THE FRESHWATER MUSSELS
OF VERMONT

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INTRODUCTION

There are 17 species of freshwater mussels native to Vermont's streams, rivers, ponds, and lakes. Mussels are invertebrate animals, bivalves, in the class Mollusca. They are related to freshwater and marine clams, and, more distantly, snails. Mussels and clams are in the mollusk class Pelecypoda. One species of mussel, the eastern pearlshell, is in the family Margaritiferidae. All other native Vermont mussels are in the family Unionidae. One non-native species, the zebra mussel, in the family Dreissenidae, is presently found in Lake Champlain.

Worldwide, there are nearly 1,000 species of freshwater mussels. In North America, which is considered to be the center of unionoid mussel distribution, as many as 300 species are recognized by some authorities. The greatest diversity is found in the Mississippi-Tennessee-Ohio River system. Of these, 72% are considered to be endangered, threatened, or of special concern (Williams et al. 1993). Vermont, with 17 species, has the richest mussel diversity in the six-state New England region. Several species reach their northeastern range limits in western Vermont in the Lake Champlain drainage (Smith 1985a).

At one time in Vermont, mussels were commercially harvested for the button industry. With the advent of plastics and the decline in use of mussel nacre for buttons, this industry waned. Commercial mussel harvesting for the cultured pearl industry now takes place in the Midwest; none of the species found in Vermont are important to this industry.
ECOLOGY AND LIFE HISTORY OF MUSSELS

Unionid mussels and the eastern pearlshell spend their adult lives situated in the bottom substrates of streams or lakes feeding on microscopic plants and animals. They are sedentary, rarely moving more than a few meters in a lifetime. They feed by filtering algae, diatoms, and plankton from the water column. Because of their sedentary nature and filter-feeding habit, mussels are considered to be good indicators of water quality (Neves 1993).

Freshwater mussels have a unique reproductive strategy; most species utilize one or more fish species as temporary hosts for their larvae (glochidia). The breeding cycles of mussels are generally either short-term or long-term. Short-term breeding involves egg fertilization, development and release of glochidia all within the same year. Long-term breeding involves fertilization in the summer with the female mussel holding the glochidia in her gills (marsupia) through the winter months until releasing them the following spring.

During reproduction, male mussels release sperm into the water column. Sperm is then fortuitously picked up by the female through her inhalent aperture (Figure 4) while filtering. Egg and partial larval development take place within the female. It is believed that larval development for most species must be completed with a host fish. Larval mussels attach to the gills or fins of the host, depending upon mussel group, where they feed as a blood parasite for periods ranging from a week or so to several weeks. When metamorphosis of the young mussel is complete, it drops from the host to the stream or lake bottom, where further development as a bivalve mussel begins. For up to two years, juvenile mussels, containing a single byssal thread, will remain near the substrate/water interface feeding by using the foot to extract food particles from interstitial spaces within the sand, gravel, or other substrate particles.

The host fish species for most mussels are unknown. Of all North American species, only about 25% of the mussel-fish host relationships have been reported, and only about 20% of those relationships have been subjected to laboratory experiments demonstrating transformation of glochidia to juvenile mussels (Hoggarth 1992).

The lifespans of freshwater mussels vary considerably by species. The dwarf wedgemussel probably lives no longer than 15 years, while the eastern pearlshell has been documented to live for at least 100 years.

THREATS FACING MUSSEL POPULATIONS

There is little quantitative historical information about the distribution and abundance of different mussel species in Vermont, which makes it difficult to document definitive population trends and their causes. We do know that the upper Connecticut River population of the dwarf wedgemussel has declined; historically it was known to occur at least as far north as Bloomfield and south into Connecticut. Certain other species have apparently always been rare.
Habitat loss is believed to be the most significant factor leading to declines in mussel populations. Construction of dams, regulation of river flows, gravel mining, siltation, and channelization alter river bottom habitat, making it unsuitable for mussels. Neves (1993) reports that heavy metal contamination, chorine, ammonia, and industrial and municipal effluents have been shown to be highly toxic to aquatic invertebrates. Unfortunately, there is little information regarding levels of various contaminants that result in mortality, reproductive failure, or reduced growth and fitness in mussels. The zebra mussel, a recent invader to Lake Champlain, may also result in significant losses in native mussel populations (Hebert et al 1991). Zebra mussels attach to native mussels as well as any hard surface, and in only a few years may reach astronomical numbers. Large numbers of zebra mussels may completely envelope native mussels, thereby preventing the natives from feeding, reproducing, or even moving.

HISTORICAL AND CURRENT INVENTORIES OF VERMONT MUSSELS

The earliest recorded observations on the freshwater mussel fauna of North America came as descriptions of shells proposed as new species. Early collectors were hasty but diligent in their efforts to describe nearly every specimen that entered their cabinet. Probably the most prolific of these early, ardent conchologists was Isaac Lea, a business man living in Philadelphia. Lea's avocation and passion was collecting freshwater mussels, a pursuit that took him far and wide in eastern North America and Europe in search of shells and the company of other conchologists of his time. It was thus logical, therefore, that the first observation of a Vermont mussel was by Lea (1834a) who published a description of "Symphynota benedictensis" (Lea 1834). In his contemporary "Observations on the genus Unio" (Lea 1834b), he elaborated on his description, detailing the circumstances under which he found the original specimen which occurred on an 1829 trip to Canada via a Lake Champlain steamboat. The form was subsequently collected by John Jay, a noted physician, who listed it in his catalog of shells (Jay 1839), later to become the foundation of the American Museum of Natural History's mollusk collection. Two years later, Charles B. Adams, a member of the faculty of Middlebury College, published a list of mollusks collected from the Middlebury area of Vermont (Adams 1841). The list was elaborated and expanded into the "Fresh-water shells of Vermont" (Adams 1842) which appeared in Zadock Thompson's "Natural History of Vermont". In this subsequent list, Adams provided a description of "Unio compressus var. plebius", the second freshwater mussel described from Vermont. Lea's Symphynota benedictensis and Adam's Unio compressus var. plebius are not now recognized and are considered synonyms of Pyganocon grandis and Lasmigona compressa, respectively.

