

FRESHWATER MUSSEL ASSESSMENT

29 October 2007



Authors

Beth I. Swartz
Maine Department of Inland Fisheries and Wildlife
650 State Street
Bangor, Maine 04401

and

Ethan Nedeau
BIODRAWVERSITY
46 Pomeroy Lane
Amherst, MA 01002

MAINE DEPARTMENT OF INLAND FISHERIES AND WILDLIFE
WILDLIFE DIVISION
RESOURCE ASSESSMENT SECTION



TABLE OF CONTENTS

	Page
INTRODUCTION.....	5
NATURAL HISTORY.....	6
Systematics.....	6
General Description.....	6
General Distribution and Status.....	9
Life History.....	15
Life Cycle.....	15
Growth.....	19
Habitat.....	20
Role in Natural Ecosystems.....	23
SPECIES PROFILES.....	26
Eastern Pearlshell.....	26
Description.....	26
Distribution and Status.....	27
Habitat.....	28
Reproduction.....	28
Brook Floater.....	29
Description.....	29
Distribution and Status.....	29
Habitat.....	31
Reproduction.....	31
Triangle Floater.....	32
Description.....	32
Distribution and Status.....	32
Habitat.....	33
Reproduction.....	33
Creeper.....	34
Description.....	34
Distribution and Status.....	34
Habitat.....	35
Reproduction.....	35
Eastern Floater.....	36
Description.....	36
Distribution and Status.....	36
Habitat.....	37
Reproduction.....	37

TABLE OF CONTENTS (continued)

	Page
Alewife Floater	37
Description	37
Distribution and Status	38
Habitat	38
Reproduction	38
Eastern Elliptio	39
Description	39
Distribution and Status	39
Habitat	40
Reproduction	40
Tidewater Mucket	41
Description	41
Distribution and Status	41
Habitat	42
Reproduction	42
Yellow Lampmussel	43
Description	43
Distribution and Status	43
Habitat	45
Reproduction	45
Eastern Lampmussel	45
Description	45
Distribution and Status	46
Habitat	46
Reproduction	46
RESEARCH AND MANAGEMENT	47
Regulatory Authority	47
Maine Endangered Species Act	48
Natural Resource Protection Act	49
Water Classification Program	50
Mandatory Shoreland Zoning	51
Comprehensive Growth Management Act	52
Site Location of Development Act	53
Various acts concerning fishways	53
Clean Water Act	54
Past Goals and Objectives	55
Past Research and Management	55
Current Research and Management	66
Research and Management Needs	67

TABLE OF CONTENTS (continued)

	Page
HABITAT ASSESSMENT	72
Past Habitats	72
Current Habitats	73
Projected Habitats	74
Yellow Lampmussel.....	76
Tidewater Mucket.....	78
Brook Floater.....	79
POPULATION ASSESSMENT.....	81
Past Populations.....	81
Current Populations.....	81
Projected Populations.....	83
Yellow Lampmussel.....	83
Tidewater Mucket.....	86
Brook Floater.....	88
Limiting Factors and Threats	91
USE AND DEMAND ASSESSMENT	94
SUMMARY AND CONCLUSIONS	97
LITERATURE CITED	99
APPENDICES	
Appendix 1. Confirmed hosts for the freshwater mussels of Maine	110
Appendix 2. Occurrences of the Yellow Lampmussel in Maine	111
Appendix 3. Occurrences of the Tidewater Mucket in Maine.....	113
Appendix 4. Occurrences of the Brook Floater in Maine	115

LIST OF FIGURES

Figure 1. Shell morphology of a typical freshwater mussel	7
Figure 2. Gross anatomy of a typical freshwater mussel.....	8
Figure 3. Maine's native freshwater mussel species	10
Figure 4. Mantle lure of a female yellow lampmussel from Maine.....	18
Figure 5. Occurrences of the Yellow Lampmussel in Maine.....	85
Figure 6. Occurrences of the Tidewater Mucket in Maine	87
Figure 7. Occurrences of the Brook Floater in Maine	90

INTRODUCTION

Since 1968, the Maine Department of Inland Fisheries and Wildlife (MDIFW) has developed and refined wildlife species assessments to formulate management goals, objectives, and strategic plans. Assessments are based upon available information and the judgments of professional wildlife biologists responsible for individual species or groups of species. This document represents the first planning effort undertaken for Maine's ten species of freshwater mussels, four of which are currently recognized by some level of state listing status.

Assessments provide the background for species planning initiatives. A "Natural History" section reviews biological characteristics useful to understanding status. A "Research and Management" section outlines relevant rules and regulatory authority, recaps previous and ongoing research and management, and assesses information gaps and management needs. Past, current, and projected conditions are discussed individually for "Habitat", "Population", and "Use and Demand". Finally, the major points of an assessment are recounted in "Summary and Conclusions."

Prior to statewide surveys conducted by MDIFW in the 1990s, little was known about the distribution and status of Maine's freshwater mussels. Since then, knowledge of and conservation efforts for this faunal group have grown significantly. In 2000, MDIFW produced "The Freshwater Mussels of Maine" (Nedeau et al. 2000) -- a comprehensive book summarizing much of what we now know about the life history, distribution, status, conservation needs, and value of the State's freshwater mussel fauna. This assessment draws heavily on the information presented in the book, with updates from recent and ongoing research and management efforts by MDIFW and its partners.

NATURAL HISTORY

Systematics

Freshwater mussels belong to a large and diverse phylum of animals called the Mollusca, which is second only to the Arthropoda (insects, spiders, and crustaceans) in terms of global diversity. Within Mollusca, mussels are members of class Bivalvia (or Pelecypoda), commonly referred to as the bivalves. Also included in this group are the commercially important clams, oysters, and scallops. Most bivalves live in marine environments, though there are several families that are found almost entirely in freshwater. All freshwater mussels are in the order Unionoida and superfamily Unionacea. There are two families, Margaritiferidae and Unionidae, and nearly 300 species of freshwater mussels native to North America (Turgeon et al. 1988). Margaritiferidae is a small family with only five species found on this continent, one of which occurs in Maine. All other North American species belong to the family Unionidae. Eight genera and ten species are native to Maine (Nedeau et al. 2000).

General Description

External Morphology. Like all bivalves, mussels possess a pair of matched shells (valves) that protect the animal from the surrounding environment (Figure 1). Composed of calcium carbonate and protein, shell material is secreted by the animal as it grows. Freshwater mussel shells range in size from 1.5 to 10 inches long, though rarely exceed 6 inches in Maine. The outside of each valve is covered with a protein-rich material called periostracum that is relatively impermeable to water and protects the

underlying shell from erosion. The periostracum exhibits a broad range of colors and patterns among different species, and is one feature used in identification. Internally, the shell is lined with an iridescent pearly material called nacre, which provides an additional layer of protection.

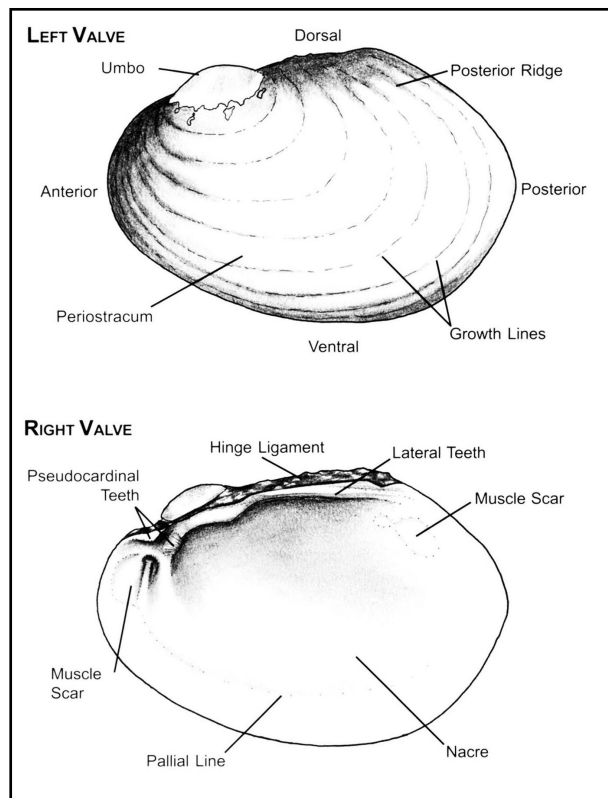


Figure 1. Shell morphology of a typical freshwater mussel (*drawing by E. Nedeau*).

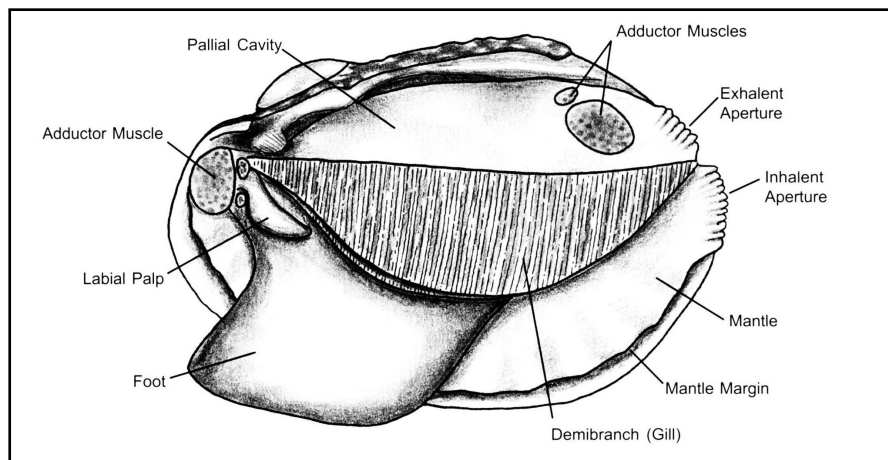
The two halves of a mussel shell are essentially mirror images of each other and are connected along the hinge by an elastic-like ligament. Two large, powerful adductor muscles located toward the anterior and posterior ends of the mussel are used to pull the valves together. The adductor muscles and hinge ligament act in opposition to each other -- when adductor muscles are relaxed, the ligament causes the shell to gape or open. The attachment site of these muscles can be seen on the shells as large muscle scars.

The beak, or umbo, is the swollen area along the dorsal slope of a mussel shell from where 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 -- pseudocardinals and laterals. Pseudocardinals are short heavy teeth located immediately below the umbo,

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 hinge teeth are highly variable among species. The most important characteristics used to identify freshwater mussels are shell shape, the nature of the periostracum and nacre, and hinge teeth morphology.

Internal Morphology. The body of a freshwater mussel (Figure 2) is enveloped within a flap-like sheet of tissue called the mantle, which lines the interior of the shell and secretes the shell material. The mantle is attached to the shell by the dorsal muscles and at the pallial line (Figure 1). 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.

Most major organs are situated within the mantle (or pallial) cavity. A pair of large gills (demibranchs) is located on each side of the body and extends across the entire pallial cavity. Gills serve three essential functions in the freshwater mussel: they



are sites of gas exchange, much like the gills of other aquatic animals; they are used to filter materials (water, food, and sperm) that enter

Figure 2. Gross anatomy of a typical freshwater mussel (internal organ anatomy not illustrated) (drawing by E. Nedeau).

through the inhalent aperture; and, in the female mussel, they contain specialized regions called marsupia that are designed to hold unfertilized eggs and incubate developing larvae.

Internally, mussels have a digestive system similar to that of other animals. Food consists primarily of detritus, bacteria, algae, and other microscopic organisms that are suspended in the water column. 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 excreted through the anal opening 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 used primarily for locomotion and also as a food-gathering organ in 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 extending and probing or digging with its foot, a freshwater mussel can pull itself deeper into the substrate, or move horizontally along the bottom (Lewis and Riebel 1984).

General Distribution and Status

Distribution. There are nearly 1000 species of freshwater mussels worldwide. They are found in lakes, rivers, and streams on all continents except Antarctica, including large islands such as New Zealand and the Japanese archipelago. North America supports the greatest diversity of freshwater mussels on the planet, with 297 species. Over half of these species 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 Valley) has a very low diversity of freshwater mussels, with only 12 species present.

Ten species of freshwater mussels have been documented in Maine (Figure 3). An eleventh species, the Newfoundland floater (*Pyganodon fragilis*), has been reported, but these records are believed to be misidentifications (Hanlon and Smith 1999). All of

<p>Eastern Pearlshell (<i>Margaritifera margaritifera</i>)</p> <p>Brook Floater (<i>Alasmidonta varicosa</i>)</p> <p>Triangle Floater (<i>Alasmidonta undulata</i>)</p> <p>Creeper (<i>Strophitus undulatus</i>)</p> <p>Eastern Floater (<i>Pyganodon cataracta</i>)</p> <p>Alewife Floater (<i>Anodonta implicata</i>)</p> <p>Eastern Elliptio (<i>Elliptio complanata</i>)</p> <p>Tidewater Mucket (<i>Leptodea ochracea</i>)</p> <p>Yellow Lampmussel (<i>Lampsilis cariosa</i>)</p> <p>Eastern Lampmussel (<i>Lampsilis r. radiata</i>)</p>

Maine's freshwater mussel species are part of the Northern Atlantic Slope fauna, which is a group of 17 species. 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.

Figure 3. Maine's native freshwater mussel species.

Some Northern Atlantic Slope species have a broad geographical

distribution, such as the creeper (*Strophitus undulatus*), which is found throughout the Mississippi River basin, and the eastern pearlshell (*Margaritifera margaritifera*), which is found throughout the Northern Hemisphere, including Europe. Seven of the Northern Atlantic Slope species are not found in Maine. Three of those species are known from adjacent states or provinces, but have never been documented despite extensive surveys: 1) the federally endangered dwarf wedgemussel (*Alasmidonta heterodon*), which is native to 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); 2) the eastern pondmussel (*Ligumia nasuta*), which is found in southeastern Massachusetts and New Hampshire, but appears to have never dispersed to the coastal plain ponds of southern Maine; and 3) the Newfoundland floater, which has a northerly distribution, occupying rivers and lakes in Newfoundland, northern Quebec, and perhaps parts of New Brunswick, but for which taxonomy and identification often is questioned (Kat 1983, Hanlon and Smith 1999) and no Maine specimens are confirmed.

In general, rivers and streams support a higher diversity of freshwater mussels than lakes and ponds. The greatest diversity of freshwater mussels in Maine is found in the Kennebec and Penobscot River drainages of midcoast and central Maine. Rivers of southern Maine have fewer species than rivers of central Maine. 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 also may be a reflection of the region's recent (400-year) history of land and water use by humans.

Rivers east of the Penobscot drainage contain six to seven mussel species, although neighboring tributaries within 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 River drainage from several Downeast rivers, yet their mussel faunas are distinctly different. The lakes and rivers of northwestern and northern Maine contain the State's lowest diversity of mussels, with only two species found consistently and a maximum of five found at a single location. The eastern lampmussel (*Lampsilis r. radiata*), yellow lampmussel (*Lampsilis cariosa*), tidewater mucket (*Leptodea ochracea*), brook floater (*Alasmidonta varicosa*), creeper and alewife floater (*Anodonta implicata*)

are all absent from the major drainages of the north (St. John, Aroostook, Fish and Allagash Rivers). This low diversity in northern Maine is likely a result of New England's glacial history and the natural history of freshwater mussels -- 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).

Within watersheds, waterfalls can act as natural constraints on fish dispersal and may explain the distribution patterns of mussels within a river system. For example, the six species absent from northern Maine are found in the lower St. John River in New Brunswick (Clarke 1981b, Dwayne Sabine, New Brunswick Department of Natural Resources, *personal communication*, April 10, 2007), where Grand Falls may have prevented fish and mussel dispersal into upper reaches of the watershed in Maine. In the North Branch, South Branch, upper East Branch, and upper West Branch of the Penobscot River, mussel diversity is notably less than in the mainstem below a series of waterfalls blocking upstream movement of some fish species. The Mattawamkeag and Passadumkeag Rivers, two large tributaries of the Penobscot, lack natural falls and have a greater diversity of mussels than any of the upper branches of the Penobscot.

Status. Freshwater mussels are one of the most imperiled groups of animals in North America (Master et al., 1998). Of the nearly 300 species found in the United States, 70 (24%) are currently listed as endangered or threatened under the federal Endangered Species Act, 17 (6%) are considered candidates for federal listing (USFWS Threatened and Endangered Species System 2007), and 35 (12%) are believed to be extinct (Bogan 1996). At the state level, approximately 75% of the country's mussel

fauna is listed as endangered, threatened, special concern, or extirpated in some part of their range (Williams et al. 1993). These dramatic declines have largely been caused by habitat degradation and loss during a century and more of pollution, dams, stream channelization, dredging, and sedimentation of our once clean, free-flowing rivers and streams. Overharvest and poaching of shells for sale to the Orient's pearl culture industry, and the recent invasion of a prolific competitor, the zebra mussel (*Dreissena polymorpha*), jeopardize many native North American mussel populations (Luoma 1997, Neves 1993).

In general, Maine's freshwater mussel fauna has fared relatively better than that of many states: no species are known to have been extirpated, the State's freshwater habitats are reasonably clean or have improved in water quality, and the zebra mussel has not yet found its way into Maine's waterways. While few records exist to document the historical occurrence and distribution of Maine's mussel species, information on their current status is available from a statewide atlas project conducted by MDIFW during the 1990s (see Past Research and Management). During these surveys, a variety of qualitative data (including species presence/absence, relative abundance, evidence of reproduction or mortality, habitat quantity and quality, and potential threats) were collected to aid in status assessment. As a result, two species -- the yellow lampmussel and tidewater mucket -- were listed as "threatened" under the Maine Endangered Species Act in 1997. Both share a restricted distribution in Maine, being found in only the St. George, Penobscot, and lower Kennebec River watersheds. Within these drainages, their distributions are further limited -- possibly a result of past fragmentation by dams and other habitat alterations. While some apparently large and healthy

populations of both species exist, many observations have consisted of only a few live individuals or spent valves.

In 2007, the brook floater was added to the State's threatened species list. Although more widely distributed than the two other listed mussels, the brook floater also is restricted in distribution and may have been extirpated from at least two historical locations. A highly isolated population in the Pleasant River (Cumberland Co.) is the only known occurrence in southern Maine, and the species is only sparsely distributed in central and midcoast regions -- suggesting that additional populations may have been lost. Nearly 70% of all brook floater observations in Maine are based on ≤ 10 live animals or relict shells only, and large numbers or evidence of recruitment have rarely been observed.

One additional species, the creeper, is listed as a species of special concern in Maine. This mussel is fairly well-distributed but rarely found in abundance. Typically, fewer than ten individuals are observed at a single location. Until listing criteria were revised in 2006, the triangle floater (*Alasmidonta undulata*) also was considered a species of special concern because of severe declines in other parts of its range. In Maine, however, this mussel is widely distributed and occasionally found in abundance. Its original listing primarily was to recognize conservation concern for this species elsewhere, the significant role Maine may play as a refugium if its populations continue rangewide decline, and the need for long-term monitoring to detect similar declines in Maine. In 2007, the triangle floater was recommended for removal from the State's special concern list when "declines elsewhere" was eliminated as a criteria for listing status.

The remaining five mussel species native to Maine are considered currently to be secure. The eastern lampmussel and alewife floater have limited distributions but often are abundant. The alewife floater is expected to expand its distribution as more dams are removed from Maine rivers and passage for anadromous fish hosts is increased (see Life History). The eastern pearlshell often is not abundant but occurs in nearly every watershed in the State. This species could experience declines if global warming alters Maine's stream temperatures and salmonid fish communities. The eastern elliptio (*Elliptio complanata*) and eastern floater (*Pyganodon cataracta*) are widespread and abundant and are Maine's most common mussel species. Both have broad environmental tolerances and inhabit a variety of habitats. More specific information about the distribution and status of Maine's freshwater mussels can be found in the Species Profiles beginning on page 26.

Life History

Life Cycle. Freshwater mussels usually are dioecious, meaning there are both male and female individuals. Males release sperm into the water through their exhalent aperture, and females filter sperm out of the water with their gills. Eggs are fertilized in the specialized marsupia of the female gills. The prospect of successful fertilization can be quite low, especially if population density is very low. Freshwater mussels can increase the chance of successful fertilization by moving closer together during the spawning season (Amyot and Downing 1998). Some, and perhaps many, species can become hermaphrodites capable of self-fertilization under conditions of low population

density, low percentage of males present, or other factors favoring hermaphroditism (van der Schalie 1970, Kat 1984, Bauer 1987a, Downing et al. 1993, Neves 1997).

After fertilization, embryos develop into larvae called glochidia and are held within the female's gills for various amounts of time depending on the species of mussel. In some species, fertilization occurs in the summer or early fall and the glochidia are retained 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 bradytictic and two are tachytictic (see Species Profiles).

