

Chapter 27

Freshwater mussels (Bivalvia: Margaritiferidae, Unionidae) of the Atlantic Maritime Ecozone

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Abstract: Of the 55 species of freshwater mussels recorded in Canada, 19 or 20 (36%) occur in the Atlantic Maritime Ecozone. Four of these species are found nowhere else in Canada, including *Alasmidonta heterodon* (Lea), *Alasmidonta varicosa* (Lamarck), *Lampsilis cariosa* (Say), and *Leptodea ochracea* (Say). With the exception of a few historic records from outside the ecozone in the St. Lawrence River, *Anodonta implicata* Say in Canada is also restricted to the Atlantic Maritime Ecozone. *Alasmidonta heterodon* is officially listed as extirpated in Canada. *Lampsilis cariosa* occurs in only two river systems and is listed federally as a species of special concern. *Alasmidonta varicosa*, with populations scattered across a limited list of river systems in New Brunswick and Nova Scotia, was recently listed federally as a species of special concern. *Obovaria olivaria* (Rafinesque), which occurs in the Quebec portion of the Atlantic Maritime Ecozone as well as in Ontario, is very rare and its national status is under review. Limited historic data combined with recent field surveys suggests that the freshwater mussel fauna of the Atlantic Maritime Ecozone has declined over the past century. Although some mussels in the ecozone are still widespread and abundant, species such as *Margaritifera margaritifera* (Linnaeus) may be experiencing reduced recruitment owing to the decline of *Salmo salar* Linnaeus, the principal host fish for this mussel. Among the primary environmental stressors that impact the freshwater mussel fauna in the Atlantic Maritime Ecozone are the construction of dams and dikes, water pollution, the destruction or modification of the riparian zone, the introduction of non-indigenous species, and sedimentation. The long-term survival of freshwater mussels within the ecozone will also depend on the conservation of native freshwater fishes, which serve as hosts for the metamorphosis and dispersal of the mussel larval stage. For some mussel species, only a subset of probable host fish has been identified in the ecozone. Drainages within the Atlantic Maritime Ecozone with the most diverse assemblages of fishes generally also harbour the greatest number of mussel species. Four river systems in the ecozone, the Miramichi (NB), Restigouche (NB), Saint John (NB), and St. François (QC), are comprised of multiple drainages. Among these, the Saint John and the St. François, with 11 and 14 mussel species, respectively, stand out as the most diverse. Not surprisingly, the Saint John River supports up to twice as many species of freshwater fish as the Miramichi and Restigouche. In some mussel-diverse watersheds, such as the Cumberland Basin and River Philip Composites, in the vicinity of the New Brunswick and Nova Scotia border, few obligate freshwater fish are present, suggesting that anadromous and catadromous fish are important hosts for the glochidia produced within these mussel assemblages. Three of the 15 ecoregions in the Atlan-

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tic Maritime Ecozone that are richest in freshwater mussel diversity are located in southern New Brunswick and southeastern Quebec. Yet, there are also significant populations of endemics and disjuncts present in the Fundy Coast, South Central Nova Scotia Uplands, and Southwest Nova Scotia Uplands ecoregions. Better data on the genetics of specific mussel populations, particularly for mussels of the genus *Pyganodon*, as well as freshwater mussel – host fish relationships, are needed to fully understand current zoogeographic patterns of Atlantic Maritime Ecozone unionoids and successfully address conservation concerns for this fauna.

Résumé : Des 55 espèces de moules d'eau douce répertoriées au Canada, 19 ou 20 (36 %) sont présentes dans l'écozone maritime de l'Atlantique. Quatre de ces espèces ne se trouvent nulle part ailleurs au Canada, notamment l'alasmidonte naine (*Alasmidonta heterodon* Lea), l'alasmidonte renflée (*Alasmidonta varicosa* Lamarck), la lampsile jaune (*Lampsilis cariosa* Say) et la leptodée ocre (*Leptodea ochracea* Say). À l'exception de quelques relevés historiques extérieurs à l'écozone maritime de l'Atlantique effectués dans le fleuve Saint-Laurent, l'anodonte du gaspé (*Anodonta implicata* Say) est limitée au Canada à l'écozone maritime de l'Atlantique. L'alasmidonte naine (*Alasmidonta heterodon*) est officiellement répertoriée comme disparue du Canada, la lampsile jaune (*L. cariosa*) est présente dans seulement deux réseaux hydrographiques et est répertoriée au niveau fédéral en tant qu'espèce préoccupante, et l'alasmidonte renflée (*A. varicosa*), avec des populations réparties sur une liste limitée de réseaux hydrographiques du Nouveau-Brunswick et de Nouvelle-Écosse, a été récemment répertoriée au niveau fédéral en tant qu'espèce préoccupante. L'obovarie olivâtre (*Obovaria olivaria* Rafinesque), présente dans la partie québécoise de l'écozone maritime de l'Atlantique ainsi que dans l'Ontario, est très rare et son statut national est à l'étude. Les données historiques limitées, combinées aux plus récentes études sur le terrain, laissent entendre que la faune des moules d'eau douce de l'écozone maritime de l'Atlantique a diminué au cours du siècle dernier. Bien que certaines moules de l'écozone maritime de l'Atlantique demeurent répandues et abondantes, il se peut que des espèces telles que la mulette-perlière de l'Est (*Margaritifera margaritifera* Linnaeus) connaissent un recrutement réduit en raison de la diminution du saumon de l'Atlantique (*Salmo salar* Linnaeus), le principal poisson-hôte pour cette moule. Au nombre des principaux stressés environnementaux ayant une incidence sur les moules d'eau douce de l'écozone maritime de l'Atlantique, on note la construction de barrages et de digues; la pollution de l'eau; la destruction ou la modification de la zone riveraine; l'introduction d'espèces non indigènes; la sédimentation. La survie à long terme des moules d'eau douce au sein de l'écozone maritime de l'Atlantique dépendra aussi de la conservation des poissons d'eau douce indigènes, qui servent d'hôtes pour la métamorphose et la dispersion des moules au stade larvaire. Par ailleurs, un seul sous-ensemble de poissons-hôtes pour certaines espèces de moules est connu dans cette écozone. Les bassins hydrographiques de l'écozone maritime de l'Atlantique contenant les assemblages de poissons les plus variés abritent généralement aussi le plus grand nombre d'espèces de moules. Quatre des réseaux hydrographiques de l'écozone maritime de l'Atlantique, la rivière Miramichi (N.-B.), la rivière Restigouche (N.-B.), la rivière Saint-Jean (N.-B.) et la rivière Saint-François (QC), sont constitués de plusieurs bassins hydrographiques. Parmi ceux-ci, les réseaux hydrographiques des rivières Saint-Jean et Saint-François, avec respectivement 11 et 14 espèces de moules, se distinguent comme ceux présentant le plus grand nombre d'espèces. Fait non étonnant, la rivière Saint-Jean abrite jusqu'à deux fois plus d'espèces de poissons d'eau douce que la Miramichi et la Restigouche. Dans certains bassins hydrographiques riches en espèces de moules, comme le bassin de Cumberland et les tributaires de la rivière Philip, à proximité de la frontière du Nouveau-Brunswick et de la Nouvelle-Écosse, peu d'espèces de poissons strictement d'eau douce sont présentes, ce qui semble indiquer que les poissons anadromes et catadromes sont d'importants hôtes pour les glochidiums produits dans les assemblages de moules. Trois des quinze écorégions comprises dans l'écozone maritime de l'Atlantique les plus riches en diversité de moules d'eau douce sont situées dans le sud du Nouveau-Brunswick et dans le sud-est du Québec. D'importantes populations d'espèces endémiques et isolées sont encore présentes dans les écorégions de la côte de Fundy, des hautes terres du centre-sud de la Nouvelle-Écosse, et des hautes terres du sud-ouest de la Nouvelle-Écosse. Des données plus précises sur la génétique des populations de moules, en particulier sur les moules du genre *Pyganodon*, ainsi que sur les relations entre les moules d'eau douce et leurs poissons-hôtes, sont nécessaires pour vraiment comprendre les modèles zoogéographiques actuels des moules d'eau douce de l'écozone maritime de l'Atlantique et pour répondre adéquatement aux préoccupations en matière de conservation de cette faune.

Introduction

The living members of the subclass Paleoheterodonta are represented by a unique group of large bivalves referred to as freshwater mussels, or less frequently as freshwater clams or naiads. These molluscs are found in various types of freshwater habitats on all continents, except Antarctica. There are approximately 800 living species worldwide (Lydeard et al. 2004; Christian and Harris 2008; Bogan 2008; Bogan and Roe 2008). Freshwater mussels belong to the order Unioniformes and the superfamily Unionacea, which comprises six families. Two of these families occur in North America: Unionidae (with 49–51 genera) and Margaritiferidae (with 2 genera) (Turgeon et al.

1998; McMahon and Bogan 2001; Bogan 2008; Bogan and Roe 2008).

This chapter is primarily an overview of the diversity, geographical distribution, and conservation status of the freshwater mussels of the lake and river systems of the Atlantic Maritime Ecozone (AME). The region encompasses New Brunswick, Nova Scotia, and Prince Edward Island, Îles de la Madeleine, and that part of Quebec extending from the Gaspé Peninsula southwesterly through the Appalachian complex of eastern Quebec to the United States border south of Sherbrooke. We also provide information on mussel origin and postglacial dispersal, life history, and ecosystem function. Sections on environmental stressors affecting freshwater mussels and

Table 1. The freshwater mussels of the Atlantic Maritime Ecozone.