A year after Adam's second list was published James DeKay produced his voluminous work on the natural history of New York which provided an account on the freshwater mollusks (DeKay 1843). Though concerned primarily with the New York fauna, several Lake Champlain records of freshwater mussels were given and all are known from the Vermont side as well. Vermont species were subsequently included in the earliest list of
New England Mollusca (Stimpson 1851); however, little information was provided concerning Vermont species beyond that already provided by Adams (1842). A hiatus existed for the next sixty years during which no published studies on Vermont mussels were produced. At the end of the period, a significant paper was published by C.T. Simpson (1896). While not concerned with the Vermont fauna per se, the paper highlighted the importance of the connection of Lake Champlain with the St. Lawrence River and Great Lakes drainage systems as an explanation for the relatively high diversity of the Lake Champlain mussel fauna of Vermont compared to the rest of New England.

In the absence of organized studies, collecting of Vermont shells nonetheless gathered momentum during the latter nineteenth century and several private collections were amassed by the turn of the twentieth century, most notably those in the possession of Byron Ruggles, George Perkins, and Asa Grey. At the same time institutional and private museums were beginning to accumulate specimens of freshwater mussels from Vermont. In the first comprehensive listing of New England freshwater mussels of the Twentieth Century (Davis 1905), some of the principal collectors and institutions of the day and the Vermont shells they possessed were listed. With passing of time, most of the private collections, through wills or simply lost interest, found their way to fewer and fewer museums. In the New England region, the majority of these collections came to reside at either the Boston Society of Natural History or the Museum of Comparative Zoology at Harvard University. The Boston Society of Natural History then published the most extensive compilation of New England mollusk species to date (Johnson 1915), part of an entire volume with several numbers devoted to the fauna of New England.

During the remainder of the first half of the century, Vermont came to be visited by a number of noted malacologists, who while presumably vacationing, collected specimens throughout and especially the northern part of the state. Frank Baker, one of the most prolific students of freshwater malacology of his time, collected in northern Vermont and produced a short note on a few species of the Lake Memphremagog drainage (Baker 1928). The next year William J. Clench published a semi-popular article on New England freshwater mollusks (Clench 1929). It is possible that the last sentence of the paper, "A detailed study of the distribution of the numerous species [of the Lake Champlain region] would lead to many interesting results as to possible routes of migration and relationship with forms in other regions", inspired Clench, along with Ruth D. Turner of Harvard University, to travel the shore of Lake Champlain during the 1940's and later for the purpose of collecting specimens to be used for just such a study. The resulting Clench and Turner collections, currently in the Museum of Comparative Zoology, are among the most complete, both geographically and systematically, of any Vermont collection to this point. Enriching these collections was the transfer of the Boston Society of Natural History's large freshwater mussel collection to Harvard University.

Towards the end of the Clench and Turner "era" of collecting, Arthur Clarke and Herbert Athearn, both with extensive experience in freshwater mussels of northeastern North
America, visited the state and made collections principally in the Lake Champlain region. Despite the apparent interest of these and other malacologists in Vermont malacology, and rumoured plans to synthesize the data, no comprehensive work on the fauna was produced during the entire period from Adams' (1842) treatise through to the 1980's other than Johnson's (1980) review of post-Pleistocene distributions in New England and elsewhere. Beginning in the 1970's, D. G. Smith commenced a survey of freshwater mussels of Vermont and carried out several field studies in areas of the state largely omitted by previous collectors. Data contained in many of the earlier collections housed in the Museum of Camparative Zoology, the American Museum of Natural History, and the New York State Museum were included with Smith's collection data, maintained in the Museum of Zoology, University of Massachusetts, to complete studies on the distribution of freshwater mussels of Vermont (Smith 1982, 1985a).

From the late 1970s to the present, interest in the status and distribution of Vermont's mussel fauna has grown, owing in part to the plight of freshwater mussels on a continent-wide basis. The most exhaustive mussel surveys have taken place in the Connecticut River mainstem, West River, and lower reaches of the tributaries of Lake Champlain.

Records of freshwater mussels presented in this publication were compiled from museum collections, private individual shell collections, and field records of biologists currently working in Vermont. Herbert Athearn, Arthur Clarke, William Clench, Mark DesMeules, Chris Fichtel, Steven Fiske, Larry Master, Carl Pagel, Doug Smith, Ruth Turner, and Susi von Oettingen are responsible for most of the mussel records. Records from a total of 270 sampling stations throughout the state are presented in this atlas. Figure 1 shows the distribution of these mussel sampling stations. Site-specific historic (those prior to 1970) records are scarce therefore we do not differentiate between current and historic records in this atlas. We do differentiate between sampling points where mussels were found and where they were not. This report on mussel distribution is not necessarily complete; some streams have been undersampled or not sampled at all, while many lakes have never been surveyed. The authors hope this atlas will spur additional interest in freshwater mussels, and that the atlas will be updated in the future to reflect additional locations and changes in species distributions.

STATUS OF MUSSELS IN VERMONT AND GENERAL COMMENTS ON DISTRIBUTION

Few mussel species are common in Vermont today. Only in some rivers, streams, and lakes is the eastern elliptio abundant. The eastern floater and eastern lampmussel are also relatively common, but only in certain streams and lakes.

Five mussel species - eastern elliptio, eastern lampmussel, squawfoot, triangle floater, and eastern floater - are found throughout the state and in both streams and lakes. Three mussel species - dwarf wedgemussel, brook floater, and alewife floater - are found only in the
Connecticut River drainage. Seven mussel species - black sandshell, pink heelsplitter, fragile papershell, fluted-shell, pocketbook, giant floater, and cylindrical papershell - are found only in the Lake Champlain drainage. The creek heelsplitter is found in the Lake Champlain and St. Francis River drainages, both of which are part of the St. Lawrence River system. The eastern pearlshell is restricted mostly to softwater streams.

