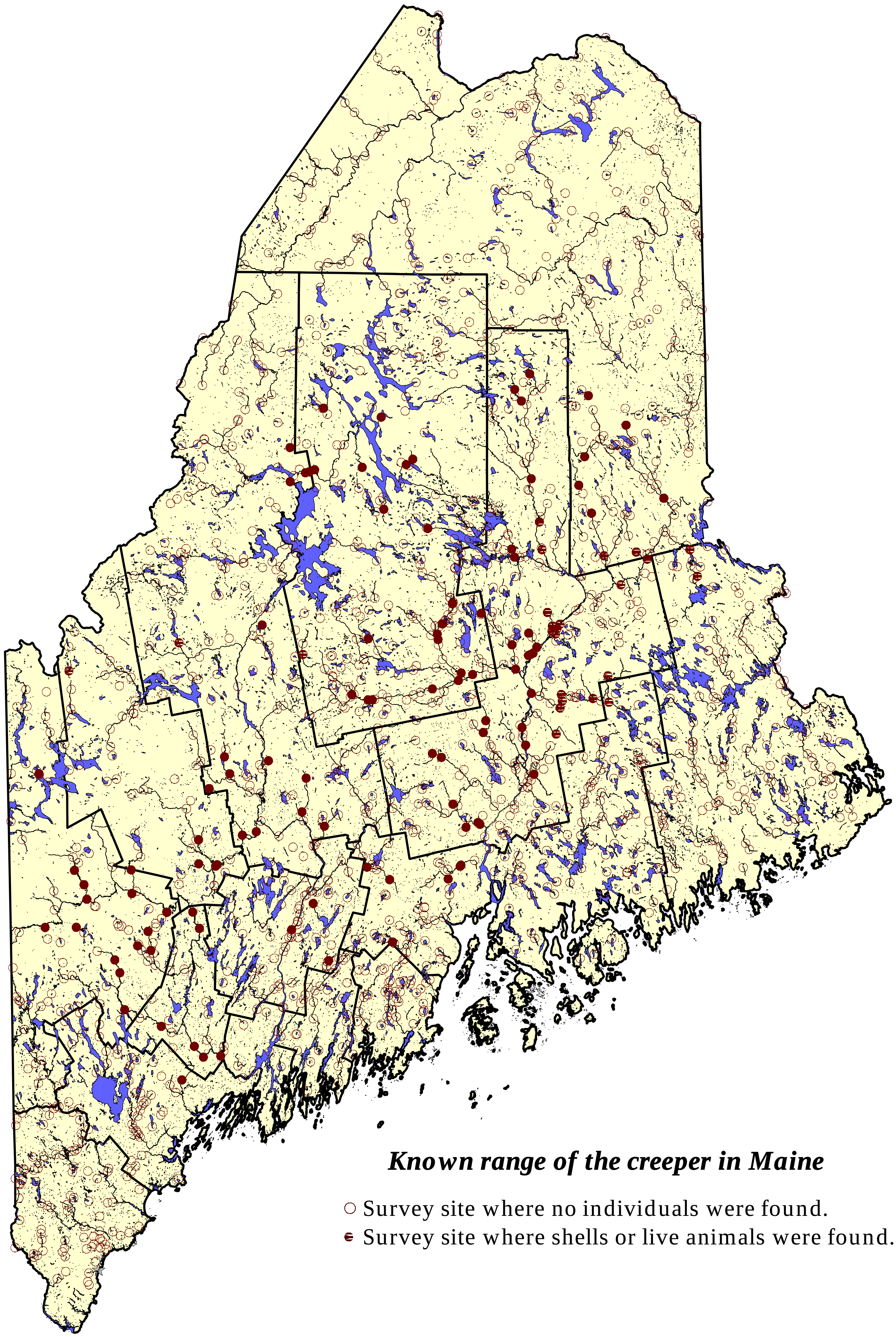
Habitat: The creeper has been found only in streams and rivers in Maine (and sometimes in impounded river sections), though elsewhere it is reported to live in lakes. It can tolerate a range of flow conditions, but is rarely found in high-gradient streams of mountainous regions. Lake outlets are especially productive habitats for this species. It seems to prefer sand and fine gravel substrates.

Reproductive Characteristics: The creeper is a long-term brooder, with eggs being fertilized in the summer and glochidia released the following spring. One study found that glochidia can transform into juveniles without a fish host (Lefevre and Curtis 1911). This is one of the few studies to show such a reproductive trait among unionaceans, and though it is widely cited in the scientific literature, no one has since been able to support these findings for the creeper. Other species have been shown to be able to metamorphose without a vertebrate host, but further work is needed to determine if the creeper has this ability. There are a number of confirmed vertebrate hosts, including the largemouth bass (*Micropterus salmoides*), creek chub (*Semotilus atromaculatus*), fallfish (*Semotilus corporalis*), fathead minnow (*Pimephales promelas*), golden shiner (*Notemigonus crysoleucas*), common shiner (*Luxilus cornutus*) slimy sculpin (*Cottus cognatus*), bluegill (*Lepomis macrochirus*), longnose dace (*Rhinichthys cataractae*), yellow perch (*Perca flavescens*), and several other darters and minnows not found in Maine (Wicklow and Beisheim 1998, Watters et al. 1999, Gray et al. 1999). Recently the Atlantic salmon was found to be a suitable host (Barry Wicklow, Saint Anselm College, *personal communication*). Wicklow and Beisheim (1998) also reported that larvae (but not adults) of the northern two-lined salamander (*Eurycea bislineata*) were suitable hosts. Given its tremendously broad geographical distribution, host-suitability studies must be assessed carefully because individuals living in Maine would probably not be able to parasitize the same fish as individuals living in Texas.

Conservation: Although the creeper is widely distributed in Maine, it is rarely abundant. Usually fewer than ten individuals are found at a single location, and there is considerable question about the long-term viability of such small populations. Consequently, Maine has listed the creeper as special concern. The only other northeastern state to list the creeper is Massachusetts (special concern). Like the other special concern species in Maine, it prefers clean, flowing water, and thus habitat degradation and pollution have probably affected this species in similar ways.

Known Range of the Creeper in Maine

County	Specific Waterbodies
Androscoggin	Androscoggin R, Little Androscoggin R
Aroostook	Mattawamkeag R (EB, WB, MB), Molunkus S, Wytopitlock S, Fish S
Cumberland	Chandler R
Franklin	Baker S, Kennebago R, Sandy R, Wilson S, Webb R
Hancock	Nicatous S
Kennebec	Outlet S, Sheepscot R (WB)
Knox	
Lincoln	
Oxford	Nezinscot R (EB, WB), Ellis R, Androscoggin R, Little Androscoggin R, Mill B, Alder R, Spears S
Penobscot	Piscataquis R, Madagascal S, Passadumkeag R, Seboeis S, Mattamiscontis S, Penobscot R (MB, EB, WB), Dead S (WB, MB), Souadabscook S (MB, WB), Black S, Kenduskeag S, French S, Olamon S, Medunkeunk S, Sawtelle B, Great Works S, Millinocket S, Seboeis R, Mattawamkeag R
Piscataquis	Piscataquis R (WB, MB), Pleasant R (EB, MB), Pine S, Ragged S, Seboeis L Outlet, Russell S, Duck B, Soper B, Cuxabexis S, Onawa L, Loon S, Nahmakanta S, Kingsbury S
Sagadahoc	Androscoggin R
Somerset	Fall B, Elm S, Black B, Carrabassett S, Penobscot R (WB), Wesserunsett S (WB, MB), Sandy R, Gilman S, Sandy S, Lemon S, Little Spencer S, Carry B
Waldo	Marsh S, Saint George R, Halfmoon S, Twentyfive Mile S
Washington	Baskahegan S
York	



Known range of the creeper in Maine

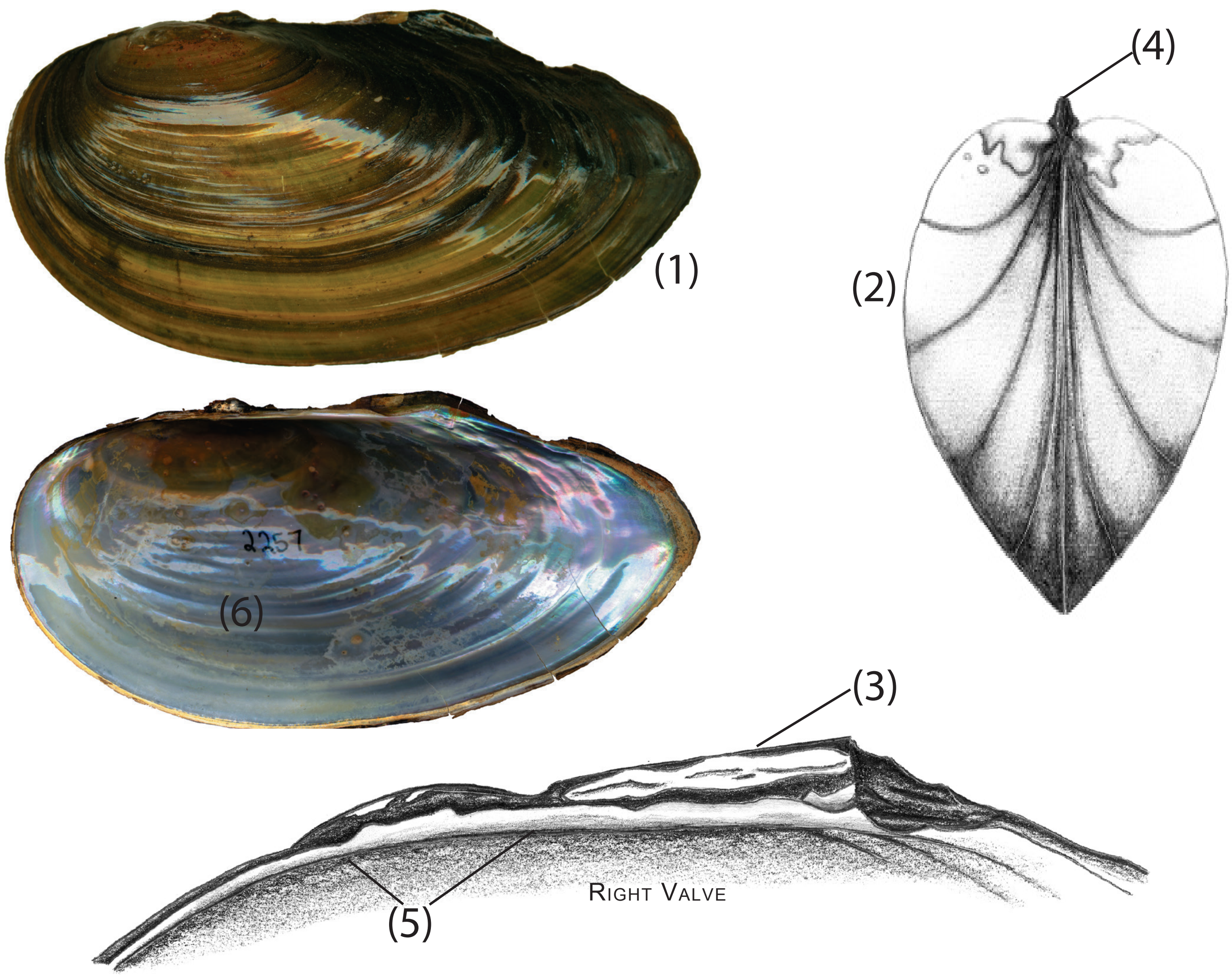
Despite its enormous size, Moosehead Lake supports only three species of mussels, including the eastern floater. ETHAN NEDEAU

Eastern Floater
Pyganodon cataracta (Say, 1817)

Description: This is a medium-sized to large (usually < 6.5 inches) mussel with a very fragile shell. The shape is usually elongate and slightly rounded (1), and the valves are laterally inflated (2). The hinge ligament is either straight or has a slight upward curve (3), and the beaks are slightly inflated and project above the hinge line (4). The beak sculpture consists of a series of double-looped concentric bands **(see page 76)**. The shells are uniformly thin, and application of slight pressure on the dorsal and ventral surfaces will cause the valves to spread apart (**see page 56**). Hinge teeth are entirely absent (5). The shell is smooth with prominent growth annuli and sometimes faint rays. The periostracum is yellowish, greenish, or brownish-black. The nacre is usually silvery white or a metallic blue, sometimes with a yellowish tinge (6).

Confusing Species: The eastern floater is distinguished from the Newfoundland floater by its **beak sculpture**: the Newfoundland floater has single-looped bands, and the eastern floater has double-looped bands (**see page 76**). However, excessive shell erosion often prevents use of this characteristic. Although color is often an inconsistent trait, the eastern floater usually has some green on the shell, whereas the Newfoundland floater is brown to straw yellow. Without the benefit of beak sculpture, it would be very difficult to reliably distinguish between the eastern floater and the Newfoundland floater. In fact, these two species are thought to hybridize where their ranges overlap, making reliable identification virtually impossible. The eastern floater can be distinguished from the alewife floater by its uniformly thin shell. The creeper may sometimes be confused with the eastern floater because it seems to lack hinge teeth and has a fragile shell; however, the creeper has rudimentary pseudocardinal teeth, tends to be smaller and darker, lacks a straight hinge ligament, and is more elongate and laterally compressed.

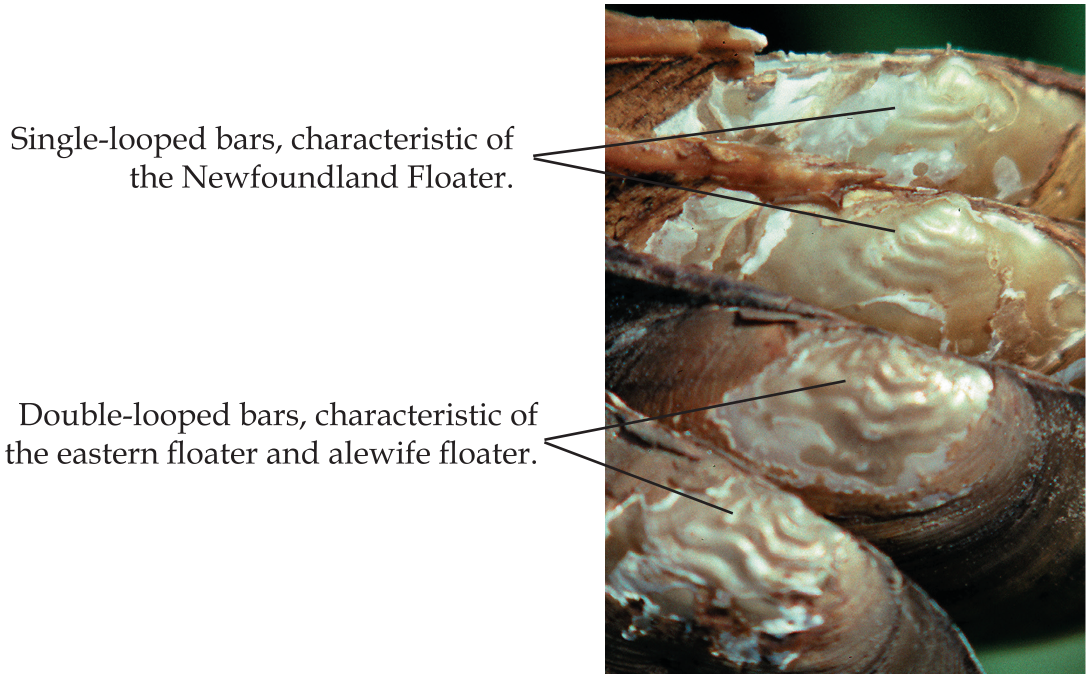
Range: The eastern floater is found in Atlantic coastal drainages from Georgia to Nova Scotia, though it is less common in the southern parts of its range. It is also found in the lower St. Lawrence River drainage, and its range extends westward to the Great Lakes. This is the second most common species in Maine, occurring in every major watershed.