Scientific name	English name	French name ^a
Superfamily: Unionoidea (synonym: Unionacea)		
Family Margaritiferidae		
<i>Margaritifera margaritifera</i> (Linnaeus, 1758)	Eastern Pearlshell	Mulette-perlière de l'Est
Family Unionidae		
Subfamily Unioninae		
<i>Alasmidonta heterodon</i> (Lea, 1830)	Dwarf Wedgemussel	Alasmidonte naine
<i>Alasmidonta marginata</i> Say, 1818	Elktoe	Alasmidonte rugueuse
<i>Alasmidonta undulata</i> (Say, 1817)	Triangle Floater	Alasmidonte à fortes dents
<i>Alasmidonta varicosa</i> (Lamarck, 1819)	Brook Floater	Alasmidonte renflée
<i>Anodonta implicata</i> Say, 1829	Alewife Floater	Anodonte du gaspateau
<i>Anodontoides ferussacianus</i> (Lee, 1834)	Cylindrical Papershell	Anodonte cylindrique
<i>Lasmigona compressa</i> (Lea, 1829)	Creek Heelsplitter	Lasmigone des ruisseaux
<i>Lasmigona costata</i> (Rafinesque, 1820)	Flutedshell	Lasmigone cannelée
<i>Pyganodon cataracta</i> (Say, 1817)	Eastern Floater	Anodonte de l'Est
<i>Pyganodon fragilis</i> (Lamarck, 1819)	Newfoundland Floater	Anodonte de Terre-Neuve
<i>Pyganodon grandis</i> (Say, 1829)	Giant Floater	Grande Anodonte
<i>Strophitus undulatus</i> (Say, 1817)	Creeper	Strophite ondulé
Subfamily Ambleminae		
<i>Elliptio complanata</i> (Lightfoot, 1786)	Eastern Elliptio	Elliptio de l'Est
<i>Lampsilis cardium</i> Rafinesque, 1820	Plain Pocketbook	Lamsile cordiforme
<i>Lampsilis cariosa</i> (Say, 1817)	Yellow Lampmussel	Lampsile jaune
<i>Lampsilis radiata radiata</i> (Gmelin, 1791)	Eastern Lampmussel	Lampsile rayée
<i>Leptodea ochracea</i> (Say, 1817)	Tidewater Mucket	Leptodée ocre
<i>Ligumia recta</i> (Lamarck, 1819)	Black Sandshell	Ligumie noire
<i>Obovaria olivaria</i> (Rafinesque, 1820)	Hickorynut	Obovarie olivâtre

^aFrench names of mussels are based on Martel et al. 2007.

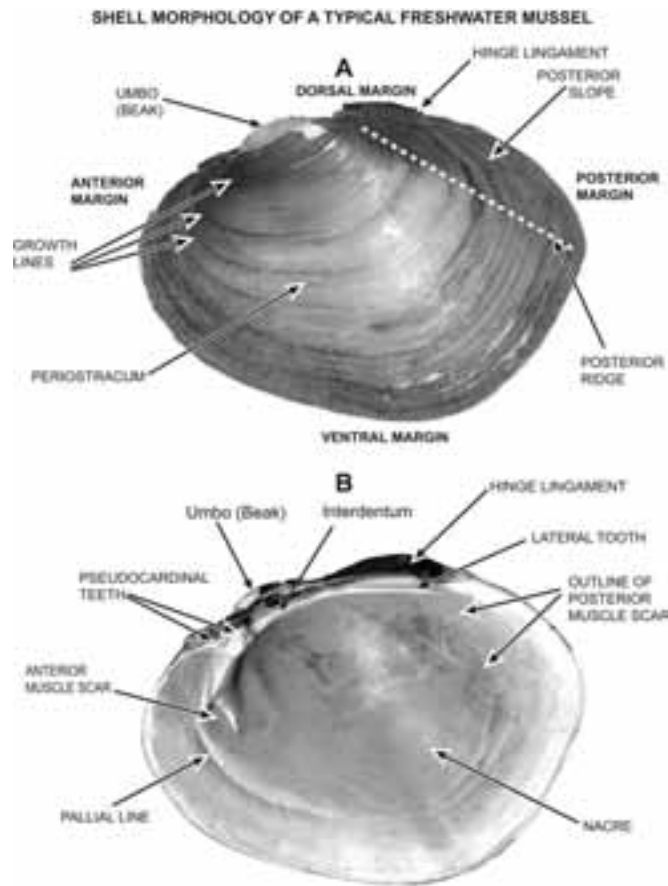
recommendations for the future preservation of this unique fauna within the AME are also included.

For the first time, detailed maps showing distribution by watershed for 19 of the 20 species (Table 1) of freshwater mussels occurring within the AME are presented. These maps and the discussions that follow are based largely on 3433 mussel specimen records, mostly housed in museum collections, which we assembled for this chapter. Most of these records are housed in the collections of the New Brunswick Museum, the Nova Scotia Museum of Natural History, and the Canadian Museum of Nature mollusc collection (CMNML). Additional sources of specimen and literature records include the Nova Scotia Department of Natural Resources, Ministère des Ressources naturelles et de la Faune du Québec, Atlantic Canada Conservation Data Centre, Ohio State Museum of Biological Diversity, University of Michigan Museum of Zoology, Royal Ontario Museum, Florida Museum of Natural History, and the Illinois Natural History Survey, as well as Athearn (1961), Athearn and Clarke (1962), Hanson and Locke (2001), Beaudet et al. (2002), Caissie (2005), Beaudet (2006), Caissie and Audet (2006), Davis (2007), Thériault et al. (2007), and S. von Oettingen (US Fish and Wildlife Service, pers. comm. to D.L.S., 2002). Although we believe these records include most of the extant mussel records from the AME up to 2007, it is important to note that representation from the region remains incomplete. In particular, drainages of northern New Brunswick, parts of southwestern Nova Scotia, the Gaspé, and the lower St. Lawrence region of the AME and Prince Edward Island require further investigation.

The Unionacea is the only group of bivalves in North America represented solely by native species. Together they comprise a group of ecologically important macroinvertebrates known for their ability to filter water while partially buried in the bottom of river and lake systems. Of moderate to large-size bivalves (Fig. 1), adult shell length may range from about 30 mm in small forms to well over 200 mm in some large species. Body mass sometimes exceeds 400 g. The shell is composed of two valves united by a strong dorsal hinge, which can open or close by means of anterior and posterior adductor muscles. In many species, the valves also include hinge teeth (pseudocardinal and lateral) near the dorsal ligament. These hinge teeth allow a tight and strong alignment of the valves upon closing.

Although freshwater mussels are sighted commonly along the shorelines of inland waterways, observers are surprised to learn that North America, with about 300 known taxa, has the highest diversity of freshwater mussels in the world (Williams et al. 1993; Master et al. 1998; Turgeon et al. 1998; McMahon and Bogan 2001; Bogan 2008; Bogan and Roe 2008). The freshwater mussel life cycle is also unique among molluscs. At a very early stage during life, freshwater mussel embryos or larvae, referred to as glochidia, must attach to a host fish. The mussel, parasitic during its larval developmental period, is also dependent on the fish host for its upstream and downstream dispersal (Kat 1984; Mackie 1984; Watters 1994). After a period of attachment on the host, the tiny metamorphosed mussel drops off and settles to the bottom, where it begins the benthic life it will follow as an adult (Lefevre and Curtis 1912; Kat 1984).

Fig. 1. Shell morphology of a typical freshwater mussel. (A) External view of left valve. (B) Internal view of right valve. *Lampsilis cariosa*.



Although diverse and widespread on this continent, freshwater mussels are among the most imperiled North American animals. Over 70% of the species are considered to be endangered, threatened, rapidly declining, or presumed extinct (Bogan 1993, 1996a; Williams et al. 1993; Ricciardi et al. 1998; Lydeard et al. 2004). The proportion of species at risk is higher than that of any other faunistic group on the continent (United States: Stein and Flack 1997; Canada: Metcalfe-Smith and Cudmore-Vokey 2004). Christian and Harris (2008) also note that 99% of all molluscs that have become extinct in the historic period are non-marine, and primarily freshwater. As many as 35 freshwater mussel taxa unique to the United States are presumed to have become extinct during the past century (Turgeon et al. 1998; Lydeard et al. 2004). In Canada, Metcalfe-Smith et al. (1998a) report on the drastic decline of the freshwater mussel fauna across the Laurentian Great Lakes basin during the past 140 years. Such catastrophic declines in freshwater mussel populations across North America, and in other parts of the world, has led to increased research on their biology, ecology, and conservation (Strayer et al. 2004).