The dwarf wedgemussel is listed by the Federal Government and the State of Vermont as Endangered. In Vermont waters it is presently known to inhabit only an 18-mile stretch of the Connecticut River. The brook floater, listed as Threatened in Vermont, is found only in the West River from Jamaica to Brattleboro. The black sandshell, listed as Threatened in Vermont, is found in the Poultny River and Otter Creek below the first falls on each river, and possibly in limited numbers in the southern portion of Lake Champlain. The species has always been rare in Vermont and currently its numbers are low; it is unclear whether the species is reproducing. The eastern pearlshell, listed as Threatened in Vermont, is found in five stream systems, all but one (Lewis Creek) are softwater streams. Its numbers are low in all but the Winooski River above Plainfield and in Kingsbury Branch, a tributary of the upper Winooski River.

From an examination of Figure 1, it is apparent that sampling effort has been concentrated in the Lake Champlain Lowlands, southern Connecticut River Valley, and northeastern Vermont. Less sampling has been undertaken in the central portion of the state because of its relatively steep topography and preponderance of rocky, high-gradient streams, which are generally not suitable freshwater mussel habitat. Figure 2 depicts mussel distribution in Vermont by watershed. It is readily apparent that the Lake Champlain Basin supports the highest diversity. Certain watersheds, such as the Passumpsic River (northeast), White River (eastcentral), Deerfield River (southcentral), and tributaries of the Hudson River (southwest) are depauperate, perhaps due to past and/or present land and river uses or because these drainages were always species-poor.

SEARCHING FOR MUSSELS

Mussels are located by searching for shells along the shores of rivers and lakes, and by searching a river or lake bottom for live mussels. Searching for live mussels typically involves a wooden viewing box or plastic bucket fitted with plexiglas or glass which facilitates viewing the river or lake bottom in shallow water. In deeper water or where there is concern about trampling mussels, snorkeling is the preferred method. Snorkeling affords a wider and often closer view of the river or lake bottom and affords better protection to mussels. In water deeper than four or five feet, SCUBA is the most efficient means of conducting surveys for mussels.

Most surveys are centered around easy access points, such as bridge crossings, but more comprehensive surveys are accomplished using canoes or boats which facilitate searching extensive reaches of streams between bridge crossings. In order to minimize the effects of
Figure 1

Freshwater Mussel Sampling Locations

Legend

- At Least One Freshwater Mussel Species Present

Freshwater Mussels of Vermont
human disturbance normally associated with bridge crossings, observers often walk upstream
and/or downstream quite a distance from these crossings. C. Fichtel attempted to survey at
least 200 ft, and up to one mile, above and/or below all bridge crossings where mussel
surveys were conducted.

Virtually all streams, with the exception of bouldery, steep gradient streams, have the
potential for supporting mussels. Certain mussels are found frequently in headwater streams
provided that suitable substrates (i.e., gravel, cobble, sand, silt, or mixtures of these) are
present for burrowing.

KEEPING RECORDS AND ETHICAL/LEGAL CONSIDERATIONS

Collecting live mussels should be avoided; depletion of native populations can result.
Whenever possible, photographs or shells from already dead mussels should be taken as
permanent records of a species' occurrence at a site. Care should be taken during stream or
lake surveys not to step on live mussels because shells, especially of smaller species, can be
easily smashed. Snorkeling is the preferred survey method for preventing mussel injury or
death.

A Federal endangered species permit is required for anyone proposing to handle or collect
dwarf wedgemussels. The U.S. Fish and Wildlife Service issues these permits. Also, in
Vermont, anyone proposing to handle live specimens or collect shells of the following
species: dwarf wedgemussel, brook floater, eastern pearlshell, or black sandshell, must
obtain a Vermont endangered species permit issued by the Secretary of the Vermont Agency
of Natural Resources. The Nongame & Natural Heritage Program should be contacted for
an application. The Nongame & Natural Heritage Program may require a scientific
collecting permit for anyone planning to collect other species of mussels not covered by State
or Federal endangered species laws.

It is important to document any new Vermont locations for mussels. Photographs, shells,
and/or written records of mussels found in Vermont waters should be sent to the following
address: Zoologist, Nongame & Natural Heritage Program, Vermont Fish and Wildlife
Department, 103 South Main Street, Waterbury, Vermont 05671-0501. Please include the
collector's name, address, name of the stream, river, or lake where the collection was made,
precise directions to the collection point (a map is helpful), date of the collection, and other
everal notes. If new, exceptional records require the collection of voucher specimens,
procedures for preparing the specimens should follow Smith (in review).

HOW TO IDENTIFY MUSSELS

Several characters are useful when trying to identify mussels. With a live mussel in hand,
only the characteristics of the outer shell and mantle will aid in identification. Shell shape,
dimensions, and color (including presence or absence of rays) are most diagnostic, while
beak ridges are sometimes useful if the periostracum is not badly eroded (see Figure 3). Several characters of the mantle, such as presence or absence of papillae, fusion of mantle edges, mantle color, and presence of specially modified mantle flaps (Smith 1991), can readily distinguish most species when observed filtering in river or lake bottom substrate (see Figure 4). Mussels in the genera *Lampsilis* and *Ligumia* have a highly modified ventral mantle, especially in the females. When identifying mussels from shell material, presence/absence and size of lateral and pseudocardinal hinge teeth, inner shell (nacre) color, and presence/absence of shell thickenings or pitting all aid in distinguishing species.
EXTERNAL SHELL CHARACTERISTICS

Dorsal

- Beak (umbo)
- Posterior ridge
- Periostracum (outer shell surface)
- Growth lines