Habitat: The eastern floater is found in a wide variety of habitats, including small streams, rivers, ponds, and lakes. It is usually confined to slow-moving portions of riverine environments, in sandy or muddy substrates. It is one of the few species that can tolerate the deep silt substrates found in the deeper water of most lakes and ponds. Its thin shell allows it to "float" on these soft substrate types.

Reproductive Characteristics: The eastern floater is a long-term brooder — eggs are fertilized in August and glochidia are released the following spring. Given its broad range in a variety of habitat types, it probably uses a number of host fish (many other anodontines, including the genera *Anodonta* and *Pyganodon*, are known to be host generalists). The common carp (*Cyprinus carpio*), bluegill (*Lepomis macrochirus*), pumpkinseed sunfish (*Lepomis gibbosus*), yellow perch (*Perca flavescens*), three-spined stickleback (*Gasterosteus aculeatus*), and white sucker (*Catostomus commersoni*) are among the suspected hosts (Hoggarth 1992, Watters 1994, Gray et al. 1999). Since only three of these fish are native to New England, it is likely that other species also serve as hosts.

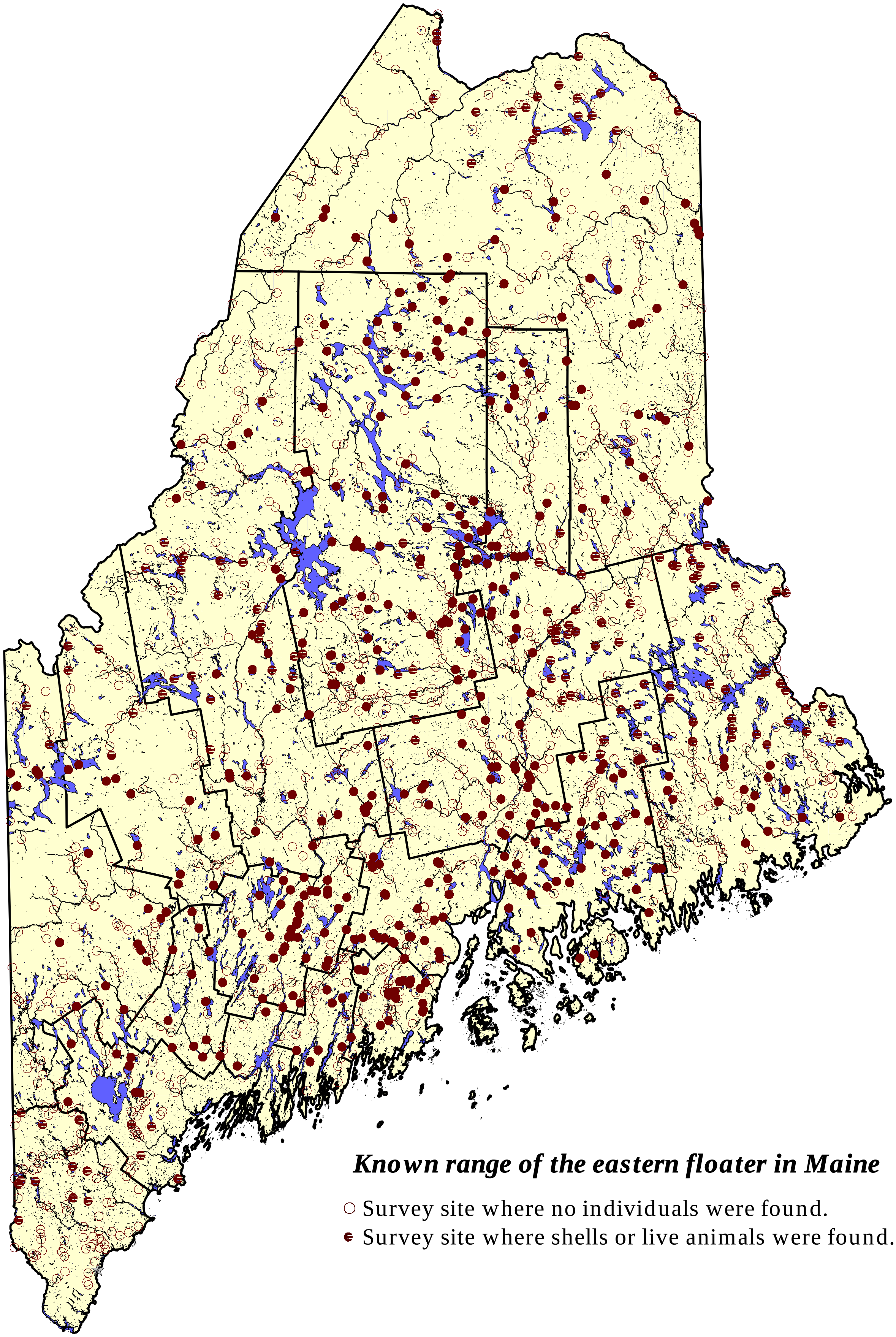
Conservation: The eastern floater has a rather broad environmental tolerance and low host specificity, and thus it is widespread and common throughout much of its range. It will remain an important biomonitor of the health of our aquatic ecosystems in the future.



Known Range of the Eastern Floater in Maine

County	Specific Waterbodies
All Maine Counties	The eastern floater has been found at nearly 600 locations in Maine, and in every major watershed. Individual waterbodies are too numerous to list.

These individuals are more yellow than typical eastern floaters. They were collected from Hale Pond in Piscataquis County.
ETHAN NEDEAU



Known range of the eastern floater in Maine

○ Survey site where no individuals were found.
● Survey site where shells or live animals were found.

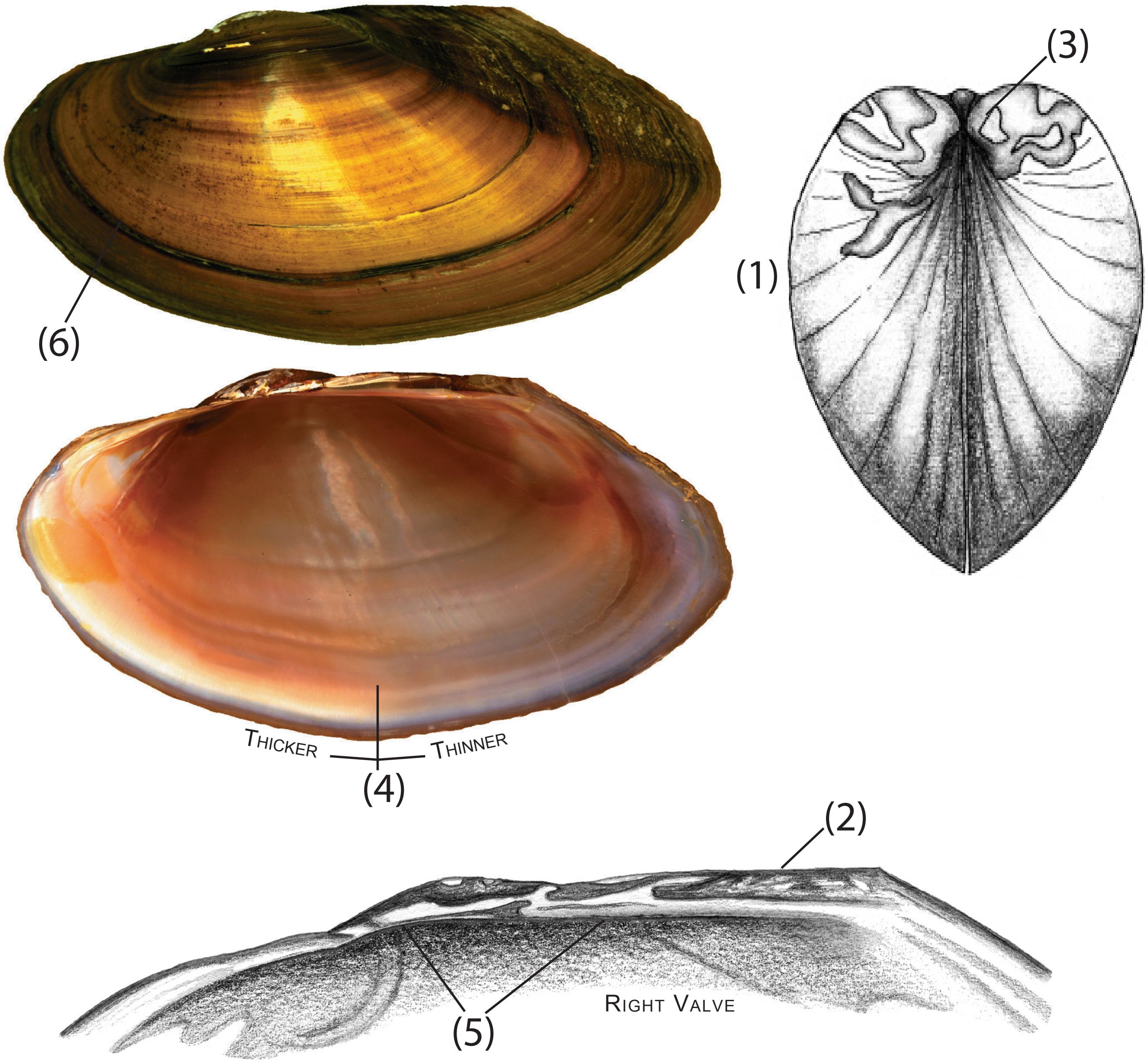
Damariscotta Lake in Maine's midcoast region supports one of the best alewife runs in the state and a healthy population of alewife floaters. ETHAN NEDEAU

Alewife Floater
Anodonta implicata Say, 1829

Description: This is a medium-sized to large (usually < 6.5 inches) mussel. The shell is usually much longer than it is wide, and is somewhat laterally inflated in cross section (1). The hinge ligament is long and straight (2), and the umbos are usually prominent and raised above the hinge line (3). The beak sculpture consists of a series of double-looped concentric bands (**see page 76**). The shell is relatively thin, and application of moderate pressure on the dorsal and ventral surfaces will cause the shells to gape (**see page 56)**. Each valve has a pronounced thickening along the antero-ventral margin that is evident only internally (4). Hinge teeth are entirely absent in this species (5). The shell is smooth, and ranges in color from green to straw yellow to brown or black. Growth annuli are usually prominent on the periostracum (6), and young specimens sometimes have shell rays. The nacre is pale copper, pinkish, or white.

Confusing Species: The alewife floater is most frequently confused with the closely related eastern floater and Newfoundland floater. Both of these species lack hinge teeth, but have uniformly thin shells. The Newfoundland floater has a beak sculpture consisting of single-looped bars, whereas both the alewife floater and the eastern floater have double-looped bars (**see page 76**). The creeper has only a rudimentary pseudocardinal tooth and may be mistaken for the alewife floater, but it does not have the pronounced thickening along the antero-ventral margin, nor does it have the long, straight hinge ligament characteristic of the alewife floater.

Range: The alewife floater is found along Atlantic coastal drainages from the Potomac River system in Maryland to Nova Scotia and New Brunswick. It is found in nearly all of the coastal watersheds in Maine, and as far inland as its anadromous fish hosts once traveled.



Habitat: The alewife floater is found in streams, rivers, and lakes. It occurs in a wide range of substrate types, including silt, sand, and gravel. Its distribution is closely tied to that of its anadromous fish hosts.

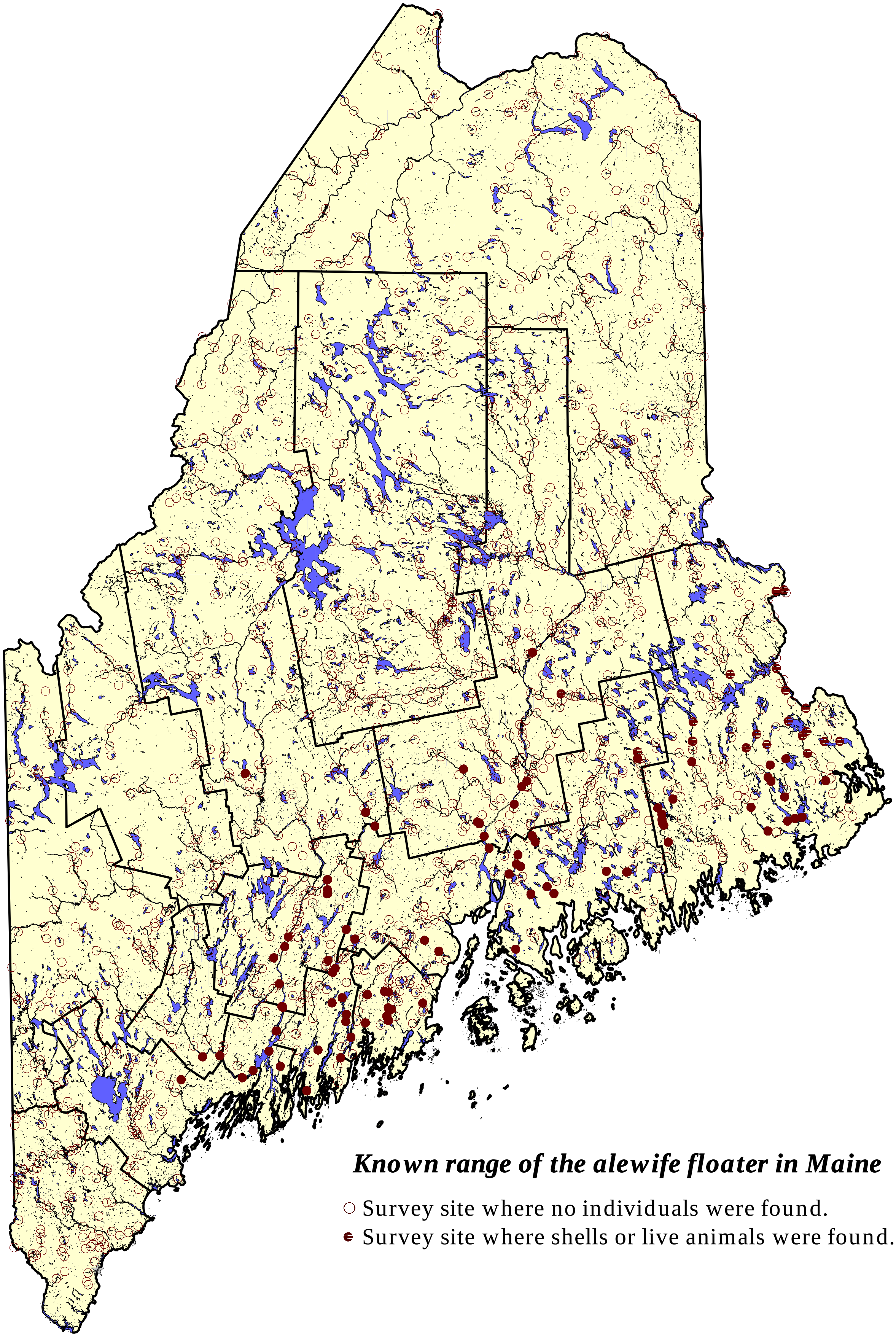
Reproductive Characteristics: The alewife floater is a long-term brooder — eggs are fertilized in August and glochidia are released the following spring. The alewife (*Alosa pseudoharengus*) is a confirmed host (Davenport and Warmuth 1965), though other anadromous clupeids — shad (*Alosa sapidissima*) and blueback herring (*Alosa aestivalis*) — are probably also suitable hosts.