Many regions of North America now have only a fraction of their historic freshwater mussel populations (Rhoads 1899; Taylor and Spurlock 1982; Parmelee 1988; Peacock et

al. 2005). Canada is no exception, where surveys show that some regions have lost much of their freshwater mussel fauna. This is especially the case where human populations are concentrated (Metcalf-Smith et al. 1997, 1998a). Many mussel species in Canada are now considered at risk, and one is already officially extirpated. The introduction of the invasive Eurasian zebra mussel (*Dreissena polymorpha* (Pallas)) and the quagga mussel (*Dreissena bugensis* Andrusov) has exacerbated the problem of declining freshwater mussel populations in the Laurentian Great Lakes basin (Schloesser and Nalepa 1994; Nalepa et al. 1996). This problem continues to spread across watersheds in Canada (Riccardi et al. 1996; Martel et al. 2001), including the St. Lawrence River in Quebec. Ricciardi et al. (1998) concluded that the introduction of the zebra mussel has accelerated regional extinction rates of North American freshwater mussels tenfold. These authors note that, coupled with environmental degradation, 60 mussel species in the Mississippi River basin are threatened with global extinction as a result of impacts from invasive dreissenid mussels.

In Canada, the status of freshwater mussel populations is a matter of growing concern for provincial and federal natural resource agencies (Metcalf-Smith and Cudmore-Vokey 2004). There is evidence that the freshwater mussel fauna of the AME has declined over the past century, especially during the last 50 years (Hanson and Locke 2000, 2001; Sabine et al. 2004). During this period human populations have increased around waterways, hydroelectric dams have been built, and forestry and agriculture practices have had a negative impact on river systems. Based on assessments by the Committee on the Status of Wildlife in Canada (COSEWIC), three freshwater mussel species that are restricted to the AME in Canada are now listed under the federal Species at Risk Act; *Alasmidonta heterodon* (Lea) is the first invertebrate to be officially listed as extirpated from Canada (COSEWIC 1999), while *Lampsilis cariosa* (Say), known from two AME river systems, has been listed as a species of special concern (COSEWIC 2004). The status of a third species, *Alasmidonta varicosa* (Lamarck), which occurs only in some rivers of Nova Scotia and New Brunswick, has recently been assessed as special concern (COSEWIC 2009). Other species of freshwater mussels unique to the AME region may have also experienced declines in their limited Canadian distributions. While the conservation and restoration of freshwater mussel populations can play an important role in preserving and restoring river systems, it is clear that this component of freshwater biodiversity needs protection, both within the AME and elsewhere.

Life history of AME freshwater mussels

Habitat

Freshwater mussels are found in a variety of permanent freshwater habitats, including streams, rivers, lakes, canals, and reservoirs. They also occasionally inhabit permanent ponds and marshes with good water circulation, usually those that are connected to a nearby lake or river system.

Although large lakes can sometimes harbour many species of freshwater mussels, it is in river systems that mussel diversity is highest. Possible explanations for this include the following: (i) river systems are older and geologically more stable habitats than lakes; (ii) rivers provide more heterogeneous habitats, through gradients in water flow along their length, and varying substrates; (iii) rivers often harbour a greater diversity of potential host fish species than lakes.

Some freshwater mussel species can flourish in a wide range of habitats, including both lakes and rivers. In the AME, such species include *Elliptio complanata* (Lightfoot), *Lampsilis radiata* (Gmelin), *Pyganodon cataracta* (Say), *Pyganodon fragilis* (Lamarck), *Pyganodon grandis* (Say), and occasionally *Alasmidonta undulata* (Say) (Clarke 1981a; Nedeau et al. 2000). Other species, including *Margaritifera margaritifera* (Linnaeus) and *Alasmidonta varicosa* are only found in river or running-water environments. Typically, running-water species are unable to survive in lakes or in impounded segments of rivers.

Stream or river size, as well as water velocity, influence the diversity, distribution and abundance of freshwater mussels (Clarke 1981a; Strayer 1993). Some species, such as *M. margaritifera*, commonly occur in the upstream sections of watersheds or in small or moderate size streams or rivers. Others, such as *L. cariosa*, prefer the larger, wider, more downstream river sections. Generally, the most favorable habitats for unionoid mussels are found in the middle and lower sections of the watershed, and it is here that both the greatest abundance and diversity of mussels often occur. Headwater streams, with their steeper gradients, coarser substrates, and narrower channels typically display a reduced diversity of mussels. The farthest upstream sections of the headwaters, with the steepest, most fast-flowing stream gradients, are typically devoid of unionoids.

Freshwater mussels often display species-specific substrate preferences. While some species inhabit coarse substrates such as gravel, others prefer finer sediments, such as sand, silty sand, silt, or even clay (Clarke 1981a). River or lake bottoms heavily covered by bedrock, boulders or large cobbles support few species or individuals, since these types of substrates are not favorable for burrowing or horizontal movement.

Freshwater mussels are found in a wide range of water depths, from a few centimeters in shallow streams, to depths of 4–10+ m in deep rivers or lakes (McMahon and Bogan 2001). However, most mussels are found at depths between 0.3 and 4 m. They cannot survive when exposed to air for extended periods of time, such as during a rapid reduction of water level above or below a dam, as they desiccate and die.

The bedrock underlying the river or lake system also plays a role in controlling freshwater mussel diversity. Moderate to large river systems with underlying sedimentary rocks, such as limestone or marble, often have the richest mussel communities (Clarke 1981a). In such river systems the high concentrations of calcium ions (high pH) minimize chemical erosion of the shell and are favorable to tissue growth, shell deposition,

and shell repair (McMahon and Bogan 2001).

The quality as well as quantity of woodland vegetation growing along the river or lake margin, also called the riparian zone, is of considerable importance for some unionoid mussels (Morris and Corkum 1996). Some AME unionoids, such as *M. margaritifera*, thrive in small to moderate-size streams or rivers where the riparian zone is thick and lush. Such healthy vegetation at the river's edge provides shelter and shaded areas necessary for the mussel's host fishes, brook trout (*Salvelinus fontinalis* (Mitchill)), and Atlantic salmon (*Salmo salar* Linnaeus).

Freshwater mussels, as a rule, inhabit river or lake systems with very good to reasonably good water quality. Studies have shown that increased siltation, due to human activity and land use, for example, can result in catastrophic declines in mussels (Anderson et al. 1991; Vaughn 1997), and that no mussels are found in grossly polluted water (Clarke 1981a). Moreover, because the life cycle of freshwater mussels is intricately linked to that of local host fishes, habitats that display rich and diverse unionoid communities necessarily includes rich and diverse fish communities (Clarke 1981a; Watters 1992).

Filter-feeding and behavior of freshwater mussels in the AME

Freshwater mussels feed by efficiently filtering planktonic food particles present in the water column. The freshwater mussel gut can contain a long list of planktonic food particles of less than 20 µm in size, including phytoplankton, bacteria (including fecal coliforms), zooplankton, such as rotifers, and detritus. Unionoids may also be capable of assimilating dissolved organic matter (McMahon and Bogan 2001; Vaughn and Hakenkamp 2001; Vaughn et al. 2008). Estimates of filtration rates range from 0.5 and 3+ L/h (Kryger and Riisgard 1988; also review by Vaughn et al. 2008). Galbraith et al. (2009) compared the gill morphology among four widely distributed freshwater mussel species and noted significant differences in gill surface morphology. These differences include total gill surface area, density of latero-frontal cirri, and the number of cilia per cirral plate. One of the conclusions is that differences in gill morphology among the various species of mussels may allow the species to utilize different planktonic food resources. Differences may also be related to other gill functions, including respiration or brood storage (Galbraith et al. 2009).

In temperate and northern climates freshwater mussels display distinct seasonal cycles in feeding, growth, spawning, and in some species, hibernation. Seasonal timing of breeding varies among Canadian unionoid mussels; some species release their larvae in the summer, while others do so through much of the fall, or even under the ice during winter or early spring (Clarke 1981a; Nedeau et al. 2000). Active filter feeding by AME freshwater mussels is also seasonal and largely depends on the timing of planktonic or primary production. In southern Canada, including the AME, the period of most intense filter feeding usually begins by late April–May. At this time the ice on lakes and rivers disappears and photoperiod rapidly increas-

es. This period of intense feeding, accompanied by rapid shell and soft tissue growth, can last until October, when water temperature and photoperiod begin to decrease. During filter feeding, when oxygen exchange through the gills also occurs, the siphonal apertures of the mussel can be seen when live mussels are examined in situ. Mantle flaps and apertures are sometimes quite distinctive (Fig. 2).

Little is known about the behavior and life history of AME freshwater mussels during the winter. Feeding and movement are certainly reduced at this time, although some species do reproduce and release their glochidia during winter (Clarke 1981a). In the fall, individuals of some species, including *E. complanata*, burrow into the sediments and disappear below the surface (Amyot and Downing 1991, 1997; Martel, pers. obs). While they may not be visible during SCUBA diving conducted in late fall or winter, *E. complanata* can be found in large numbers by simply digging into the sediment by hand (Martel, pers. obs). Caution must be taken when conducting field surveys in the fall, since surface counts alone can significantly underestimate the number of mussels present. In spring, the buried *E. complanata* resurface and assume their typical upright filter-feeding position. Amyot and Downing (1997) also observed that the greatest horizontal movement in *E. complanata* occurs during spring and early summer, when the species is spawning. Most freshwater mussels are capable of active crawling, using the foot to move the shell through the sediment. *Elliptio complanata* is one of the most active mussels in eastern Canada and is capable of crawling many metres over 24 h. Amyot and Downing (1998) observed that population aggregations in this species varied over the season. The clumping together of these mussels during summer spawning may have a functional reproductive role in that sperm are provided a greater chance of reaching the eggs brooded inside the gills of the female.