Glochidia of nearly all freshwater mussels require a vertebrate host to complete larval development and reach the juvenile stage. The majority of species use fish as hosts (Kat 1984), although some also can use amphibians (Watters 1997, Watters and O'Dee 1998). When environmental conditions are right, females release glochidia into the water column through their exhalent aperture. Some of the factors that are thought to govern the timing of glochidial release include the presence of migratory or nesting fish (Davenport and Warmouth 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 only a short period of time on their own, so they must quickly find and attach to a suitable host. Many freshwater mussels are host-specific, requiring one or more particular fish species to complete their development (Haag et al. 1995) (see Appendix 1 for a list of hosts for Maine mussel species). The chance of a

glochidium successfully finding and attaching to a suitable host is low. Freshwater mussels compensate for this uncertainty by producing very large numbers of glochidia -- ranging from 200,000 to 17,000,000 per reproductive season (Kat 1984, Bauer 1994). They also display a remarkable array of adaptations to ensure that glochidia come in contact with a potential host (Kat 1984). Many species release glochidia in a matrix of mucous called a conglutinate that remains intact in the water column. These conglutinates often resemble food items of fish in both color and shape (Kat 1984, Hartfield and Hartfield 1996) and likely have a greater chance of encountering a host than randomly dispersed glochidia. 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 mucous. The 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 other lampsilines have brightly pigmented mantle margins that also resemble minnows, complete with eyespots (Figure 4). The female pulses 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 glochidia of some species possess a sensory hair that is thought to aid in the detection of or attachment to a host (Kat 1984). Some have hooks on the valve margins that allow them to penetrate scales or fins (Kat 1984, Pekkarinen 1996), whereas others have rounded margins and are more specialized for attaching to gill filaments (Kat 1984). Soon after attachment, the glochidium becomes encysted in the host tissue and receives nutrients from the host as it develops (Arey 1932a, Arey 1932b, Kat 1984).



Figure 4. Mantle lure, resembling a small minnow, of a female yellow lampmussel from Maine (*photo by Philip Wick*).

This parasitic stage lasts from six to 160 days depending on the species and environmental conditions, especially water temperature (McMahon 1991). Deleterious effects on the host fish are rarely observed, mainly because infection rates are typically 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 existence. For species with strict habitat requirements, the location where a juvenile drops is an important factor that determines its survival. Little is known, however, about the habitat ecology or post-settlement movement of juvenile mussels (Neves and Widlak 1987). As adult mussels are virtually sedentary, the parasitic phase

is the only time that significant dispersal can take place. Colonization of new habitats, restocking of depleted populations, and exchange of genetic material between populations are largely dependent on the movement of infected host fish.

Growth. Freshwater mussels undergo the greatest shell growth in their first four to six years of life (Coker et al. 1921, Payne and Miller 1989, McMahon 1991). Juvenile mussels can be crushed by shifting sediments or eaten by predators, therefore it is important that the shell grow quickly to provide a protective barrier between the animal and its environment. Because juveniles allocate most of their energy to shell growth, comparatively little is allocated to soft-tissue growth, and especially to reproductive development. The average age at sexual maturity in freshwater mussels is generally greater than six years (McMahon 1991).

The growth rate of mussels depends on a number of factors, including 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. Most mussels burrow into the sediment in winter and enter a dormant period (Balfour and Smock 1995, Amyot and Downing 1997). At the end of each growth period, they produce a growth ring (annulus) that is seen externally as a dark band of periostracum along the shell margin. Since these rings are laid down annually, they can be used to estimate age of some species, particularly in younger specimens. However, determining age from external growth rings often is unreliable due to shell erosion, obscurity of bands on dark-colored valves, difficulty in distinguishing annual growth rings from occasional stress-produced bands, and the inability to count closely deposited bands near the shell margin of older individuals

(Ansell 1968, Coon et al. 1977, Lutz and Rhoades 1980). Neves and Moyer (1988) found the counting of internal growth annuli -- viewed upon thin-sectioning of shell material -- to be a much more reliable method of aging freshwater mussels.

The spacing of shell annuli also is used to infer growth rates and determine the productivity of mussel populations (Negus 1966, Strayer et al. 1981, Muller and Patzner 1996). Age structure, size structure, and growth rates of freshwater mussel populations are used to determine if a population is declining, increasing, or remaining stable. 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, growth rates also are used to assess the long-term health of aquatic ecosystems (McCuaig and Green 1983, Metcalfe-Smith and Green 1992).

Once they reach maturity, 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 among the longest living of invertebrates, with an average life span of 73 years being reported for some populations in Germany (Bauer 1987a) and a maximum life span that may reach up to 200 years (Mutvei et al. 2001). One individual recently collected from Sunkhaze Stream (Penobscot County) was documented to be over 120 years old (Philip Wick, MDIFW, *personal communication*).

Habitat. Freshwater mussels are found in a variety of permanent aquatic habitats, including both flowing and standing water. They reach their greatest diversity in flowing waters, where a variety of habitat types and conditions are offered along the length of a stream. However, they rarely are found in high-gradient streams because of

the extremes in hydrology (especially spring floods and late summer dry periods) and geology (extensive bedrock substrate). They do not typically occur in swamps, marshes, bogs, intermittent streams, or ponds smaller than a few acres in size, unless the pond is an impounded section of a stream or has been stocked by humans.

The microhabitat preferences of freshwater mussels are difficult to generalize. Some species occupy a variety of habitats, whereas others are much more specialized. Species living in lakes and ponds (e.g., eastern floater, eastern elliptio and eastern lampmussel in Maine) usually do not show a strong habitat preference. In general, freshwater mussels are typically found in sand, gravel, and cobble substrates in shallow waters (< 30 feet) and they 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, can tolerate deep silt and mud. Species living in streams and rivers (e.g., eastern pearlshell and brook floater in Maine) often have more specialized microhabitat requirements. Many cannot tolerate standing water or even small amounts of silt.

The most important microhabitat variables for riverine mussels are depth, current velocity, 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, and 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 or more per month to seek out suitable habitat conditions (Johnson 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 an important role and includes variables such as soil types, drainage patterns, and topography. Physical geography and climate strongly influence water chemistry and flow patterns in a watershed or region. These exert considerable influence on the distribution patterns of mussels (Strayer 1983, 1993, Di Maio and Corkum 1995). Habitat connection 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. This species often will be found in small coolwater tributaries of large rivers (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 also will contain a diverse mussel assemblage. 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 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).

Role in Natural Ecosystems

Freshwater mussels play an important role in aquatic food webs, nutrient cycling, water quality, and in the structure of the benthic environment (Strayer 1994, Strayer et al. 1999). Whereas an individual mussel can filter only a tiny amount of water compared to the total volume of a lake or stream, the filter-feeding activity of an entire mussel community removes large quantities of suspended material from the water column -- including detritus, bacteria, algae, and other microscopic organisms -- and may reduce turbidity (Strayer et al. 1999). Most of these nutrients are quickly released back to the aquatic ecosystem by biodeposition and excretion.

Because freshwater mussels often make up the largest proportion of the total biomass of aquatic animals in a lake or river, they can have a significant influence on nutrient cycling in aquatic systems by converting food resources into forms readily assimilated by other plants and animals. Negus (1966) reported that in the Thames River (England), freshwater mussels (excluding shells) comprised more than 90% of the biomass of bottom fauna, and was twice that 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 carbon. They have the capacity to retain energy and nutrients for years or even decades, whereas the turnover 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 substrate, they “stir up” the sediment and enhance the exchange of nutrients and important elements such as oxygen between the water column and substratum (McCall et al. 1979, Nalepa et al. 1991). They also affect other qualities of the substrate, including retention of organic material, substrate heterogeneity, and sediment porosity (McCall et al. 1979). Freshwater mussels can actually promote the diversity and abundance of other aquatic organisms by improving local conditions (Sephton et al. 1980).

Freshwater mussels also provide a colonization surface for other aquatic 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 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. One family of water mites is named the Unionicolidae in reference to its close relationship 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 diversity of invertebrate and vertebrate predators (Fuller 1974). Flatworms, leeches, and crayfish are able to eat small juveniles. Some species of fish, including carp, sturgeon, shad, freshwater drum, catfishes, sunfishes, and suckers, prey on freshwater mussels (McMahon 1991) -- although most fish cannot eat mussels larger than a half-inch in length. Mammalian predators include otters, mink, muskrats, raccoons, and skunks (Neves and Odom 1989, Jokela and Mutikainen 1995). Muskrats and otter are effective predators of freshwater mussels, often leaving hundreds of shells in piles (middens) along the shoreline.

Like many aquatic organisms, freshwater mussels are sensitive to contaminants and changes in their environment -- a vulnerability compounded by specific habitat and fish host requirements, an inability to leave their surroundings, and a long lifespan. Consequently, they are valuable indicators of water quality and ecosystem health.

SPECIES PROFILES

The following species accounts are excerpts from *The Freshwater Mussels of Maine* by Nedeau et al. (2000). This publication should be referred to for more specific information, including identification diagrams, range maps and locations of known occurrences. Appendix 1 lists confirmed and suspected host species.

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”. The valves are usually laterally compressed, with low umbos. The shell is smooth, brown to golden-brown in juveniles and nearly black in adults. Rays are rarely present. The periostracum is thick and durable, and tends to not show much erosion, even in older individuals. Pseudocardinal teeth are well developed -- the left valve has two and the right valve has one. Lateral teeth are absent. The nacre is usually white, with distinctive “pits” in the central region -- each with a faint “tail” pointing toward the beak cavity, 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.

Distribution and Status. 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 includes Scandinavia and northern Europe. It is North America's only native mussel whose range extends beyond the continent.

This species is widely distributed throughout nearly every watershed in Maine, though it is not common in northern, western, and extreme southern regions of the State. In many streams where it has been documented, only a few old individuals were found. Evidence of recent recruitment often is not observed, compared to what is seen for other mussel species during visual searches. The loss and degradation of clean riverine habitat along the Atlantic coast likely has affected this species. Several authors have provided evidence that the eastern pearlshell is intolerant of eutrophication (Bauer 1988, Buddensiek 1995); thus, landscape disturbance such as intensive agriculture and urbanization may have reduced its distribution or abundance. Potential effects of global warming on stream thermal regimes and salmonid populations in the Northeast could also negatively affect this freshwater mussel.

Although currently ranked G4 (apparently secure) by NatureServe (2007), the eastern pearlshell has experienced severe declines across northern and central Europe and in some parts of its North American range. The species currently is listed as endangered under the International Union for the Conservation of Nature (IUCN) Red List Category (IUCN 2006) and as Special Concern by the American Fisheries Society (Williams et al. 1993). It is state-listed as endangered in Rhode Island, threatened in Vermont and special concern in Connecticut.

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

Reproduction. This species has the most primitive reproductive characteristics of any Maine freshwater mussel. It has the highest fecundity (> 17 million glochidia produced annually) reported for any unionacean and the smallest glochidia (Bauer 1987a, 1994). It can also become hermaphroditic when population densities are very low. Bauer (1987a) reports a mean age at sexual maturity of 20 years. Individuals are known to live for up to 200 years (Mutvei et al. 2001), making it one of the longest-living invertebrate species ever documented. Native host fish in Maine include the brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) (Smith 1976; Bauer 1987b; Cunjak and McGladdery 1991). The introduced brown trout (*Salmo trutta*) and rainbow trout (*Salmo gairdnerii*) also may serve as hosts (Karna and Millemann 1978, Young et al. 1987). 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.

Brook Floater *Alasmidonta varicosa* (Lamarck, 1819)

Description. This is a small to medium-sized (usually ≤ 3 inches) mussel, and in profile often has a characteristic “Roman nose” shape. The ventral margin usually is flattened or indented, so that if the bottom of the mussel were placed on a flat surface the shell would not rock forward. The valves are moderately inflated, giving the mussel a swollen appearance in cross section. The periostracum is yellowish-green in young animals to brownish-black in mature specimens and usually has broad, dark rays that extend from the umbo. A diagnostic feature for this species is a series of ridges and wrinkles along the dorso-posterior slope, perpendicular to the growth lines. Pseudocardinal teeth are present but poorly developed -- there is just a small knob-like tooth on each valve. 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.

Distribution and Status. The brook floater is found in streams and rivers of the Atlantic coastal region, from South Carolina to Nova Scotia. 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, its current distribution is largely restricted to the Penobscot River watershed and several Downeast river systems, with scattered populations also found in the middle Kennebec and a few, small midcoast drainages. An isolated population in the Pleasant River (Cumberland Co.) is the only known

occurrence in southern Maine. This species may have been extirpated in at least two rivers (Dennys River in Washington County, Presumpscot River in Cumberland County), where efforts to relocate previously known or expected populations have been unsuccessful. Its absence from most watersheds in southern, midcoast, and central portions of the State suggests the brook floater may have experienced additional extirpations in Maine.

In other parts of its Atlantic Slope range, significant declines and extirpations are well documented for the brook floater. Because this species requires free-flowing rivers and streams with excellent water quality, and is sensitive to habitat degradation and changes in its environment, it has been severely affected by dams and other forms of stream alteration, and by water quality degradation. Where it is found, the population often consists of a small number of aging individuals, with little evidence of recruitment. In Maine, a similar pattern has been observed with nearly 70% of all observations based on ≤ 10 live animals or relict shells only. Significant populations or young individuals have rarely been observed during visual searches. However, surveys have detected what appear to be relatively large, healthy populations on several rivers (e.g., East Branch Pleasant River, Passadumkeag River, St. George River). Consequently, Maine likely will figure prominently in this species' rangewide conservation, having more documented extant populations than the remainder of the Northeast combined.

The brook floater is listed as a threatened species in Maine, and as endangered or threatened in nearly every other state where it is found, including all northeastern states. It is believed to be extirpated from Rhode Island and Delaware. This mussel was formerly listed as a Category 2 species by the U.S. Fish and Wildlife Service, and is

currently being considered for a status review. It is ranked G3 (vulnerable) by NatureServe (2007) and listed as threatened by the American Fisheries Society (Williams et al. 1993).

Habitat. The brook floater inhabits flowing-water habitats, from small streams to large rivers. It does not inhabit high-gradient streams with very fast water and coarse substrate (cobble and boulders), nor is it usually found in slow water. Strayer and Ralley (1993) did 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. It frequently is 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). In Maine, the brook floater often is encountered in association with rooted aquatic vegetation.

Reproduction. 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. Longnose dace (*Rhinichthys cataractae*), blacknose dace (*Rhinichthys atratulus*), golden shiners (*Notemigonus chrysoleucas*), pumpkinseed sunfish (*Lepomis gibbosus*), slimy sculpins (*Cottus cognatus*), and yellow perch (*Perca flavescens*) serve as potential hosts for this species under laboratory conditions (Wicklowsky and Richards 1995, Schulz and Marbain 1998, Barry Wicklowsky, St. Anselm College, *personal communication*).

Triangle Floater *Alasmidonta undulata* (Say, 1817)



Description. This is a small to medium-sized (usually ≤ 3 inches) mussel with a somewhat squat, triangular appearance in profile. The ventral margin is rounded, so that it rocks evenly when placed on a flat surface. The umbos are somewhat prominent and raised above the hinge line. The periostracum is smooth, and may vary in color from yellowish-green to nearly black. The periostracum also has prominent colored rays extending from the umbos, though they often are obscured in older, darker individuals. Pseudocardinal teeth are well developed and buttressed by a heavy ridge. 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. The foot is usually white, but infrequently is cantaloupe-colored, similar to that of the brook floater.

Distribution and Status. The triangle floater is more widely distributed than other New England *Alasmidonta*. 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, whereas Johnson (1970) indicated the Cooper-Santee River system in North Carolina as the southern limit for this species. It is found in most Atlantic coastal drainages northward to Nova Scotia, and also westward into tributaries of the lower St. Lawrence, such as the Ottawa River. It is found in nearly every watershed in Maine, although sparsely distributed in northern and western regions.

The triangle floater may be experiencing declines in southern parts of its range, where its preferred habitat (streams and small rivers) may be particularly threatened by habitat destruction and pollution. In Maine, it is widespread but rarely abundant, although it probably is more abundant than in other states to the south. Therefore, habitats in Maine may be a particularly important refugium for this species if its populations continue to decline in other parts of its range. The triangle floater is listed as endangered in Maryland, threatened in New Jersey, and special concern in Massachusetts. It is ranked G4 by NatureServe (2007) and listed as special concern by the American Fisheries Society (Williams et al. 1993).

Habitat. The triangle floater most often is found in streams and rivers, but also occurs in lakes and ponds, where it is never very abundant. It does not exhibit a particularly strong substrate preference, but is frequently encountered in sand and gravel.

Reproduction. The triangle floater is a long-term brooder, with fertilization taking place in summer and release of glochidia occurring the following spring. Confirmed hosts include the common shiner (*Luxilus cornutus*), blacknose dace, longnose dace, white sucker (*Catostomus commersoni*), pumpkinseed sunfish, fallfish (*Semotilus corporalis*), largemouth bass (*Micropterus salmoides*), slimy sculpin, and several other fish species not found in New England (Watters et al. 1999; Barry Wicklow, St. Anselm College, *personal communication*). Recent studies at the University of Maine also identified the white perch (*Morone americana*) as a potential host (Kneeland 2006).

Creeper *Strophitus undulatus* (Say 1817)

Description. This is a small to medium-sized (usually < 3 inches) mussel. The valves are laterally compressed, and the umbos are not prominent and barely raised above the hinge line. The shell is thin, fragile, and somewhat rough due to prominent growth lines. The beak sculpture is usually coarse and prominent, 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. Lateral teeth are absent. The nacre is usually white or bluish-white, and is conspicuously dull yellow or greenish toward the beak cavity.

Distribution and Status. The creeper is one of the most widely distributed mussel 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. In Maine, it is found in most major watersheds, but is sparsely distributed. The creeper is conspicuously absent from the Downeast rivers, and from northern and southernmost parts of the State.

Although this species is fairly well-distributed in Maine, it is rarely found in abundance. In statewide surveys, usually fewer than ten individuals have been observed at a single location, and it is recorded as “fairly common” at only three sites.

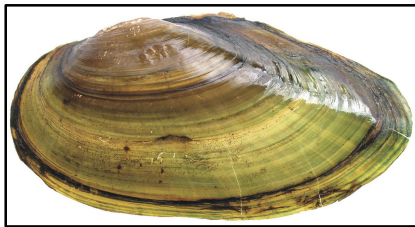
Concern for the long-term viability of such potentially small populations, as well as threats to habitat quality, resulted in the creeper being listed as special concern in Maine. Because this species prefers clean, flowing water, it may have been negatively affected by stream alteration and water quality degradation in some parts of its range. The only other northeastern states to list the creeper are Massachusetts, Rhode Island, and New Jersey, where it also is listed as special concern. It is ranked G5 (secure) by NatureServe (2007) and currently stable by the American Fisheries Society (Williams et al. 1993).

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

Reproduction. The creeper is a long-term brooder, with eggs being fertilized in the summer and glochidia released the following spring. Numerous fish hosts have been identified, including the largemouth bass, creek chub (*Semotilus atromaculatus*), fallfish, fathead minnow (*Pimephales promelas*), golden shiner, common shiner, slimy sculpin, bluegill (*Lepomis macrochirus*), longnose dace, blacknose dace, yellow perch, and Atlantic sturgeon (*Acipenser oxyrhyncus*) (Wicklow and Beisheim 1998; Watters et al. 1999; van Snik Gray et al. 1999, 2002). Recently, the Atlantic salmon also was found to be a suitable host (Barry Wicklow, St. Anselm College, *personal communication*). The red-spotted newt (*Notophthalmus viridescens*) (van Snik Gray et

al. 1999, 2002) and larvae (but not adults) of the northern two-lined salamander (*Eurycea bislineata*) (Wicklow and Beisheim 1998) also can serve as glochidial hosts. Glochidia of the creeper may transform into juveniles without a host (Lefevre and Curtis 1911), although there are no recent studies to support these findings.

Eastern Floater *Pyganodon cataracta* (Say, 1817)



Description. This is a medium-sized to large (usually < 6.5 inches) mussel with a fragile shell. The shape is usually elongate and slightly rounded, and the valves are laterally inflated. The hinge ligament is either straight or has a slight upward curve, and the beaks are slightly inflated and project above the hinge line. The beak sculpture consists of a series of double-looped concentric bands. The shells are uniformly thin, and the application of slight pressure on the dorsal and ventral surfaces will cause the valves to spread apart. Hinge teeth are entirely absent. 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.

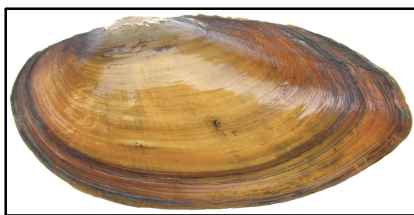
Distribution and Status. The eastern floater is found in Atlantic coastal drainages from Georgia to Nova Scotia, though it is less common in the southern parts of its range. It also is found in the lower St. Lawrence River drainage, and its range extends westward to the Great Lakes. This species has a rather broad environmental tolerance and low host specificity, and thus is widespread and common throughout much of its range. In Maine, it is the second most common species, occurring in every

major watershed. It is ranked G5 by NatureServe (2007) and listed as currently stable by the American Fisheries Society (Williams et al. 1993).

Habitat. The eastern floater is found in a variety of habitats, including small streams, rivers, ponds, and lakes. It usually is confined to slow-moving portions of riverine environments in sandy or muddy substrates. It is one of the few species that can tolerate deep silt substrates found in the deeper water of most lakes and ponds.