Ventral

From Pennak (1978)

INTERNAL SHELL CHARACTERISTICS

Center

- Lateral hinge teeth
- Interdentum
- Beak cavity
- Beak (umbo)
- Pseudocardinal teeth
- Muscle scars
- Anterior
- Muscle scars
- Pallial line
- Nacre (inner shell surface)

Ventral

From Pennak (1978)
MANTLE FEATURES OF UNIONID MUSSELS

SIDE VIEW OF A UNIONID MUSSEL

Supra anal aperture
Exhalent aperture
Mantle
Inhalent aperture

A SPECIES OF LAMPSILIS AS SEEN FROM BELOW SHOWING MODIFIED MANTLE

Foot
Mantle flap of Lampsis radiata
Inhalent aperture

From Smith (1991)
EASTERN PEARLSSHLL  [Margaritifera margaritifera (Linn., 1758)]

Eastern pearlshells are found in the Winooski River and Lewis Creek systems of the Lake Champlain drainage, and the West River, Passumpsic River, and Nulhegan River systems of the Connecticut River drainage. A badly-worn shell fragment was found in the Coaticook River (St. Lawrence River system) in 1993, but no live mussels were located. The eastern pearlshell is currently found in the following locations: Lewis Creek (locally common in Hinesburg and Monkton), Moose River (Concord and Victory), Nulhegan River (rare in Ferdinand and Lewis), West River (uncommon in Jamaica and occasional in Londonderry), and Winooski River. In the Winooski system, the pearlshell is apparently absent below Montpelier, uncommon in the mainstem between Montpelier and Plainfield, common above Plainfield and in the Kingsbury Branch (East Montpelier), and rare in the Dog River (Berlin).

In Vermont waters, this species is found in streams with firm sandy bottoms, often amidst gravel, cobbles, or small boulders. Occasionally they are found tucked in among tightly packed cobbles and gravel. They have not been found in lakes.

Large (120+ mm [5+ inches] long) and presumably old mussels have a nearly black periostracum with a slight to pronounced ventral curvature; smaller individuals are brownish without a curve. Pearlshells never show color rays on the outer shell (Smith 1991). The whitish nacre shows distinctive pits with trails radiating from them. There are well-developed pseudocardinal teeth, but no lateral teeth. There is no fusion in the mantle separating the inhalent and exhalent apertures; this is the easiest means for recognizing smaller pearlshells.

Known host fishes for the eastern pearlshell in New England include salmonids, such as brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) (Smith 1976). The influence of stream stocking of brown trout on the distribution of this species is unknown.
The eastern elliptio is the most widely distributed and most common mussel in Vermont, occurring in lakes, rivers, and streams, and is found in nearly every type of bottom substrate. This species is probably the most abundant mussel species in most lakes where it may number in the thousands. Where it occurs in rivers, the elliptio is usually the most common species. In some streams (e.g., Lewis Creek and West River), it is less common than other species. The eastern elliptio is found in a wide variety of bottom substrates, including sand, silt, clay, sand and gravel, gravel, cobble, and amidst large rocks. The densest riverine elliptio beds generally occur along the banks of streams. For example, in the lower Poultney River (West Haven), a single mussel bed contained nearly 1,700 elliptios.

This mussel’s appearance is variable, and it can resemble other species. The elliptio’s most distinctive feature is its shape, which is roughly trapezoidal. This is a medium to large mussel (120 mm [4.8 inches] in length). Adults usually have a dark brown or blackish periostracum with a distinctive rounded ridge running from the beak to the posterior apex. The nacre is pinkish-purple. The hinge teeth are well-developed and complete. Young elliptios have a tan or yellowish outer shell, which is sometimes rayed.

The yellow perch (*Perca flavescens*) is the only known host fish for the glochidia; however, other fish species may serve as hosts. Female elliptios are short-term breeders, being gravid from spring to late summer.
Freshwater Mussels of Vermont

Legend

- Species Present
The eastern lampmussel is common in the Connecticut, Missisquoi, Lamoille, Missisquoi, and Poultney rivers, and Otter Creek. It is uncommon in the West River. It is most abundant in Lake Champlain where it is nearly equal in abundance to the eastern elliptio, usually numbering in the hundreds or thousands within a bed. It is also common in Lake Memphremagog. The lampmussel has also turned up in some smaller lakes, such as Echo Lake (Charleston). In the Connecticut River and rivers draining into Lake Champlain, the lampmussel is far less common than the eastern elliptio, but is the second most common species. This mussel occurs in a variety of bottom substrates, including silt, sand, gravel and sand, and a matrix of sand, gravel, cobble, and rock.

The periostracum of the eastern lampmussel is yellowish-brown, greenish-brown, or brown, and usually rayed, especially in younger individuals. Lampmussels are medium-sized (100 mm [4 inches] in length). The posterior end of males is narrowly rounded, while in females the posterior end is broadly expanded and rounded. A posterior ridge is mostly absent compared to the elliptio. The nacre is usually white, but can also be pinkish or salmon. Hinge teeth are well-developed and complete, that is, with both pseudocardinal and lateral teeth present. The mantle of this species, especially in females, has conspicuous fleshy tubercles and a pigmented flap-like extension (Smith 1991). In younger animals the mantle is very dark, becoming lighter in older individuals. The taxonomic relationship between Lake Champlain populations and those farther to the west is unresolved. There is no eyespot. These mantle projections may serve in some way to attract fish.