Growth and longevity of freshwater mussels

Many freshwater benthic macroinvertebrates, such as pulmonate snails, larval insects, and small crustaceans have an annual life cycle, typically living about a year. In contrast, freshwater mussels live much longer. In Canada, freshwater mussels of most species reach 6–15+ years (e.g., Metcalfe-Smith and Green 1992). Life spans of many decades are also observed in some species. *Margaritifera margaritifera* often reach 20–40+ years of age in Quebec (Martel, unpublished data), while in Europe, this mussel has been shown to live for over 100 years (Carell et al. 1987). Freshwater mussels, along with some marine clams known to live well over a century (Schöne et al. 2005; Strahl et al. 2007), are therefore some of the longest-lived animals on earth.

Determining age and growth in freshwater mussels involves counting the number of annual growth rings present in the shell. In temperate and northern climates, a period of winter growth cessation typically results in narrow, dark, shell secretion bands. These are sometimes visible externally, although if the rings are close together, the most precise counting method

requires that thin shell sections be cut with fine geological diamond saws and examined.

The usefulness of dendrochronological cross-dating methods for studying growth patterns and longevity in freshwater mussels has been studied by Rypel et al. (2008). Using 13 species of mussels, thin shell sections showed that shell growth was synchronous among species, even from different rivers, and that shell growth was negatively correlated with stream flow. This would seem to support the idea that shell growth increments are formed annually.

Mark–recapture methods have also been used to estimate age and growth of freshwater mussels. Anthony et al. (2001) conclude that mussels can be significantly older than predicted by annual ring counts alone. However, Haag (2009) has demonstrated that repeated handling of mussels during marking and remeasuring can lead to significant reductions in growth, leading to multiple additive sources of bias.

Reproduction in AME freshwater mussels

Reproduction in freshwater mussels involves parasitism of fishes during the larval stage and is unique among molluscs. An understanding of this complex relationship between mussels and their host fishes (Fig. 3) is crucial to understanding patterns of diversity, distribution, and conservation among freshwater mussels in the AME.

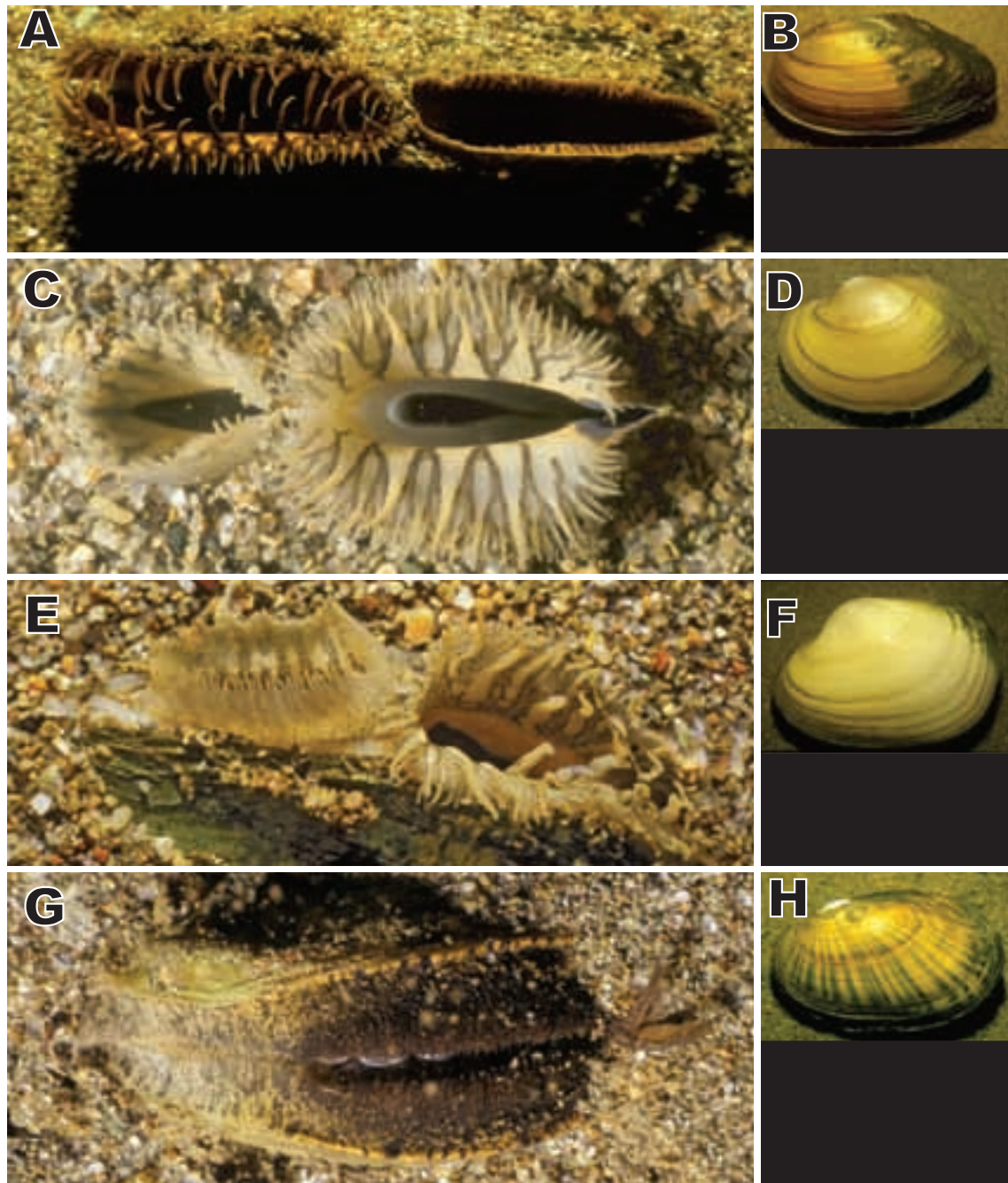
Gonochorism, sexual dimorphism

Among most North American freshwater mussel species, the sexes are separate (gonochoristic or dioecious) (Hoeh et al. 1995; Parmelee and Bogan 1998). Hermaphroditism does occur, but generally appears to be rare (Haag and Staton 2003), with the exception of mussels of the subfamily Ambleminiinae (Mackie 1984; Parmelee and Bogan 1998), where it is linked to the gill structures required to brood glochidia. The AME mussel species in which hermaphroditic individuals have been recorded include *M. margaritifera*, *Alasmidonta marginata* Say, and *Lasmigona compressa* (Lea) (Smith 1976; van der Schalie 1970; Bauer 1987).

Gills of female mussels modified for brooding specialised larvae

During the final steps of unionoid ovulation, mature oocytes are transferred from the ovary via the oviduct to specialized brood pouches located within the numerous gill lamellae (Mackie 1984; Tankersley and Dimock 1992; McMahon and Bogan 2001). These brood pouches, brood chambers, or marsupia, are made up of compartments where the eggs, and eventually larvae, are held. The proportion of the gill filaments that are used for brooding varies among species. In most freshwater mussels, brooding occurs only within the inner portion of the left and right demibranchs. However, in some species, brooding occurs in both inner and outer (i.e., all four) demibranchs (Williams et al. 2008). Inside the marsupia, the eggs eventually develop into specialized larvae called glochidia, the parasitic larval form unique to unionoid mussels (Fig. 4A, B) (Mackie

Fig. 2. In situ underwater photographs of live freshwater mussels taken while scuba-diving off Middle Island, Saint John River, near Oromocto, New Brunswick, 26–27 September 2005. Pictures depict a close-up of the siphonal apertures, mantle display (one species only), and a side view of a live shell removed from the sandy bottom and manually placed for the photograph. (A, B) *Anodonta implicata*, siphons and shell. (C, D) *Leptodea ochracea*, siphons and shell. (E, F) *Lampsilis cariosa*, siphons and shell. (G, H) *Lampsilis radiata*, mantle display and shell. Underwater photographs by A.L. Martel.