Conservation: The alewife floater is fairly widespread and common in coastal regions of Maine, though it seems to be more prevalent Down East where rivers have been less affected by dam construction and watershed disturbance. Fish passage facilities have been shown to facilitate population expansion by enhancing the passage of its anadromous hosts (Smith 1985). Damariscotta Lake in Lincoln County has an exceptional population of alewife floaters, largely because it supports one of the best alewife runs in the state. The species was likely extirpated from a number of rivers in southern Maine that historically lost their alewife runs because of dam construction.

This alewife fishway on the Damariscotta River allows tens of thousands of alewife to make their annual spawning migration into Damariscotta Lake. Removal of this fishway would block the alewife migration, and eventually extirpate alewife floaters from the lake. ETHAN NEDEAU

Known Range of the Alewife Floater in Maine

County	Specific Waterbodies
Androscoggin	Androscoggin R
Aroostook	
Cumberland	Androscoggin R, Chandler R
Franklin	
Hancock	Hot Hole P, Lower Patten P, Donnell P, Phillips L, Card Mill S, Walker P, Long P, Great P, Narraguagus R, Toddy P, Orland R, Moosehorn S, Patten S
Kennebec	Kennebec R, Sheepscot R (WB), Sebasticook R, Pattee P, Cobbosseecontee S, Long P
Knox	Maces P, Seven Tree P, North P, South P, Round P, North P Outlet, Saint George R
Lincoln	Damariscotta L, Dyer Long P, Sherman L, Medomak R, Medomak P, Sheepscot R, Knickerbocker P, Pemaquid P, Pemaquid R
Oxford	
Penobscot	Souadabscook S, Penobscot R, Kenduskeag S, Passadumkeag R
Piscataquis	
Sagadahoc	Kennebec R, Androscoggin R, Merrymeeting Bay, Nequasset P
Somerset	Sebasticook R
Waldo	Pitcher P, Sheepscot P, Penobscot R, Tilden P, Branch P, Sebasticook R
Washington	Northern S, Love L, Saint Croix R, Round L, Rocky L, Hadley L, Gardner L, Crawford L, Machias R (MB, EB), Woodland Flowage, Big Musquash S, Cathance L, Narraguagus R, Meddybemps L, First Machias L, Boyden L, Pleasant R, Cathance S, Dennys R
York	

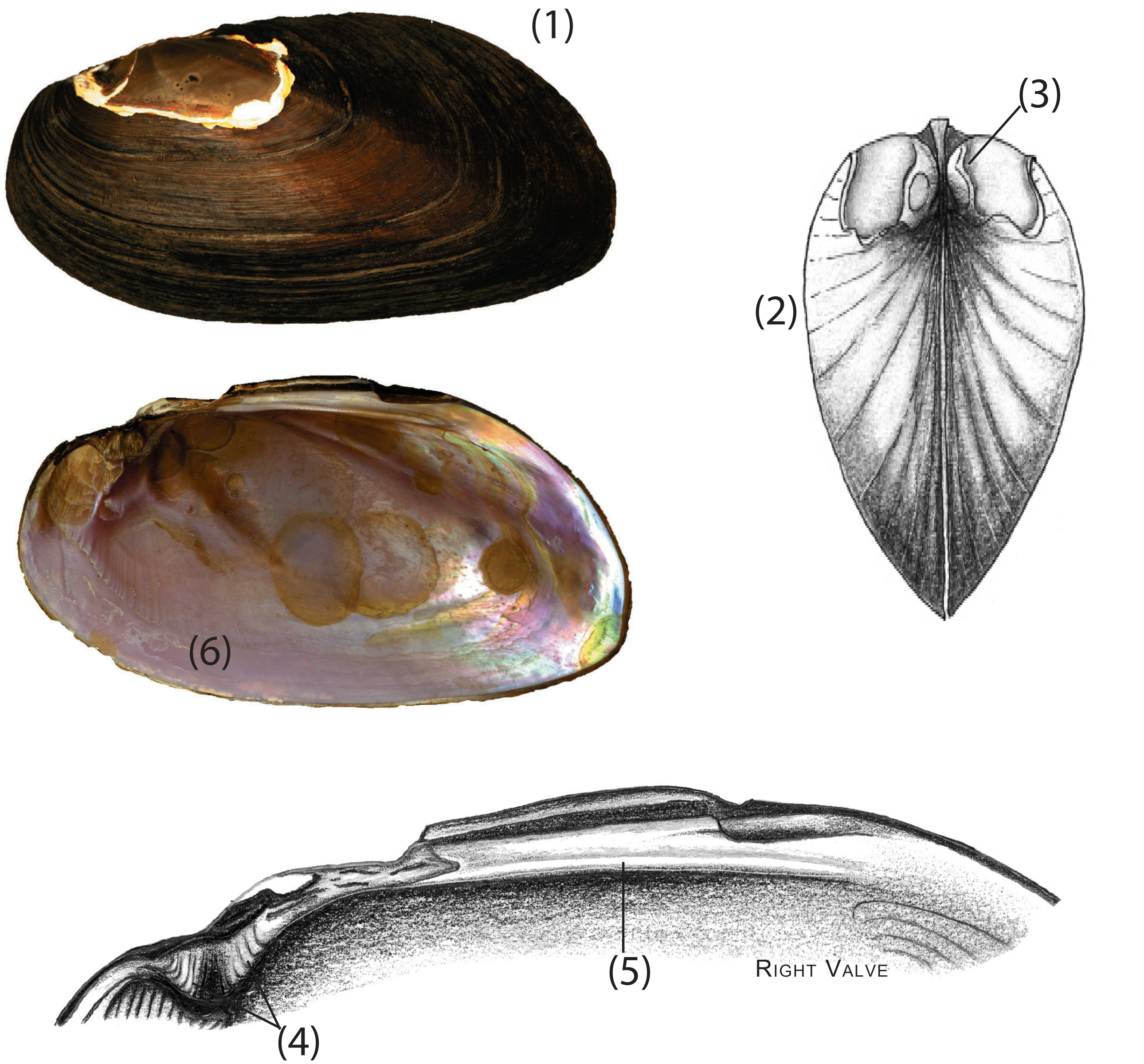

Known range of the alewife floater in Maine
Survey site where no individuals were found.
Survey site where shells or live animals were found.

The eastern elliptio is found in nearly every river and lake in the state, including some island ponds such as Bubble Pond on Mount Desert Island. ETHAN NEDEAU

Eastern Elliptio
Elliptio complanata (Lightfoot, 1786)

Description: This is a medium-sized to large (usually < 5 inches), heavy-shelled mussel. Its shape is extremely variable. The most "typical" shell shape is quadrate or rectangular (1). The valves are usually laterally compressed (2), and the umbos are not very prominent (3). The periostracum is usually tan or brownish in younger individuals to dark brown or black in adults, and there are sometimes rays on the periostracum. Pseudocardinal teeth are well developed — the left valve has two and the right valve has one (4). Lateral teeth are also well developed — the left valve has two and the right valve has one (5). The nacre is purplish or rose-colored in freshly killed specimens (6) to chalky white in older shells. The mantle margin is gray, white, or reddish, without any distinct patterns or modifications, and the foot is white.

Confusing Species: The freshwater mussel most commonly found in Maine is the eastern elliptio. Since most other species are not nearly as widespread, it would be valuable to check the range maps and habitat requirements of other species before spending time trying to differentiate them. Because the eastern elliptio has such a variable shape, it is sometimes confused with the eastern pearlshell, eastern lampmussel, and creeper. The ventral margin of the elliptio is less curved than that of the eastern lampmussel, it is more laterally compressed, and it usually does not have rays on the periostracum. Live specimens of young elliptios resemble the creeper, and often the only reliable way to distinguish them is to use the "squeeze test" (**see page 56**). Some elliptios resemble young eastern pearlshells. Internally, these species are very easy to tell apart since the pearlshell does not have lateral teeth. Though the eastern pearlshell is usually more elongate and "banana-shaped" than the elliptio, occasionally elliptios will also be elongate. The eastern pearlshell has a peculiar habit of "sputtering and wheezing" when removed from the water, a trait not observed for elliptios. The mantle margins of the eastern pearlshell are dark gray or black, and there is no



separation between the inhalent and exhalent apertures. Habitat is often a key piece of information to distinguish these two, since the eastern pearlshell is not found in lakes, ponds, or most of the larger rivers.

Range: The eastern elliptio occurs along the Atlantic coast from Nova Scotia to Florida. It is also found in the St. Lawrence drainage, some of the Great Lakes (Lake Superior, upper Lake Huron, and Lake Ontario), and the southern James Bay drainages. It is found in virtually every water body in Maine that is capable of supporting mussels.

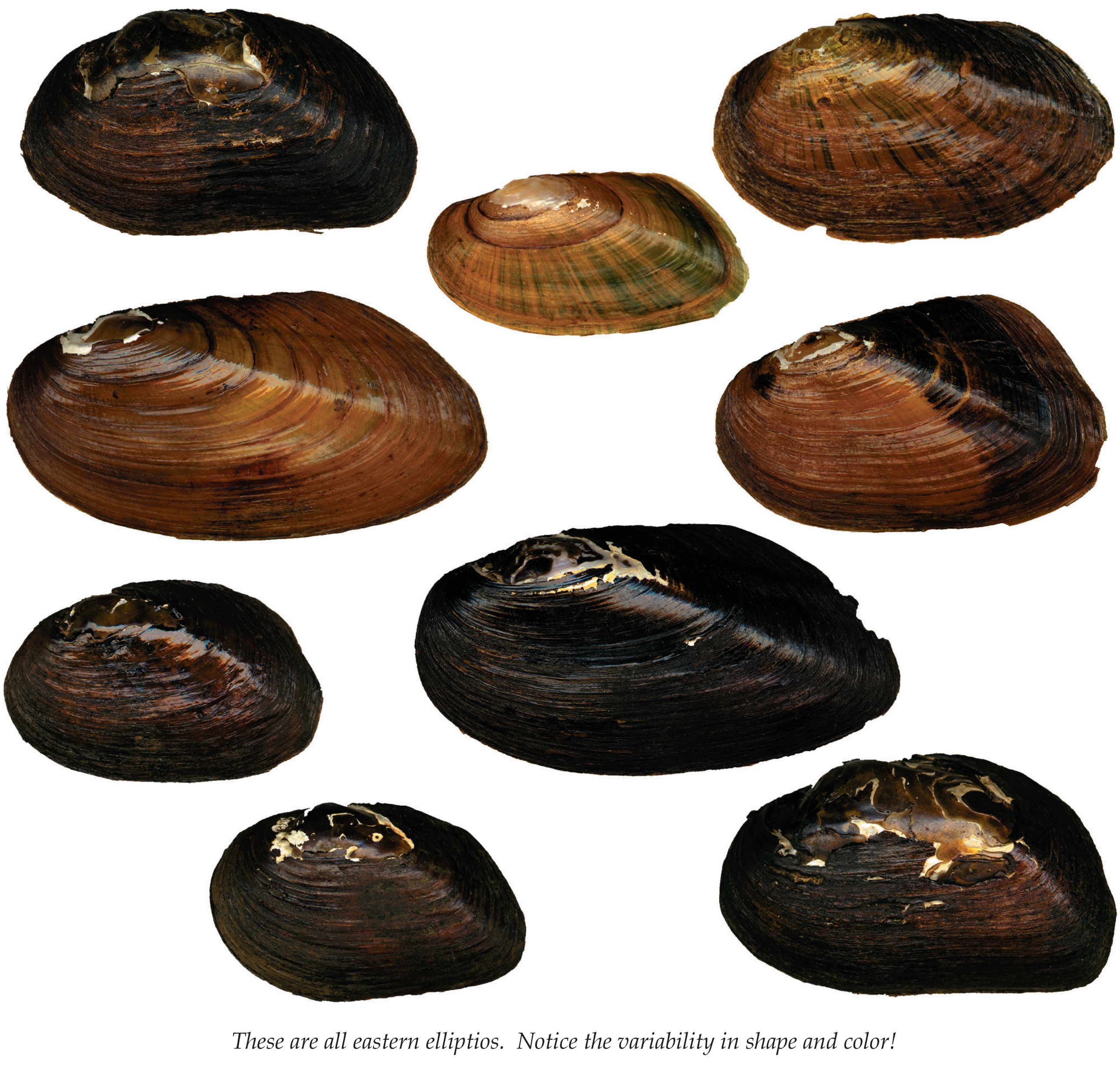
Habitat: The eastern elliptio is found in a wide variety of habitats, including small streams, large rivers, freshwater tidal waters (such as the lower Kennebec), and all types of ponds and lakes. It is found in clay, mud, sand, gravel, and cobble bottoms. The only habitats that appear to be unsuitable for this species are the deep semi-liquid silt characteristic of deeper portions of lakes and the rocky bottoms of small high-gradient mountain streams. Even sites that have been heavily influenced by habitat disturbance or pollution usually support populations of the eastern elliptio, suggesting that it has a wide environmental tolerance and a capacity to quickly colonize new habitats.

Reproduction: This species is a short-term brooder — fertilization takes place in early spring and glochidia are released later in the summer. Confirmed hosts include the yellow perch (*Perca flavesens*), banded killifish (*Fundulus diaphanus*), and largemouth bass (*Micropterus salmoides*) (Watters 1994, Wiles 1975). Given how widespread and common the eastern elliptio is in eastern North America, it probably uses a wide variety of fish hosts.