Reproduction. The eastern floater is a long-term brooder. Eggs are fertilized in August, and glochidia are released the following spring. Given its occurrence in a variety of habitat types, it probably uses a variety of host fish. Many other anodontines, including the genera *Anodonta* and *Pyganodon*, are known to be host generalists. The common carp (*Cyprinus carpio*), bluegill, pumpkinseed sunfish, yellow perch, threespine stickleback (*Gasterosteus aculeatus*), and white sucker are among the suspected hosts (Hoggarth 1992, Watters 1994, van Snik 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.

Alewife Floater *Anodonta implicata* (Say, 1829)



Description. This is a medium-sized to large (usually < 6.5 inches) mussel. The shell usually is much longer than it is wide, and is somewhat laterally inflated in cross section. The hinge ligament is long and straight, and the umbos are usually prominent and raised above the hinge line. The beak sculpture consists of a series of double-looped concentric bands. The shell is relatively thin, but each valve has a pronounced thickening along the antero-ventral margin that is

evident only internally. Hinge teeth are entirely absent. 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, and young specimens sometimes have shell rays. The nacre is pale copper, pinkish, or white.

Distribution and Status. The alewife floater is found along Atlantic coastal drainages from the Potomac River system in Maryland to Nova Scotia. In Maine, the alewife floater is fairly widespread and common in waterbodies throughout much of the coastal region. It is conspicuously absent, however, from Maine's southern coast where it was likely extirpated from rivers that lost their alewife runs because of past dam construction. Historically, this mussel probably was distributed as far inland as its anadromous fish hosts once traveled. Its present upstream distribution likely is reduced by blockages to fish passage. Damariscotta Lake in Lincoln County has an exceptional population of alewife floaters, largely because it supports one of the best alewife (*Alosa pseudoharengus*) runs in the State. Fish passage facilities have been shown to facilitate population expansion by enhancing the passage of anadromous hosts (Smith 1985).

The alewife floater is ranked G5 by NatureServe (2007) and listed as currently stable by the American Fisheries Society (Williams et al. 1993).

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

Reproduction. The alewife floater is a long-term brooder. Eggs are fertilized in August, and glochidia are released the following spring. The alewife is a confirmed host

(Davenport and Warmouth 1965). Other suspected host fish include the white sucker, threespine stickleback, white perch, and pumpkinseed sunfish (Davenport and Warmouth 1965; Wiles 1975a). Kneeland (2006) also identified blueback herring (*Alosa aestivalis*) and striped bass (*Morone saxatilis*) as probable hosts.

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, but the most typical shell shape is rectangular. The valves usually are laterally compressed, and the umbos are not very prominent. The periostracum usually is tan or brownish in younger individuals to dark brown or black in adults, and there sometimes are rays on the periostracum. Pseudocardinal and lateral teeth are well developed -- the left valve has two of each and the right valve has one of each. The nacre is purplish or rose-colored in freshly killed specimens and chalky white in older shells. The mantle margin is gray, white, or reddish, without any distinct patterns or modifications, and the foot is white.

Distribution and Status. The eastern elliptio occurs along the Atlantic coast from Nova Scotia to Florida. It also is found in the St. Lawrence drainage, the southern James Bay drainage, and some of the Great Lakes (Lake Superior, upper Lake Huron, and Lake Ontario). In Maine, it is found in virtually every water body capable of supporting mussels and often is very abundant. The eastern elliptio is one of only 75 or so mussel species in North America whose populations are currently stable or even

increasing. It is ranked G5 by NatureServe (2007) and listed as currently stable by the American Fisheries Society (Williams et al. 1993).

Habitat. The eastern elliptio is found in a variety of habitats, including small streams, large rivers, freshwater tidal waters (such as the lower Kennebec River), 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 deep semi-liquid silt and the rocky bottoms of small high-gradient 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. Hosts include the yellow perch, banded killifish (*Fundulus diaphanus*), largemouth bass, bluegill and pumpkinseed (Young 1911; Matteson 1948; Wiles 1975b; Watters 1994; Watters et al. 2005). Recent studies at the University of Maine identified the white perch, smallmouth bass (*Micropterus dolomieu*), redbreast sunfish (*Lepomis auritus*), alewife, threespine stickleback, brook trout, black crappie (*Pomoxis nigromaculatus*), and white sucker as potential hosts (Kneeland 2006). Given the abundance and widespread distribution of the eastern elliptio in eastern North America, the species probably uses a variety of fish hosts rangewide.

Tidewater Mucket *Leptodea ochracea* (Say, 1817)



Description. This is a medium-sized (usually < 3 inches) mussel, somewhat resembling a marine quahog. The shell is rounded or oval in outline, and the valves are laterally inflated. The umbos and ligament are usually prominent and raised above the hinge line.

The valves are strong but uniformly thin. Hinge teeth are thin and delicate -- the left valve has two pseudocardinal and two lateral teeth, and the right valve has two pseudocardinal teeth and one lateral tooth. Pseudocardinal teeth are thin, elongate, and located well anterior of the beak. 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. Dark interannular lines also may be evident on clean shells. The nacre usually is pinkish or salmon colored and translucent. The mantle margin usually is gray or yellowish-gray and not heavily pigmented. Sexually mature females appear slightly more rounded at the posterior end of the animal.

Distribution and Status. The tidewater mucket is found in Atlantic coastal drainages from Georgia to Nova Scotia. In Maine, it is known only from the St. George, Penobscot, and lower Kennebec River drainages, including Merrymeeting Bay. Its distribution is similar to that of the yellow lampmussel, though it has not been found in the Mattawamkeag and East Branch Penobscot River watersheds where the lampmussel is well-documented. Despite its common name, the tidewater mucket is found quite far inland -- as far as Millinocket Lake in the Mount Katahdin region.

The tidewater mucket has been declining throughout its range, prompting many states to consider it for endangered or threatened species listing status. The reasons for its decline are unknown but probably reflect a cumulative effect of habitat destruction and pollution. In at least one instance (lower Hudson River), competition with the zebra mussel may have resulted in extirpation (Strayer and Jirka 1997). In Maine, some healthy populations do exist -- especially in lakes and rivers of the lower Kennebec and Penobscot River drainages -- but this species often is scarce where it is found, and populations appear restricted and fragmented within the three watersheds. Consequently, it has been listed as threatened in Maine since 1997. The tidewater mucket also is listed as threatened in Connecticut, New Jersey, and North Carolina, and as special concern in Massachusetts and Maryland. It is ranked G3G4 (vulnerable) by NatureServe (2007) and is listed as near threatened on the IUCN Red List Category (IUCN 2006) and special concern by the American Fisheries Society (Williams et al. 1993). As with several other declining species, Maine may serve as an important refugium if tidewater mucket populations become extirpated elsewhere along the Atlantic seaboard.

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.

Reproduction. The tidewater mucket is a long-term brooder. Eggs are fertilized in late summer, and glochidia are released the following spring. Recent studies (see Past Research and Management) have confirmed the white perch as a suitable host for this species and identified the banded killifish and alewife as potential hosts (Kneeland 2006, Wick 2006).

Yellow Lampmussel *Lampsilis cariosa* (Say, 1817)



Description. This is a medium-sized to large (usually < 4.5 inches) mussel that is distinctly yellow and oval-shaped, somewhat resembling a marine quahog. The valves are inflated in cross section, and the umbos are quite prominent and raised above the hinge line. The shell is strong and thick, especially toward the anterior end. The periostracum often is bright yellow in young 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. The nacre usually is white or bluish-white. Pseudocardinal teeth are well developed -- the left valve has two and the right valve has two or three. Pseudocardinals are usually stout, with distinct striations on the surface, and are located nearly directly under the beak. Lateral teeth also are well developed -- the left valve has two and the right valve has one. The female mantle margin often is brightly pigmented, with a conspicuous fleshy flap and dark “eyespot” resembling a minnow (see Figure 4) displayed during the breeding season. Mature females are considerably more rounded toward the posterior ventral margin than males and immature females.

Distribution and Status. The yellow lampmussel is distributed throughout the Atlantic drainages from Georgia to Nova Scotia. In Maine, its distribution is limited to the St. George, Penobscot, and lower Kennebec River watersheds, where often it co-exists with the tidewater mucket. Unlike the mucket, however, this species occurs

farther north and east in the upper reaches of the Penobscot River watershed where it is found in the East Branch Penobscot and Mattawamkeag River drainages.

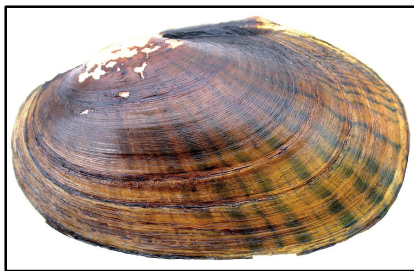
The yellow lampmussel has been declining throughout its range, prompting many states to list it as an endangered or threatened species. The reasons for its decline are unknown, but probably reflect a cumulative effect of habitat alteration and water quality degradation. This species also may be hybridizing with *Lampsilis ovata* and *Lampsilis cardium* in some parts of its range, further jeopardizing its future status (Kelly 2004). In Maine, occurrences of the yellow lampmussel are limited and often further fragmented within the three watersheds where it occurs. Many observations are of only a few individuals or relict valves. Until recently, it was thought to be extirpated from the lower Kennebec River, but several individuals were found during the Edwards Dam removal in 1999. Some large and healthy populations do exist, such as in the Sebasticook, St. George, and Passadumkeag Rivers, and Maine likely will play an important role in this species' conservation if populations are extirpated elsewhere throughout its range.

Like the tidewater mucket, the yellow lampmussel has been state-listed as threatened since 1997. It also is listed as threatened in New Jersey, endangered in Massachusetts and North Carolina, and extirpated in New Hampshire and Maryland. It was thought to be extirpated in Connecticut, but a single live individual recently was discovered in the Connecticut River (Victoria 2006). This species formerly was listed as a Category 2 species by the U.S. Fish and Wildlife Service. It is ranked G3G4 (vulnerable) by NatureServe (2007), and is listed as special concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), endangered by the IUCN Red List, and threatened by the American Fisheries Society (Williams et al. 1993).

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

Reproduction. This species is a long-term brooder. Eggs are fertilized in late summer, and glochidia are released the following spring. It is one of the few species in New England that uses a modified mantle flap as a lure to attract host fish. Recent studies (see Past Research and Management) have confirmed the white perch, yellow perch, and largemouth bass as suitable hosts for this species, and identified the banded killifish, chain pickerel (*Esox niger*), white sucker, and smallmouth bass as potential hosts (Kneeland 2006, Wick 2006).

Eastern Lampmussel *Lampsilis r. radiata* (Gmelin, 1791)



Description. This is a medium-sized to large (usually <5 inches), heavy-shelled mussel. The shape is oval or slightly rounded, and the valves typically are only moderately inflated in cross section. The hinge ligament usually is prominent, and the umbos are not very prominent and barely raised above the hinge line. The shell is yellowish-green in younger individuals to brownish-green or black in older specimens. There usually are numerous green rays on the periostracum, although these sometimes are obscured in older individuals. Hinge teeth are well developed -- the left valve has two pseudocardinal and two lateral teeth, and the right valve has two or three pseudocardinal teeth and one lateral tooth. The nacre typically is white, pink, or bluish-white. The female's mantle margin usually is lightly to darkly

pigmented, with fleshy tubercles and flap extensions. Mature females usually are more rounded toward the posterior ventral margin than males or immature females.

Distribution and Status. 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, but is primarily absent from northern, western, and southernmost regions. Where it does occur, it often is found in abundance. 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 is ranked G5 by NatureServe (2007), but is state-listed as threatened in New Jersey and special concern in Rhode Island.

Habitat. This species inhabits a variety of aquatic habitats, including small streams, large rivers, ponds, and lakes. It is found in a variety of substrates, though most often it is encountered in 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. This species has been documented to parasitize a number of warmwater fishes, including yellow perch, white perch, largemouth bass, smallmouth bass, black crappie, bluegill, and pumpkinseed sunfish (Tedla and Fernando 1969a, 1969b; Hanek and Fernando 1978; Watters 1994; O'Dee and Watters 2000; Watters et al. 2005; Kneeland 2006).

RESEARCH AND MANAGEMENT

Regulatory Authority

Under Title 12 MRSA, the Maine Department of Inland Fisheries and Wildlife is charged to “preserve, protect and enhance the inland fisheries and wildlife resources of the state; to encourage the wise use of these resources; to ensure coordinated planning for the future use and preservation of these resources; and to provide for the effective management of these resources” (Chpt. 903, §10051). “Wildlife” is defined as “any species of the animal kingdom, except fish, which is wild by nature, whether or not bred or reared in captivity, and includes any part, egg or offspring of the animal, or the dead body or parts of the animal” (Chpt. 901, §10001).

Unless listed as endangered or threatened, however, invertebrates are currently provided only minimal protection under Maine law. Except for commercial take of snakes and turtles, the laws that govern hunting, trapping, and possession of Maine’s wildlife (Chpt. 915) pertain solely to “wild birds” and “wild animals”. By definition, “wild animals” includes only mammals (Chpt. 901, §10001) -- thus excluding invertebrates from any closed season or general possession coverage. Except for listed species, invertebrates also are excluded from scientific collection permit requirements by the same definition (MDIFW Rules, Chpt. 7, Part VI, Section 7.60). Permits are required, however, to possess for exhibition purposes (Chpt. 915, §12152), import or introduce into the state (§12155), or take or transport within the state for breeding and advertising purposes (§12157), because these laws refer to all “wildlife”, which includes invertebrates.

The following state and federal regulations are the most important regulatory tools in Maine for conservation of freshwater mussels and the aquatic ecosystems upon which they depend:

Maine Endangered Species Act (Title 12 MRSA, Chapter 925)

The Maine Endangered Species Act, first enacted in 1975, prohibits the take, exportation, hunting, trapping, possession, processing, offering for sale, selling, transporting, feeding, baiting or harassing of any endangered or threatened species of fish and wildlife, including invertebrates (§12808). These prohibitions encompass both negligent and intentional acts. “Take” is defined as the act or omission that results in the death of any endangered or threatened species (§12808). “Harass” means an intentional or negligent act or omission that creates the likelihood of injury to wildlife by annoying it to such an extent as to significantly disrupt normal behavioral patterns (Chapter 901, §10001). Because the tidewater mucket, yellow lampmussel, and brook floater are officially listed as threatened in Maine, they are the only freshwater mussel species fully protected from these activities.

In 1988, an amendment to the Maine Endangered Species Act enabled the Commissioner of Inland Fisheries and Wildlife to designate areas currently or historically providing physical or biological features essential to the conservation of an endangered or threatened species as “Essential Habitat” (Chapter 925, §12804, subsection 2; MDIFW Rules, Chpt. 8, Section 8.05). Under this act, state agencies and municipal governments may not permit, license, fund, or carry out projects that would significantly alter an Essential Habitat or violate protection guidelines adopted for the habitat. These habitats and their protection guidelines first must be defined and

mapped by MDFIW, and adopted through public rule-making procedures. To date, Essential Wildlife Habitat has been designated only for the bald eagle, piping plover, least tern, and roseate tern. If necessary, the rule also could be used to protect habitat for listed freshwater mussel species.

A 1999 amendment also allows the Commissioner to permit the “incidental” take of any endangered or threatened species (§12808). There are three provisions of the Incidental Take Permit (subsection 3):

- 1) such taking is incidental to, and not the purpose of, carrying out an otherwise lawful activity;
- 2) the taking will not impair the recovery of any endangered species or threatened species; and
- 3) the person develops and implements an incidental take plan approved by the Commissioner.

Natural Resource Protection Act (Title 38 MRSA, Chpt. 3, subchpt. 1, Article 5-A)

The Natural Resource Protection Act (NRPA) provides the primary state legislation protecting Maine’s freshwater resources by recognizing rivers and streams, great ponds, freshwater and coastal wetlands, and Significant Wildlife Habitats as resources of state significance. It establishes environmental standards to prevent the degradation of these resources, and authorizes the Maine Department of Environmental Protection (MDEP) to enforce them in organized townships. Specifically, the NRPA prohibits without a permit activities that may potentially harm a protected resource, including dredging; bulldozing; removing or displacing soil, sand, vegetation, or other materials; draining or otherwise dewatering; filling; or construction, repair or alteration of permanent structures.

“Significant Wildlife Habitat” protected under NRPA is defined to include several habitat types that could be relevant to protecting freshwater mussel habitat, including habitat for species on the state or federal lists of endangered or threatened species, inland waterfowl and wading bird habitat, and critical spawning and nursery areas for Atlantic salmon. These areas must first be identified and mapped by MDIFW (or Atlantic Salmon Commission) and, along with habitat protection guidelines and permit review criteria, adopted by MDEP through public rulemaking. MDIFW cooperates regularly with MDEP to review permit applications for projects falling within a Significant Wildlife Habitat. To date, Significant Wildlife Habitat has been designated only for seabird nesting islands, coastal and inland waterfowl and wading bird habitats, significant vernal pools, and shorebird nesting, feeding and roosting sites. This habitat protection tool also could be used to protect habitat for Maine’s listed freshwater mussel species.

Water Classification Program (Title 38 MRSA, Chpt. 3, subchpt. 1, Article 4-A)

This legislation establishes a water quality classification system that allows the State to manage its surface waters to protect the quality of those waters and, where water quality standards are not being achieved, to enhance water quality. It recognizes the value of proper management of water resources in promoting the public’s general welfare, and declares the State’s objective to restore and maintain the chemical, physical and biological integrity of the State’s waters and to preserve certain pristine state waters. Specifically, this objective is to be achieved by: a) eliminating, where appropriate, the discharge of pollutants into the State’s waters; b) disallowing discharge

of pollutants into any state water without first providing the degree of treatment necessary to allow those waters to attain their classification; and c) ensuring water quality sufficient to provide for the protection and propagation of fish, shellfish and wildlife and provide for recreation in and on the water.

Opportunity exists for closer cooperation and communication between MDIFW and MDEP under the Water Classification Program to identify state waters of high value to freshwater mussels (particularly listed species) that may benefit from increased water quality standards. These water bodies or river segments could be reviewed for reclassification to a higher standard where appropriate.

Mandatory Shoreland Zoning (*Title 38 MRSA, Chpt. 3, subchpt. 1, Article 2-B; MDEP Rules Chpt. 1000*)

This state legislation requires all municipalities to adopt, administer, and enforce ordinances that regulate land use activities within 250 feet of a great pond, river, freshwater and coastal wetland, including all tidal waters, and within 75 feet of a stream. The purposes of these ordinances include preventing water pollution, protecting economic and ecological resources from the effects of flooding and erosion, and protecting fish and wildlife habitat. The Act requires that the Board of Environmental Protection establish minimum guidelines for such ordinances, and that municipalities adopt shoreland zoning ordinances consistent with, or no less stringent than, those minimum guidelines.

Provisions also are included that govern establishment of various use districts within the shoreland zone. Within each district, the Board prescribes uses that may be allowed with or without conditions and establishes criteria for the issuance of permits

and nonconforming uses. In areas identified as Resource Protection districts, some development activities (e.g., commercial and industrial developments, road construction, marinas, parking facilities) are prohibited, and others require permit applications for approval. In general, MDIFW does not review town permit applications but often is consulted by municipal officials in permitting and comprehensive planning. This provides an opportunity to relay concerns for freshwater mussels when appropriate.

Comprehensive Growth Management Act (Title 30-A MRSA)

This act lists State goals required in all municipalities to guide local comprehensive planning and land use management (§§4312, 4326). It encourages towns to plan for protection of the State's water resources and other critical natural resources, including without limitation, wetlands, wildlife and fisheries habitat. It similarly enables Significant Wildlife Habitats identified under NRPA, and other wildlife habitat information, to be provided to the Department of Economic and Community Development for use by towns in their comprehensive planning processes. MDIFW routinely reviews town comprehensive plans and provides feedback on wildlife habitat conservation standards. Strategies that would benefit freshwater mussels include the protection of water quality and maintenance of riparian buffers. In unorganized townships, the Land Use Regulation Commission administers a comprehensive plan with similar purposes for "wildlands" under its jurisdiction (12 MRSA, §§685A-C).

Site Location of Development Act (Title 38 MRSA, Chpt. 3, §484(3); MDEP Rules, Chpt. 375, §§12, 15)

This state law includes provisions to regulate the location and extent of development projects to prevent degradation of the natural environment, including wildlife and fisheries habitat. Specifically, MDEP regulations enumerate that there will be no unreasonable disturbance to habitat for state or federally listed endangered or threatened species, and recognize the importance of preserving unusual natural areas - including important wildlife habitats for rare or endangered species. Developments of state or regional significance that may substantially affect the environment (e.g., those >20 acres, mineral extractions, most residential subdivisions >15 lots on 30 or more acres, or, for commercial subdivisions >5 lots on 20 or more acres, and transmission lines >100 kV; §§482, 487-A) require approval by MDEP or certified municipalities (§485-A). When such projects potentially affect the habitat of rare freshwater mussels, MDEP consults with MDIFW for potential management restrictions and conditions associated with the Site Law Permit.

Various acts concerning fishways in inland and coastal waterways (Title 12 MRSA, Chpt. 605, subchapter 4)

This legislation grants the Department of Marine Resources authority to require fish passage facilities in dams where they are needed to conserve, develop, or restore anadromous fisheries or to protect or enhance rare, endangered, or threatened fish species (§6121). Facilitating fish passage over dams that previously served as barriers to the movements of both migrating and local fish populations can significantly improve

host fish availability, dispersal, and gene flow for populations of mussels that have become isolated or fragmented by dams.