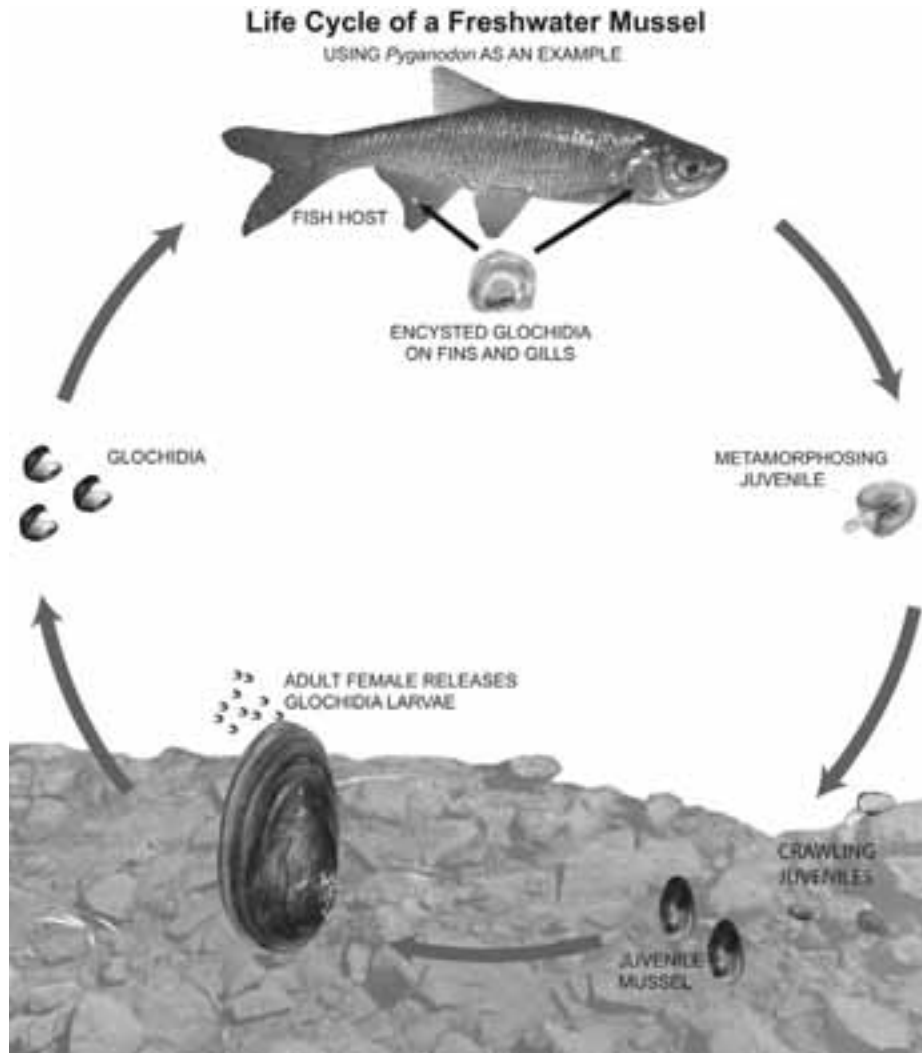
1984; Zardus and Martel 2002; Williams et al. 2008). The general morphology, anatomy, and dimensions of the glochidia vary among species, with even closely related mussels often displaying significant differences in glochidial form (Hoggarth 1999). Sizes of glochidia range from about 70–80 μm in *M. margaritifera* (Bauer 1994; Pekkarinen and Valovirta 1996)

to over 350 μm for the glochidia of anadontine mussels, such as *Pyganodon* spp. (Hoggarth 1999).

Male spawning and fertilisation of brooded eggs

In the male mussel the testis secrete and accumulate sperm cells that are eventually released into the water at the time of

Fig. 3. Life cycle of a freshwater mussel, *Pyganodon cataracta*. Glochidia of this species typically attach to fish fins, but occasionally attach to gills.

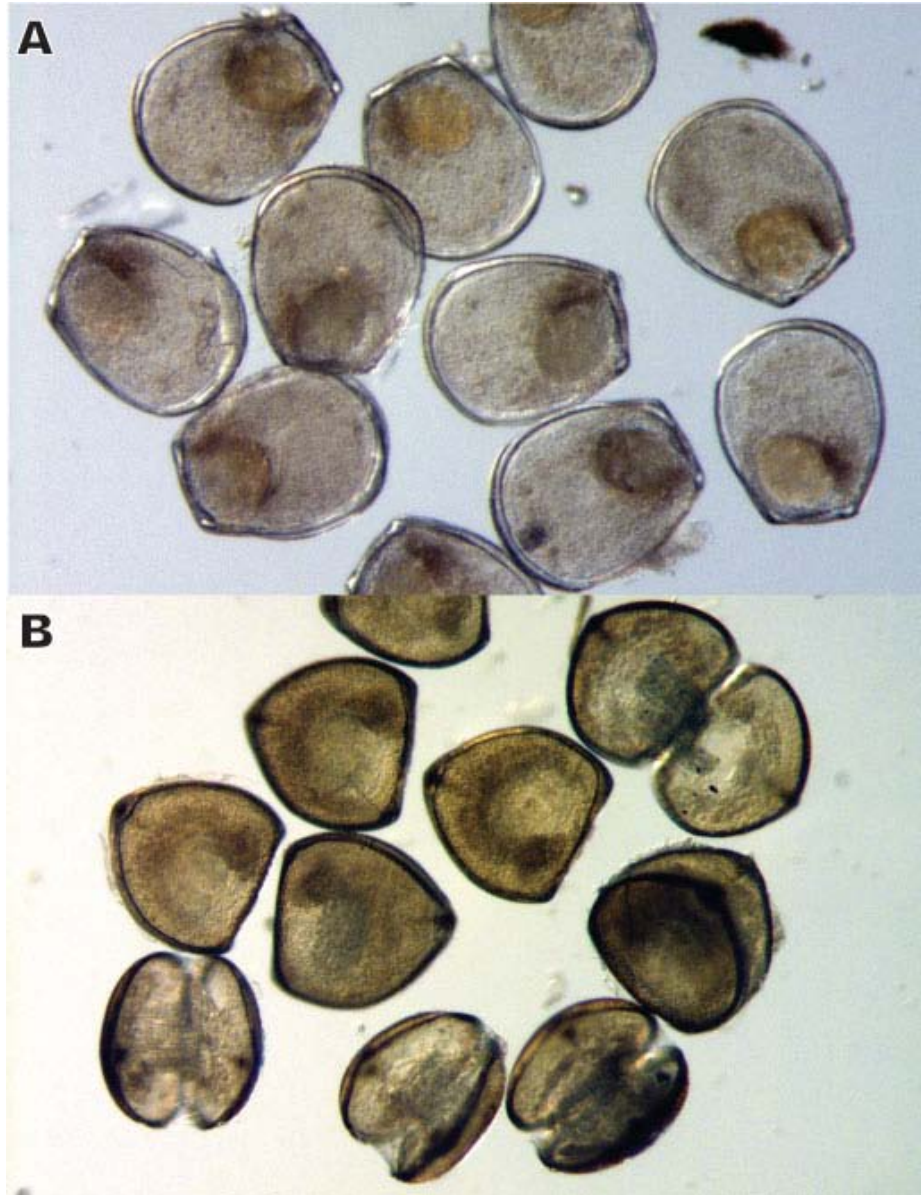


spawning. Prior to male spawning, breeding females transfer oocytes from the ovary to the marsupium. As the female filters water during feeding, sperm released from upstream or nearby males is drawn into the female mantle cavity with the inhalant water current. Here, sperm enter the egg-filled marsupial pouches through numerous micropores, and thus fertilize the eggs (McMahon and Bogan 2001; Parmelee and Bogan 1998). When mussels are present at extremely low densities (e.g., $<1/m^2$), and distances between individuals are great, reproductive success may be poor. In rare or declining species, the chances for unassisted recovery of the population may be limited. However, Neves (1997) notes that some rare riverine mussels are commonly gravid and show evidence of high fertilization success. This suggests that facultative hermaphroditism, and possibly self-fertilization, may occur more frequently among freshwater mussels than is generally believed (Neves 1997). Clearly, our knowledge of unionoid reproductive biology remains incomplete, especially when mussels are rare or persist at low densities.

Gravidity and brooding period

After fertilization, embryos develop into mature glochidia. They remain in the marsupial pouches for a few weeks to many months, depending on the species. In some species, females brood glochidia throughout the fall and winter, and gravid females can be found in a population from early fall until the next spring. Such species are called long-term brooders or bradytic (Mackie 1984). Other species brood their glochidia for only a short time during the summer months, and are referred to as short-term brooders, or tachytic (Mackie 1984). In the AME region, examples of long-term brooders include *A. varicosa*, *L. cariosa*, and *P. cataracta*. Species such as *E. complanata* and *M. margaritifera* are short-term brooders (Clarke 1981a; Nedeau et al. 2000). Unfortunately, details on the precise timing of breeding, the length of the brood period, and the time of glochidial release, are largely unknown among freshwater mussels in the AME. Watters and O'Dee (2000) examined the timing of glochidial release in five North American freshwater mussel species, including *L. radiata* and *P. grandis*,

Fig. 4. (A) Microphotograph of the hookless glochidium larvae of the eastern lampmussel *Lampsilis radiata*. Glochidia from the marsupial chambers of a gravid female from the rivière St. François, Quebec. The longest dimension of the larvae is 270–290 μm . (B) Microphotograph of the hooked glochidium larvae of the eastern floater *Pyganodon cataracta*. Glochidia from the marsupial chambers of a gravid female from a pond on Prince Edward Island (CMN-MOL 26236). The longest dimension of the larvae is 340–360 μm .



which occur in the AME. They note that each species releases larvae at different temperatures, calling some species “winter-releasers”, and others “summer-releasers” (Waters and O’Dee 2000). They suggest that the applicability of the terms bradyctic and tachytic should be reevaluated.

In some species, mature glochidia are released from marsupial compartments in strands, amorphous clumps, or in packets bound together by stretchable mucus secreted by the gills (Haag and Warren 2003; Martel. pers. obs). These glochidia-laden mucus strands are designed to snare nearby fish. In

becoming entangled around the head, gills, or fins, the likelihood that some glochidia will succeed in attaching onto the host fish is enhanced (Haag and Warren 2003). This strategy may be widespread among freshwater mussels, although further research is needed to confirm this.