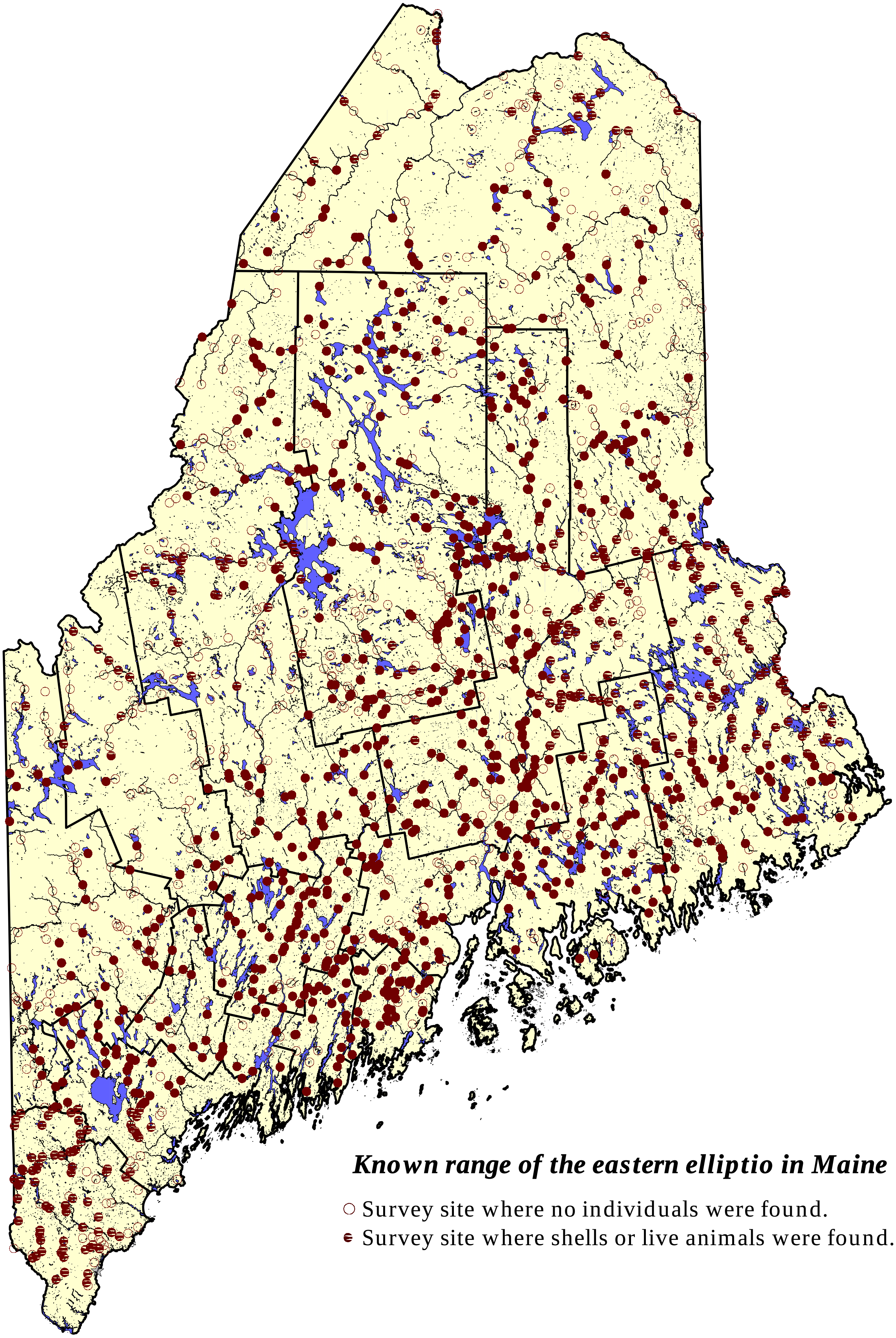
Conservation: The eastern elliptio is one of the 75 or so mussel species in North America whose populations are currently stable or even increasing. It is often used in toxicological studies to determine its tolerance of and response to different types of pollutants, and it is used in other types of ecological and biological research. Given its abundance in many habitats, it probably plays a very important ecological role.

Known Range of the Eastern Elliptio in Maine

County	Specific Waterbodies
All Maine Counties	The eastern elliptio has been found at over 1100 locations in Maine, and in every major watershed. Individual waterbodies are too numerous to list in this table.



These are all eastern elliptios. Notice the variability in shape and color!



Known range of the eastern elliptio in Maine

○ Survey site where no individuals were found.
● Survey site where shells or live animals were found.

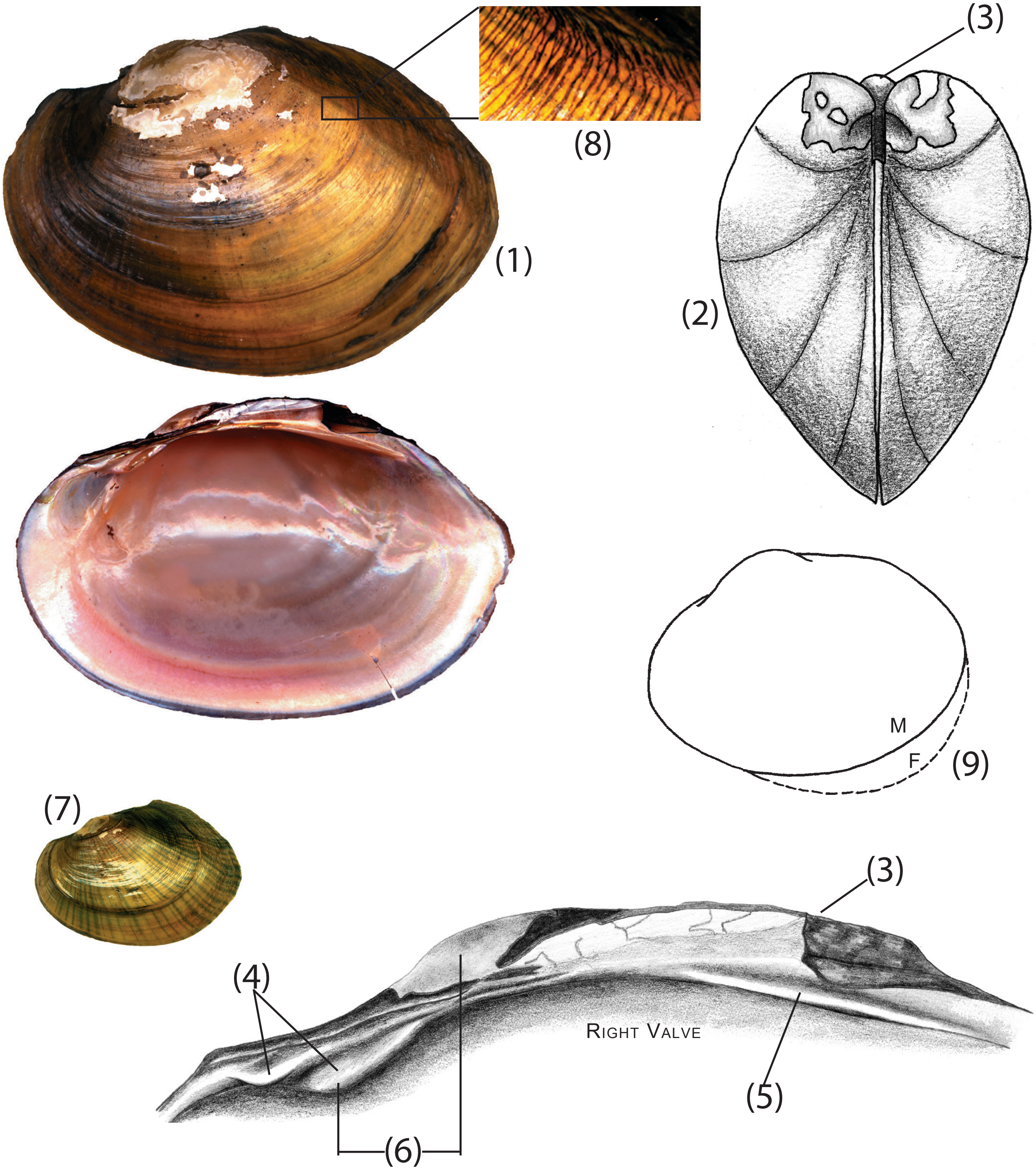
The Passadumkeag River, a major tributary of the Penobscot River, supports a healthy population of tidewater muckets - as well as all other species known from Maine. ETHAN NEDEAU

Tidewater Mucket
Leptodea ochracea (Say, 1817)

MAINE THREATENED SPECIES

Description: This is a medium-sized (usually < 3 inches) mussel, superficially resembling a marine quahoag. The shell is rounded or oval in outline (1), and the valves are laterally inflated (2). The umbos and ligament are usually prominent and raised above the hinge line (3). The valves are strong but uniformly thin. Hinge teeth are thin and delicate — the left valve has two pseudocardinal teeth and two lateral teeth, and the right valve has two pseudocardinal teeth (4) and one lateral tooth (5). Pseudocardinal teeth are rather thin and elongate, and are located well anterior of the beak (6). The periostracum is usually yellowish or greenish-brown, often with a bronze or reddish-yellow cast. Fine green rays are sometimes evident on the shell, especially in younger specimens (7). Dark interannular lines may also be evident on clean shells (8). The nacre is usually pinkish or salmon color and translucent. The mantle margin is usually gray or yellowish-gray and not heavily pigmented. Sexually mature females appear swollen (slightly more rounded) toward the rear of the animal (9).

Confusing Species: It is often very difficult to distinguish this species from the yellow lampmussel (Johnson 1947), especially for the novice. There are several differences that will nearly always lead to proper identification. The tidewater mucket is smaller, with a thinner shell and more delicate hinge teeth. It is not nearly as yellow as the yellow lampmussel, and it often has dark interannular lines on the periostracum. The nacre is usually pinkish or salmon colored, whereas it is white or bluish-white in the yellow lampmussel. Pseudocardinal teeth are thin and elongate, whereas the yellow lampmussel usually has thick, blunt pseudocardinals with some striations on the surface. The pseudocardinals are also situated far forward of the beak, in comparison to almost directly under the beak in the yellow lampmussel. Some rayed individuals can resemble the eastern lampmussel, though eastern lampmussels are not nearly so rounded in outline or fat in cross section.



Range: The tidewater mucket is found in Atlantic coastal drainages from Georgia to Nova Scotia. In Maine it is known only from Merrymeeting Bay and the St. George, Penobscot, lower Kennebec, and lower Androscoggin River drainages. Its distribution is very similar to that of the yellow lampmussel, particularly in ponds and lakes. Despite its common name, it is found quite far inland — as far as Millinocket Lake in the Mount Katahdin region.

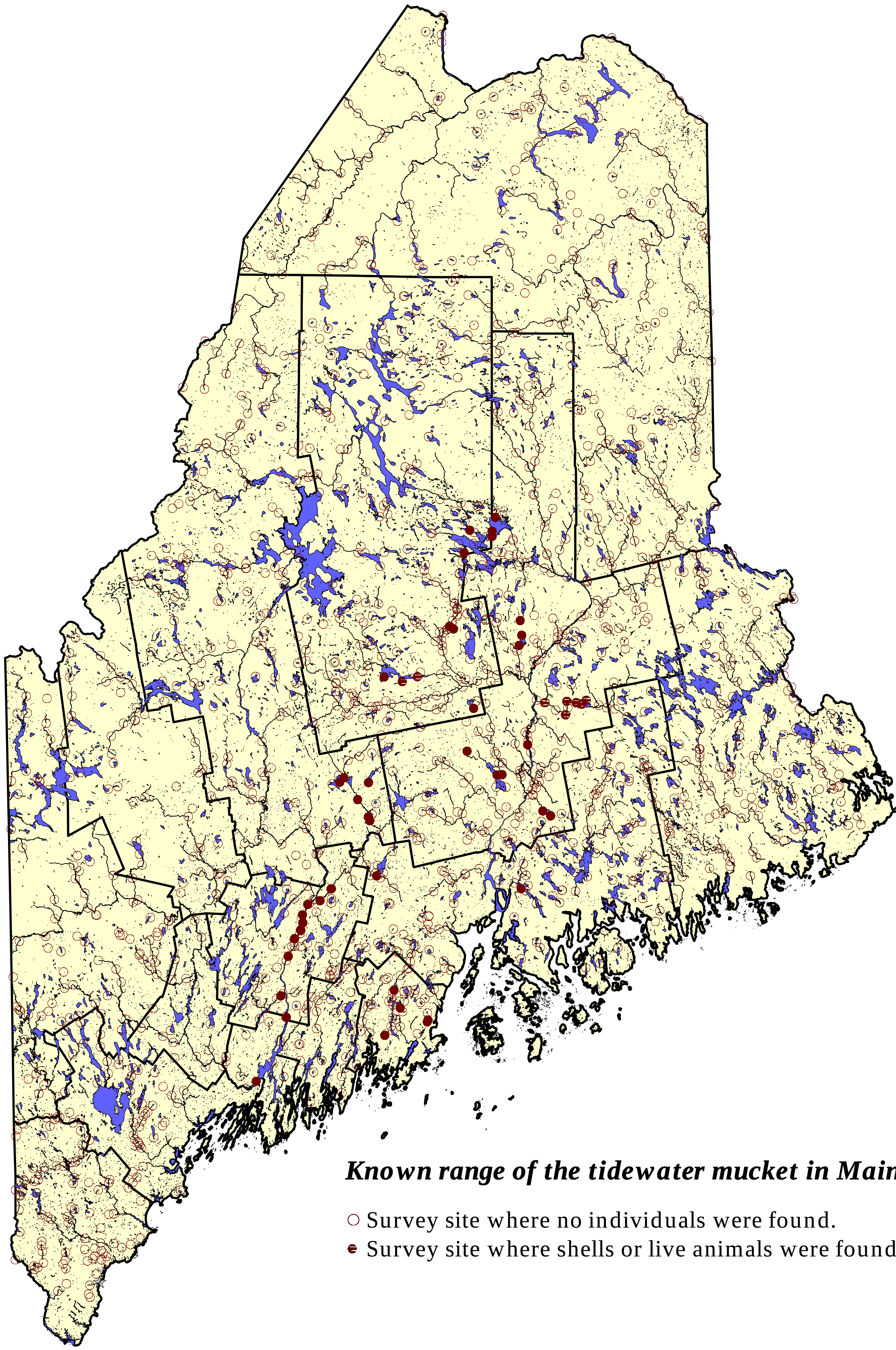
Habitat: The tidewater mucket seems to prefer coastal lakes, ponds, and slow-moving portions of rivers, including artificial impoundments. It is found in a variety of substrates, including silt, sand, gravel, cobble, and occasionally clay.

Reproductive Characteristics: The tidewater mucket is a long-term brooder — eggs are fertilized in late summer and glochidia are released the following spring. The host fish are unknown. It seems likely that at least one of its hosts is an anadromous species because of its distribution in tidewater areas. However, there are no anadromous fish in some lakes of the upper Penobscot drainage where this species occurs, though anadromous fish historically were able to reach these lakes (such as Jo-Mary Lake and Millinocket Lake in the Katahdin region).