Clean Water Act (U.S.C. Title 33, Chpt. 26)

This federal legislation, first enacted in 1972, establishes the basic structure for regulating discharges of pollutants into the waters of the United States. It gives the U.S. Environmental Protection Agency the authority to implement pollution control programs such as setting wastewater standards for industry and water quality standards for all contaminants in surface waters. It also makes it unlawful for any person to discharge any pollutant from a point source into navigable waters, unless a permit is obtained under its provisions.

The Clean Water Act funds the construction of sewage treatment plants under the construction grants program and recognizes the need for planning to address the critical problems posed by nonpoint source pollution. It employs a variety of regulatory and nonregulatory tools to sharply reduce direct pollutant discharges into waterways, finance municipal wastewater treatment facilities, and manage polluted runoff. These tools are employed to achieve the broader goal of restoring and maintaining the chemical, physical, and biological integrity of the nation's waters so that they can support the protection and propagation of fish, shellfish, and wildlife and recreation in and on the water. This legislation does not address freshwater mussels specifically, unless federally endangered species are involved.

Past Goals and Objectives

There are no past goals and objectives for freshwater mussels in Maine.

Past Research and Management

Prior to the 1990s, little was known about the distribution and status of freshwater mussels in Maine. Naturalists had collected shells from Maine's waters since the beginning of the 19th century (Lermond 1908; Nylander 1943; Martin 1995), yet the historical data were scant and often lacking information necessary to verify or reconfirm records in modern times. By the 1980s, many state and federal agencies and private conservation organizations were documenting startling declines in freshwater mussel diversity throughout North America. Some of the species reported to occur in Maine were recognized by other states as needing protection, or as candidates for federal listing, yet their status in Maine was unknown.

In the mid 1980s, the Maine Natural Heritage Program undertook some of the first modern mussel surveys in the State with funding support from MDIFW's Endangered and Nongame Wildlife Grants Program. These surveys (Albright 1991) were limited and focused primarily on the brook floater, which at the time was a candidate for federal listing. In 1991, MDIFW began seeking outside funds to conduct additional surveys for the brook floater and other rare mussel species, including the yellow lampmussel, which also was a federal candidate. These early surveys were facilitated by annual awards from the U.S. Fish and Wildlife Service via Cooperative Endangered Species Conservation Fund (i.e., "Section 6") grants, and soon developed into a comprehensive, systematic survey of all freshwater mussel species. Additional

funding support came later from the Environmental Protection Agency's State Wetland Protection Development Grants. The primary goals of this survey were to document species occurrence and obtain baseline data on the current distribution, relative abundance, and conservation status of all of Maine's freshwater mussels. During 1992 - 1997, approximately 1600 sites on rivers, streams, lakes and ponds were surveyed statewide as part of the Maine Freshwater Mussel Atlas Project. A voucher collection of nearly 3500 specimens was established, and a database was created to track all mussel survey data.

Following completion of the statewide surveys, MDIFW successfully obtained funding from the Maine Outdoor Heritage Fund to summarize the status of Maine's freshwater mussels in the initial draft of this document and in an outreach guide to promote appreciation and understanding of this faunal group. This work also was supported by the U.S. Fish and Wildlife Service and Maine's Endangered and Nongame Wildlife Fund. In 2000, "*The Freshwater Mussels of Maine*" (Nedeau et al. 2000) was published. This book summarizes the ecology, conservation, management, collection, identification, and distribution of freshwater mussels in Maine. It has become an invaluable resource to inform landowners, land trusts, watershed groups, town governments, state and federal agencies, private organizations, industries, consultants, and the general public about freshwater mussels.

In conjunction with ecoregional surveys for rare species, MDIFW has continued to fill in survey gaps and look for new occurrences of listed mussel species. During 1998 - 2006, an additional 90+ sites were surveyed, resulting in new information about the distribution and occurrence of both rare and common mussels. All known

occurrences for the four rarest species (tidewater mucket, yellow lampmussel, brook floater, and creeper), including those documented by outside sources, have been incorporated into Maine's Natural Heritage Program database -- part of a nationwide network tracking information about the status and locations of rare species. These occurrences are recorded and mapped using national standards of Heritage Program methodology, and the information is provided to MDIFW regional staff, state and federal resource agencies, landowners, land trusts, and other users for project planning, permit review and other conservation measures.

Information obtained from statewide mussel surveys also has enabled MDIFW to identify those species needing special protection. In 1997, when invertebrates were listed under the Maine Endangered Species Act for the first time, the inclusion of freshwater mussels on the state list was based on results of the statewide survey. Two species, the tidewater mucket and yellow lampmussel, were listed as threatened, and three additional species (creeper, triangle floater, and brook floater) were listed as special concern¹. Since then, MDIFW has provided guidance and management recommendations to avoid and minimize potential conflicts with listed mussel species for a variety of projects. Environmental permit reviews involving mussel conservation concerns have ranged in scope and intensity, from repairs of small, lowhead dams to removal of large, hydropower dams; from road repair to new bridge construction; and from sunken log salvage to installation of major utility crossings. In some cases, only a few individuals may have been affected; in others, perhaps thousands. Incidental Take Plans were developed for several major projects. Examples of past projects where

¹ In 2007, the listing status of the brook floater was upgraded to "threatened" and the triangle floater was removed from the special concern list.

state-listed freshwater mussels played a prominent role in environmental permit reviews and project planning are listed below:

Lowell Tannery Dam, Passadumkeag River (1998). MDIFW was notified by the dam owner of plans for reservoir drawdown prior to dam repairs. Pre-project surveys determined that four state-listed species occurred in the impoundment. Consequently, MDIFW recommended that water levels be dropped only five feet, instead of the proposed 20 feet, and that a temporary cofferdam be installed so that repairs could be completed without further dewatering the reservoir. Limited recovery and relocation efforts were conducted by a small crew of MDIFW staff during the dewatering phase, and >250 yellow lampmussels and tidewater muckets were moved into deeper water to prevent mortality.

Fort Halifax Dam, Sebasticook River (1998, 2002 to present). In the summer of 1998, a drawdown prior to dam repairs caused extensive mortality of both state-threatened species. Unfortunately, dam operators were not aware of the presence of rare species in the impoundment. In order to assess mortality, MDIFW requested the hydro company intensively survey all exposed substrate for listed species. Approximately 1500 tidewater muckets and yellow lampmussels were found to have perished.

In 2002, dam owners initiated the permit process to decommission and remove the nearly 100-year old structure as an alternative to providing permanent fish passage. MDIFW requested pre-project surveys of the five-mile long impoundment and development of an Incidental Take Plan (ITP) to minimize loss of the two listed species. The ITP includes provisions for recovery and relocation of all rare species located

during and after dewatering. It also provides for a limited post-monitoring effort to determine the success of the relocation effort. Since legal proceedings have delayed the removal of Fort Halifax Dam well beyond the plan's approval date, and new information is now available to suggest revisions are needed (see below), MDIFW and the applicant will need to revisit the ITP prior to dam removal.

Edwards Dam, Kennebec River (1999). Extensive surveys (shoreline searches, bucket surveys, and SCUBA) of this 17-mile long impoundment were conducted by MDIFW prior to the removal of Edwards Dam to look for state-listed species, especially the tidewater mucket and yellow lampmussel. During the dam removal and dewatering phase, a large team of state and federal biologists and volunteers scoured shorelines to move exposed mussels into deeper water. The yellow lampmussel, which had not been documented in the lower Kennebec River for nearly 100 years, was found during the relocation effort. A total of 607 tidewater muckets, 16 yellow lampmussels, and dozens of creepers and triangle floaters were relocated. Post-monitoring to assess survival of relocated mussels did not occur.

Maritimes & Northeast Pipeline Project (mid 1990s, ongoing reviews). This major utility line affects dozens of waterbodies statewide, including numerous sites where state-listed mussel species are documented. MDIFW requested pre-project surveys at all stream crossings where listed species might be affected, recommended preferred crossing techniques to minimize loss, and requested relocation of state-listed species in areas where loss was unavoidable. Survey data and voucher specimens from these surveys were incorporated into the MDIFW Freshwater Mussel Database.

Third Augusta Bridge, Kennebec River (2002). MDIFW worked with the Maine Department of Transportation to coordinate pre-project SCUBA surveys and develop an ITP to minimize loss of listed species during construction of the new bridge. Intensive surveys of the project area documented only two tidewater mucketts. These individuals were relocated upriver and no post-monitoring was required.

Sennebec Dam, St. George River (2002). The deteriorating Sennebec Dam was proposed to be removed and replaced with a rock ramp to allow fish passage while maintaining water levels in Sennebec Pond. MIDFW worked with Trout Unlimited to develop an ITP that included pre-project surveys of the proposed construction and drawdown areas, relocation of all rare mussels found to the pond above the dam site, and development of outreach materials (i.e., information kiosk for local boat launch, educational packet for local schools) to raise awareness of freshwater mussels in the St. George River watershed. As a result, a few hundred yellow lampmussels and several tidewater mucketts were moved out of the construction and dewatering zone.

In recent years, MDIFW also has collaborated with University of Maine scientists on several research projects that address issues critical to freshwater mussel conservation in Maine. Significant funding for these studies was obtained from the State Wildlife Grant program, Maine Outdoor Heritage Fund, U.S. Fish and Wildlife Service, and Maine Endangered and Nongame Wildlife Fund. These research projects are summarized below.

Conservation Genetics of Two Rare Freshwater Mussels: The Tidewater Mucket (*Leptodea ochracea*) and the Yellow Lampmussel (*Lampsilis cariosa*)

(M.S. thesis completed by Morgan W. Kelly, August 2004). Understanding the distribution of genetic diversity in populations is valuable to developing effective conservation plans for rare species. Measurements of genetic diversity can indicate the potential viability and fitness of a population; and maintenance of genetic diversity is important to preserving the local adaptations and future evolutionary potential of a species. This research investigated the population genetic structures of the state-threatened yellow lampmussel and tidewater mucket by analyzing DNA markers (microsatellite loci) to assess population-level genetic variation within and among the three river drainages where these rare mussels occur. It also sought to determine if barriers to fish host movement, such as dams, were indirectly affecting genetic structure through reproductive isolation of populations.

Study results indicated that both species had significant genetic differences among populations. For *L. cariosa*, significant differences were observed both within and between drainages. By contrast, significant differences were observed within but not between drainages for *L. ochracea*. Although *L. cariosa* exhibited significant isolation by distance, there was no correlation between genetic distance and the number of intervening dams for either species after correcting for the effects of geographic distance. This research will contribute to the understanding of population-level management units for conservation of these rare species in Maine, and aid in making informed decisions during relocation efforts about where to move mussels that ensures the least genetic divergence. This will be particularly important in light of pending and increasing dam removals in Maine, which are likely to require translocations of both species.

A second part of this research looked at the rangewide taxonomy of both species, using DNA sequences of the mitochondrial ND1 gene. Findings indicated that *L. cariosa* and *L. ochracea* each form well-supported monophyletic lineages. However, individuals from the Potomac River drainage identified as *L. cariosa* on the basis of morphology had the DNA of *Lampsilis cardium* or *L. ovata*, while individuals identified as *L. ovata* from the St. Lawrence River drainage had the DNA of *L. cariosa*. This discrepancy between morphology and DNA sequence data is evidence for hybridization of *L. cariosa* with the other *Lampsilis* species in the Potomac River and St. Lawrence drainages -- having implications to longterm conservation efforts, and federal and state listing statuses for the yellow lampmussel.

Fish Hosts and Demographics of *Lampsilis cariosa* and *Leptodea ochracea*, Two Threatened Freshwater Mussels in Maine (M.S. thesis completed by Philip C. Wick, August 2006). Part one of this research addressed the need to identify potential fish hosts for Maine's two threatened mussel species. Host information is lacking for many freshwater mussel species throughout North America, yet it is critical to making informed management decisions and ensuring adequate conservation measures. This study artificially infected several species of native fishes with glochidia of the yellow lampmussel and tidewater mucket. The parasitized fish were maintained in the laboratory to document successful transformation of glochidia to juvenile mussels. Transformed juvenile lampmussels were recovered from both yellow and white perch, whereas the tidewater mucket successfully transformed only on white perch. Alewife also were identified as a possible host for the tidewater mucket, but none of the parasitized fish survived long enough for transformation to take place.

Part two of this research examined the demographics and densities of yellow lampmussel and tidewater mucket populations at five sites where relatively large populations of both species were known to occur: Sebasticook River, Unity Pond, and Sandy Stream in the Kennebec River drainage; Seven Tree Pond in the St. George River drainage; and Millinocket Lake in the Penobscot River drainage. Surveys were conducted using excavated 0.25m² quadrats combined with length at age estimates derived from internal annuli counts. Mean densities of *Lampsilis cariosa* ranged from 0.1/m² to 1.6/m², and densities of *Leptodea ochracea* ranged from 0/m² to 0.3/m² (by comparison, densities of the common eastern elliptio ranged from 0.4/m² to 27.6/m²). *L. cariosa* ranged in age from one to >20 years, whereas *L. ochracea* ranged from one to ten years. All five populations showed some evidence of recent recruitment, as well as a wide distribution of older animals.

Identification of Fish Hosts for Wild Populations of Rare Freshwater Mussels (*Lampsilis cariosa* and *Leptodea ochracea*) Using a Molecular DNA Key (M.S. thesis completed by Stephen C. Kneeland, August 2006). This study sought to determine if the hosts previously identified in the lab by Wick (2006) act as hosts in natural populations, and also to assess additional species as possible hosts by sampling naturally parasitized fish in the wild. To identify glochidia, a species-specific molecular identification key utilizing restriction fragment length polymorphism patterns of the mitochondrial ND1 gene was developed and tested for accuracy prior to sampling. Fish were captured at 13 localities and in all three drainages where both species previously had been documented. The fish hosts identified in laboratory conditions for both mussel species were confirmed from naturally parasitized fish. Five additional

species (largemouth bass, banded killifish, chain pickerel, white sucker, and smallmouth bass) were found to be potential hosts for *L. cariosa* -- one of which, the largemouth bass, has since been confirmed as a suitable host in laboratory experiments done elsewhere (Eads et al. 2007). One species (banded killifish) was identified as a potential new host for *L. ochracea*. For both species, the white perch was the most commonly used and heavily infected host fish.

Methods for the Translocation of the Yellow Lampmussel (*Lampsilis cariosa*) and the Tidewater Mucket (*Leptodea ochracea*) in the Fort Halifax Dam Impoundment of the Sebasticook River, Maine (M.S. thesis completed by Jennifer E. Kurth, May 2007). Pending removal of the Fort Halifax Dam, this study assessed populations of the two listed species in the impoundment and determined the effects of within and between waterbody translocations on survival. Qualitative and quantitative surveys were performed to document the mussels' current distribution and abundance in the project area and to guide future recovery and relocation efforts. In a 2004 pilot study, a co-occurring common species (eastern lampmussel) was translocated within the impoundment and to two other sites within the watershed: Unity Pond and Sandy Stream, which had been proposed as relocation sites following dam removal. The feasibility of using Passive Integrated Transponder (PIT) tags to track and monitor translocated mussels was investigated for the first time and found to be effective (72-80% recovered using PIT pack searches vs. 30-47% recovered using visual searches alone). In 2005, the translocation experiment was repeated with yellow lampmussels and tidewater muckets. Recapture rates of the PIT-tagged listed mussels were 57-90% for yellow lampmussels (0-7% mortality) and 30-86% for tidewater muckets (4-6%

mortality). A high percentage of mussels moved to Sandy Stream were either not recovered or found >100 meters from their original translocation position due to extreme sediment redistribution during high spring flows. As a result, Sandy Stream was not recommended as a suitable relocation site for maximizing survival and monitoring relocation success. The information obtained from this research will be invaluable in revisiting the Incidental Take Plan prepared for the relocation and monitoring of rare mussels affected by the removal of Fort Halifax Dam.

Landscape Control of the Distribution of Two Rare Atlantic Slope Freshwater Mussels in Maine, the Yellow Lampmussel (*Lampsilis cariosa*) and the Tidewater Mucket (*Leptodea ochracea*). (Final report for the Maine Cooperative Fish and Wildlife Research Unit prepared by Cynthia S. Loftin, December 2005).

This study sought to identify landscape-scale factors denoting suitable habitat for yellow lampmussels and tidewater muckets in Maine. Watershed analysis based on available GIS data layers and mussel survey data indicated that these species occupy streams with similar characteristics. Both were found in streams with forested riparian zones as the dominant cover type, and there was a greater proportion of wetland area in occupied reaches and contributing watersheds than was present statewide. Wetland comprised a greater proportion of the buffer of reaches occupied by tidewater muckets than those with yellow lampmussels. Both species occupy reaches that are longer, have larger contributing areas, more upstream connecting first order streams, and lower gradients than unoccupied reaches -- characteristics that indicate conditions creating hydrological stability. Muckets were found more often in reaches connected upstream to shorelines of large streams or rivers and downstream to shorelines of large streams

and lakes; downstream connections were less often to small streams. Yellow lampmussels were found at sites most often connected to streams and shorelines of large rivers and less often to lakes, and where stream order was greater and cumulative watersheds larger. The number of dams did not differ between reaches with or without either species, but the total dam height per stream mile in contributing areas where the mussels were absent exceeded that of where they were present. Percent calcareous bedrock in the total upstream drainage area was greater in reaches containing tidewater mussels than where they were not found, reflecting the near-coastal distribution of this species in Maine. In contrast, watersheds occupied by yellow lampmussels contained less calcareous bedrock in the upstream drainage area. Attempts to develop logistic regression models describing features of watersheds occupied by these rare species were unsuccessful; their low number of occurrences distributed across a broad range of conditions resulted in unreliable models.

Current Research and Management

MDIFW continues to incorporate targeted surveys for rare mussels in ecoregional surveys and, beginning in 2008, will focus on survey gaps in the central and western mountains and foothills. The Department also responds regularly to information requests and permit reviews where potential concerns for listed or rare mussels exist. The recent initiation of the *Penobscot River Restoration Project* will require longterm involvement by MDIFW as this precedent-setting endeavor develops and unfolds. This project seeks to remove both the Veazie and Great Works Dams, and partially breach

the Howland Dam, in a stretch of the Penobscot River where all four of Maine's rarest species are known to occur.

As part of the process to update Maine's endangered species list, MDIFW recently completed a status review for all ten of the State's freshwater mussel species. As a result, the brook floater was proposed and approved for listing as threatened. Another important ongoing status review is taking place as part of *Maine's Comprehensive Wildlife Conservation Strategy* (MDIFW 2005). During this planning process, the status and conservation needs of all Maine's mussels are reviewed and prioritized. The tidewater mucket, yellow lampmussel, and brook floater all have been identified as priority species of greatest conservation need.

MDIFW regularly inputs new survey and occurrence data into both the Freshwater Mussel Survey Database and the Natural Heritage Program database, and provides updated locational information to staff and outside users. Currently, all occurrence data for the four species tracked in the Heritage database (yellow lampmussel, tidewater mucket, brook floater, and creeper) are being reviewed to rank and delineate occurrence polygons (vs. points as currently mapped) based on standardized Heritage Program methodology. These new occurrence and map representations will improve the information available to MDIFW and others for habitat conservation and management actions.

Research and Management Needs

Rangewide, there are tremendous gaps in knowledge about the general life history, biology, and conservation needs of freshwater mussels. Identification of fish

hosts continues to be an important research need. In Maine, potential hosts identified for the yellow lampmussel and tidewater mucket by Kneeland (2006) based on naturally parasitized fish need to be confirmed in the laboratory². Other species of fish that have not yet been sampled also could be investigated.

One of the most important research and management needs for freshwater mussels in Maine is the development and implementation of a longterm population-monitoring program. This is especially important for listed species, but some level of monitoring should be included for common species as well. Currently, most of what is known about the status of Maine's mussel populations is qualitative in nature, and based almost entirely on observations recorded during the statewide surveys (i.e., presence/absence, relative abundance, evidence of reproduction). Baseline quantitative data on population size, age structure, and other demographic parameters are not available to accurately assess status, determine recovery potential, or monitor trends on a local or statewide scale. Given the severe declines experienced elsewhere by some of Maine's native species, and the significant role the State may ultimately play in their rangewide conservation, having baseline population data and a longterm monitoring plan in place will be central to a successful conservation strategy.

In areas where listed species potentially are affected by water management schemes, cooperative agreements should be developed with industries and landowners controlling flow and water levels to ensure minimal loss of rare mussels during normal operations and repairs. As dam removal efforts continue to grow in Maine, investigating the effects of habitat change and fish community redistribution on the yellow

² Fish host confirmation requires investigative trials in both nature and the laboratory in order to document successful transformation and determine host effectiveness in natural ecosystems.

lampmussel and tidewater mucket is critical to understanding the significance of impoundments to their longterm conservation. Techniques and protocols to recover, hold, relocate, and mitigate for rare mussels following dam removals and other projects that directly affect their populations need to be further developed and refined. In particular, longterm post-monitoring should be implemented in order to measure the success of relocation and other conservation efforts.