The yellow perch is the only known host fish species for the eastern lampmussel. This is a long-term breeder, with females gravid from late July-August to late summer of the following year.
EASTERN LAMPMUSSEL *Lampsilis radiata*

Legend

- • Species Present

*Freshwater Mussels of Vermont*
The distribution of the pocketbook in Vermont includes only Lake Champlain and its major tributaries upstream to their principal fall-lines. This is a mussel of the Interior Basin of North America reaching its northeastern range limit in the St. Lawrence River and Lake Champlain. It apparently is not common, except in the Poultney River where it ranks as the third most abundant mussel species. Other Vermont tributaries of Lake Champlain in which the pocketbook is found are: Missisquoi River (Swanton and Highgate), Lamoille River (Milton and Colchester), Lewis Creek (Ferrisburgh), and Otter Creek (Ferrisburgh and Vergennes). It has also been found in the littoral zone of Lake Champlain in Colchester; presumably it is found in low numbers in other littoral areas of the lake. Substrates where it is found include loose to firmly-packed sand or gravel and sand, and silty sands.

The taxonomy of the pocketbook in the Lake Champlain drainage is uncertain. *Lampsilis cardium*, the plain pocketbook, closely resembles *L. ovata*. Based on shell characteristics alone, it appears that *Lampsilis ovata* occurs here, but characteristics of both species can be observed in many individuals from the Lake Champlain drainage. Younger specimens tend to display more *ovata*-like characters that grade into *cardium*-like features in older specimens. Genetic studies may help resolve the issue.

These are medium to large mussels (120+ mm [5+ inches] in length), and the shell is quite heavy, thick and inflated. The sexes are distinctive in this species. Males are ovate to elliptical; females are ovate to nearly round. The posterior ridge is prominently sharp-angled, especially in younger individuals. The outer shell is yellowish to brownish-yellow, usually with thin to wide dark (sometimes greenish) rays. The nacre is white or nearly so. The hinge teeth are thick and well-developed. Older individuals of this species get to be heavy and quite large (up to 150 mm [6 inches] long, 100 mm [4 inches] high, and 75 mm [3 inches] wide). The mantle is highly modified and pigmented. The flap is streaked and has an eyespot. The pocketbook is a long-term breeder with full maturation of the glochidia attained in late July-early August and released by early July of the following year (Holland-Bartels and Kammer 1989).
POCKETBOOK *Lampsilis ovata*

Freshwater Mussels of Vermont

Legend

- Species Present
The squawfoot has a widespread distribution in Vermont. This species is found mostly in streams, and occasionally in lakes, including Lake Champlain. Rivers in which it occurs include the Black (Irasburg), Black (Ludlow), Connecticut, Lamoille, Missisquoi, Moose, Nulhegan, Poultney, West, and Winooski Rivers, Lewis and Otter Creeks, and Indian Brook (Colchester). Rarely is the squawfoot found to be common. The greatest densities were found in Lewis Creek (0.8 mussels/m²) and the lower Poultney River (0.5-2.0 mussels/m²). Substrate is variable, but the squawfoot appears to be most common aggregates of gravel and sand.

The squawfoot is a small to medium-sized mussel (70 mm [2.8 inches] in length). The largest squawfoots observed by the authors in Vermont were 105 mm (4.2 inches) found in the upper Black River in Ludlow.

The periostracum is black or brown, and rays are not generally visible. The nacre is bluish-white with a brown ventral border and a pinkish cast in the beak cavity. The lateral hinge teeth are absent. The pseudocardinal hinge teeth are represented only by a slight swelling on the hinge line. In the Missisquoi River and Stone Bridge Brook, where the squawfoot overlaps in distribution with the cylindrical floater, it can be distinguished by that species by beak sculpture. Squawfoot beak sculpture consists of 4-5 concentric ridges parallel to the growth lines (Clarke 1981).

Laboratory transformation of squawfoot glochidia has occurred on creek chub (Semotilus atromaculatus) and largemouth bass (Hoggarth 1992). Glochidia are released by the female in the spring.
SQUAWFOOT  *Strophitus undulatus*

*Freshwater Mussels of Vermont*

**Legend**

- **Species Present**
The eastern floater is one of Vermont's most common mussel species. The species' distribution is probably more widespread than the map indicates; relatively few lakes and ponds have been surveyed. It is found in rivers and streams, but appears to be most common in lakes and ponds. It is often the second in abundance to the eastern elliptio in lakes. River or lake bottom habitat includes sand, silty sand, or sand and gravel.

The eastern floater is a fragile, thin-shelled mussel. Adults average 90 mm (3.6 inches) in length, but attain lengths of 160 mm (6.4 inches) or more. The largest individuals in Vermont have been found in Dead Creek (Addison), Dead Creek (Fairfield), and Goslant Pond (Marshfield). Periostracum color is variable and can be brown, greenish, or even bright gold, such as mussels from Bristol Pond. The nacre is silvery-white, occasionally with blue or yellowish tones. Hinge teeth are absent. Beak sculpture, when visible, consists of 6 or more double-looped, curved bars without nodules.

The host fish species for the eastern floater are not known. Glochidia have been recorded on white sucker (*Catostomus commersoni*), pumpkinseeds (*Lepomis gibbosus*), and carp (*Cyprinus carpio*) but transformation has not been confirmed (Hoggarth 1992). The eastern floater is a long-term breeder spawning in late summer and releasing glochidia in May of the following year.
EASTERN FLOATER *Pyganodon c. cataracta*

*Freshwater Mussels of Vermont*

**Legend**

- **Species Present**
GIANT FLOATER  

*Pyganodon grandis* (Say, 1829)

In Vermont, the giant floater is found in Lake Champlain and at least the following tributary streams - Missisquoi River, Lamoille River, Otter Creek, East Creek, Hubbardton River, Poultney River, and Winooski River. It is a species of the Interior Basin of North America reaching its northeastern range limit in the Lake Champlain drainage. This species appears to be most abundant in the Missisquoi River and littoral areas of Lake Champlain. Only Smith (1985a) found this species above the principal fall-line on one of these rivers (Otter Creek). Substrates in which this mussel is found include sand, sand and gravel, silty sand, and clay.