In other taxa, glochidia are arranged tightly into fusiform, structurally distinct, packets called conglutinates, which are secreted by the gills (McMahon and Bogan 2001). Conglutinates may contain tens of thousands of glochidia; they remain intact upon release, enclosing the glochidia until a host fish bites and

attempts to eat the conglutinate. Conglutinates may be highly specialized structures, elongate and colourful, sometimes with eye spots and complex lateral pigmentation that mimics fish prey and serves to attract hosts (Haag et al. 1995). Details on the formation and morphology of conglutinates remain unknown for most North American freshwater mussels.

The fish connection in freshwater mussel propagation

The most unique feature in the reproductive biology of the freshwater mussel is the link to fishes. The life cycle of essentially all North American freshwater mussels involve one or more fish hosts (McMahon and Bogan 2001). The glochidium attaches to the fish by clamping two tiny valves onto the fish gills or fins. It is while attached to the fish that glochidia complete the last phase of development before metamorphosing into juvenile mussels. The likelihood of an individual glochidium attaching to a host fish, completing metamorphosis, and settling to the bottom as a juvenile mussel is extremely low (Jansen and Hanson 1991). Very high fecundity is thus a necessity for freshwater mussels. The brood pouches of an adult female *M. margaritifera* may contain over 10 million glochidia (Bauer 1987, 1994). This low probability of attachment to a host fish is countered by the opportunity for dispersal, both upstream and downstream. Upstream dispersal would be otherwise limited for a sessile, benthic organism (Kat 1984; McMahon and Bogan 2001).

Glochidia commonly attach to either the gills or the fins of fishes, although other parts of the host body may also be used (Jansen 1991; Martel and Lauzon-Guay 2005). Glochidia that usually attach to fish gills are small (70–250 µm) and typically hookless. In the AME, hookless glochidia that attach to the gills include those of *M. margaritifera* (Cunjak and McGladery 1991) and species of the subfamily Ambleminae (e.g., *Elliptio*, *Lampsilis*, *Ligumia*, *Obovaria*) (Fig. 4A). Glochidia that attach to fins, or perhaps the head and body, are larger (300–380+ µm) and equipped with specialized hooks or barbs, enabling a more effective attachment to the fish. Glochidia with hooks are observed in mussels of the subfamily Unioninae, including species of the genera *Alasmidonta*, *Anodonta*, and *Pyganodon* (Fig. 4B). Hooked glochidia are also commonly observed attached to the gills of fish (Jansen 1991), especially when they are present on individual fish in large numbers (Martel and Lauzon-Guay 2005).

Display of a “lure” in lampsiline mussels: attracting host fishes

The common glochidial release strategy is for the female to discharge her brood when a suitable host fish passes nearby or touches her. In this way, some glochidia may succeed in attaching to the fish. It appears that mussels can respond to the proximity of a fish by releasing glochidia when siphons or mantle are touched or through shadows cast on the mussel as a fish swims nearby (McMahon and Bogan 2001). However, in mussels belonging to the genus *Lampsilis*, females display highly modified mantle margins or flaps, which mimic small

fish, terrestrial insects, or aquatic macro-invertebrates (Fig. 2G) (Haag and Warren 1999). These modified mantle margins are located ventral to the inhalant siphon and are expanded and displayed during the breeding season. In gravid females of *L. radiata* the mantle flaps consist of 5–9 elongate papillae located below the inhalant siphonal aperture. When the female is partly buried, these are visible just above the sediment surface (Fig. 2G) and attract the fish to the female mussel (Kat 1984; Haag et al. 1995; Haag and Warren 1999). In *L. cariosa* and *L. cardium* (Rafinesque), the mantle flaps of these AME species mimic eye spots, elongate tail, and dorsal fins or spines of small fish. Once fully extended, these flaps can be rhythmically pulsed by the female mussel and are effective in luring predatory fishes that may serve as suitable hosts for the glochidia. When a fish strikes at the mantle lure, the valves of the shell contract, pressing on the brood chamber and releasing a cloud of tiny glochidia (Haag and Warren 1999). These specialized mantle flaps are unique adaptations that significantly increase the likelihood that the glochidia will attach to suitable host fishes, thus greatly enhancing the mussel’s chances to complete its life cycle and disperse within the watershed.

Glochidia development, metamorphosis, and release

Glochidia that succeed in attaching to a suitable host fish are encysted, a process that results in the glochidia being covered by a layer of host epithelial tissue. While encapsulated on the fish, the glochidium will gradually transform and metamorphose into a small juvenile mussel. There is usually no shell growth of the glochidium while on the fish. However, in *M. margaritifera*, there is significant growth of the glochidial shell while encysted. Glochidia of this species grow from about 70 to over 400 µm during the many months they are encysted. (Wachtler et al. 2001). During metamorphosis of the glochidium, larval structures are lost and replaced by juvenile or adult structures, including a tiny foot, two adductor muscles, and gill buds (Zardus and Martel 2002). At the time of release, the newly metamorphosed freshwater mussel excysts from the fish and settles to the bottom, beginning its benthic life.

Predators

The muskrat (*Ondatra zibethicus* (Linnaeus)) is the chief predator of freshwater mussels (Oesch 1984; Hanson et al. 1989; McMahon and Bogan 2001), including those species found in the AME. Muskrats often leave piles of shells, termed muskrat middens, on or near the shore at favorite feeding spots (Hanson et al. 1989). If carefully examined, such shell piles can provide information on the diversity of unionid mussels present in the area. Muskrat predation can be a significant source of mortality among mussels (Hanson et al. 1989) and a concern where muskrats are abundant and feed on rare or endangered mussels (Neves and Odom 1989). Although there is little data concerning predation pressures on mussels in the AME, mammals and reptiles that occur in the ecozone and are known elsewhere to prey on mussels include the river otter (*Lontra canadensis* (Schreber)), the raccoon (*Procyon lotor*

(Linnaeus)), the American mink (*Neovison vison* (Schreber)), and turtles (Oesch 1984; McMahon and Bogan 2001).

Certain fishes present in the AME region are molluscivores and are also suspected to be important predators of freshwater mussels. These fishes include bottom-dwelling species such as sturgeons (*Acipenser* spp.) and suckers (*Catostomus* spp.) (McMahon and Bogan 2001). Small, thin-shelled juvenile mussels are likely preyed upon by other fish taxa that forage on the bottom. Very little is known about fish predation on freshwater mussels in Canadian waters.

Conservation genetics

In recent years, there has been an increase in the number of North American studies on the population genetics of rare or imperiled mussels. Such investigations are important because the artificial propagation and or reintroduction of mussels from one river or watershed to another must consider genetic variation and the different morphologies sometimes observed in the wild within species (Zanatta et al. 2007; Zanatta and Murphy 2008). Two recent studies that have focused on the genetics of freshwater mussels of the genus *Pyganodon*, and have in part covered the AME, include Cyr et al. (2007) and Stanton (2008).

Origin and postglacial dispersal

Freshwater mussels are believed to have originated from marine bivalves (Watters 2001). With their larvae attaching to fish, which are highly motile organisms, unionoids have gradually colonized freshwater ecosystems. The freshwater mussels of the superfamily Unionacea found in today's lake and river systems have a long freshwater fossil history, dating as far back as the Triassic period, over 200 million years ago (Haas 1969; Watters 2001). This suggests that, at the time the world's continents formed a single supercontinental landmass, mussels were already important components of freshwater ecosystems.

On their own, freshwater mussels have limited powers of movement; they cannot pass over land from one drainage basin to another and are largely dependent on fish for their dispersal (Johnson 1980). It has therefore been generally accepted that current freshwater mussel distributions are a reflection of the history of drainage connections, which allowed fish to disperse among river systems. These historic drainage connections may have been quite different in the past than those observed today (Strayer and Jirka 1997; Nagel 2000). Sepkoski and Rex (1974) have also proposed that fish movement through episodic stream capture is not the sole means of dispersal for unionoids; these authors suggest birds as agents, either through gravid mussels clamping onto the feet of birds, or a more likely scenario in which fish-eating birds might carry parasitized fish or parts of fish between neighboring river systems. Fish stocking efforts may also obscure natural distributional patterns that reflect historical relationships among populations of mussels (Strayer and Jirka 1997; Nagel 2000). Nevertheless, natural dispersal via host fishes from one or more glacial refugia, with

subsequent changes in drainage patterns and perhaps extinction events, would appear to be largely responsible for the mussel distribution patterns we see today within the AME. Dispersal abilities among mussel species may also be influenced by the natural history of the fish host, and this may in turn be reflected in levels of genetic variability among mussel populations. Kat and Davis (1984), partly on the basis of allozymic data collected in Nova Scotia, suggest that mussels dependent on anadromous host fishes show less divergence among populations than do species with strictly freshwater host fishes, perhaps because the greater movements of these fish among river systems reduced the isolation between populations.

The origin of the modern eastern North American mussel fauna, the most diverse in the world, is unclear. Comparative morphology of fossil and modern species, suggests that there are Asian, European, and western North American elements present in the fauna, as well as a large number of eastern North American endemics (Watters 2001). Like the rest of the flora and fauna of the AME, all of the mussel species now present in the region colonized the area after the close of the last glacial period, some 11 ka. There are 11 (or 12, depending on taxonomy) widespread, or characteristic, mussel species of the AME that one can consider the core fauna. These species are part of an Atlantic Slope group of about 40 species, ranging from the lower St. Lawrence River and Newfoundland and Labrador, south to the Altamaha River Basin of Georgia (Parmalee and Bogan 1998). Within this region, distinct southern and northern mussel assemblages have been recognized (Johnson 1970; Parmalee and Bogan 1998). The core unionoid fauna of the AME is encompassed by 15 species that constitute the Northern Atlantic Slope assemblage, which extends north from the York River system, Virginia (Johnson 1980).