The effects of contaminants on Maine's mussel populations also should be investigated. As benthic suspension feeders, freshwater mussels are exposed to contaminants in both the sediment and water column. They are effective bioaccumulators and often are used as sentinel species in biomonitoring studies. Elevated contaminant concentrations from anthropogenic sources are a probable contributing factor to widespread declines in mussel diversity and abundance (Naimo 1995, Wang et al. 2007, Bringolf et al. 2007b). Mercury, polychlorinated biphenyls (PCBs), pesticides, paper mill effluents, ammonia, wastewater pharmaceuticals, and other pollutants all have been documented to effect the survivorship, behavior, and physiology of freshwater mussels under certain conditions and life stages (Fuller 1974, Moulton et al. 1996, Newton 2003, Bringolf et al. 2007a), and all are present in Maine waters (MDEP 1996). Other potential threats and limiting factors also need to be identified.

A potential management need is the development and implementation of commercial harvest regulations for all species of freshwater mussels. Currently, only species listed under the Maine Endangered Species Act receive any protection from take. While Maine's freshwater mussels are not as commercially valuable as those in

other regions of the country, they do have some limited consumptive use potential. Although the full magnitude is undocumented, several credible reports are known of large numbers (thousands) being harvested from Maine rivers for sale to the biological laboratory supply industry (Fred Kircheis and Tom Schaeffer, MDIFW, *personal communication*). Over the past several years, MDIFW has also received increasing numbers of inquiries about restrictions on the consumptive use and commercial harvest of freshwater mussels, with interests ranging from freshwater pearl culture to human food production to bait supply. Given the freshwater mussel's unique life history traits (e.g., long life span, long age to sexual maturity, low recruitment, immobility), unregulated harvest and overcollection -- particularly for species that are already rare or populations that are already stressed -- could result in severe declines or local extirpations.

Outreach is a significant, ongoing need for freshwater mussel conservation. While efforts have improved in recent years as a result of MDIFW's listing process and survey efforts, the general public still has a limited understanding of and appreciation for freshwater mussels and other aquatic invertebrates. Outreach to landowners, industries, and municipalities with the potential to affect (e.g., alter water quality, riparian habitat, flow regimes or impoundment levels) sites with listed mussels is especially important. Involvement of local watershed groups in the monitoring and conservation of mussels could enhance outreach and improve MDIFW's ability to develop a statewide conservation and monitoring program. Outreach efforts to help prevent the introduction of exotic competitors such as the zebra and quagga mussel (*Dreissena bugensis*), or

invasive plants that degrade freshwater habitats (i.e., Eurasian milfoil, didymo algae), also should be increased.

Finally, management guidelines for use in permit review, land use planning, project design, and habitat conservation need to be developed to assist resource agencies, municipalities, landowners, and others in successfully considering the needs of freshwater mussels. In particular, standardized recommendations for riparian buffers associated with projects potentially affecting high value river reaches (e.g., development, forestry activities) should be established and consistently implemented.

HABITAT ASSESSMENT

General Habitat Assessment

Past Habitats. Maine has approximately 5,800 lakes and ponds and more than 30,000 miles of streams and rivers, which provide a tremendous amount of habitat for freshwater mussels. Except for during glacial periods when Maine was ice-covered and post-glacial periods prior to isostatic rebound when much of Maine was inundated with seawater, the amount of available habitat has not been a limiting factor. More recently, however, the quality and character of freshwater habitat has been affected by human activity and demands on water resources. Damming of rivers and streams for mills, water storage, and transporting timber has been a central feature in the history and development of Maine since the earliest days of European settlement. Thousands of dams were built from the colonial period to the present (Hasbrouck 1984), greatly modifying Maine's river systems and altering fish communities and the amount and quality of habitat available for freshwater mussels.

Prior to modern-day water quality regulatory standards, many of Maine's waterbodies also were significantly altered and degraded by adjacent land use and dumping of industrial, commercial, and domestic waste. Throughout the 18th and 19th centuries, well over a million acres of Maine's forests were cleared for agriculture and timber harvest (Coolidge 1963) -- with little regard for protection of riparian areas or reducing the effects of erosion, sedimentation, or nutrient input. At the peak of Maine's lumbering operations, there were nearly 1300 sawmills on Maine's lakes and rivers generating sawdust, bark and logs. Much of this debris was dumped directly into the

State's waters, forming extensive deposits over the substrate (Nylander 1914, Wood 1961), some of which are still evident today. Throughout the 19th and into the mid 20th century, textile factories, pulp and paper mills, tanneries, and other industries also dumped their waste directly into Maine's rivers. Even well into the 1970s, many Maine communities continued to pump raw industrial and residential sewage directly into rivers and coastal areas (Maine Water Resources Plan 1969, Hasbrouck 1984). While documentation is lacking on the specific effects these and other historical degradations had on Maine's freshwater mussels, there can be little doubt that some populations of mussels, fish, and other aquatic life were significantly reduced.

Current Habitats. Maine likely has nearly the same amount of freshwater habitat as just prior to European colonization. The suitability of certain habitats for specific mussels, however, has been altered from historical conditions by flow and channel modification, pollution, and changes to the distribution and abundance of host fish. Although many older dams have washed away or been removed, there are still approximately 750 registered³ dams in Maine -- of which 125 are hydro power generating or storage dams (Dana Murch, MDEP, *personal communication*, June 8, 2007). These structures have altered flow patterns, habitat characteristics and fish communities, and may have caused local extirpations of some mussel species such as the alewife floater in southern coastal watersheds and the brook floater in the Presumpscot River. Alternatively, construction of dams may have increased habitat

³ Does not include dams smaller than 2 feet high or impounding less than 15 acre-feet of water, dams sufficiently breached to not meet size criteria, or old log driving dams no longer being maintained.

availability for species that prefer lentic conditions to riverine habitats. Large impoundments (e.g., Flagstaff Lake, Pemadumcook Lake, Chesuncook Lake) represent an enormous increase in habitat for species such as the eastern elliptio and eastern floater that successfully inhabit standing water habitats. Other impoundments, such as one on the Passadumkeag River upstream of the dam in Burlington, probably represent a significant habitat loss for species like the brook floater and eastern pearlshell that require flowing water environments.

Because of environmental legislation and other conservation programs, the quality of Maine's freshwater habitats has improved greatly over the last several decades. The advent of habitat protection and restoration measures such as environmental regulations governing land and water use, municipal sewage treatment plants, erosion and sedimentation control measures, pollution control programs and discharge standards, fish passage facilities, and other conservation efforts have helped improve water quality and protect habitat integrity in Maine's waterways. While pollution remains an ongoing conservation concern for aquatic ecosystems, these improvements likely are positively affecting freshwater mussel populations in some of Maine's once heavily degraded waterbodies.

Projected Habitats. Future habitat availability is difficult to predict for freshwater mussels as a group because each species will respond differently to modification or restoration of habitat, fish communities, and water quality. Effective outreach and compliance with existing environmental regulations should help protect freshwater mussel habitat in the future. However, despite great improvements in water quality, contamination from point and non-point source pollution likely will continue to affect

habitat quality for mussels. Dioxin, mercury, PCBs, phosphorus, untreated municipal wastewater, and other toxins continue to be serious problems for some Maine lakes, ponds, rivers, and streams (MDEP 2006).

As human populations increase, there also may be increasing conflict over water-use. Extraction of groundwater for industrial, commercial, agricultural, and residential purposes may lower the water table enough to cause rivers to lose water to, rather than recharge from, a groundwater supply. This is occurring in many watersheds in eastern Massachusetts and has several negative consequences for aquatic ecosystems, including reduced water availability, high temperatures, concentration of pollutants, and low dissolved oxygen (Trout Unlimited 2006). Sensitive freshwater mussels likely would be lost from these rivers.

As more dams are removed from Maine's rivers and streams, the amount and quality of riverine habitat should increase for species such as the brook floater and creeper, which require clean, free-flowing water. Conversely, habitat would be reduced for species that prefer standing or slow water environments and softer substrates, such as the eastern floater. The benefit to species such as the tidewater mucket and yellow lampmussel is less clear. Both mussels inhabit impoundments, but no data exist to compare their success in this artificial lentic environment versus a natural lake or free-flowing river. The increased access to anadromous fish species following dam removal or installation of fish passage would increase the extent of habitat available to species such as the alewife floater that rely on anadromous fish hosts.

One environmental trend that may significantly affect future habitat quality and availability for some freshwater mussel species is global warming. The northeastern

United States is expected to be strongly affected by climate change, resulting in the loss of significant portions of our existing cold and coolwater fisheries. This has important negative implications for freshwater mussels that rely on cold and coolwater fishes as hosts, such as the eastern pearlshell, but may increase habitat availability for habitat generalists such as the eastern elliptio and eastern floater.

A brief assessment of past, current and projected habitat for Maine's three listed species of freshwater mussels is provided below.

Yellow Lampmussel

Historical records for this species in Maine are scant, but documented reports prior to recent statewide surveys indicate that this mussel was known from both flowing and standing water habitats. Since neither of these habitat types was or is limiting in the State, the restricted distribution of this species is more likely a result of other factor(s) such as glacial history or watershed scale parameters. Today, the yellow lampmussel is found in as many or more lakes and ponds than rivers or streams, although this does not seem to be the case in other parts of its range where it is considered primarily a river species. While it seems to prefer gravel, sand, and cobble, it has been found on a variety of substrates indicating that this alone is not a strong habitat predictor. Nor are fish hosts likely a limiting factor for this mussel. Its confirmed hosts -- the white perch, yellow perch, and largemouth bass -- are widely distributed in Maine and found in a variety of aquatic habitats.

Within the three drainages where the yellow lampmussel occurs, the species is not found everywhere that potentially suitable habitat is present. Its distribution is

further restricted within each watershed, even where there appears to be similar habitat connecting populations. Dams have fragmented all of the major river systems where this species is found, but its tolerance of lentic habitat has allowed it to successfully occupy impounded sections of rivers. However, often it is observed that yellow lampmussels in an impoundment are concentrated in the upper reach, where substrates are coarser and cleaner, flow is greater, and water depth is shallower. This would seem to indicate that this mussel does have some preferred range or combination of habitat preferences and tolerances, and likely experienced some level of habitat loss from dams and other alterations that resulted in changes to habitat characteristics such as flow, temperature, substrate, depth, water chemistry, and water quality.

Current and future habitat quality and availability for this species likely depend on the ability of natural resource protection laws and regulations to maintain and enhance water quality and habitat integrity in Maine's aquatic ecosystems. Outreach and cooperative agreements with landowners and managers who have direct influence on mussel habitat (e.g., managed flow regimes, water level manipulation) also may be important for ensuring long term viability of habitat at some sites. It is possible that as more dams are removed and Maine's riverine habitat quality improves, habitat will increase for this mussel. Finally, determining specific habitat preferences and limiting factors will help maximize the success of future conservation and recovery efforts, including selection of survey, relocation and introduction sites, and providing habitat management recommendations.

Tidewater Mucket

A past, current, and projected habitat analysis for the tidewater mucket is nearly identical to what has been noted above for the yellow lampmussel. These two species have very similar distributions in Maine and often co-occur in the same waterbodies. A few differences have been observed, however, that may indicate some divergence in habitat preferences or tolerances between them. The tidewater mucket seems to have a greater tolerance for softer substrates (i.e., silt, clay) and slower water. Unlike the yellow lampmussel, it is found in ponds and lakes throughout its range and, in Maine, has been more frequently observed in lower reaches of impoundments. Consequently, the longterm effects of past dam construction and future dam removals on habitat availability and quality for this species are unclear.

The tidewater mucket also is found in lower reaches of a watershed (e.g., Merrymeeting Bay), many river miles below the nearest yellow lampmussel occurrence in both the Penobscot and Kennebec Rivers. Within upper reaches of these two watersheds, there are several waterbodies where one species is found but not the other. In the large Mattawamkeag River drainage of the Penobscot watershed, the mucket appears to be absent entirely. Whether these differences reflect disparities in habitat preferences, life history strategies, or the loss of habitat suitability for one species or the other is not known. As noted for the yellow lampmussel, quantifying the tidewater mucket's specific habitat preferences and limiting factors is needed to better understand its current distribution and habitat requirements, as well as its future recovery potential.

Brook Floater

The brook floater is found in flowing-water habitats, from small streams to large rivers, where it prefers moderate flow rates and coarse sand and gravel substrates. The amount of stream and riverine habitat in Maine with seemingly ideal habitat for this species was and is vast, yet its current distribution is known to be fairly restricted to a handful of watersheds in midcoast, central, and Downeast regions of the State. Because historical records are extremely limited, it is difficult to assess potential changes from past habitat availability. However, the brook floater cannot tolerate standing water and is sensitive to changes in habitat integrity and water quality. In addition, its hosts are comprised primarily of small-bodied, fluvial specialists whose populations may be negatively affected by habitat modification, introduction of larger predatory fish species, and changes in thermal regime. Past degradations to Maine rivers from water pollution, dams, and other habitat alterations likely had significant effects on the suitability and availability of habitat for this species. The fragmentation of extant occurrences, as well as conspicuous gaps in distribution throughout coastal and central Maine, suggest that the brook floater may have been extirpated from some rivers.

Current and future habitat quality and availability for this species likely depend on the ability of natural resource protection laws and regulations to maintain and enhance water quality and habitat integrity in Maine's riverine ecosystems. Outreach and cooperative agreements with landowners and managers who have direct influence on mussel habitat (e.g., managed flow regimes, water level manipulation) also may be important for ensuring long term viability of habitat at some sites. It is likely that as

more dams are removed and Maine's riverine habitat quality improves, habitat will increase for this mussel. Finally, determining specific habitat preferences and limiting factors will help maximize the success of future conservation and recovery efforts, including selection of survey, relocation, and introduction sites, and providing habitat management recommendations.

POPULATION ASSESSMENT

General Population Assessment

Past Populations. Except for some scant, isolated, and sometimes questionable records from the 19th and early 20th centuries, information on historical populations of freshwater mussels in Maine is very limited. Presumably, species with broad habitat preferences and low host specificity, such as the eastern elliptio, were at least as abundant and widespread as they are today. Likewise, species that are more sensitive to habitat changes or perturbations are more likely to have suffered declines in population size and distribution as a result of habitat alterations and degradations during the past few centuries. There is some evidence suggesting that species may have been extirpated from some rivers, including the brook floater from the Presumpscot and Dennys Rivers, and the alewife floater from southern coastal watersheds. A true assessment of past populations is not possible, however, for any of Maine's freshwater mussel species.

Current Populations. As a result of the Maine Freshwater Mussel Atlas Project, excellent information exists on the current distribution and relative abundance of all the State's mussel species. Whereas some species are widespread, others exhibit restricted distributions that might be explained by one or more factors, such as fish host distribution, habitat loss, landscape patterns, or Maine's glacial history. For example, the eastern lampmussel appears confined to a narrow band across central portions of the State, and is largely absent from northern, western, Downeast, and extreme southern regions. Where it does occur, this species often is abundant and appears to

tolerate a variety of habitat and environmental conditions. Therefore, it is more likely the current distribution of this mussel has been limited by landscape factors or zoogeography, rather than by human influences. In contrast, the current distribution of the alewife floater demonstrates large gaps between coastal watersheds, a truncated distribution in upper river reaches, and an obvious absence from southern coastal areas. This current pattern likely reflects a significant reduction from the species' historical natural distribution, as hundreds of dams have blocked passage of its anadromous fish hosts on Maine rivers for over three hundred years.

Information on the status of Maine's freshwater mussel populations is largely limited to qualitative data (e.g., relative abundance, observed density, evidence of reproduction) collected during recent statewide surveys. Although it is apparent that some species are abundant and presumably doing well, others are more frequently documented in low numbers and densities, and with little evidence of recruitment. Populations also vary from site to site -- a particular species may carpet the river bottom in one location, but be much less abundant or absent at another. There are many rivers and lakes in Maine with extremely low observed population densities of certain species, especially those listed as threatened and special concern. Without past population data, however, it may be difficult to determine whether these species naturally occur at low population densities or if humans or other factors have caused population declines. Likewise, without quantitative survey data to measure population demographics and a current baseline from which to monitor longterm trends, an accurate population assessment is not possible, particularly for the rarer species.

Limited quantitative survey data are available for several populations, primarily of the yellow lampmussel and tidewater mucket (see below). Wick (2006) measured demographics of these two listed species at five sites, and Kurth (2007) intensively surveyed these species in the Fort Halifax impoundment on the Sebasticook River.

Projected Populations. Future population trends will depend on a variety of environmental factors such as flow modification, pollution, changes in fish communities, climate change, and restoration of natural habitats. The response of each species to these changes will vary according to its ecological tolerance, life history, and dispersal ability. Compliance with environmental regulations, as well as proactive conservation and management actions such as outreach, river restoration, maintenance of riparian buffers and flow management agreements, should help maintain or improve current populations. Translocation of individuals to suitable yet previously unoccupied habitats is a potential method for increasing the numbers and occurrences of listed species, if warranted under an approved recovery plan. However, a comprehensive understanding of the potential threats and limiting factors influencing freshwater mussel populations in Maine is lacking.

A brief assessment of past, current and projected populations for Maine's three listed species of freshwater mussels is provided below.

Yellow Lampmussel

Historical (pre-1984) records for this species are known only from nine sites, five of which are from the St. George River (Appendix 2). Anecdotal information on population size or status is not reported with any of these records. Recent

comprehensive surveys have significantly increased the number and distribution of documented occurrences for this mussel (Appendix 2), which appears to be confined to the Penobscot, St. George, and lower Kennebec River watersheds (Figure 5). Surveys also reconfirmed its presence at all previously known sites. Limited by scant historical data, there is no evidence to suggest that past populations have been extirpated -- although numbers and distributions likely have been reduced at some locations, particularly in the Kennebec River watershed.

Several sites where this species is present have relatively large and apparently healthy populations, including the West Branch Mattawamkeag and lower Sebasticook Rivers, and Sennebec Pond. Typically it is observed in extremely low numbers and densities. Limited quantitative survey data do exist for this mussel at several sites (see Past Research and Management), but baseline population estimates and demographics are lacking for nearly all populations.

Without baseline data and a longterm monitoring program, future population trends of this species cannot be measured. It is likely that currently stable populations would remain so as long as habitat quality (including fish host availability) and regulatory protection are maintained or enhanced. Existing and potential threats and limiting factors are not fully understood for this mussel. For example, the short and long-term implications of increasing dam removals on Maine rivers could have significant effects on the future size and status of many yellow lampmussel populations. Whether the presumed net gain in habitat quality outweighs the net loss from mortality, habitat alteration, and fish host redistribution has yet to be determined.

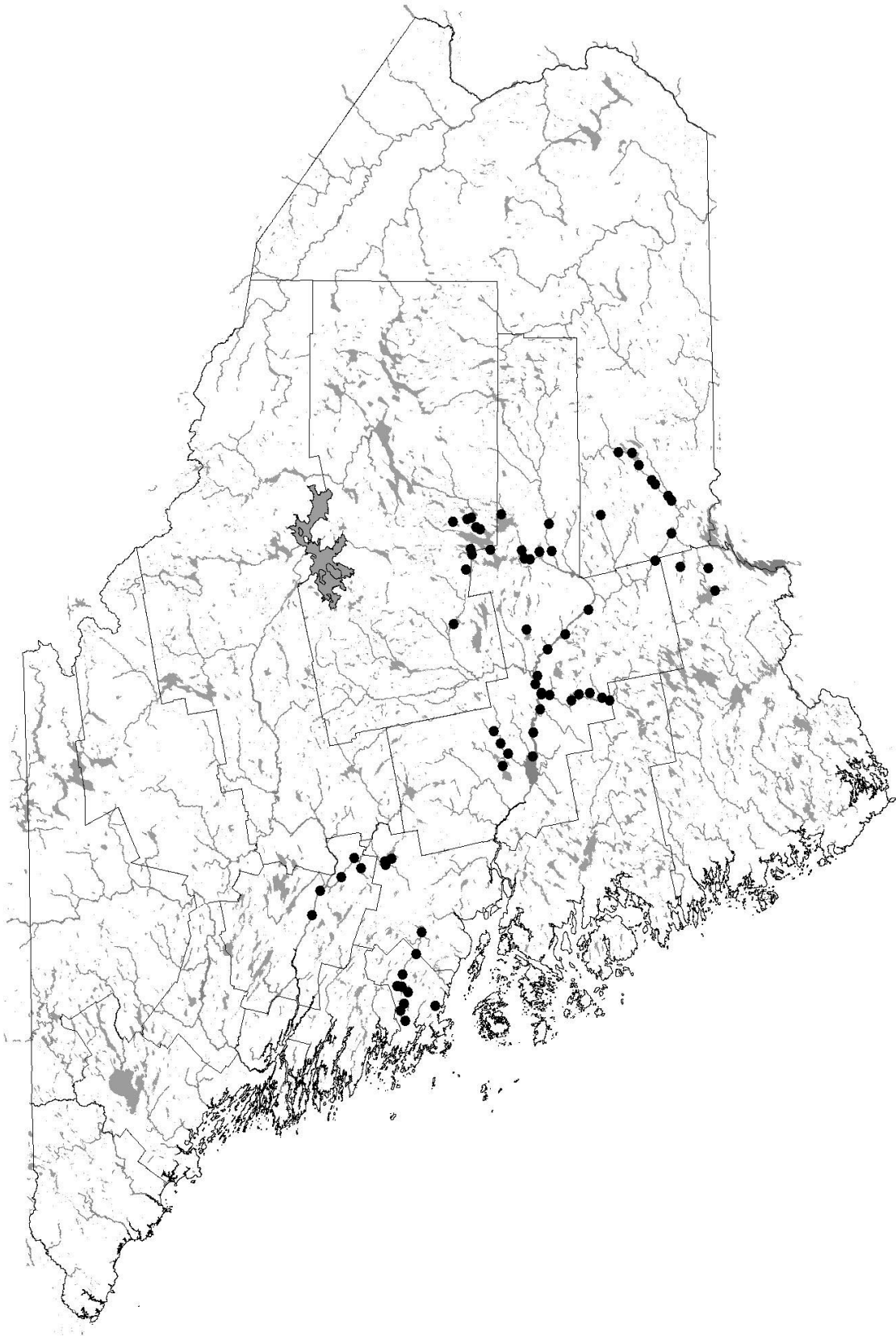


Figure 5. Occurrences of the Yellow Lampmussel in Maine.