Conservation: This species is listed as threatened in Maine. Although some healthy populations do exist — especially in lakes and rivers of the lower Kennebec and Penobscot River drainages — this species is often scarce where it is found, and populations may be in decline. The tidewater mucket has been declining throughout its range, prompting many states to list it as endangered or threatened. It is currently listed as threatened in Connecticut and special concern in Massachusetts. It may have been extirpated from the Hudson River in recent years. The reasons for its decline are unknown, but probably reflect a cumulative effect of habitat destruction and pollution, and in at least one instance (lower Hudson River), competition with the zebra mussel. As with the yellow lampmussel, Maine's healthy populations of the tidewater mucket may serve as important refugia if other populations along the Atlantic seaboard are extirpated.

Known Range of the Tidewater Mucket in Maine

County	Specific Waterbodies
Androscoggin	
Aroostook	
Cumberland	
Franklin	
Hancock	Alamoosook L
Kennebec	Sebasticook R, Kennebec R, Outlet S, Cobbosseecontee S
Knox	Chickawaukee P, Crawford P, Sennebec P, South P, North P, Seven Tree P
Lincoln	Sidensparker P
Oxford	
Penobscot	Millinocket L, South Branch L, Pushaw L, Little Pushaw P, Saponac P, Passadumkeag R, Little Mattamicontis L, Penobscot R, Mud P, Chemo P, Cold Stream P (possibly extirpated)
Piscataquis	Sebec L, Ebeemee L, Boyd L, Lower Jo-Mary L, Passamagamet L
Sagadahoc	Androscoggin R, Kennebec R, Merrymeeting Bay
Somerset	Sebasticook R, Indian P, Douglas P, Great Moose L
Waldo	Sandy S, Unity P
Washington	
York	



Known range of the tidewater mucket in Maine

○ Survey site where no individuals were found.

● Survey site where shells or live animals were found.

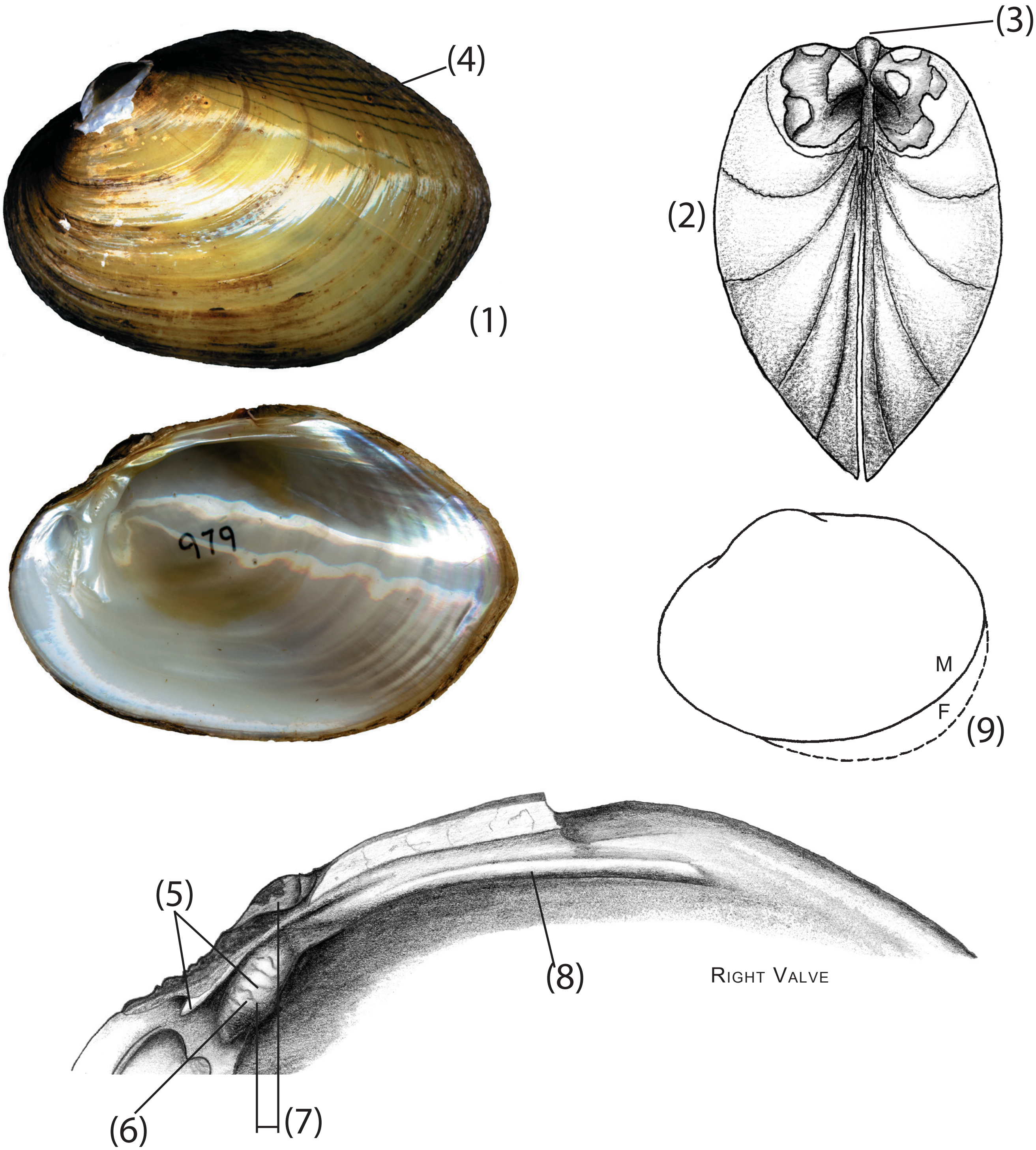
Sennebec Pond is one of several ponds in the St. George River watershed where the yellow lampmussel exists. JAIME HASKINS

Yellow Lampmussel
Lampsilis cariosa (Say, 1817)

MAINE THREATENED SPECIES

Description: This is a medium-sized to large (usually < 4.5 inches) mussel that is distinctly yellow and oval-shaped — superficially resembling a marine quahoag (1). The valves are inflated in cross section (2) and the umbos are quite prominent and raised above the hinge line (3). The shell is strong and thick, especially toward the anterior end. The periostracum is often bright yellow in younger or healthy specimens, though it becomes yellowish or reddish-brown in older individuals. Some individuals (particularly young ones) have faint green rays on the periostracum, especially toward the dorsal posterior region (4). The nacre is usually white or bluish-white. Pseudocardinal teeth are well developed — the left valve has two and the right valve has two or three (5). Pseudocardinals are usually stout, with distinct striations on the surface (6), and are located nearly directly under the beak (7). Lateral teeth are also well developed — the left valve has two and the right valve has one (8). The female mantle margin is often brightly pigmented, with a conspicuous fleshy flap and a dark "eyespot" near the inhalent aperture. Mature females are considerably more rounded toward the posterior ventral margin than males and adolescent females (9).

Confusing Species: It is often very difficult to distinguish this species from the tidewater mucket (Johnson 1947), especially for the novice. Variability in the coloration of the periostracum and shape of the hinge teeth may cause difficulty in identification. The yellow lampmussel is larger, with a thicker shell and more robust hinge teeth. It is usually a brighter yellow than the tidewater mucket, and the nacre is usually white or bluish-white, whereas it is pinkish or copper-colored in the tidewater mucket. The mantle margin of the yellow lampmussel is usually brightly pigmented and has fleshy extensions. The pseudocardinal tooth on the right valve is located almost directly under the umbo, whereas it is located well forward of the umbo in the tidewater mucket. Pseudocardinal teeth are thick and blunt, with some striations on the surface. In the tidewater mucket, pseudocardinal teeth are thin and elongate, without such striations. The yellow lampmussel lacks the dark interannular lines that are evident on tidewater mucket shells.



Range: The yellow lampmussel is distributed throughout the Atlantic drainages from Georgia to Nova Scotia and Cape Breton Island. In Maine it is known only from the Penobscot, St. George, and lower Kennebec River watersheds.

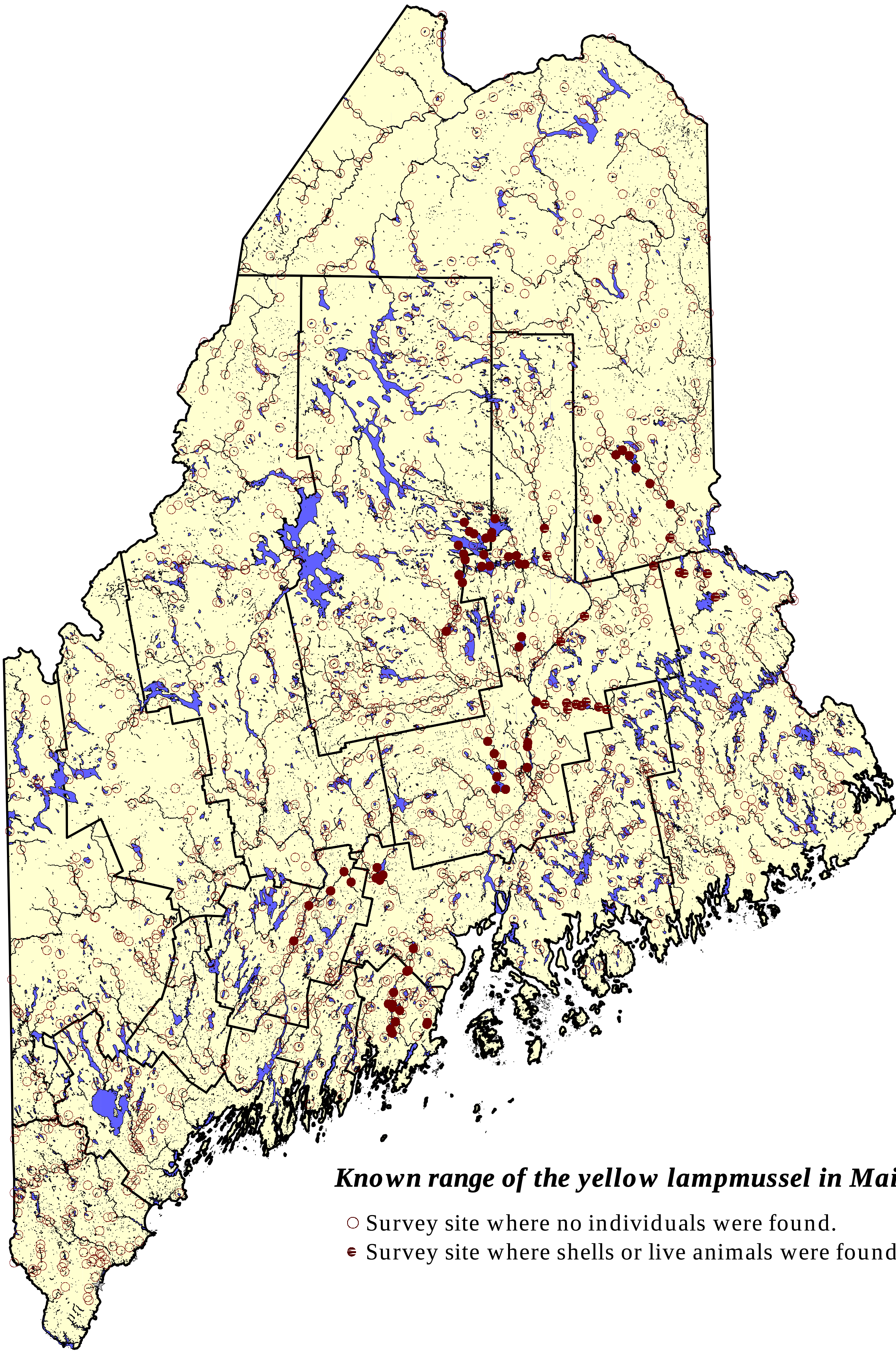
Habitat: The yellow lampmussel seems to prefer medium to large rivers, although in Maine it is also found in lakes and ponds and seems to do well in impounded sections of rivers. It exists in a variety of substrate types, including silt, sand, gravel, and cobble.

Reproductive Characteristics: This species is a long-term brooder — eggs are fertilized in late summer and glochidia are released the following spring. The host fish is unknown, though it is likely a species that has at least some affinity for coastal areas. Other species in the genus use a variety of warmwater fish species, including percids (perch and walleye) and centrarchids (sunfishes and bass). It is one of the few species in New England that uses a modified mantle flap to attract host fish.

Conservation: This species is listed as threatened in Maine. It is found in relatively few sites, and population densities are often very low. Scientists suspected that it was extirpated from the Connecticut River in Massachusetts until live specimens were discovered in 1996-1999. It was thought to be possibly extirpated from the lower Kennebec River until it was rediscovered in the summer of 1999. This species has been declining throughout its range, prompting many states to add it to their lists of endangered and threatened species. It is currently listed as endangered in Massachusetts, and special concern (possibly extirpated) in Connecticut. It was a candidate for federal listing prior to the elimination of this list by Congress in 1995. The reasons for its decline are unknown, but probably reflect a cumulative effect of habitat degradation and pollution. Maine has some very healthy populations of the yellow lampmussel (especially in the Sebasticook River, St. George River, middle Penobscot River, and Passadumkeag River) that may play an important role in the species' conservation if populations are extirpated elsewhere along the Atlantic seaboard. This species may be hydridizing with *Lampsilis ovata* and *Lampsilis cardium* in the western part of its range, and the genetic integrity of Maine populations may be important to the future conservation of this species.

Known Range of the Yellow Lampmussel in Maine

County	Specific Waterbodies
Androscoggin	
Aroostook	Mattawamkeag R (MB, WB), Mattawamkeag L, Molunkus S
Cumberland	
Franklin	
Hancock	
Kennebec	Sebasticook R, Kennebec R, Messalonskee S, Fifteenmile S
Knox	Saint George R, Chickawaukee P, Crawford P, Seven Tree P, Round P, Sennebec P, North P, South P
Lincoln	
Oxford	
Penobscot	Penobscot R (MB, WB, EB), Passadumkeag R, Dead S (MB, WB), Saponac P, Pushaw S, Pushaw L, Mattawamkeag R, South Branch L, Madagascal S, Pemadumcook Chain L, Millinocket L, Millinocket S Middle Jo-Mary L, Upper Jo-Mary L
Piscataquis	Lower Jo-Mary L, Middle Jo-Mary L, Upper Jo-Mary L, Pemadumcook Chain L, Passamagamet L, Pleasant R (EB), Penobscot R (WB)
Sagadahoc	
Somerset	
Waldo	Quantabacook L, Unity P, Saint George R, Sandy S, Twentyfive Mile S
Washington	Crooked Brook Flowage, Upper Hot Brook L, Baskahegan L, Baskahegan S
York	



Known range of the yellow lampmussel in Maine

○ Survey site where no individuals were found.
● Survey site where shells or live animals were found.