Johnson (1970) suggests that the mussels that now occupy the AME are of Interior Basin origin, originating in refugia south of the Terminal Moraine (Johnson 1980), while Clarke (1981b) proposes that the Atlantic coastal region was populated with unionoids dispersing from an Atlantic Coastal Plain refugium to the south. Strayer and Jirka (1997) and Nedeau et al. (2000) suggest that a portion of the northeast mussel fauna likely survived in a Northeastern Coastal Plain refugium off Nova Scotia. They hypothesize that mussels dispersed westward from refugia near the Grand Banks and Sable Island following the receding ice. Clear breaks in mussel distributions along the northeastern seaboard around southern Maine would appear to support this hypothesis, explaining disjunct populations of some mussel species within the AME, including *Alasmidonta heterodon*, *A. varicosa*, *L. cariosa*, and *Leptodea ochracea* (Say). However, recent models of deglaciation in Atlantic Canada suggest that the ice margin lay close to the edge of the continental shelf at the last glacial maximum (Shaw et al. 2002, 2006), providing no opportunity for offshore glacial refugia in the region. It now seems more likely that post-glacial extinction events and perhaps isolated founder events have produced the disjunct freshwater mussel distributions we see today in the AME.

Other species, such as populations of *L. radiata*, may have survived in a more southerly Atlantic Coastal Plain refugium, dispersing northeasterly and entering the AME via the Champlain Basin (see Nedeau et al. 2000). On the basis of genetic data, Kat and Davis (1984) have suggested that both *E. Complanata* and *L. radiata* entered Nova Scotia from the north via the Isthmus of Chignecto, rather than from offshore refugia. Molecular genetic data collected in the future may help to confirm or refute some of these hypotheses. Unfortunately, with the only Canadian population of *A. heterodon* extirpated from the AME (Hanson and Locke 2000), a unique element, perhaps derived from an Atlantic Coastal Plain refugium, is now gone. Genetic evidence now suggests dispersal from perhaps several coastal plain refugia in the region of the Carolinas by widespread AME amphibians and reptiles (see McAlpine 2010), and one can speculate that other aquatic species followed a similar pattern.

The remaining eight species of mussels recorded in the AME, additional to the core fauna, have very limited distributions in the ecozone, but are clearly of Mississippian (= Interior Basin of Johnson (1970)) origin. All are confined to the Quebec portion of the AME.

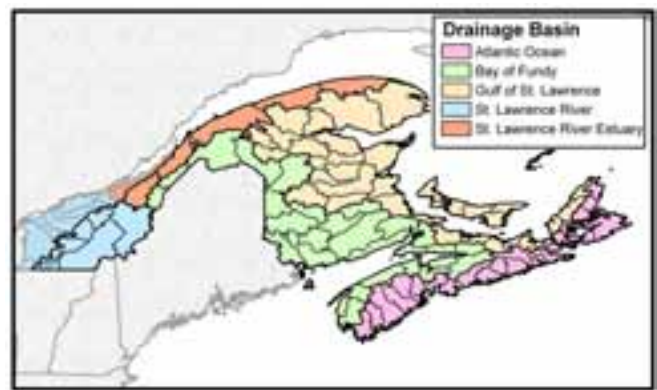
Zoogeography and distribution

In this chapter we follow the terminology of Burch (1975) for the major drainage regions of central and eastern North America, the portion of the continent of concern for the species described here. These major drainage regions, starting from the east, include the following: Atlantic Slope drainage (river systems emptying directly into the Atlantic Ocean), Great Lakes and St. Lawrence River drainage, Mississippi River drainage, and Hudson Bay drainage.

Undoubtedly, as further surveys are carried out and under-sampled areas are visited, some of our comments on mussel diversity in specific drainages within the AME (Fig. 5) will be shown to be incorrect or incomplete. For mapping purposes, we have shaded the drainages where mussel species have been recorded within the AME portions of those watersheds. Along the New Brunswick – Maine border, and in southwestern Quebec along the boundary between the AME and the Mixedwood Plains Ecozone, this has meant that mussel species may have been recorded within the drainage, but to date these occurrences fall outside the boundaries of the AME. Where Nedeau et al. (2000) cite mussel diversity for overlapping drainages as higher in Maine, we have used the higher figures.

Parmalee and Bogan (1998) recognize 12 distinct freshwater mussel faunal provinces or regions on the North American continent. The 12 unionoid faunal provinces differ from each other in overall species composition and species richness. Species richness within each one varies from nearly 200 taxa in the Cumberlandian faunal province, the richest unionoid region in the world, centered in the state of Tennessee, to less than 10 species for the Pacific faunal province. Intermediate species diversities are observed in the other unionoid faunal provinces of

Fig. 5. The five drainage basins of the Atlantic Maritime Ecozone.



North America (Parmelee and Bogan 1998). In comparison to other regions of Canada, the AME, with 20 species recorded, has a fairly high diversity of freshwater mussels. In Canada, only the Mixedwood Plains Ecozone, with 41 species, supports a higher diversity. With the exception of lakes or rivers that are highly polluted or degraded, freshwater mussels are more or less ubiquitous in the region and are present in nearly every watershed in the AME, often in great abundance.

Unionoids found in the AME region of Canada are for the most part members of the Northern Atlantic Slope freshwater mussel fauna (Parmelee and Bogan 1998). Four freshwater mussel species found exclusively in watersheds of the Atlantic coastal region (i.e., east of the Appalachian Mountains) and also present in the AME are among those that characterize this fauna (Johnson 1970). These include *A. heterodon*, *A. varicosa*, *L. cariosa*, and *L. ochracea*. In Canada, these species are unique to the AME region, being found nowhere else in the country. An additional unique Atlantic Slope species, *Pyganodon fragilis* (Lamarck), has also been reported in the AME region, although the validity of this taxon is unclear. This species is not considered here in our comments on zoogeography and distribution (it is treated in the AME species account section, although not mapped), and our numbers do not incorporate this species. Over a third of AME mussels have ranges that largely occupy the Mississippian Basin faunal province. In the AME these species are known from only a few sites/specimens in southeastern Quebec and are not part of the core AME freshwater mussel fauna.

On the basis of the records available for the AME (Fig. 6), the unionoid fauna of the region can be divided into four groups, with Groups 1–3 making up the core AME mussel fauna:

Group 1 (four species): *Margaritifera margaritifera*, *Elliptio complanata*, *Anodonta implicata* Say, and *Pyganodon cataracta*. All these species are widespread across New Brunswick, and mainland Nova Scotia, and also occur on Cape Breton Island. Three of the species appear to have more limited distributions in the Quebec portion of the AME, and one is absent. Two of the four species (*M. margaritifera* and *P. cataracta*) occur on Prince Edward Island, and one (*E. complanata*) occurs on Îles de la Madeleine.

Fig. 6. Sampling effort for freshwater mussels in the Atlantic Maritime Ecozone region. Each dot represents a historical or recent record (all available sources).



Group 2 (two species): *Lampsilis radiata* and *Alasmidonta undulata* (Say). These two species are relatively widespread in New Brunswick and the Quebec part of the AME, but have much more limited distribution in Nova Scotia, and are absent from Prince Edward Island.

Group 3 (five species): *Alasmidonta heterodon* (extirpated), *Alasmidonta varicosa* (Lamarck), *Lampsilis cariosa*, *Leptodea ochracea*, and *Strophitus undulatus* (Say). These five species have restricted and disjunct distributions in New Brunswick and Nova Scotia and are absent from Prince Edward Island. *Strophitus undulatus* also has an apparently disjunct occurrence in two watersheds in the Quebec portion of the AME.

Group 4 (eight species): *Alasmidonta marginata*, *Anodontoideus ferussacianus* (Lea), *Lasmigona compressa*, *Lasmigona costata* (Rafinesque), *Pyganodon grandis*, *Lampsilis cardium*, *Ligumia recta* (Lamarck), and *Obovaria olivaria* (Rafinesque). Unlike the preceding species, whose ranges center on the Northern Atlantic Slope, all of these species have distributions that mostly occupy the Mississippi Basin. Essentially, they occur in the AME as spill-over from the Mixedwoods Plains Ecozone. In the AME all these species are restricted to one or a few rivers in the Eastern Townships of Quebec, with their presence in the AME documented on the basis of few specimens. Two thirds of them (6 species) are known in the AME only from the rivière St. François, which is the largest St. Lawrence River tributary occurring within the AME.

To some degree, the AME mussel fauna supports Watters (1992) statement that unionid diversity is directly related to the number of fish species present. Certainly, ecoregions incorporating drainage basins within the AME with some of the more diverse assemblages of fishes do harbour higher numbers of mussel species (Fig. 7, Tables 2 and 3). Therefore, we find high mussel diversity (11 species) in the Bay of Fundy drainage, especially the St. Croix, Saint John, Kennebecasis, and Petitcodiac rivers in southern New Brunswick. This is an area Curry and Gautreau (2010) have identified as having as many as 26 species of strictly freshwater fish. The rivière St. François supports 14 mussel and 32 freshwater fish species along

that portion of the river that occurs in the AME of Quebec. It is worth noting that many of the mussels in the rivière St. François are Group 4 species. The Petitcodiac, with its diverse, and until recently, unique assemblage of mussel species, appears to be something of an anomaly in that this drainage supports a relatively modest number of fish species (Table 2). Drainages on Prince Edward Island and within the Gaspé, with 4–15 species of fish, support 1–4 mussel species.