Tidewater Mucket

Past, current, and projected population assessments for this species are similar to those of the yellow lampmussel. Historically, the tidewater mucket was reported from eight sites (Appendix 3) -- five of which are the same early St. George River sites as for the yellow lampmussel. As with the lampmussel, population information was not recorded for these locations, and the number and distribution of currently known occurrences has increased significantly with statewide survey efforts (Appendix 3). The tidewater mucket has been reconfirmed at all previously known sites but Cold Stream Pond (Penobscot Co.), where the species is thought to be extirpated.

Also confined to the Penobscot, St. George, and lower Kennebec River watersheds (Figure 6), the tidewater mucket often is found at the same sites as the yellow lampmussel. A noticeable exception to this is the mucket's absence from the Mattawamkeag River drainage, where the lampmussel is fairly well distributed. In contrast, the mucket's current distribution extends into areas where the lampmussel appears to be absent: higher reaches of the Sebasticook River drainage, lower reaches of the Penobscot and Kennebec River drainages, and the Sebec River watershed (Piscataquis Co.). Whereas gross differences in distribution might be explained by landscape scale conditions, or more intrinsic factors such as fish hosts or habitat tolerances, this species likely also experienced reductions in the number and distribution of some populations over the past few centuries. However, based on numbers recovered during the Edwards Dam removal, plus its broader distribution in the

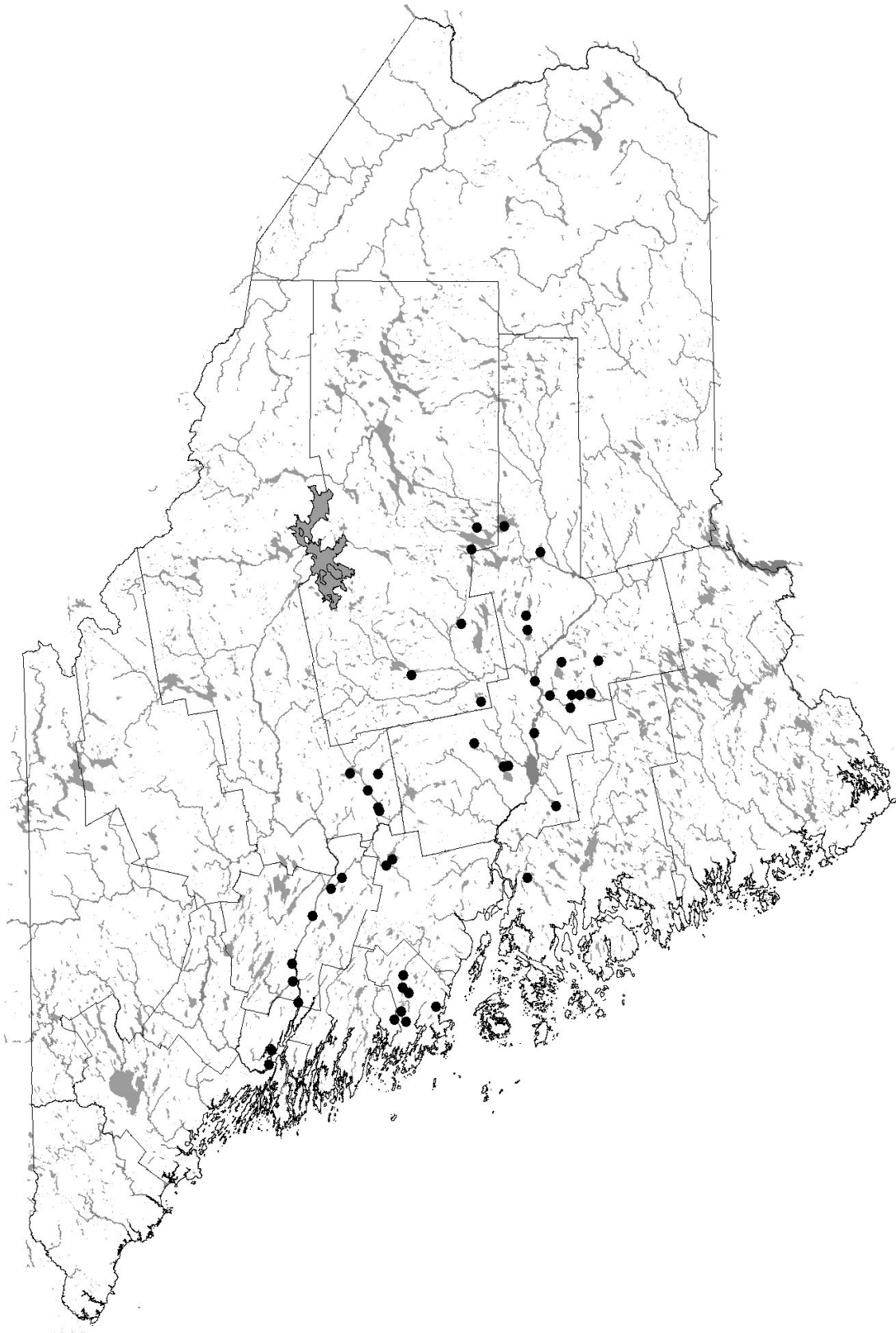


Figure 6. Occurrences of the Tidewater Mucket in Maine.

watershed, the tidewater mucket may have fared better than the yellow lampmussel in the Kennebec River drainage.

A number of locations seem to support relatively large populations of tidewater muckets, with many young individuals observed (e.g., Kennebec and Sebasticook Rivers, Mud Pond (Old Town, Penobscot Co.)). At most sites where the species occurs, however, only a few individuals have been found. Limited quantitative survey data also exist for the same sites as the yellow lampmussel (see Past Research and Management), but baseline population estimates and demographics are lacking for nearly all populations.

Without baseline data and a longterm monitoring program, future population trends of this species cannot be measured. It is likely that currently stable populations would remain so as long as habitat quality (including fish host availability) and regulatory protection are maintained or enhanced. However, existing and potential threats and limiting factors are not fully understood. As with the yellow lampmussel, the short and long-term implications of increasing dam removals on Maine rivers could have significant effects on the future size and status of many mucket populations -- particularly since this species seems to tolerate quieter waters and softer substrates.

Brook Floater

Only three historical Maine records are known to exist for this species (Appendix 4). Following completion of MDIFW's recent statewide surveys, the number and distribution of documented occurrences have been greatly increased (Appendix 4). Its distribution is now known to be concentrated in the Penobscot River watershed, with scattered

populations also present in the Kennebec River drainage and several small midcoast and Downeast rivers. A highly isolated occurrence in the Pleasant River (Cumberland Co.) is southern Maine's only known brook floater population (Figure 7).

The brook floater's extreme isolation in southern Maine and its conspicuous absence from many coastal river systems and major drainages in midcoast and central regions may indicate this species has experienced local extirpations. Within the large Kennebec River watershed, this mussel has been documented only at a few sites in the mid portion of the drainage -- suggesting that its distribution in this major river system has been contracted. Recent attempts to reconfirm the species in the Dennys River (Washington Co.), where it was last observed in 1985, have been unsuccessful. Numerous surveys specifically focused on locating the brook floater in the Presumpscot River (Cumberland Co.) and its lower tributaries, where it would be expected to occur based on its upstream presence in the Pleasant River, also have failed. Of all Maine's freshwater mussels, the brook floater is most likely to have been significantly affected by past alterations and degradations of the State's rivers and streams. Declines and extirpations resulting from dams, bridge and road construction, stream channelization, and water quality degradation are well documented in other parts of this species' range (NatureServe 2007), and there is no reason to assume Maine mussels would have been immune to similar habitat alterations.

Several sites where this species is present have relatively large and apparently healthy populations, including the East Branch Pleasant (Piscataquis Co.), Passadumkeag (Penobscot Co.), and St. George (Knox and Waldo Co.) Rivers. More than any other Maine mussel, however, the brook floater typically is observed in

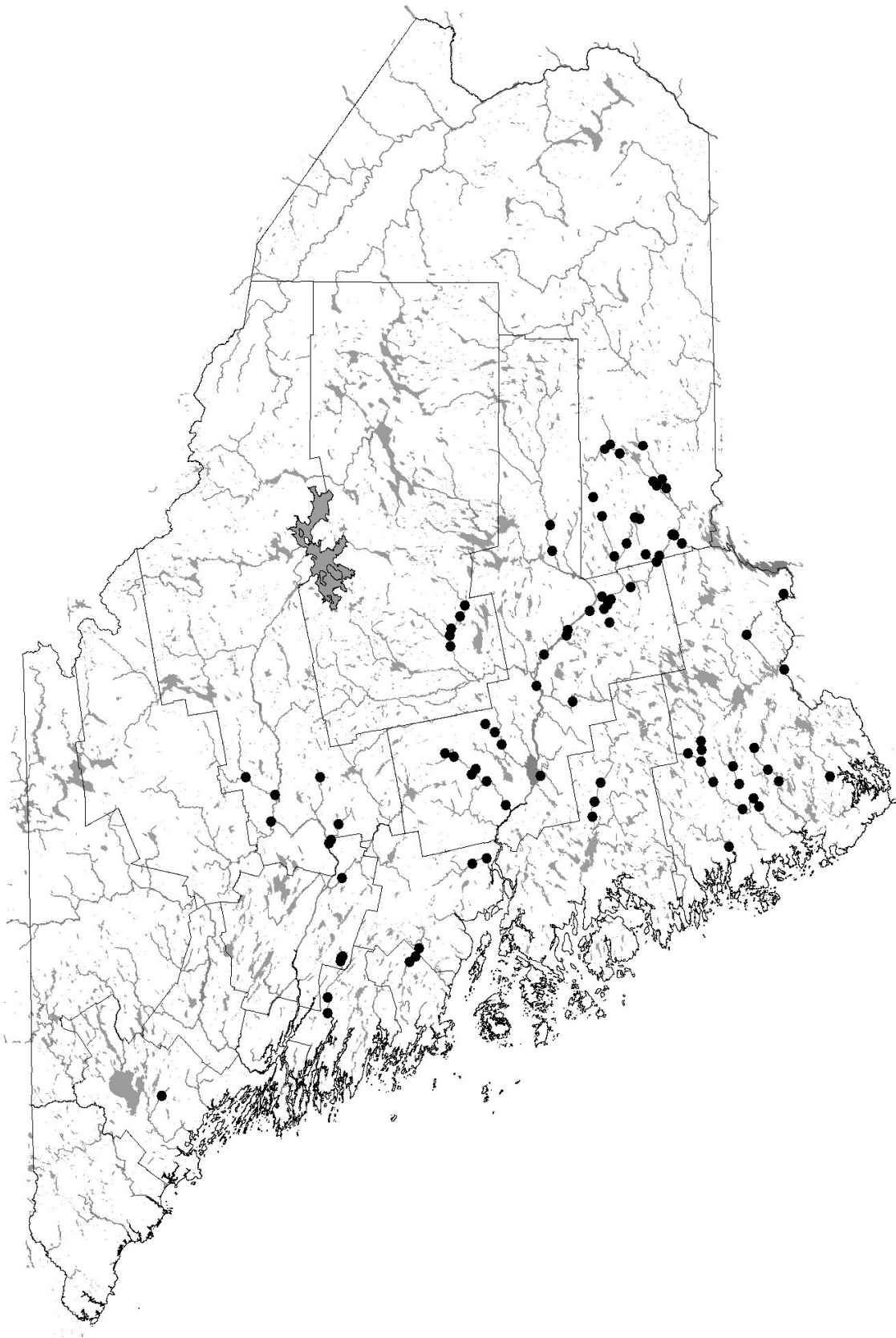


Figure 7. Occurrences of the Brook Floater in Maine.

very low numbers and densities -- nearly 70% of all observations are based on ≤ 10 live animals or only relict shells. Young individuals rarely are observed during qualitative visual searches.

The current status of the brook floater can only be assessed based on qualitative data gathered during past statewide surveys. Without quantitative survey efforts and a longterm monitoring program, determinations of local and statewide population sizes and trends cannot be made. Likewise, the longterm viability of small, low density populations of brook floaters is unknown. It is likely that currently stable populations would remain so as long as habitat quality (including fish host availability) and regulatory protection are maintained or enhanced. The growing trend of dam removals and river restoration projects in Maine is likely to have a significant positive influence on some of the State's brook floater populations by increasing flow rates and improving stream habitat quality. However, existing and potential threats and limiting factors are not fully understood for this mussel. Its current rangewide rarity may indicate some other factor(s) is contributing to population declines or preventing recovery.

Limiting Factors and Threats

Factors that determine patterns of distribution and abundance in freshwater mussel populations are not completely understood and may vary among species and locations. Generally, species having a narrower range of habitat preferences, such as the brook floater or eastern pearlshell, would be expected to be limited by specific habitat parameters (e.g., flow, temperature, substrate) to a greater degree than habitat generalists, such as the eastern elliptio or eastern floater. Mussel density or distribution

within a waterbody, however, often is not strongly correlated with simple microhabitat variables (Strayer 1981; Strayer and Ralley 1993; Layzer and Madison 1995). Loftin (2005) looked at potential landscape-level factors controlling the distribution of tidewater mussels and yellow lampmussels in Maine, and found some correlations with watershed size, accumulative dam height, number of first order streams in the watershed, and proportion of the watershed that is forested, but was unable to develop reliable models to predict their occurrence due to their low numbers across a broad range of conditions.

Seasonal or sporadic stressors such as severe oxygen deficiencies, extreme water level fluctuations, reduced flows, low food availability, and heavy or prolonged siltation can influence mussel occurrences and survival. Disease, parasites, and predation also may be limiting, particularly on a local scale. Competition from the introduced zebra mussel is a severe limiting factor for many native freshwater mussel populations where this exotic invasive mollusk has become established. Fortunately, the zebra mussel has not yet been documented in Maine, where the low calcium concentration and low pH of most waterbodies may limit its risk of introduction (Whittier et al. 1995). Although a significant threat in some parts of the country, unregulated or illegal harvest has been reported only sporadically in Maine, but may have reduced some local populations.

Due to the unique life cycle of unionids, specific fish hosts must be present in order for most species to successfully reproduce. The availability of fish hosts is therefore a potentially significant limiting factor, particularly for mussel species that are restricted to just one or a few host species. Natural or anthropogenic factors that affect

fish community composition, distribution, and movement also can have significant effects on mussel populations. Specifically, loss or degradation of host habitat and barriers to host movement such as dams and impoundments can result in local extirpation of mussel populations and prevent unionid migration and the exchange of genetic material among populations (Watters 1996; Vaughn 1997).

Habitat alterations and degradations resulting from human use of water resources have severely threatened freshwater mussel populations rangewide. Water quality degradation from point and nonpoint source pollution and poor land use practices, as well as stream habitat alteration from dams, impoundments and channelization, continue to pose significant threats to mussel populations. Water level manipulations and drawdowns from agricultural withdrawal, hydropower generation, and dam repair or removal can reduce available habitat and cause extensive mortality of exposed mussels. Major construction and utility projects (e.g., bridge construction, utility line crossings) also can degrade or alter habitat and result in mortality if efforts are not undertaken to conserve mussel populations present in the project area. The effects of global warming on aquatic habitats (e.g., host availability, water temperature, invasive species, changes in storm flows and low flows) pose potential future threats to some species of freshwater mussels that rely on coolwater fish hosts (e.g., eastern pearlshell) or have a narrow range of habitat tolerances (e.g., brook floater).

USE AND DEMAND ASSESSMENT

Freshwater mussels have long been important to humans. Historically, indigenous tribes in North America used their meat as a food source (Parmalee and Klippel 1974) and their shells and pearls as decorations (e.g., jewelry, ornaments) and implements (e.g., spoons, hide scrapers, hoes). In modern societies, freshwater mussels also have had considerable economic importance. Beginning in the 1800s, a commercial fishery was established in some parts of the country to harvest mussel shells for the manufacture of buttons. This fishery peaked in the early 1900s when over 40 million gross⁴ of buttons were produced -- representing a 12.5 million dollar industry (Fassler 1997). By the mid 20th century, however, the invention and widespread use of plastic brought the shell button industry to a close.

In the early 1900s, a cultured pearl industry arose using beads cut from freshwater mussel shells as seed pearls in marine oysters. Dominated by the Japanese, this industry largely has been supplied by North American mussel shells (Fassler 1997). In 1991, the commercial export value of shells shipped to Japan from the United States (10,000 metric tons annually) was estimated at \$70 million dollars (Ahlstedt and McDonough 1993). This fishery has since declined dramatically due to declining mussel populations and harvest restrictions by many states. New England's freshwater mussels were spared this commercial harvest pressure because species native to the region are generally small and thin-shelled.

⁴ One gross equals a twelve dozen (i.e., 144 buttons).

Although Maine's mussels never have been a significant economic resource, they have experienced some unknown level of consumptive use for profit. Several large-scale collections for sale to the biological supply industry have been reported to MDIFW over the past decade, and numerous inquiries have been received about harvest restrictions and commercial use of freshwater mussels for human consumption, freshwater pearl production and bait supply.

Prior to invertebrates being listed under Maine's Endangered Species Act, freshwater mussels largely had gone unnoticed by the general public. Today, even with three species listed as state-threatened, they still are unknown to many of Maine's citizens due to their inconspicuous nature. Continuing public outreach to increase awareness of and appreciation for freshwater mussels and their role in the aquatic environment could increase the use and demand for these invertebrates from a larger segment of the public. An estimated 91% of Maine's adult citizens engaged in some nonconsumptive use of wildlife and expended more than \$50 million in 1988 (Boyle et al. 1990). As the popularity of photography and nature study and appreciation grows, and as awareness of the diversity of Maine's wildlife resources grows, the demand for observational and photographic use of rare species, such as endangered or threatened invertebrates, will increase. As interest in these species intensifies, there will likely be increased public demand for interpretive and educational materials to explain and justify species and habitat protection measures.

Increasing numbers of U.S. citizens desire preservation of the greatest diversity of species possible, at state, national, and global levels (Kellert 1980). These desires are based on increasing public perception of scientific, utilitarian, and cultural values of

biological diversity, as well as ethical arguments for preserving plant and animal species that are endangered by the actions of human society. At the state level, public support for preserving biodiversity in Maine is growing and is reflected in strong state legislation to protect endangered and threatened wildlife and their habitats. Regardless of the appeal and familiarity of an individual species, public demand for the conservation of rare species, especially those listed as endangered or threatened, is unequivocally mandated in the preamble to the Maine Endangered Species Act of 1975:

“The Legislature finds that various species of fish or wildlife have been and are in danger of being rendered extinct within the State of Maine, and that these species are of aesthetic, ecological, educational, historical, recreational, and scientific value to the people of the State. The Legislature, therefore, declares that it is the policy of the State to conserve, by according such protection as is necessary to maintain and enhance their numbers, all species of fish or wildlife found in the State, as well as the ecosystems upon which they depend.”

As such, MDIFW is committed to preserving the diversity of all wildlife in the state and is entrusted with the preservation of Maine’s natural heritage for future generations. This responsibility is manifested by an increasing commitment to management and research programs that protect and enhance endangered and threatened species of all taxa. The protection and ecological understanding of even inconspicuous species, such as freshwater mussels, are vital to proper ecosystem management and to the preservation of Maine’s natural heritage.

SUMMARY AND CONCLUSIONS

Freshwater mussels are one of the most imperiled faunal groups in North America. Of nearly 300 species native to the U.S., approximately 75% are considered to be endangered, threatened, or special concern at the state and federal levels, and 35 species are believed already extinct. Degradation and loss of habitat resulting from human use such as dams, stream channelization, and water pollution -- combined with overharvest and competition from invasive species -- have led to these declines. Ten species are documented to occur in Maine, three of which are state-listed as threatened and one as special concern. No species are known to have been extirpated from the State, although local populations are likely to have been lost. Currently, state wildlife laws provide little regulatory protection for freshwater mussels and other invertebrates unless they are listed under Maine's Endangered Species Act.