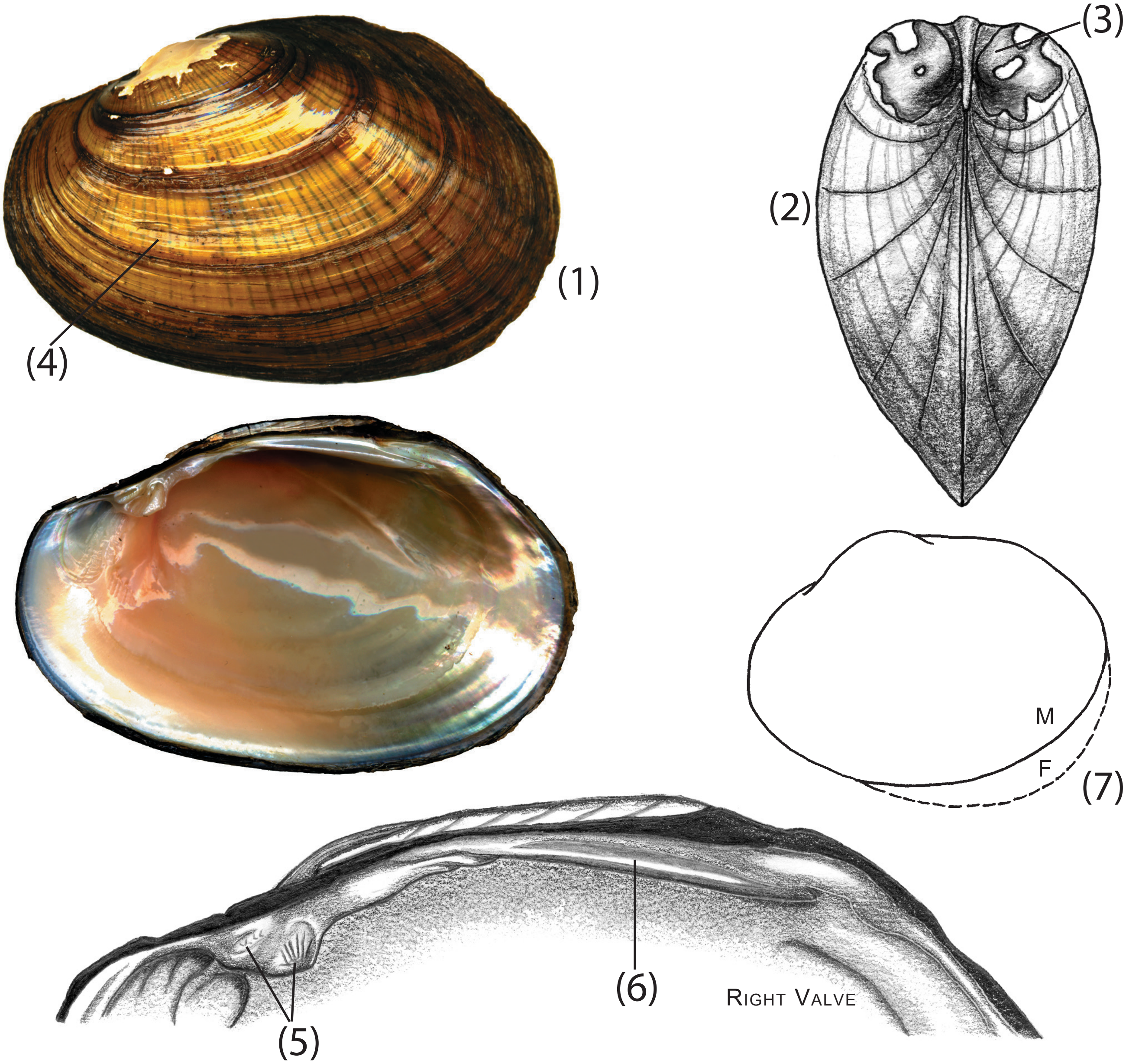
Alamoosook Lake in western Hancock County supports a good population of eastern lampmussels and state-threatened tidewater muckets. MARK McCOLLOUGH

Eastern Lampmussel
Lampsilis radiata radiata (Gmelin, 1791)

Description: This is a medium-sized to large (usually <5 inches), heavy-shelled mussel. The shape is oval or slightly rounded (1), and the valves are usually only moderately inflated in cross section (2). The hinge ligament is usually prominent, and the umbos are not very prominent and barely raised above the hinge line (3). The shell is yellowish-green in younger individuals to brownish-green or black in older specimens. There are usually numerous green rays on the periostracum (4), though these are sometimes obscured in older individuals. Hinge teeth are well developed — the left valve has two pseudocardinal teeth and two lateral teeth, and the right valve has two or three pseudocardinal teeth (5) and one lateral tooth (6). The nacre is usually white, pink, or bluish-white. The female's mantle margin is usually lightly to darkly pigmented, with fleshy tubercles and flap extensions. Mature females are usually more rounded toward the posterior ventral margin than males or adolescent females (7).

Confusing Species: The eastern lampmussel is often confused with the eastern elliptio, with whom it shares all of its range. The eastern lampmussel is usually more oval-shaped and laterally inflated than the eastern elliptio, and it nearly always has prominent rays on the periostracum. However, the eastern elliptio shows a great deal of variability in size and shape, so one must be careful when relying on these characteristics. The eastern lampmussel has a whitish or pinkish nacre, whereas the eastern elliptio has a more purplish nacre (in freshly dead specimens). The mantle margin of the eastern elliptio is not modified or pigmented. The eastern lampmussel may also be confused with the tidewater mucket or yellow lampmussel, though both of these species are more oval-shaped and inflated in cross section, and their yellowish periostracum usually does not have abundant shell rays.

Range: The eastern lampmussel is widely distributed in Atlantic coastal drainages from South Carolina to Nova Scotia, as well as the lower St. Lawrence River drainage. In Maine it is very common in lakes and rivers of the central portion of the state.



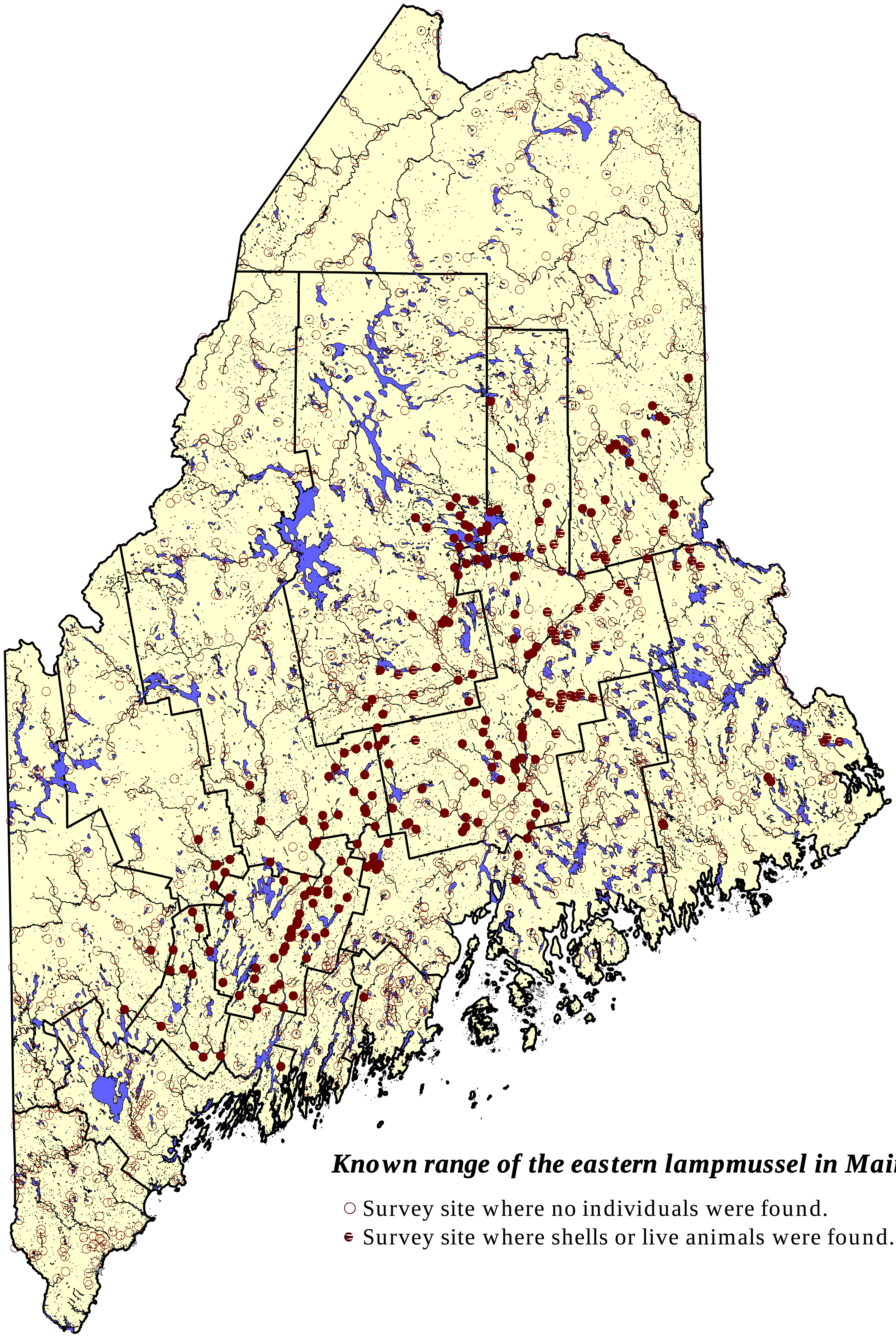
Habitat: This common species inhabits a variety of aquatic habitats, including small streams, large rivers, ponds, and lakes. It is found on a wide variety of substrate types, though it seems to prefer sand or gravel.

Reproduction: The eastern lampmussel is a long-term brooder — eggs are fertilized in mid to late summer and glochidia are released the following spring. Females have a modified mantle flap to attract host fish, though it is not as impressive as that of the yellow lampmussel. This species has been reported to parasitize a number of warm-water species, including yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), black crappie (*Pomoxis nigromaculatus*), and pumpkinseed sunfish (*Lepomis gibbosus*) (Watters 1994). No experimental studies of host fish suitability have been conducted in New England.

Conservation: Like the eastern elliptio and eastern floater, the eastern lampmussel is doing well throughout its range, with stable or increasing populations. This may be because of its ability to tolerate a range of environmental conditions, or its ability to parasitize a number of common fish species. It will remain an important biomonitor of the health of aquatic ecosystems in the future.

Known Range of the Eastern Lampmussel in Maine

County	Specific Waterbodies
Androscoggin	Androscoggin R, Little Androscoggin R, Martin S, Nezinscot R, Androscoggin L, Big Bear P
Aroostook	Molunkus S, Meduxnekeag R, Big B, Mattawamkeag R (WB, MB), Molunkus L, Macwahoc S, Cochrane L, Mattawamkeag L, Lower Macwahoc L, Drews L, Plunkett P, Skagrock B, Skitacook L, Mattaseunk L
Cumberland	
Franklin	Crowell P, Sandy R, Baker S, Wilson S, Little Norridgewock S
Hancock	Alamoosook L, Long P
Kennebec	Outlet S, Cobbosseecontee S, China L, Messalonskee S, Pattee P, McGrath P, Kennebec R, Carrabassett S, Nehumkeag P, Echo L, Sebasticook R, Parker P, Pleasant P, Lovejoy P, Fifteenmile S, Sand P, Cobbosseecontee L, Cochnewagon P, Togus P, Threemile P, Webber P
Knox	Medomak R
Lincoln	
Oxford	Little Androscoggin R, Nezinscot R (EB)
Penobscot	Souadabscook S (MB, WB), Pushaw S, Madagascal S, Passadumkeag R, Saponac P, Dead S (WB, MB), Pushaw L, Little Pushaw P, Kenduskeag S, Garland P, Plymouth P, Martin S, Chemo P, Eddington P, Piscataquis R, Mattakeunk S, Penobscot R (MB, EB, WB), Pleasant L, Wassookeag L, Sebasticook R (MB, EB), Olamon S, Hermon P, Salmon S, Salmon Stream L, Mattanawcook P, Center P, Little Mattamiscontis L, South Branch L, Mattawamkeag R, Pemadumcook Chain L, Middle Jo-Mary L, Millinocket L, Nollesemic L, Big Mud B, Medunkeunk S, Seboeis R, Mattamiscontis S, Sunkhaze S, Mattagodus S, Millinocket S, Mud B
Piscataquis	Pleasant R (EB, WB), Upper Togue P, Sebec L, Center P, Piscataquis R, Passamagamet L, Upper Ebeemee L, Hurd P, Ebeemee L, Lower Jo-Mary L, Upper Jo-Mary L, Pemadumcook Chain L, Boyd L, Nahmakanta L, Sebec R, Manhanock P, Penobscot R (WB), Lower Togue P
Sagadahoc	Nequasset P, Androscoggin R, Kennebec R
Somerset	Kennebec R, Indian P, Douglas P, Mill S, Sebasticook R, Whites P, Lake George, North P, Ripley P, Mainstream P, Great Moose L, Carrabassett S, Sibley P
Waldo	Sebasticook R, Unity P, Carlton S, Sandy S, Twentyfive Mile S
Washington	Narraguagus R, Mattakeunk L, Boyden L, Moosehorn B, Upper Hot Brook L, Crooked Brook L, Round L, Baskahegan S, Machias R (EB), Baskahegan L
York	


Known range of the eastern lampmussel in Maine
Survey site where no individuals were found.
Survey site where shells or live animals were found.

Dwarf Wedgemussel
Alasmidonta heterodon (Lea, 1830)

FEDERALLY ENDANGERED
NOT REPORTED IN MAINE

Description: This is a small (usually ≤ 1.5 inches) mussel with a characteristic "wedge" shape (1). The posterior end of the shell is somewhat pointed (2). The valves are usually laterally compressed (3), though mature females tend to be somewhat swollen. The shell is smooth and may be yellowish-brown, olive-brown, or blackish-brown in color. Young individuals may have greenish rays on the periostracum, but adults typically lack rays. The hinge teeth are quite delicate. This is the only species in the genus *Alasmidonta* in New England that has lateral teeth — one in the left valve and two in the right valve (4), which is the reverse of all other North American species that possess lateral teeth. It also has pseudocardinal teeth — two in the left valve and one in the right valve (5). The nacre is bluish-white and often iridescent along the posterior margin (6).