This mussel is a thin-shelled species with a slight dorsal wing posterior to the beak. The beak is inflated above the hinge line. Shape is ovate, and the outer shell color is shiny yellow-brown, greenish, or greenish-brown. Inner shell color is white, sometimes with a bluish or salmon tinge. There are no hinge teeth. In contrast to the eastern floater, the beak sculpture of the giant floater has nodulous, double-looped bars. Some very large specimens (length 160 mm [6.4 inches]) are found in Dead Creek, where presumably an abundance of nutrients (from livestock in the watershed) encourages optimum growth in this species. Lake Champlain specimens of 110 mm (4.4 inches) are more typical.

The host fish include longnose gar (*Lepisosteus osseus*), blacknose dace (*Rhinichthys atratulus*), blackchin shiner (*Notropis heterodon*), and Iowa darter (*Etheostoma exile*). The giant floater is a long-term breeder, with spawning in August and release of glochidia in May or June of the following year.
GIANT FLOATER  *Pyganodon grandis*

**Legend**

- **Species Present**
Zebra mussel

Pink heelsplitter

Creek heelsplitter

Fragile papershell

Fluted-shell

Squawfoot
In Vermont, the fluted-shell is found only in tributaries of Lake Champlain. This is another of the Mississippi Basin species that reaches its northeastern range limit in the Lake Champlain drainage. Adams (1841) first documented this species in Vermont. Most records of this species are from downstream of the principal fall-lines, but on Otter Creek, the fluted-shell is found as far up as Cornwall. It has not been recorded in Lake Champlain or other lowland lakes or ponds. It is often found in association with other mussel species, and is not found in large numbers. In the lower Poultney River, densities of 0.8 mussels/m² have been recorded (Fichtel 1994 pers. obs.). Fluted-shells are found in a variety of bottom substrates, including silt, coarse and fine sands, gravel, and aggregates of cobble, gravel, and sand.

This is a medium-sized mussel (90 mm [3.6 inches] in length). Fluted-shells are laterally compressed which makes them appear somewhat flattened. The most diagnostic feature is the ‘washboard’ effect, or series of parallel ridges on the dorso-posterior surface of the periostracum. Periostracum color is variable, and the nacre is white, bluish-white, or yellowish-white. The pseudocardinal hinge teeth are strong and well-developed but the lateral teeth are weak or absent. There is an interdental projection in the left valve (Clarke 1981). Vermont fluted-shells have an orange-colored foot, another diagnostic feature of this species.

The host fish species for the fluted-shell is not known. The species is a long-term breeder spawning in late summer and releasing glochidia in the late spring of the following year.
The creek heelsplitter is a species which is often found in headwater streams of the St. Lawrence drainage and has not been found in lakes. It is not restricted to the Lake Champlain basin, but most records are from the basin. In 1993, the species was discovered in the Coaticook River (Norton), a tributary of the St. Francis River, which enters the St. Lawrence River downstream from the Richelieu River. Pond Brook (Colchester) is the smallest stream in which this species has been found to date. Adams (1841) first documented this species in Vermont. It is found in Otter Creek in Mt. Tabor nearly to the headwaters.

This is a small to medium-sized mussel averaging 60 mm (2.4 inches) in length. The diagnostic features include a somewhat flattened (laterally compressed) appearance, a slight dorso-posterior wing, strong, forward-projecting preudocardinal hinge teeth, an obvious interdental projection, and long, narrow lateral hinge teeth. The periostracum color is yellowish or greenish brown to brown and the nacre color is silvery or bluish white.

The host fish species for the creek heelsplitter is not known. This species is thought to be hermaphroditic (i.e., sperm and eggs are produced in the same individual). The creek heelsplitter is a long-term breeder which spawns in late summer and releases glochidia in late spring or early summer of the following year.
CREEK HEELSPRITTER *Lasmigona compressa*

Legend

- **Species Present**
ALEWIFE FLOATER  \textit{[Anodonta implicata (Say, 1829)]}

The alewife floater is presently found only in the Connecticut River below Bellows Falls within the range of the shad \textit{(Alosa sapidissima)}, one of its suspected, but unconfirmed fish hosts. Smith (1985b) reported that prior to 1970, the alewife floater was not known to occur above Hartford, Connecticut. This species appears to be indicative of the success of clupeid fish restoration in the Connecticut River. While not abundant at this time, it is most common below Vernon Dam. It shares habitat with the eastern elliptio, eastern lampmussel, triangle floater, and eastern floater, with which it can be easily confused.

The shell is elongated, generally without the slight upward curve which characterizes the eastern floater. Most characteristic is a pronounced thickening of the anteroventral portion of the adult shell. The nacre is pinkish or salmon. This is a medium to large mussel (110 mm [4.4. inches] in length).

It is suspected that one or more anadramous clupeid fish species serve as hosts for the alewife floater, but no experimental evidence exists documenting successful transformation of glochidia. Laboratory transformation has been documented with glochidia on white suckers, pumpkinseed, and white perch \textit{(Morone americana)} (Hoggarth 1992).
ALEWIFE FLOATER *Anodonta implicata*

*Freshwater Mussels of Vermont*

**Legend**
- • *Species Present*
The fragile papershell is another Interior Basin species with its northeastern range limit in Lake Champlain and some of its tributary streams. It inhabits the Missisquoi (Swanton and Highgate), Lamoille (Milton and Colchester), Winooski (Burlington and Colchester), and Poultney (West Haven) rivers, and Otter Creek (Ferrisburgh and Vergennes), only below their principal fall-lines. It has been found in littoral areas of Lake Champlain near the deltas of the Lamoille and Winooski Rivers. This is not a common species; the greatest densities have been recorded in the lower Poultney River. The fragile papershell is most often found anchored in sand, gravel and sand, silty sand, and clayey silt.