Historical data on the distribution and status of freshwater mussels in Maine is limited. Since the early 1990s, comprehensive statewide survey efforts by MDIFW have significantly increased knowledge of these species. Cooperative projects with the University of Maine also have led to advances in understanding important ecological and conservation issues such as fish host identification, conservation genetics, and relocation strategies. Additional research is needed to investigate life histories, influences of contaminants, significance of impoundments, and effects of dam removals, and to identify other key threats and limiting factors to rare mussels. Important management needs include implementation of a long-term population monitoring scheme, development of management guidelines for projects potentially affecting rare

mussels, establishment of co-operative habitat management agreements with hydro companies and other large landowners, investigating the need for establishing regulatory protection for all of Maine's freshwater mussel species, improving habitat quality through river restoration and water quality enhancement, and developing more effective outreach materials.

Unlike in other parts of the country, freshwater mussels currently do not have significant commercial value in Maine. However, their ability to improve water quality, nutrient cycling, and substrate conditions and their role as food for many fish and wildlife species make them important components of Maine's stream, river, lake, and pond ecosystems. Their life history traits also lend them to serve as valuable indicators of aquatic ecosystem health. Maine's freshwater mussel fauna has fared relatively well compared to populations in many other states, and the State ultimately may serve as an important refugium for species that have been lost elsewhere. However, threats to habitat quality persist, and several species are rare enough to warrant state-listing. The development of goals and objectives for conserving and managing this group of species will greatly enhance MDIFW's ongoing efforts to protect and promote freshwater mussels as an important part of Maine's natural heritage.

LITERATURE CITED

- Ahlstedt, S. A. and T. A. McDonough. 1993. Quantitative evaluation of commercial mussel populations in the Tennessee River portion of Wheeler Reservoir, Alabama. Pages 38-49 *in*: K.S. Cummings, A.C. Buchanan, and L.M. Koch, eds. Conservation and management of freshwater mussels. Proceedings of a UMRCC symposium, 12-14 October 1992, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.
- Albright, J. 1991. A survey of selected rare invertebrate species of Maine. A report to the Endangered and Nongame Wildlife Grants Program, Maine Department of Inland Fisheries and Wildlife, Bangor, ME 04401.
- Amyot, J. and J. A. Downing. 1997. Seasonal variation in vertical and horizontal movement of the freshwater bivalve *Elliptio complanata* (Mollusca: Unionidae). *Freshwater Biology* 37:345-354.
- Amyot, J. and J. A. Downing. 1998. Locomotion in *Elliptio complanata* (Mollusca: Unionidae): a reproductive function? *Freshwater Biology* 39:351-358.
- Ansell, A.D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographic range. *Journal du Conseil* 31:364-409.
- Arey, L. B. 1932a. The formation and structure of the glochidial cyst. *Biological Bulletin* 52:212-221.
- Arey, L. B. 1932b. The nutrition of glochidia during metamorphosis. *Journal of Morphology* 53:201-219.
- Balfour, D. L. and L. A. Smock. 1995. Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca: Unionidae) in a headwater stream. *Journal of Freshwater Ecology* 10:255-268.
- Bauer, G. 1987a. Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *Journal of Animal Ecology* 56:691-704.
- Bauer, G. 1987b. The parasitic stage of the freshwater pearl mussel (*Margaritifera margaritifera* L.) III. Host relationships. *Archiv fuer Hydrobiologie Suppl.* 76(4):413-423.
- Bauer, G. 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in central Europe. *Biological Conservation* 45:239-253.
- Bauer, G. 1994. The adaptive value of offspring size among freshwater mussels (Bivalvia: Unionoidea). *Journal of Animal Ecology* 63:933-944.

- Beckett, D. C., B. W. Green, S. A. Thomas, and A. C. Miller. 1996. Epizotic invertebrate communities on Upper Mississippi River unionid bivalves. *The American Midland Naturalist* 135:102-114.
- Boyle, K.J., S.D. Reiling, M. Tiesl, and M.L. Phillips. 1990. A study of the economic impact of game and non-game species on Maine's economy. Staff Paper No. 423, Dept. of Agriculture and Resource Economics, University of Maine. 119 pp.
- Bringolf, R., R. Heltsley, C. Eads, T. Newton, S. Fraley, D. Shea, and W. G. Cope. (2007a, March 14). *Environmental occurrence of fluoxetine and its effects on freshwater mussel reproduction*. Presentation at the 5th biennial Freshwater Mollusk Conservation Society Symposium, Little Rock, Arkansas.
- Bringolf, R., S. Mosher, P. Lazaro, C. Eads, C. Barnhart, D. Shea, and W. G. Cope. (2007b, March 14). *A comprehensive assessment of the hazards of current use pesticides to native freshwater mussels*. Presentation at the 5th biennial Freshwater Mollusk Conservation Society Symposium, Little Rock, Arkansas.
- Buddensiek, V. 1995. The culture of juvenile freshwater pearl mussels *Margaritifera margaritifera* L. in cages: a contribution to conservation programmes and the knowledge of habitat requirements. *Biological Conservation* 74:33-40.
- Clarke, A. H. Jr. 1981a. The tribe Alasmidontini (Unionidae: Anodontinae), Part I: *Pegias*, *Alasmidonta*, and *Arcidens*. *Smithsonian Contributions to Zoology*, Number 326. Smithsonian Institution Press, Washington D. C. 101pp.
- Clarke, A. H. Jr. 1981b. The freshwater molluscs of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada. 446pp.
- Coker, R. E., A. F. Shira, H. W. Clark, and A. D. Howard. 1921. Natural history and propagation of fresh-water mussels. *Bulletin of the U.S. Bureau of Fisheries* (Document 893) 37:75-181.
- Coolidge, P. T. 1963. *History of the Maine woods*. Furbish-Roberts Printing Company, Inc., Bangor, Maine. 805pp.
- Coon, T. G., J. W. Eckblad, and P. M. Trygstad. 1977. Relative abundance and growth of mussels (Mollusca: Eumellibranchia) in pools 8, 9, and 10 of the Mississippi River. *Freshwater Biology* 7:279-285.
- Cunjak, R. A. and S. E. McGladdery. 1991. The parasite-host relationship of glochidia (Mollusca: Margaritiferidae) on the gills of young-of-the-year Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology* 69:353-358.
- Cvancara, A. M. 1972. Lake mussel distribution as determined with SCUBA. *Ecology* 53:154-157.

- Davenport, D. and M. Warmouth. 1965. Notes on the relationship between the freshwater mussel *Anodonta implicata* Say and the alewife *Pomolobus pseudoharengus* (Wilson). *Limnology and Oceanography* 10, Supplement: R74-R78.
- Di Maio, J. and L. D. Corkum. 1995. Relationship between the spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. *Canadian Journal of Zoology* 73:663-671.
- Downing, J. A., Y. Rochon, M. Perusse, and H. Harvey. 1993. Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanata*. *Journal of the North American Benthological Society* 12:148-156.
- Eads, C., C. J. Kittel, G. Wilson, R. J. Bradford, A. E. Bogan, and J. F. Levine. (2007, March 13). *Propagation and culture of freshwater mussels in North Carolina (2004-2006)*. Poster presented at the 5th biennial Freshwater Mollusk Conservation Society Symposium, Little Rock, Arkansas.
- Fassler, C. R. 1997. The American mussel crisis: effects on the world pearl industry. Pages 265-277 in: K. S. Cummings, A. C. Buchanan, C. A. Mayer, and T. J. Naimo, eds. Conservation and management of freshwater mussels II: initiatives for the future. Proceedings of a UMRCC symposium, 16-18 October 1995, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.
- Fuller, S. L. H. 1974. Clams and mussels (Mollusca: Bivalvia). Pages 215-273 in: C. W. Hart, Jr. and S. L. H Fuller, eds. *Pollution Ecology of Freshwater Invertebrates*. Academic Press, New York.
- Ghent, A. W., R. Singer, and L. Johnson-Singer. 1978. Depth distributions determined with SCUBA, and associated studies of the freshwater unionid clams *Elliptio complanata* and *Anodonta grandis* in Lake Bernard, Ontario. *Canadian Journal of Zoology* 56:1654-1663.
- Haag, W. R. and M. L. Warren Jr. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. *Canadian Journal of Fisheries and Aquatic Sciences* 55:297-306.
- Haag, W. R., R. S. Butler, and P. D. Hartfield. 1995. An extraordinary reproductive strategy in freshwater bivalves: prey mimicry to facilitate larval dispersal. *Freshwater Biology* 34:471-476.
- Hanek, G. and C. H. Fernando. 1978. Spatial distribution of gill parasites of *Lepomis gibbosus* (L.) and *Ambloplites rupestris* (Raf.). *Canadian Journal of Zoology* 56(6):1235-1240.
- Hanlon, S. D. and D. G. Smith. 1999. An attempt to detect *Pyganodon fragilis* (Mollusca: Unionidae) in Maine. *Northeastern Naturalist* 6:119-132 .

- Hartfield, P. and E. Hartfield. 1996. Observations on the conglomerates of *Ptychobranthus greeni* (Conrad 1834) (Mollusca: Bivalvia: Unionoidea). The American Midland Naturalist 135:370-375.
- Hasbrouck, S. 1984. Maine rivers and streams. Resource Highlights, The Land and Water Resources Center, University of Maine, Orono, Maine. August edition. 12pp.
- Hoggarth, M. A. 1992. An examination of the glochidia-host relationships reported in the literature for North American species of Unionacea (Mollusca: Bivalvia). Malacology Data Net 3(1-4):1-30.
- IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 03 July 2007.
- Johnson, R. I. 1970. The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the southern Atlantic Slope region. Bulletin of the Museum of Comparative Zoology 140(6):263-450.
- Johnson, S. L. (1999, March 17-19). *Habitat suitability criteria for freshwater mussels: can mussels seek out suitable habitat?* Presentation at the 1st Symposium of the Freshwater Mollusk Conservation Society, Chattanooga, Tennessee.
- Jokela, J. and P. Mutikainen. 1995. Effect of size-dependent muskrat (*Ondatra zibethica*) predation on the spatial distribution of a freshwater clam, *Anodonta piscinalis* Nilsson (Unionidae, Bivalvia). Canadian Journal of Zoology 73:1085-1094.
- Karna, D. W. and R. E. Millemann. 1978. Glochidiosis of salmonid fishes. III. Comparative susceptibility to natural infection with *Margaritifera margaritifera* (L.) (Pelecypoda: Margaritanidae) and associated histopathology. Journal of Parasitology 64(3):528-537.
- Kat, P. W. 1983. Genetic and morphological divergence among nominal species of North American *Anodonta* (Bivalvia: Unionidae). Malacologia 23:361-374.
- Kat, P. W. 1984. Parasitism and the Unionacea (Bivalvia). Biological Review 59:189-207.
- Kellert, S.R. 1980. Public attitudes towards critical wildlife and natural habitat issues. U.S. Govt. Printing Office, Wash., D.C.
- Kelly, M. W. 2004. Conservation genetics of two rare freshwater mussels: the tidewater mucket (*Leptodea ochracea*) and the yellow lampmussel (*Lampsilis cariosa*). M.S. Thesis, University of Maine.

- Kneeland, S.C. 2006 Identification of fish hosts for wild populations of rare freshwater mussels (*Lampsilis cariosa* and *Leptodea ochracea*) using a molecular DNA key. M.S. Thesis, University of Maine.
- Kraemer, L. R. 1970. The mantle flap in three species of *Lampsilis* (Pelecypoda: Unionidae). *Malacologia* 10:225-282.
- Kurth, J.E. 2007. Methods for the translocation of the yellow lampmussel (*Lampsilis cariosa*) and the tidewater mucket (*Leptodea ochracea*) in the Fort Halifax Dam impoundment of the Sebasticook River, Maine. M.S. Thesis, University of Maine.
- Layzer, J. B. and L. M. Madison. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. *Regulated Rivers: Research and Management* 10:329-345.
- Lefevre, G. and W. C. Curtis. 1911. Metamorphosis without parasitism in the Unionidae. *Science* 33:863-865.
- Lellis, W. A. and C. S. Johnson. 1996. Delayed reproduction of the freshwater mussel *Elliptio complanata* through temperature and photoperiod control. *Journal of Shellfish Research* 15:485.
- Lermond, N. W. 1908. Shells of Maine: A catalogue of the land, fresh-water and marine Mollusca of Maine. Privately published by the author, Thomaston, Maine. 46 pp. [reproduced verbatim in 1909 on pp. 217-262 of *Seventh Annual Report of the Commissioner of Agriculture of the State of Maine*].
- Lewis, J. B. and P. N. Riebel. 1984. The effect of substrate on burrowing in freshwater mussels (Unionidae). *Canadian Journal of Zoology* 62:2023-2025.
- Loftin, C. S. (2005, December). Landscape control of the distribution of two rare Atlantic Slope freshwater mussels in Maine, the yellow lampmussel (*Lampsilis cariosa*) and tidewater mucket (*Leptodea ochracea*). Final report for the Maine Cooperative Fish and Wildlife Research Unit, Orono, ME.
- Luoma, J. R. (1997, January-February). Shell Game. *Audubon*, 50-55,95.
- Lutz, R. A. and D. C. Rhoades. 1980. Growth patterns within the molluscan shell. *In: Skeletal Growth in Aquatic Organisms*. Rhoades, D. C. and R. A. Lutz, eds. Pp 203-254. Plenum Press, New York.
- Maine Department of Environmental Protection (MDEP). 2006. Draft 2006 Integrated Water Quality Monitoring and Assessment Report. Document Number: DEPLW0817. (<http://www.maine.gov/dep/blwq/docmonitoring/305b/draft.htm>)
- Maine Department of Inland Fisheries and Wildlife (MDIFW). 2005. Maine's Comprehensive Wildlife Conservation Strategy. (<http://www.maine.gov/ifw/wildlife/compwildlifestrategy/index.htm>)

- Maine Water Resources Plan: Water Supply and Sewerage Facilities. 1969. Volume 1: State Water Resources Planning. Prepared by Edward C. Jordan Co., Inc. Consulting Engineers and Planners, Portland, Maine.
- Martin, S. M. 1995. Maine's early malacological history. *Maine Naturalist* 3:1-34.
- Master, L. L., S. R. Flack, and B. A. Stein, eds. 1998. *Rivers of Life: Critical Watersheds for Protecting Freshwater Biodiversity*. The Nature Conservancy, Arlington, Virginia.
- Matteson, M. R. 1948. Life history of *Elliptio complanatus* (Dillwyn 1817). *The American Midland Naturalist* 40:690-723.
- Matteson, M. R. 1955. Studies on the natural history of the Unionidae. *The American Midland Naturalist* 53:126-145.
- McCall, P. I., M. J. S. Tevesz, and S. F. Schwelgien. 1979. Sediment mixing by *Lampsilis radiata siliquoidea* (Mollusca) from western Lake Erie. *Journal of Great Lakes Research* 5:105-111.
- McCuaig, J. M. and R. H. Green. 1983. Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 40:436-442.
- McMahon, R. F. 1991. Mollusca: Bivalvia. Pages 315-399 *in*: J. H. Thorp and A. P. Covich, eds. *Ecology and classification of North American freshwater invertebrates*. Academic Press, Inc. 911pp.
- Metcalfe-Smith, J. L. and R. H. Green. 1992. Aging studies on three species of freshwater mussels from a metal-polluted watershed in Nova Scotia, Canada. *Canadian Journal of Zoology* 70:1284-1291.
- Moulton, C. A., W. J. Fleming, and C. E. Purnell. 1996. Effects of two cholinesterase-inhibiting pesticides on freshwater mussels. *Journal of Environmental Toxicology and Chemistry* 15(2): 131-137.
- Muller, D. and R. A. Patzner. 1996. Growth and age structure of the swan mussel *Anodonta cygnea* (L.) at different depths in Lake Mattsee (Salzburg, Austria). *Hydrobiologia* 341:65-70.
- Mutvei, H. and T. Westermarck. 2001. How environmental information can be obtained from naiad shells. *Ecology and evolution of the freshwater mussels Unionidae*. K. W. G. Bauer, Berlin. Springer-Verlag: 367-378.
- Naimo, T. J. 1995. A review of the effects of heavy metals on freshwater mussels. *Ecotoxicology* 4:341-362.

- Nalepa, T. F. and J. M. Gauvin. 1988. Distribution, abundance, and biomass of freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair. *Journal of Great Lakes Research* 14:411-419.
- Nalepa, T. F., W. S. Gardner, and J. M. Malczyk. 1991. Phosphorus cycling by mussels (Unionidae: Bivalvia) in Lake St. Clair. *Hydrobiologia* 219:239-250.
- NatureServe. 2007. NatureServe Explorer: An online encyclopedia of life [web application]. Version 6.2. NatureServe, Arlington, Virginia. Available <http://www.natureserve.org/explorer>. (Accessed April 2007)
- Nedeau, E. J., M. A. McCollough, and B. I. Swartz. 2000. The Freshwater Mussels of Maine. Maine Department of Inland Fisheries and Wildlife, Augusta, ME. 118pp.
- Negus, C. 1966. A quantitative study of growth and reproduction of Unionid mussels in the River Thames at Reading. *Journal of Animal Ecology* 35:513-532.
- Neves, R. J. 1993. A State-of-the-Unionids Address. Pages 1-10 *in*: K.S. Cummings, A.C. Buchanan, and L.M. Koch, eds. Conservation and management of freshwater mussels. Proceedings of a UMRCC symposium, 12-14 October 1992, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.
- Neves, R. J. 1997. A national strategy for the conservation of native freshwater mussels. Pages 1-11 *in*: K. S. Cummings, A. C. Buchanan, C. A. Mayer, and T. J. Naimo, eds. Conservation and management of freshwater mussels II: initiatives for the future. Proceedings of a UMRCC symposium, 16-18 October 1995, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois.
- Neves, R. J. and J. C. Widlak. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. *American Malacological Bulletin* 5(1):1-7.
- Neves, R. J. and M. C. Odom. 1989. Muskrat predation on endangered freshwater mussels in Virginia. *Journal of Wildlife Management* 53:934-941.
- Neves, R. J. and S. N. Moyer. 1988. Evaluation of techniques for age determination of freshwater mussels (Unionidae). *American Malacological Bulletin* 6(2):179-188.
- Newton T. J. 2003. The effects of ammonia on freshwater unionid mussels. *Environmental Toxicology and Chemistry* 22:2543-2544.
- Nylander, O. O. 1914. Distribution of some fresh water shells of the St. John's River valley in Maine, New Brunswick, and Quebec. *The Nautilus* 27:139-141.

- Nylander, O. O. 1943. The Lymnaeidae of northern Maine and adjacent Canadian provinces and notes on Anson Allen and his collection. University of Maine Studies. 2nd Series. No. 58. 42pp.
- O'Dee, S. H. and G. T. Watters. 2000. New or confirmed host identifications for ten freshwater mussels. Pages 77-82 in R. A. Tankersley, D. I. Warmoltz, G. T. Watters, B. J. Armitage, P. D. Johnson, and R. S. Butler, eds. Freshwater Mollusk Symposium Proceedings, Ohio Biological Survey, Columbus.
- Parker, R. S., C. T. Hackney, and M. F. Vidrine. 1984. Ecology and reproductive strategy of a south Louisiana freshwater mussel, *Glebulia rotundata* (Lamarck) (Unionidae: Lampsilinae). Freshwater Invertebrate Biology 3:53-58.
- Parmalee, P. W. and W. E. Klippel. 1974. Freshwater mussels as a prehistoric food resource. American Antiquity 39:421-434.
- Payne, B. S. and A. C. Miller. 1989. Growth and survival of recent recruits to a population of *Fusconaia ebena* (Bivalvia:Unionidae) in the lower Ohio River. American Midland Naturalist 121:99-104.
- Schulz, C. and K. Marbain. 1998. Hosts species for rare freshwater mussels in Virginia. Triannual Unionid Report (15):32-38.
- Sephton, T. W., C. G. Paterson, and C. H. Fernando. 1980. Spatial relationships of bivalves and nonbivalve benthos in a small reservoir in New Brunswick, Canada. Canadian Journal of Zoology 58:852-859.
- Smith, D. G. 1976. Notes on the biology of *Margaritifera margaritifera* (Lin.) in central Massachusetts. The American Midland Naturalist 96:252-256.
- Smith, D. G. 1985. Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut River system. Freshwater Invertebrate Biology 4(2):105-108.
- Strayer, D. 1981. Notes on the microhabitats of unionid mussels in some Michigan streams. American Midland Naturalist 106:411-415.
- Strayer, D. L. 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia, Unionidae) distribution in southeastern Michigan, U.S.A. Freshwater Biology 13:253-264.
- Strayer, D. L. 1987. Ecology and zoogeography of the freshwater mollusks of the Hudson River basin. Malacological Review 20:1-68.
- Strayer, D. L. 1993. Macrohabitats of freshwater mussels (Bivalvia:Unionacea) in streams of the northern Atlantic Slope. Journal of the North American Benthological Society 12:236-246.