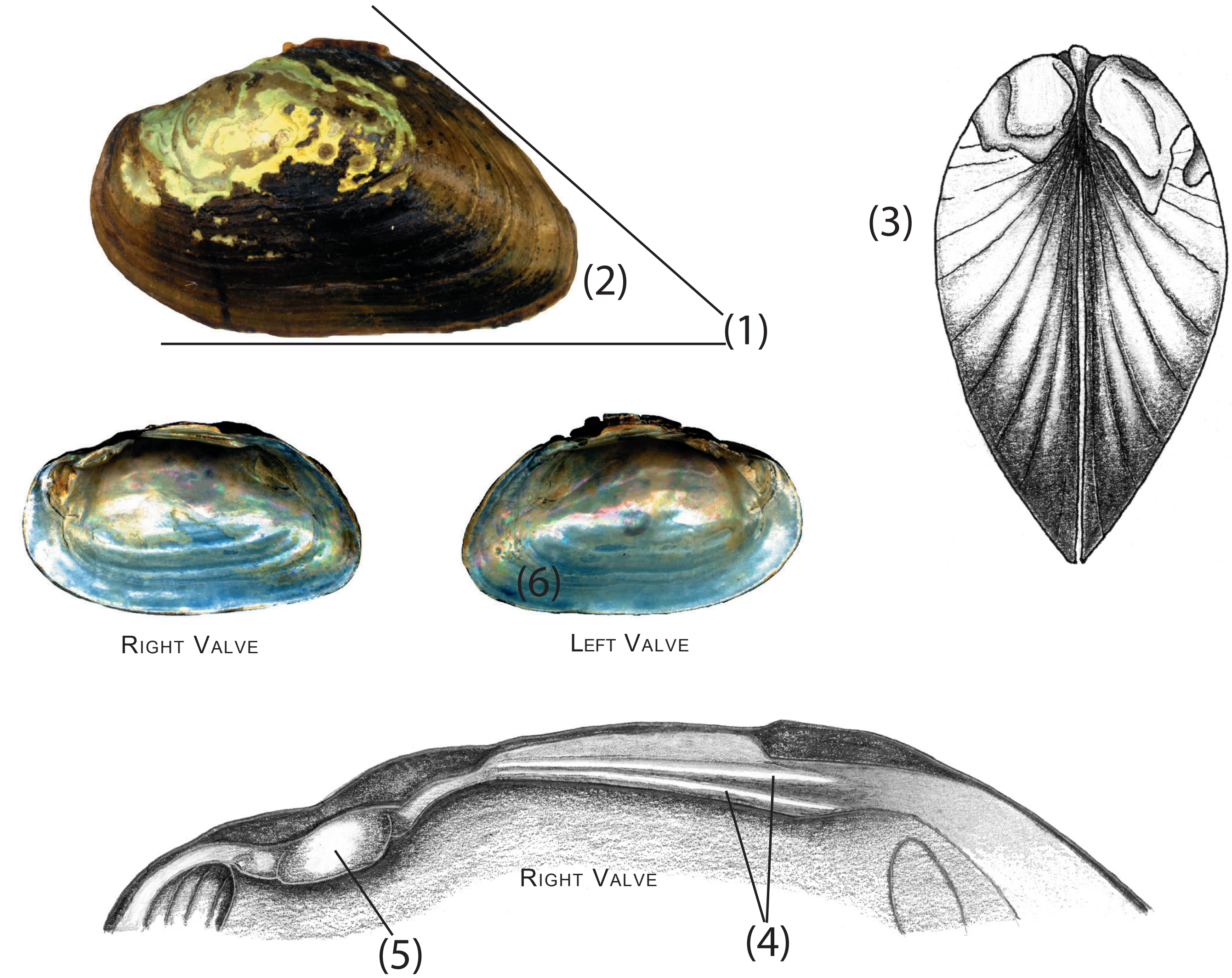
Confusing Species: The small size, wedge shape, and hinge tooth morphology of this species make shells easily distinguishable from all other species in New England. None of the species it can be confused with (brook floater, triangle floater, and creeper) have lateral teeth. However, live specimens are often difficult to distinguish from a young brook floater, triangle floater, or creeper. The dwarf wedgemussel lacks the series of ridges along the dorso-posterior slope of the brook floater. Since the dwarf wedgemussel is federally endangered, and all of the species it may be confused with are special concern in Maine, experts should verify the identity of live specimens.

Range: The dwarf wedgemussel is found in streams and rivers of the Atlantic coastal region, from North Carolina to eastern New Brunswick. In New England, it has been found in the Quinnipiac River (Connecticut), Connecticut River watershed (Connecticut, Massachusetts, Vermont, and New Hampshire), Agawam River (Massachusetts), Taunton River (Massachusetts), and Merrimac River (Massachusetts and New Hampshire). It historically was found in the Petitcodiac River (New Brunswick). However, it is believed to be extirpated from all but the Connecticut River watershed. Although it has been documented in New Hampshire and New Brunswick, it has never been found in Maine despite surveys at well over 1600 sites.

The Connecticut River and several of its tributaries support populations of the federally endangered dwarf wedgemussel.
ETHAN NEDEAU

Habitat: The dwarf wedgemussel inhabits flowing-water habitats — from small streams to large rivers. It seems to prefer slow to moderate flow conditions and is not found in high gradient streams of mountainous areas. Investigators have not found a particularly strong substrate preference for this species — it has been collected in mud, sand, and gravel habitats (Strayer and Ralley 1993, Michaelson and Neves 1995).

Reproductive Characteristics: This species is a long-term brooder — fertilization occurs in the summer or early fall, and glochidia are released the following spring. Michaelson and Neves (1995) confirmed three hosts for this species: the tesselated darter (*Etheostoma olmstedi*), Johnny darter (*Etheostoma nigrum*), and mottled sculpin (*Cottus bairdi*). Wicklow (1999) found that



the Atlantic salmon (*Salmo salar*) is also a suitable host fish. The slimy sculpin (*Cottus cognatus*) may also be a host fish (Barry Wicklow, Saint Anselm College, *personal communication*). Among the suspected hosts, only the Atlantic salmon and slimy sculpin are found in Maine (Everhart 1976).

Conservation: The dwarf wedgemussel is currently the only federally endangered freshwater mussel in New England. Historically, it was known from 70 locations in 15 major river drainages along the Atlantic coast, but now it is known from perhaps two dozen locations. It has not been found in the Petitcodiac River in New Brunswick (the only known Canadian locality) since 1963, and is presumably extirpated. The exact cause of its widespread decline is unknown, but it is probably a cumulative effect of many factors, such as habitat degradation and pollution. Its host fish have been affected by many of the same factors — many darter and sculpin species have experienced significant range reductions and have been listed as endangered, threatened, or special concern throughout their range. It is difficult to understand why the dwarf wedgemussel is not found in Maine, especially considering its occurrence in neighboring New Hampshire and New Brunswick, and because the Atlantic salmon is a suitable host. There may have been isolated populations in Maine that were quickly extirpated due to human activity, such as we have seen in the Merrimac River and Petitcodiac River. In addition to being a federally endangered species, this species is also listed as endangered by many states along the eastern seaboard from North Carolina to New Hampshire.

The eastern pondmussel is found in many streams throughout the lower Connecticut River watershed, such as the Mill River near Northampton, Massachusetts. ETHAN NEDEAU

Eastern Pondmussel
Ligumia nasuta (Say, 1817)

NOT REPORTED IN MAINE

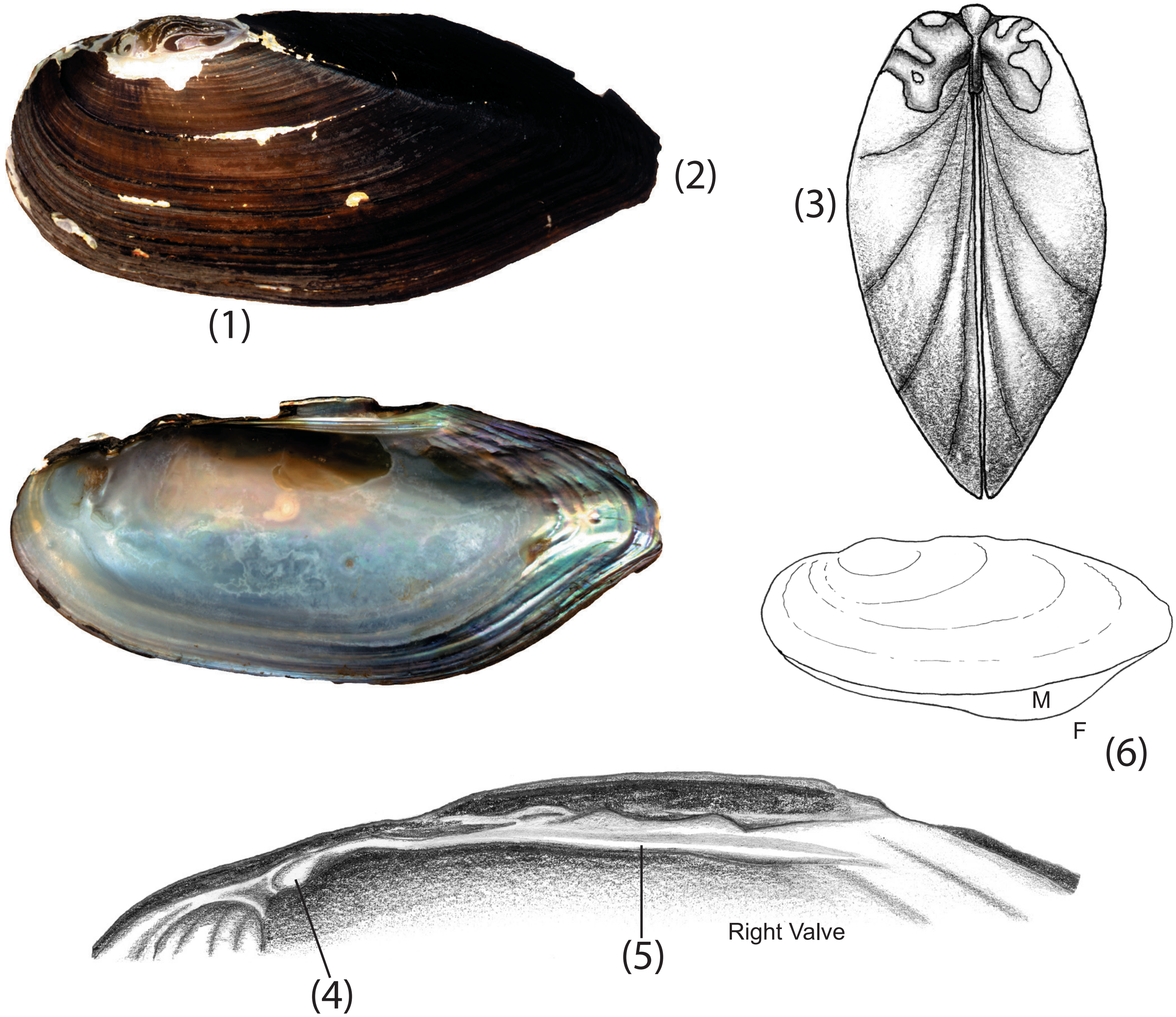
Description: This is a medium-sized to large (usually <6 inches) mussel with a distinctly narrow and elongate shape (1). The shell is usually over twice as long as it is high, and the posterior end tapers to a blunt point (2). The valves are usually laterally compressed in cross section (3), and despite being thin, they are quite strong. The shell is yellowish or greenish-black in young individuals, but usually darker in older specimens. Rays are sometimes evident on those individuals with a light-colored periostracum. Hinge teeth are well developed but delicate — the left valve has one or two pseudocardinal teeth and two lateral teeth, and the right valve has one or two pseudocardinal teeth (4) and one lateral tooth (5). The nacre is usually purple, pink, or silvery white. Mature females are distinctly swollen along the posterior ventral margin (6).

Confusing Species: This species is very distinct and could not be confused with any other species in the state.

Range: The eastern pondmussel is distributed throughout Atlantic coastal drainages from Virginia to New Hampshire and in the eastern Great Lakes region. It is found in the lower Connecticut River Valley, southeastern Massachusetts, and southern New Hampshire. It is possible that this species could be found in extreme southwestern Maine.

Habitat: This species inhabits a wide variety of habitats, including coastal ponds, slow-moving rivers, and small streams and rivers. It is found in a variety of substrate types.

Reproduction: The eastern pondmussel is a long-term brooder — fertilization occurs in late summer and glochidia are released the following spring. The host fish have not yet been determined, though the mussel's range suggests



that its hosts have some affinity for coastal areas. Closely related species have been reported to parasitize centrarchids (sunfishes and bass) as well as the banded killifish (*Fundulus diaphanus*), which has a coastal affinity.

Conservation: This species is listed as special concern in Massachusetts and Connecticut. It has a restricted distribution in New England, and many historical populations are either extinct or have declined considerably in recent decades. This is probably the result of habitat degradation and pollution.

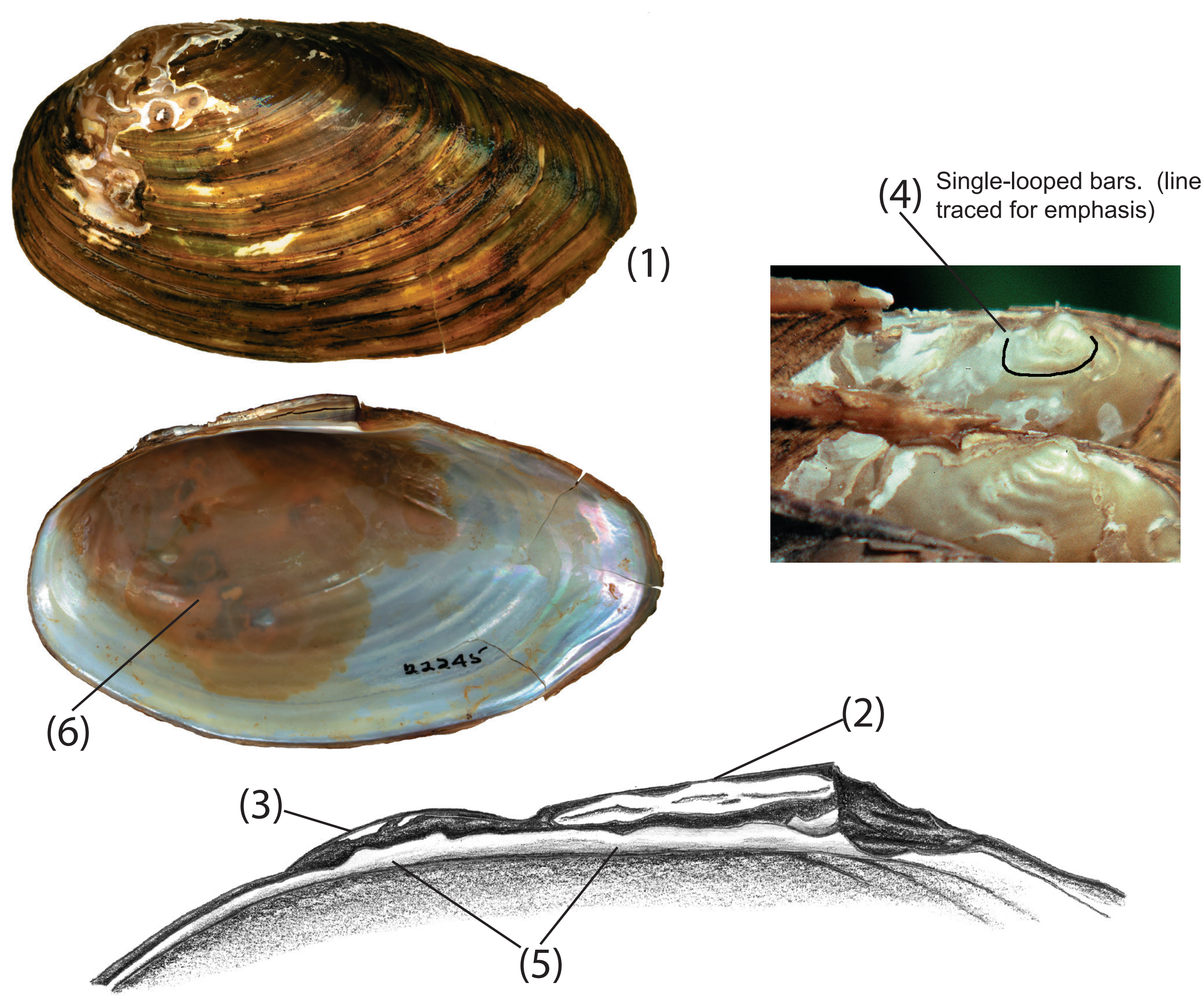
This small pond surrounded with a coniferous forest and bog plants is typical habitat for the Newfoundland floater, which is found in eastern Canada. MNAP PHOTO