This mussel is distinctive with its thin (laterally compressed), yellowish shell, ovate-oblong shape, and prominent dorsal wing. The dorsal wing is highest in juveniles and least prominent in older adults. The growth rings are typically brownish on the otherwise yellow outer shell. The inner shell color is an iridescent white. The hinge teeth are weak and narrow. This species is especially difficult to dislodge from the substrate, another apparently distinctive feature (Fichtel 1991 pers. obs.). This species is a medium to large mussel, 120 mm (4.8 inches) in length. The mantle is not modified.

The host fish may be the freshwater drum (*Aplodinotus grunniens*), but this has not been confirmed. The fragile papershell is a long-term breeder, with spawning taking place in late summer and glochidia being released in June or July of the following year.
FRAGILE PAPERSHELL *Leptodea fragilis*

*Freshwater Mussels of Vermont*

**Legend**

- **Species Present**
PINK HEELSPLITTER [Potamilus alatus (Say, 1817)]

The pink heelsplitter, a mussel of the Interior Basin, reaches into northeastern North America to the St. Lawrence River and Lake Champlain drainage. In Vermont, it occupies the Missisquoi River, Lamoille River, Winooski River, Lewis Creek, Otter Creek, Hospital Creek, and Poultney River, and only below the principal fall-lines of these rivers. It also occurs in the littoral zone of Lake Champlain. Nowhere in Vermont waters is it common. Substrates in which the pink heelsplitter is found include clay, clayey silt, sand, pea gravel and sand, and cobble/sand/silt.

This mussel is distinctive in appearance with an ovate shape, dark, almost black outer shell color, and prominent dorsal wing. The shell is moderately thick, and overall size can be quite large (up to 160 mm [6.4 inches] long). The inner shell is a striking pinkish-purple. The hinge teeth are well-developed; the pseudocardinal tooth is serrated. Young mussels have more prominent dorsal wings, and the outer shell color is greenish-brown. The mantle is not modified.

The host fish may be the freshwater drum, but this has not been verified. The pink heelsplitter is a long-term breeder spawning in late summer with release of glochidia in late May-early July of following year (Holland-Bartels and Kammer 1989).
Freshwater Mussels of Vermont

Legend

• Species Present
The black sandshell has always been rare in Vermont and is presently known to inhabit only two streams, the Poultney River (West Haven) and Otter Creek (Ferrisburg and Vergennes). Also found by Smith (1985a) in the Missisquoi River (Highgate) and Hospital Creek (Addison), it has not been found in those streams since the late 1970s. A worn shell was found on the shore of Lake Champlain in Benson in 1993, but the species has never been seen alive in Lake Champlain. This is another species of the Interior Basin mussel fauna which reaches its northeastern range limit in the Lake Champlain drainage. It is infrequently encountered in the Poultney River and Otter Creek. Poultney River mussel beds rarely yield more than one or two sandshells (Fichtel 1991). Females are almost never found, and no one has ever reported finding a juvenile sandshell alive. Whether the species' population in either river is still viable is unclear. The black sandshell is found in substrates of sand, sand and gravel, and silt.

The male black sandshell has the appearance of a long black spearpoint, while the female is broader and more rounded at the posterior end. Adults in Vermont average 130 mm (5.2 inches) long. The outer shell color is dark green to black; the inner shell color is usually white, but may be salmon or purplish. The shell is moderately inflated. The hinge teeth are well-developed. The mantle edge is modified into many long, crowded papillae and is light-colored.

The host fish for the glochidia of the black sandshell include largemouth bass and white crappie (Pomoxis annularis). This species is a long-term breeder.
BLACK SANDSHELL  *Ligumia recta*

_Freshwater Mussels of Vermont_

**Legend**
- • *Species Present*
In New England, the Connecticut River is one of only two known streams supporting the dwarf wedgemussel, encompassing an 18-mile reach from Hartford to Weathersfield. Another record from the 1970s in Thetford was not reconfirmed on two subsequent surveys. Since most of the Connecticut River is in New Hampshire, very little dwarf wedgemussel habitat actually occurs in Vermont. This species is on the Federal and both Vermont and New Hampshire endangered species lists. Records of early twentieth century collectors indicate that the dwarf wedgemussel was much more widespread, having occurred from Bloomfield, Vermont south into Connecticut. There are no records of this species in any Vermont tributaries of the Connecticut River, and none were found during surveys for this species during the period 1983-94. Population density estimates by Strayer (1995) suggest that the Connecticut River may contain one of the largest remaining populations of this species. In the Connecticut River, this species is found in shallow water (up to 5 feet deep) along both shores typically in a firmly packed aggregate of gravel, sand, cobble, and small rocks.

This is a small (maximum length of 45 mm [1.8 inches]) mussel with a somewhat trapezoidal shape. Outer shell color is dark, often with a greenish cast, and frequently eroded around the umbo. Two lateral hinge teeth are found in the right valve, one in the left. The posterior end is rounded and the ventral margin is mostly straight.

A host fish in New England is probably the tesselated darter (Etheostoma olmstedi), based on a study by Mickelson and Neves (1995) that demonstrated that dwarf wedgemussel glochidial successfully transform under experimental conditions.
DWARF WEDGEMUSSEL  

*Alasmidonta heterodon*

Freshwater Mussels of Vermont

Legend

- Species Present
In Vermont, the brook floater is found only in the lower reaches of the West River (Dummerston, Newfane, Townshend, and Jamaica), a large tributary of the Connecticut River in southeastern Vermont. A population is found to extend from about 0.5 miles below the Townshend flood control dam nearly to the Interstate 91 overpass at Brattleboro. A small population is found between the Ball Mountain and Townshend dams. However, surveys indicate that distribution of this population is not uniform, but is characterized by areas where this species is locally common, often outnumbering other mussel species. This mussel is most common within the towns of Brookline, Newfane, and Townshend. Although searched for in the upper watershed above the Ball Mountain Dam, the brook floater has never been found there. The brook floater is usually found in shallow water (less than 3 feet, though sometimes deeper). River bottom habitat used by this mussel is a matrix of firmly packed sand, gravel, cobble, with some mussels found among large rocks. Mussel beds usually support low to moderate densities of submerged aquatic plants (Elodea sp., Potamogeton spp.).