- Strayer, D. L. and J. Ralley. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society* 12:247-258.
- Strayer, D. L. and K. J. Jirka. 1997. The Pearly Mussels (Bivalva: Unionoidea) of New York State. *New York State Museum Memoir* 26. The NY State Education Department.
- Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves. *Bioscience* 49(1):19-27.
- Tedla, S. and C. H. Fernando. 1969a. Changes in the parasite fauna of the white perch, *Roccus americanus* (Gmelin), colonizing new habitats. *Journal of Parasitology* 55:1063-1066.
- Tedla, S. and C. H. Fernando. 1969b. Observations on the glochidia of *Lampsilis radiata* (Gmelin) infesting yellow perch, *Perca flavescens* (Mitchill) in the Bay of Quinte, Lake Ontario. *Canadian Journal of Zoology* 47(4):705-712.
- Trout Unlimited. 2006. A Glass Half Full. The Future of Water in New England. Available at <http://www.tu.org/site/pp.asp?c=7dJEKTNuFmG&b=2247647>.
- Turgeon, D. D., A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, D. F. E. Roper, A. Scheltema, F. G. Thompson, and J. D. Williams. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. *American Fisheries Society, Special Publication* 16: viii. 277 pp.
- van der Schalie, H. 1938. The naiad fauna of the Huron River, in southeastern Michigan. *Miscellaneous Publications of the University of Michigan Museum of Zoology* 40: 1-83 + 12 plates and 1 map.
- van der Schalie, H. 1970. Hermaphroditism among North American freshwater mussels. *Malacologia* 10:93-112.
- van Snik Gray, E. S., W. A. Lellis, J. C. Cole, and C. S. Johnson. 1999. Hosts of *Pyganodon cataracta* (eastern floater) and *Strophitus undulatus* (squawfoot) from the Upper Susquehanna River basin, Pennsylvania. *Triannual Unionid Report*, 18:6.
- van Snik Gray, E. V. S., W. A. Lellis, J. C. Cole, and C. S. Johnson. 2002. Host identification for *Strophitus undulatus* (Bivalvia: Unionidae), the creeper, in the upper Susquehanna River basin, Pennsylvania. *American Midland Naturalist*, 147:153-161.
- Vaughn, C. 1997. Regional patterns of mussel species distribution in North American rivers. *Ecography* 20:107-115.

- Victoria, J. 2006. Freshwater Mussel Thought to Be Extinct in Connecticut Recently Found. *Connecticut Wildlife* 26(5):9.
- Wang, N., C. G. Ingersoll, F. J. Dwyer, A. D. Roberts, T. Augspurger, C. M. Kane, R. J. Neves, and M. C. Barnhart. (2007, March 14). *Assessing contaminant sensitivity of early life stages of freshwater mussels*. Presentation at the 5th biennial Freshwater Mollusk Conservation Society Symposium, Little Rock, Arkansas.
- Watters, G. T. 1992. Unionids, fishes, and the species-area curve. *Journal of Biogeography* 19:481-490.
- Watters, G. T. 1994. An Annotated Bibliography of the Reproduction and Propagation of the Unionoidea (Primarily of North America). Ohio Biological Survey Miscellaneous Contributions No. 1. Vi + 158 p.
- Watters, G. T. 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoidea) and their hosts. *Biological Conservation* 78:79-85.
- Watters, G. T. 1997. Glochidial metamorphosis of the freshwater mussel *Lampsilis cardium* (Bivalvia: Unionidae) on larval tiger salamanders, *Ambystoma tigrinum* ssp. (Amphibia: Ambystomidae). *Canadian Journal of Zoology* 75:505-508.
- Watters, G. T. and S. H. O'Dee. 1998. Metamorphosis of freshwater mussel glochidia (Bivalvia: Unionidae) on amphibians and exotic fishes. *The American Midland Naturalist* 139:49-57.
- Watters, G. T., S. W. Chordas, S. F. O'Dee, and J. Reiger. (1999, March 17-19). *Host identification studies for six species of Unionidae*. Presentation at the 1st Symposium of the Freshwater Mollusk Conservation Society, Chattanooga, Tennessee.
- Watters, G. T., T. Menker, S. Thomas, and K. Kuehnl. 2005. Host identifications or confirmations. *Ellipsaria* 7(2):11-12.
- Whittier, T. R., A. T. Herlihy, and S. M. Pierson. 1995. Regional susceptibility of Northeast lakes to zebra mussel invasion. *Fisheries* 20(6): 20-27.
- Wick, P. C. 2006. Fish hosts and demographics of *Lampsilis cariosa* and *Leptodea ochracea*, two threatened freshwater mussels in Maine. M.S. Thesis, University of Maine.
- Wicklowsky, B. J. and L. D. Richards. 1995. Determination of host fish species for glochidia of the endangered freshwater mussel *Alasmidonta varicosa*. Fifth Annual Northeastern Freshwater Mussel Meeting, United States Fish and Wildlife Service, Concord, New Hampshire.

- Wicklowsky, B. J. and P. M. Beisheim. 1998. Life history studies of the squawfoot mussel *Strophitus undulatus* in the Piscataquog River watershed, New Hampshire. *Abstract*, Freshwater Mussel Symposium: Conservation, Captive Care, and Propagation, Columbus, Ohio.
- Wiles, M. 1975a. The glochidia of certain Unionidae (Mollusca) in Nova Scotia and their fish hosts. *Canadian Journal of Zoology* 53:33-41.
- Wiles, M. 1975b. Parasites of *Fundulus diaphanus* (LeSueur) (Pisces: Cyprinodontidae) in certain Nova Scotian freshwaters. *Canadian Journal of Zoology* 53(11):1578-1580.
- Williams, J. D., M. L. Warren Jr., K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18(9):6-22.
- Wood, R. G. 1961. A history of lumbering in Maine: 1820-1861. *The Maine Bulletin* 43 (15), 267pp. University of Maine Press, Orono, Maine [Originally published in 1935 as *University of Maine Studies, Second Series, No. 33*, University of Maine Press].
- Yeager, M. M., D. S. Cherry, and R. J. Neves. 1994. Feeding and burrowing behaviors of juvenile rainbow mussels, *Villosa iris* (Bivalvia:Unionidae). *Journal of the North American Benthological Society* 13:217-222.
- Young, D. 1911. The implantation of the glochidium on the fish. *University of Missouri Bulletin Science Series* 2:1-20.
- Young, M., G. J. Purser, and B. Al-Mousawi. 1987. Infection and successful reinfection of brown trout [*Salmo trutta* L.] with glochidia of *Margaritifera margaritifera* (L.). *American Malacological Bulletin* 5(1):125-128.

Appendix 1. Hosts for the freshwater mussels of Maine. Species identified as hosts but not found in Maine are not listed. An asterisk (*) indicates a suspected host.

MUSSEL SPECIES	HOSTS	SOURCE
Eastern Pearlshell <i>Margaritifera margaritifera</i>	Atlantic Salmon (<i>Salmo salar</i>), Landlocked Salmon (<i>Salmo salar sebago</i>), Brook Trout (<i>Salvelinus fontinalis</i>), Brown Trout (<i>Salmo trutta</i>), Rainbow Trout (<i>Salmo gairdnerii</i>)	Smith 1976, Karna and Millemann 1978, Young et al. 1987, Bauer 1987b, Cunjak and McGladdery 1991
Triangle Floater <i>Alasmidonta undulata</i>	Common Shiner (<i>Luxilus cornutus</i>), Blacknose Dace (<i>Rhinichthys atratulus</i>), Longnose Dace (<i>Rhinichthys cataractae</i>), Pumpkinseed Sunfish (<i>Lepomis gibbosus</i>), Fallfish (<i>Semotilus corporalis</i>), Largemouth Bass (<i>Micropterus salmoides</i>), Slimy Sculpin (<i>Cottus cognatus</i>), White Sucker (<i>Catostomus commersoni</i>), White Perch* (<i>Morone americana</i>)	Watters et al. 1999, Kneeland 2006, Barry Wicklow, St. Anselm College, <i>personal communication</i>
Brook Floater <i>Alasmidonta varicosa</i>	Longnose Dace, Blacknose Dace, Golden Shiner (<i>Notemigonus chrysoleucas</i>), Pumpkinseed Sunfish, Slimy Sculpin, Yellow Perch (<i>Perca flavescens</i>)	Wicklows and Richards 1995, Schulz and Marbain 1998, Barry Wicklow, St. Anselm College, <i>personal communication</i>
Creeper <i>Strophitus undulatus</i>	Largemouth Bass, Creek Chub (<i>Semotilus atromaculatus</i>), Fathead Minnow (<i>Pimephales promelas</i>), Bluegill (<i>Lepomis macrochirus</i>), Longnose Dace, Blacknose Dace, Fallfish, Golden Shiner, Common Shiner, Yellow Perch, Slimy Sculpin, Atlantic Salmon, Atlantic Sturgeon (<i>Acipenser oxyrhynchus</i>), Two-lined Salamander (<i>Eurycea bislineata</i>), Red-spotted Newt (<i>Notophthalmus viridescens</i>)	Hoggarth 1992, Wicklow and Beisheim 1998, van Snik Gray et al. 1999, 2002, Watters et al. 1999, Barry Wicklow, St. Anselm College, <i>personal communication</i>
Eastern Floater <i>Pyganodon cataracta</i>	White Sucker, Pumpkinseed Sunfish, Threespine Stickleback (<i>Gasterosteus aculeatus</i>), Carp (<i>Cyprinus carpio</i>), Bluegill, Yellow Perch	Wiles 1975a, Hoggarth 1992, Watters 1994, van Snik Gray et al. 1999
Alewife Floater <i>Anodonta implicata</i>	Alewife (<i>Alosa pseudoharengus</i>), American Shad* (<i>Alosa sapidissima</i>), Blueback Herring* (<i>Alosa aestivalis</i>), White Sucker*, Threespine Stickleback*, White Perch*, Pumpkinseed Sunfish*, Striped Bass* (<i>Morone saxatilis</i>)	Davenport and Warmuth 1965, Wiles 1975a, Kneeland 2006
Eastern Elliptio <i>Elliptio complanata</i>	Yellow Perch, Banded Killifish (<i>Fundulus diaphanus</i>), Largemouth Bass, Bluegill, Pumpkinseed Sunfish, White Perch*, Smallmouth Bass* (<i>Micropterus dolomieu</i>), Redbreast Sunfish (<i>Lepomis auritus</i>)*, Alewife*, Threespine stickleback*, Brook Trout*, Black Crappie (<i>Pomoxis nigromaculatus</i>)*, White Sucker*	Young 1911, Matteson 1948, Wiles 1975b, Watters 1994, Watters et al. 2005, Kneeland 2006
Yellow Lampmussel <i>Lampsilis cariosa</i>	White Perch, Yellow Perch, Largemouth Bass, Banded Killifish*, Chain Pickerel* (<i>Esox niger</i>), White Sucker*, Smallmouth Bass*	Kneeland 2006, Wick 2006
Eastern Lampmussel <i>Lampsilis radiata radiata</i>	Yellow Perch, Largemouth Bass, Smallmouth Bass, Black Crappie, Pumpkinseed Sunfish, White Perch, Bluegill	Tedla and Fernando 1969a, 1969b; Hanek and Fernando 1978; Watters 1994; O'Dee and Watters 2000; Watters et al. 2005; Kneeland 2006
Tidewater Mucket <i>Leptodea ochracea</i>	White Perch, Banded Killifish*. Alewife*	Kneeland 2006, Wick 2006

Appendix 2. Occurrences of the Yellow Lampmussel (*Lampsilis cariosa*) in Maine.

ST. GEORGE RIVER WATERSHED

St. George River mainstem (Warren, Appleton, Searsmont)
 Chickawaukie Pond¹ (Rockland, Rockport)
 South Pond¹ (Warren)
 North Pond¹ (Warren)
 Seven Tree Pond¹ (Union, Warren)
 Crawford Pond (Union, Warren)
 Round Pond (Union)
 Sennebec Pond¹ (Union, Appleton)
 Quantabacook Lake (Searsport, Morrill)

KENNEBEC RIVER WATERSHED

Kennebec River

Kennebec River mainstem¹ (Winslow, Vassalboro, Hallowell, Chelsea, Waterville, Augusta)
 Messalonskee Stream (Waterville)

Sebasticook River

Sebasticook River mainstem (Clinton, Benton, Winslow)
 Fifteen Mile Stream (Benton)
 Twenty-five Mile Stream (Unity)
 Sandy Stream (Unity)
 Unity Pond¹ (Unity, Burnham, Troy)

PENOBSCOT RIVER WATERSHED

Penobscot River

Penobscot River mainstem (Milford, Argyle Twp, Greenbush, Passadumkeag, Edinburg, Enfield, Howland, Lincoln, Chester, Winn)
 Stillwater River (Old Town)
 Pushaw Stream (Old Town, Alton)
 Dead Stream (Alton)
 West Branch Dead Stream (Bradford)
 Pushaw Lake¹ (Old Town, Glenbun, Hudson, Orono)
 South Branch Lake (Seboeis Plt, T2R8 NWP)

West Branch Penobscot River

West Branch Penobscot River mainstem (TAR7 WELS, Millinocket, T1R9 WELS)
 Dolby Pond (Millinocket, TAR7 WELS, East Millinocket, Grindstone Twp)
 Millinocket Stream (Millinocket)
 Pemadumcook Chain Lakes (T4 Indian Purchase, T3 Indian Purchase, T1R9 WELS, T1R10 WELS)

PENOBSCOT RIVER WATERSHED (continued)West Branch Penobscot River (continued)

Millinocket Lake (T1R8 WELS, T2R8 WELS, T1R9 WELS, T2R9 WELS)

Passamagamet Lake (T1R9 WELS)

Lower Jo-Mary Lake (T1R10 WELS)

Middle Jo-Mary Lake (T4 Indian Purchase, TAR10 WELS, Veazie Gore)

Upper Jo-Mary Lake (TAR10 WELS, TBR10 WELS, Veazie Gore)

First Debsconeag Lake (T2R10 WELS)

Third Debsconeag Lake (T2R10 WELS)

Debsconeag Deadwater (T2R10 WELS, T2R9 WELS, T1R9 WELS)

East Branch Penobscot River

East Branch Penobscot River mainstem (Grindstone Twp, East Millinocket)

Piscataquis River

East Branch Pleasant River (T5R9 NWP)

Passadumkeag River

Passadumkeag River mainstem (Passadumkeag, Lowell, Summit Twp, Burlington, Grand Falls Twp)

Saponac Pond (Burlington, Grand Falls Twp)

Madagascal Stream (Grand Falls Twp)

Mattawamkeag River

Mattawamkeag River mainstem (Drew Plt, Bancroft, Haynesville)

Molunkus Stream (Silver Ridge Twp)

Upper Hot Brook Lake (T8R4 NBPP, Danforth)

Lower Hot Brook Lake (T8R4 NBPP)

Crooked Brook Flowage (Danforth)

Baskahegan Lake (Brookton Twp, Topsfield)

West Branch Mattawamkeag River

West Branch Mattawamkeag River mainstem¹ (T3R3 WELS, T4R3 WELS, Island Falls)

Mattawamkeag Lake (Island Falls, T4R3 WELS)

East Branch Mattawamkeag River

East Branch Mattawamkeag River mainstem (Haynesville)

¹Reported in historical literature; species still extant at site

Appendix 3. Occurrences of the Tidewater Mucket (*Leptodea ochracea*) in Maine.

ST. GEORGE RIVER WATERSHED

Chickawaukie Pond¹ (Rockland, Rockport)
 South Pond¹ (Warren)
 Sidensparker Pond (Waldoboro, Warren)
 North Pond¹ (Warren)
 Seven Tree Pond¹ (Union, Warren)
 Crawford Pond (Union, Warren)
 Sennebec Pond¹ (Union, Appleton)

KENNEBEC RIVER WATERSHED

Kennebec River

Kennebec River mainstem¹ (Richmond, Pittston, Chelsea, Hallowell, Augusta, Sidney, Vassalboro, Winslow, Waterville)
 mouth of Androscoggin River² (Topsham, Brunswick)
 Cathance River (Bowdoinham)
 Cobbosseecontee Stream (Gardiner)

Sebasticook River

Sebasticook River mainstem (Benton, Winslow, Pittsfield, Palmyra)
 Outlet Stream (Winslow)
 Sandy Stream (Unity)
 Unity Pond (Unity, Burnham, Troy)
 Douglas Pond (Pittsfield, Palmyra)
 Indian Pond (St. Albans)
 Great Moose Pond (Harmony, Hartland, St. Albans)

PENOBSCOT RIVER WATERSHED

Penobscot River

Penobscot River mainstem (Milford, Argyle Twp, Greenbush, Enfield)
 Alamoosook Lake (Orland)
 Mud Pond (Old Town)
 Pushaw Lake¹ (Old Town, Glenbun, Hudson, Orono)
 Little Pushaw Pond (Hudson)
 Chemo Pond (Clifton, Eddington, Bradley)
 Boyd Lake (Orneville Twp)
 South Branch Lake (Seboeis Plt, T2R8 NWP)
 Little Mattamiscontis Lake (T3R9 NWP)

PENOBSCOT RIVER WATERSHED (continued)Piscataquis River

Sebec Lake (Dover-Foxcroft, Sebec, Willamantic, Bowerbank)

Ebeemee Lake (T5R9 NWP, Brownville)

Passadumkeag River

Passadumkeag River mainstem (Passadumkeag, Lowell, Summit Twp, Burlington, Grand Falls Twp)

Cold Stream Pond³ (Enfield, Howland, Lincoln)

Saponac Pond (Burlington, Grand Falls Twp)

Madagascal Pond (Burlington)

Number 3 Pond (Twombly)

West Branch Penobscot River

Dolby Pond (Millinocket, TAR7 WELS, East Millinocket, Grindstone Twp)

Millinocket Lake (T1R8 WELS, T2R8 WELS, T1R9 WELS, T2R9 WELS)

Passamagamet Lake (T1R9 WELS)

Lower Jo-Mary Lake (T1R10 WELS)

¹Reported in historical literature; species still extant at site

²Record based on spent shells; most likely drifted down with tide from Kennebec River/Merrymeeting Bay

³Historical site; population believed extirpated

Appendix 4. Occurrences of the Brook Floater (*Alasmidonta varicosa*) in Maine.***KENNEBEC RIVER WATERSHED***Kennebec River

Kennebec River mainstem (Anson, Madison)
 Carabassett Stream (Clinton, Canaan)
 Wesserunsett Stream (Cornville)
 Sandy River (Norridgewock)
 Gilman Stream (New Portland)

Sebasticook River

Sebasticook River mainstem (Benton, Winslow)

PENOBSCOT RIVER WATERSHEDPenobscot River

Penobscot River mainstem (Enfield, Mattamiscontis Twp, Lincoln, Chester, Winn)
 Marsh Stream (Frankfort, Winterport)
 Kenduskeag Stream (Bangor, Kenduskeag, Corinth)
 French Stream (Exeter, Corinth)
 Great Works Stream (Bradley)
 Dead Stream (Alton)
 West Branch Dead Stream (Bradford)

East Branch Penobscot River

East Branch Penobscot River mainstem (Medway, East Millinocket, Grindstone Twp,
 Soldiertown Twp)

Piscataquis River

Pleasant River (Brownville)
 East Branch Pleasant River (Brownville, T5R9 NWP)

Passadumkeag River

Passadumkeag River mainstem (Lowell, Summit Twp)

Mattawamkeag River

Mattawamkeag River mainstem (Winn, Mattawamkeag, Kingman Twp, Reed Plt, Drew Plt, Bancroft)
 Mattakeunk Stream (Winn)
 Molunkus Stream¹ (Macwahoc Plt, Benedicta Twp, Silver Ridge Twp)
 Macwahoc Stream (North Yarmouth Academy Grant)
 Wytopitlock Stream (Reed Plt, Glenwood Plt, T2R4 WELS)
 Baskahegan Stream (Bancroft)

West Branch Mattawamkeag River

West Branch Mattawamkeag River mainstem¹ (T3R3 WELS, Island Falls, Dyer Brook)
 Fish Stream (Island Falls, Crystal)

East Branch Mattawamkeag River

East Branch Mattawamkeag River mainstem (Forkstown Twp, T3R3 WELS, T4R3 WELS, Haynesville)

SMALL COASTAL WATERSHEDS

Presumpscot River² (Cumberland Co.)

Pleasant River (Windham)

Sheepscot River (Kennebec/Lincoln Cos.)

Sheepscot River mainstem (Alna, Whitefield)

West Branch Sheepscot River (Windsor)

St. George River (Knox/Waldo Cos.)

St. George River mainstem (Appleton, Searsmont)

Union River (Hancock Co.)

West Branch Union River (Mariaville, Amherst, Aurora)

Pleasant River (Washington Co.)

Pleasant River mainstem (Columbia Falls)

Machias River (Washington Co.)

Machias River mainstem (Northfield, T30 MD BPP, T31 MD BPP, T36 MD BPP, T37 MD BPP)

Old Stream (Wesley, Northfield)

Chain Lakes Stream (T31 MD BPP, Wesley)

West Branch Machias River (T36 MD BPP)

East Machias River (Washington Co.)

East Machias River mainstem (T18 ED BPP, T19 ED BPP, Crawford)

Dennys River (Washington Co.)

Dennys River mainstem³ (Dennysville)

St. Croix River (Washington Co.)

St. Croix River mainstem (Baileyville, Fowler Twp, Dyer Twp, Lambert Lake Twp)

Tomah Stream (Indian Twp, Waite)

¹Reported in historical literature; species still extant at site

²Probable historical site; believed extirpated

³Historical site; possibly extirpated