Newfoundland Floater
Pyganodon fragilis (Lamarck, 1819)

NOT REPORTED IN MAINE

Description: This is a medium-sized (usually < 4.5 inches) mussel with a very fragile shell. It is much longer than it is wide, slightly rounded, and the posterior end is usually bluntly pointed (1). The valves are laterally inflated in cross section. The hinge ligament is typically straight (2), and the beaks are slightly inflated and project above the hinge line (3). The beak sculpture consists of a series of single-looped concentric bars (4). The shells are uniformly thin, and application of slight pressure on the dorsal and ventral surfaces will cause the valves to spread apart (**see page 56**). Hinge teeth are entirely absent (5). The shell is smooth, with prominent growth annuli and sometimes faint rays. The periostracum is yellowish to brownish black, and the nacre is usually silvery white or bluish, sometimes with yellowish patches (6).

Confusing Species: The Newfoundland floater is distinguished from the alewife floater and eastern floater by its beak sculpture, which consists of single-looped bars (**see page 76**). However, excessive shell erosion sometimes prevents the use of this characteristic. Without the benefit of beak sculpture, it would be very difficult to reliably distinguish between the eastern floater and the Newfoundland floater. In fact, these two species are thought to hybridize where their ranges overlap, making reliable identification virtually impossible. The zone of hybridization is primarily in eastern New Brunswick and Nova Scotia, although it may extend west into Maine. The Newfoundland floater is reported not to have the green color seen in the eastern floater, though many lakes and ponds in northern Maine have populations of eastern floaters with conspicuously yellow shells (**see page 76**) It also does not have the distinct thickening along the antero-ventral shell margin that occurs in the alewife floater.



Range: This species is found throughout Newfoundland and perhaps south into other Canadian Maritime provinces including northern Nova Scotia, New Brunswick, and eastern Quebec. It might exist in some lakes and streams in northern Maine, where it is thought to hybridize with the eastern floater. However, Hanlon and Smith (1999) report that shells of the eastern floater from northern Maine were previously misidentified as the Newfoundland floater and that the Newfoundland floater has yet to be documented in the state.

Habitat: The Newfoundland floater is found in a variety of aquatic habitats, including ponds, lakes, and streams. Like other closely related species, it can tolerate silt substrates, though it is also found in sand and gravel.

Reproductive Characteristics: Virtually nothing is known about the reproductive characteristics of this species. Since it is known to hybridize with the eastern floater, it probably has a similar reproductive period, and perhaps uses the same types of host fish.

Conservation: It is difficult to judge the conservation status of this species in Maine, since we have not yet been able to determine whether it exists in the state, or to what extent it is distinct from the eastern floater. If it does occur in Maine, it is probably relatively stable because it lives in northern regions that are less influenced by human activity.

Zebra Mussel – *Dreissena polymorpha* (Pallas, 1771)
Quagga Mussel – *Dreissena bugensis* Andrusov, 1897

Description: These are small mussels (< 1 inch) whose appearance is similar to that of Maine's marine mussels. Their most distinctive trait is the dark irregular stripes on the shell surface, giving them a "zebra-like" appearance. **Byssal threads** are located ventrally and are used for attachment.

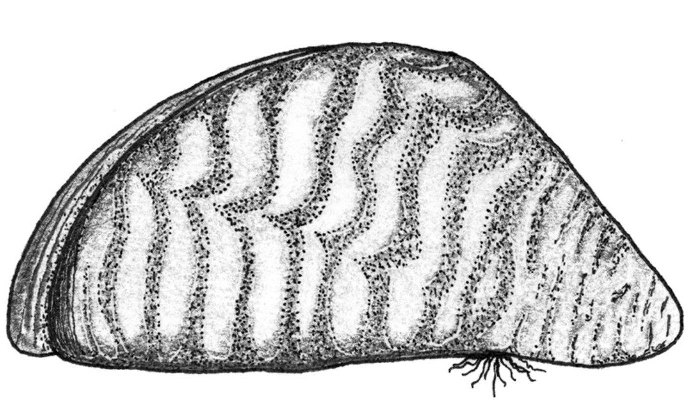
Confusing Species: Zebra mussels and quagga mussels cannot be confused with any other North American freshwater mussels.

Range: The native range of the zebra mussel and quagga mussel is the Caspian and Black Sea region of Eastern Europe. The zebra mussel was accidentally introduced into North America in the mid to late 1980s and has since spread throughout the Mississippi River Basin, Great Lakes Basin, lower St. Lawrence River, Hudson River, and numerous inland lakes. As of 2000, its range in New England included Lake Champlain in Vermont and East Twin Lake in northwestern Connecticut. The quagga mussel was discovered in the Erie Canal and Lake Ontario in 1991, and is primarily restricted to the eastern Great Lakes and the St. Lawrence River. Neither species have been found in Maine.

Habitat: Research shows that dreissenid mussels prefer large rivers and lakes with moderate to high alkalinity and calcium levels. There is considerable question about their ability to thrive in calcium-poor acidic waters of the northeast (Whittier et al. 1995). Both the zebra mussel and quagga mussel have some tolerance for salinity and may pose a threat to estuarine ecosystems such as the lower Hudson River. They attach to solid substrates — such as submerged rocks, woody debris, docks, boat hulls, water intake pipes, and native mussels — where they reach densities as high as 10,000 on a single mussel shell and 750,000 per square meter (Schloesser et al. 1996)!

Reproduction: Dreissenid mussels have different reproductive traits than native freshwater mussels. They do not require internal fertilization or a host fish. Sperm and eggs are released into the water column where fertilization takes place. The larvae, called veligers, are planktonic (drift freely with the current). After maturation the veligers settle onto a solid surface, attach with their byssal threads, and become sessile adults. Individual females produce 30,000 to 40,000 eggs per growing season.

Conservation: Since the discovery of zebra mussels in the Great Lakes in the late 1980s a great amount of research has been conducted to understand their biology, ecology, and potential effects on native organisms, ecosystems, and water-dependent industries. Very few freshwater organisms have ever elicited such an immediate and widespread "call to arms" among ecologists, engineers, industry leaders, and various outdoor recreation groups. Their effects range from colonizing and clogging intake pipes of nuclear power plants, altering the natural structure and function of aquatic ecosystems, and causing the extinction of native species.



Zebra mussels attached to a native mussel.

Glossary of Terms

Adductor Muscle: Large bundle of muscle fibers used to pull the two valves together. Freshwater mussels have two adductor muscles, located dorsally towards the anterior and posterior of the animal. Two large "scars" on the nacre indicate the attachment sites of these muscles.

Anadromous: Living in a marine environment but returning to freshwater to spawn.

Anterior: The front, or "head end" of an animal. The beak and foot of freshwater mussels are located at the anterior end.

Artificial Propagation: Bringing reproductively mature adults into a laboratory environment to ensure successful fertilization and create favorable conditions for embryonic development and juvenile survival. Also called captive breeding.

Beak: The prominent rounded or raised area along the dorsal margin of a shell valve that represents the embryonic shell. The shell grows in a concentric fashion around the beak, and all shell rays radiate from the beak.

Beak Sculpture: A pattern of wrinkles, ridges, or other markings other than color on the surface of the beak. Beak sculpture is sometimes an important taxonomic character, though it is often difficult to use because of shell erosion.

Benthic: Living in, or in close association with, the substrate of an aquatic environment.

Biodeposition: The release of ingested material back into the environment. This includes release of completely digested material (feces) and partially digested material (pseudofeces). Biodeposition refers only to release of particulate material. *See also:* **Excretion**

Biomass: The amount of living tissue mass for a population of animals.

Bradytictic: Long-term brooders; fertilization occurs in summer or fall and developing glochidia are retained in the marsupia until the following spring or summer.

Byssal Threads: A tuft of tough thread-like filaments that certain bivalved molluscs use to attach to solid objects.

Catadromous: Living in a freshwater environment but returning to a marine environment to spawn.

Compressed: Narrow, skinny, or laterally flattened.

Conglutinate: A cluster of several to thousands of individual glochidia, usually held within a mucous matrix. Release of glochidia in a conglutinate is thought to be an adaptive strategy used by freshwater mussels to ensure contact with a host fish. Conglutinates often resemble other organisms in shape and coloration.

Demibranch: One of the paired gills of a typical bivalve. Two demibranchs occur on either side of the body.

Dichotomous Key: A key used to identify organisms based on a series of paired choices between alternative character states.

Dioecious: Organisms with male and female individuals.

Dorsal: Located toward the upper or top surface. In mussels, dorsal refers to the margin where the beak and hinge are situated and from where shell growth originates.

Endemic: An organism whose native range is restricted to a particular location or region.

Eutrophication: The process by which an environment becomes richer in nutrients (especially nitrogen and phosphorus), either from natural or human sources.

Excretion: The release of dissolved inorganic nutrients from an organism, such as urea, uric acid, or ammonia.

Exhalent Aperture: An opening formed by the two mantle margins through which filtered water, waste, and gametes are expelled from the body of a mussel. The exhalent aperture is located dorsal to (above) the inhalent aperture.

Filter-Feeding: Removal of suspended material (nutrients, sediment, small organisms) from the water column using a system that involves some sort of filtering mechanism, such as gills in freshwater mussels.

Foot: A large muscular extension of the body, projecting ventrally and anteriorly. The foot is used for digging, locomotion, and feeding.

Glochidium (plural: Glochidia): The bivalved larva of a freshwater mussel.

Growth Annulus (plural: Annuli): A dark ring on the periostracum that indicates a period of little or no growth, especially during winter months. The number of growth annuli has been used to infer the age of a shell. Growth annuli can also be seen in shell cross-sections. Non-annual growth annuli are referred to as false annuli and are caused by environmental stressors.

Hermaphroditic: Capable of self-fertilization.

Hinge: Portion of the dorsal margin where the two valves articulate. This region includes the pseudocardinal and lateral teeth, and hinge ligament.

Inflated: Wide, fat, or laterally expanded.

Inhalent Aperture: An opening formed by the two mantle margins, though which water, food, and sperm are brought into the body. The inhalent aperture is located ventral to (below) the exhalent aperture.

Isostatic Rebound: The rise of land relative to the sea, following retreat of glaciers that caused the earth's crust to be compressed.

Labial Palps: A pair of structures located on either side of the mouth that sort edible from non-edible particles before delivering them to the mouth.

Lateral Teeth: Elongate hinge teeth that extend posteriorly away from the beak of each valve. These teeth interlock to create a more solid connection between the two valves. The presence and number of these teeth are important identification characteristics.

Ligament: A tough elastic-like material that connects the two valves at the hinge. The ligament acts in opposition to the adductor muscles – when adductor muscles are sliced or the animal dies, the ligament causes the two valves to gape.

Macrohabitat: Large-scale habitat variables, or variables that are strongly influenced by processes occurring at large scales, including stream size, stream gradient, hydrology, topography, land use, proximity to the ocean, water chemistry, and climate.

Macrophyte: A vascular plant, especially of aquatic environments. This does not include algae, mosses, or liverworts.

Mantle: The fleshy lining of the shell valves that encloses the body of the mussel. The mantle is responsible for secreting shell material, forms the exhalent and inhalent apertures, and also serves a sensory function.

Marsupium (plural: Marsupia): The pouch within the female demibranch (gill) that contains developing embryos.

Microhabitat: Small-scale habitat variables, including water depth, flow velocity, substrate type, patchiness of fine substrates, and presence of aquatic plants.

Midden: An accumulation of shells left by animals, such as muskrats, that consistently feed in the same location.

Nacre: The white or iridescent mother-of-pearl lining of a mussel shell. The color is variable among species and is an important identification characteristic.

Pallial Cavity: The space enclosed within the two mantle flaps, containing the mussel's body and gills. It is also called the mantle cavity.

Pallial Line: A line in the nacre along the ventral margin of the shell that indicates the attachment site of pallial line muscles that attach the mantle margin to the shell.

Periostracum: The thin, proteinaceous, and fibrous outer lining of a mussel shell. The color of the periostracum is highly variable among species and is an important identification characteristic.

Photoperiod: The relative length of daylight versus darkness.

Piscivore: An animal whose diet is comprised primarily of fish.

Posterior: The back, or "rear end" of an animal. In freshwater mussels, the exhalent and inhalent apertures are located toward the posterior end of the body.

Pseudocardinal Teeth: The thick, often stout teeth located toward the anterior end of the hinge. These are usually located below or slightly anterior to the beak. The presence, number, and size of pseudocardinal teeth are important identification characteristics.

Pseudofeces: Particulate material that is released before it is entirely digested.

Reintroduction Program: Reestablishing a population of animals where they were previously extirpated or where a population was greatly diminished because of environmental degradation or overharvest.

Relocation Program: Moving individuals out of an area prior to environmental degradation, such as habitat disturbance associated with bridge demolition.

Riparian Zone: The boundary between an aquatic and terrestrial system that contains a variety of uniquely-adapted wetland plants and animals. The riparian zone is an important source of organic matter for the aquatic environment and also influences temperature and light levels.

Tachytictic: Short-term brooders; fertilization usually occurs in the spring and glochidia are released later in the summer.

Turbidity: The amount of sediment and other material suspended in the water, which determines water clarity and visibility.

Umbo: *see* **Beak**

Valve: One of the opposing halves of a bivalved mollusk.

Ventral: Located toward the lower (bottom) surface. In mussels, ventral refers to the rounded margin opposite where the beak is situated. The foot is situated at the ventral margin.

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