This mussel can reach 70 mm (2.8 inches) in length. Its most characteristic feature is the presence of a series of small wavy ridges perpendicular to the growth lines on the dorso-posterior shell surface. The outer shell color varies from yellowish-brown to dark brown, and is usually extensively rayed. The nacre is bluish-pink. Pseudocardinal teeth exist only as weak knobs, and lateral teeth are absent. The foot is often bright pink or orange.

Barry Wicklow (1995 pers. comm.) has observed metamorphosis of glochidia when slimy sculpin (Cottus cognatus), pumpkinseed, and blacknose dace served as host species.
BROOK FLOATER *Alasmidonta varicosa*

*Freshwater Mussels of Vermont*

**Legend**

- • *Species Present*
TRIANGLE FLOATER  [Alasmidonta undulata (Say, 1817)]

The triangle floater is a widespread, but not common species in Vermont. It is found in the Connecticut, Hudson, and St. Lawrence river drainages. Most records of this species are in the middle to upper portions of streams within these major drainages, although it does occur in lakes. The largest known populations in Vermont are found in Warm Brook (Arlington), a second order tributary of the Battenkill River, the West River, and the Connecticut River. The 18-mile reach of the Connecticut River that supports the dwarf wedgemussel also supports numerous triangle floaters. It is not clear why this species is relatively uncommon; presumably past land use activities have reduced these populations. In general, this species is found in stream runs within a matrix of sand and gravel, but sometimes within shifting sands.

This species is short (55 mm [2.2 inches] long) and squat with a broadly ovate to triangular shape. The outer shell color is yellowish-green to black and is extensively rayed. The anterior portion of the shell is thickened, and the nacre is sharply bicolored, pinkish-salmon posteriorly, whitish anteriorly. The pseudocardinal teeth are large and well developed, and lateral teeth are absent.

Barry Wicklow (1995 pers. comm.) has observed metamorphosis of glochidia when the blacknose dace served as the host species. This is a long-term breeder that begins spawning in mid-summer and releases glochidia in late spring or early summer of the following year (Clarke 1981).
TRIANGLE FLOATER  *Alasmidonta undulata*

*Freshwater Mussels of Vermont*

**Legend**

- *Species Present*
The cylindrical papershell is a species of the Great Lakes-St. Lawrence system and Ohio-Mississippi system that reaches its easternmost range limit in Lake Champlain and the St. Lawrence River. In Vermont, it is presently known to live only in the Missisquoi River drainage and in Stone Bridge Brook. There is a historic (Baker, 1928) collection record from the Clyde River. One live individual and one shell were found in Stone Bridge in 1994 near the mouth of the brook. It is probable that the cylindrical papershell is found in shallow water areas of the extreme northern portion of Lake Champlain. Smith (1985a) notes that the cylindrical papershell probably reached Lake Champlain from the St. Lawrence River system via the Richelieu River. He found the species to be common in the Missisquoi River around Highgate. Substrate in which the cylindrical papershell lives in the Missisquoi River is silt and silty sand.

This species is a small to medium-sized mussel (70 mm [2.8 inches]). The most diagnostic features of this species are its moderately thin shell, inflated, nearly cylindrical, appearance, and fine beak sculpture ridges which are not parallel to the growth lines. Hinge teeth are absent. Periostracum color is brown or greenish and the nacre is bluish white. This is the only species in the subfamily Anodontinae with a papillate exhalent aperture.

The host fish species for the cylindrical papershell is not known. The mottled sculpin (Cottus bairdi) and sea lamprey (Petromyzon marinus) have been reported as hosts (Hogggarth 1992), but without confirmation that glochidia successfully transformed.
CYLINDRICAL PAPERSHELL  *Anodontaoides ferussacianus*

*Freshwater Mussels of Vermont*

**Legend**

- • *Species Present*
The zebra mussel, native to eastern Europe, is completely unlike our native freshwater mussels in appearance and biology. It is a recent addition to the mussel fauna of Vermont, first reported from southern Lake Champlain at Benson Landing in 1993. It is not yet known to occur in any other lakes or in any of Vermont’s rivers. Zebra mussels have been found at various locations in Lake Champlain attached to native mussels, but zebra mussel densities are still low relative to the Hudson and Seneca River drainages, or the Great Lakes (Kamman 1995). In 1994, zebra mussels were found to be widespread in the southern portion of Lake Champlain, in clusters north to Burlington, and individually to Rouses Point (Kamman 1995). Studies in the Great Lakes have documented up to 10,000 zebra mussels on an individual unionid mussel. Unlike our native mussels, zebra mussels attach themselves to just about any hard surface underwater, such as rocks, stumps, driftwood, piers, boat hulls, bricks, bottles, and pipes using sticky byssal threads. Kamman (1995) reported that boat owners have had to scrape zebra mussels off their boat hulls at some Lake Champlain marinas. Certain fish and waterfowl, such as the lesser scaup (*Aythya affinis*) feed on these mussels.

The zebra mussel is a thumbnail-sized mussel with a zebra-like color pattern of alternating light and dark bands across the shell. They are "D"-shaped in appearance. Average length of adult zebra mussels is 25-35 mm (1.0-1.4 inches).

Zebra mussels are extremely prolific breeders. The larvae, called veligers, unlike glochidia, are free-swimming when released by the female and are carried long distances by water currents. Veligers attach to hard surfaces with a tough, string-like byssis where they develop into mature zebra mussels. This species does not require an intermediate host species as do the native mussels. Adults lifespan is typically 2-5 years.
ZEBRA MUSSEL *Dreissena polymorpha*

**Legend**

- Species Present

*Freshwater Mussels of Vermont*
REFERENCES ON FRESHWATER MUSSELS