Three river systems in the AME, the Saint John, Miramichi, and Restigouche, all composed of multiple drainages, provide useful comparison. Among these, the Saint John River system (Fig. 8A, B, F), with 11 mussel species (all Groups 1–3), stands out as the most diverse. The Miramichi harbours 6 species, and in the Restigouche system, only 3 (*M. margaritifera*, *P. cataracta*, *S. undulata*) have been recorded. Not surprisingly then, the Saint John River supports up to twice as many species of freshwater fish as the Miramichi and Restigouche. However, portions of the Restigouche are as diverse in fish species as the Miramichi (Table 2), suggesting that additional unionoid mussel species should be present in the Restigouche or that factors additional to fish diversity are involved. Likewise, the Becancour, Yamaska, and lac Memphremagog – lac St. François drainage basins in Quebec support 38, 39, and 56 freshwater fishes respectively, and only 2, 3, and 7 mussel species. Arbuckle and Downing (2002) found a close correlation between certain landscape features (watershed slope and alluvial deposits) and mussel diversity and abundance, suggesting that fish diversity is only one of several factors influencing freshwater mussel diversity at the regional level.

Although it has yet to be tested statistically, there do appear to be correlations between fish and mussel diversity within some of the complex drainages of Nova Scotia (Table 2). River systems with low fish diversity usually support few mussel species. Conversely, the Tusket River is distinctly more diverse than surrounding watersheds in terms of both unionids and strictly freshwater fish species. The St. Marys and Musquodoboit rivers and the Mira River Composite support a diverse assemblage of small-bodied fishes, including anadro-

Fig. 7. Number of freshwater mussel species within each watershed of the Atlantic Maritime Ecozone. There has been no collecting in some watersheds, thus the “0” value.

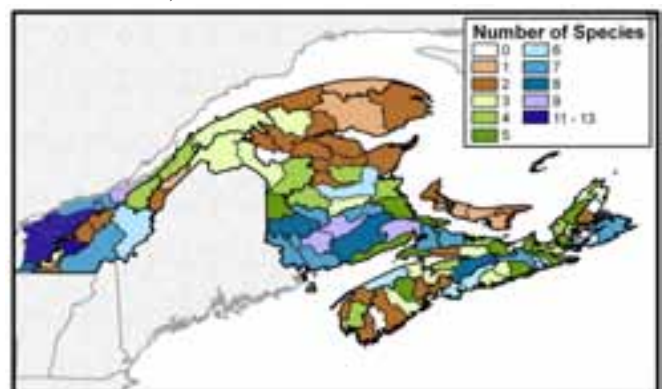


Table 2. Known number of freshwater mussel and obligate freshwater fish species by drainage basin within the Atlantic Maritime Ecozone. Where drainage basins extend outside the AME, total mussel and fish species for the basin may be greater (shown in parentheses) than totals for the AME. Totals for fish species are taken from Curry and Gautreau (2010), data supplied by the Ministère des Ressources naturelles et de la Faune du Québec, and J.F. Desroches (pers. comm. to D.F.M., 2009).

Drainage basin	Total unionoid species	Total fish species
St. Lawrence River drainages		
Lac Champlain (QC, VT, NY)	2 (9)	30
Rivière Yamaska (QC)	3 (11)	39
Lac Memphremagog – Lac St. François (QC, VT)	7	56
Rivière St. François (QC)	12 (13)	32
Rivière Nicolet (QC)	2 (11)	20
Rivière Bécancour (QC)	2 (11)	38
Rivière du Chêne Composite ^a (QC)	0 (7)	—
Rivière Chaudière Composite (QC)	6 (7)	40
St. Lawrence River Estuary drainages		
Rivière Etchemin Composite (QC)	4 (9)	26
Rivière du Loup Composite (QC)	4	22
Rivière Rimouski Composite (QC)	3	21
Rivière Matane (QC)	3	15
Rivière Madeleine Composite (QC)	2	7
Gulf of St. Lawrence drainages		
Îles de la Madeleine (QC)	1	1
Gaspé Composite (QC)	2	8
Cascapédia–Bonaventure Composite (QC)	1	15
Rivière Nouvelle (QC)	2	4
Little Main Restigouche River (NB)	0	11–15
Kedgewick River (QC, NB)	2	2
Restigouche–Patepédia rivers (QC, NB)	2	5
Upsalquitch River (NB)	2	11–15
Rivière Matepédia (QC)	3	10
Chaleur Bay Composite (NB)	2	4
Nepisiquit River (NB)	2	7–10
Acadian Peninsula Composite (NB)	2	7–10
Upper Southwest Miramichi River (NB)	4	11–15
Lower Southwest Miramichi – Cains River (NB)	3	11–15
Little Southwest Miramichi River (NB)	2	11–15
Northwest Miramichi River (NB)	4	11–15
Renous – Dungarvon – Lower Southwest Miramichi (NB)	6	11–15
Bay du Vin – Kouchibouguac River Composite (NB)	4	11–15
Richibucto–Buctouche Composite (NB)	5	11–15
Cape Tormentine Composite (NB)	5	11–15
Western Prince Edward Island (PEI)	2	4–6
West-central Prince Edward Island (PEI)	1	4–6
East-central Prince Edward Island (PEI)	1	4–6
Southeastern Prince Edward Island (PEI)	1	4–6
Northeastern Prince Edward Island (PEI)	2	4–6
River Philip Composite (NS)	7	7–10
Tatamagouche Composite (NS)	4	4–6
Pictou Composite (NS)	5	7–10

Table 2 (continued).

Drainage basin	Total unionoid species	Total fish species
Barneys River Composite (NS)	0	4–6
West River Composite (NS)	5	7–10
St. Georges Bay Composite (NS)	4	1–3
Mabou River Composite (NS)	4	4–6
Margaree River (NS)	5	4–6
Cheticamp River Composite (NS)	3	1–3
Atlantic Ocean drainages		
Ingonish Composite (NS)	3	1–3
North River (NS)	0	4–6
Middle River Composite (NS)	2	1–3
Whycocomagh Bay Composite (NS)	3	4–6
Mira River Composite (NS)	7	4–6
St. Peters Bay Composite (NS)	6	4–6
River Inhabitants (NS)	5	4–6
Milford Haven Composite (NS)	3	7–10
Salmon River – Canso Composite (NS)	5	7–10
Country Harbour River (NS)	6	7–10
St. Marys River (NS)	7	7–10
Liscomb River Composite (NS)	5	7–10
Sheet Harbour rivers (NS)	3	7–10
Tangier Composite (NS)	3	7–10
Musquodoboit River (NS)	6	7–10
Halifax Harbour Composite (NS)	6	7–10
St. Margarets Bay Composite (NS)	2	7–10
Gold River Composite (NS)	2	7–10
Lahave River (NS)	5	11–15
Medway River (NS)	3	7–10
Mersey River (NS)	2	7–10
Roseway–Jordan rivers composite (NS)	0	7–10
Clyde River Composite (NS)	2	4–6
Bay of Fundy drainages		
Tusket River (NS)	4	11–15
St. Marys Bay West Composite (NS)	2	4–6
Sissibou – Bear rivers composite (NS)	2	4–6
Annapolis River Composite (NS)	6	7–10
Cornwallis River Composite (NS)	3	1–3
Gaspereaux–Avon rivers composite (NS)	3	7–10
Kennetcook River Composite (NS)	4	11–15
Shubenacadie–Stewiacke rivers (NS)	8	4–6
North–Salmon rivers composite (NS)	3	7–10
North Cobequid Bay Composite (NS)	2	1–3
Chignecto Composite (NS)	5	4–6
Cumberland Basin Composite (NS, NB)	7	4–6
Peticodiac River (NB)	9	7–10
East Fundy Composite (NB)	5	16–20
Upper St. John – Daaquam rivers (QC, ME)	2 (3)	24
Upper St. John River – Grande Rivière Noire (QC, ME)	1 (3)	18
Upper St. John – St. François – Madawaska rivers (QC, NB, ME)	3	22
Upper St. John – Green rivers (QC, NB, ME)	3	21–30
Aroostook River (NB, ME)	6 (7)	21–30?
Tobique River (NB)	4	21–30
Upper St. John – Meduxnekeag – Becaguimec rivers (NB, ME)	5 (6)	21–30
Eel River – Mactaquac Headpond (NB)	8	21–30

Table 2 (concluded).

Drainage basin	Total unionoid species	Total fish species
Nashwaak River (NB)	7	21–30
Salmon River (NB)	7	21–30
Lower St. John River – Grand Lake (NB)	9	21–30
Oromocto River (NB)	9	21–30
Lower St. John – Kennebecasis – Canaan rivers (NB)	8	21–30
Magaguadavic River – West Fundy Composite (NB)	7	21–30
St. Croix – Digdeguash rivers (NB, ME)	7	21–30
Lower Bay of Fundy Islands (NB)	0	1–3

^a<9 km² of the of the extreme headwaters of the drainage basin occur in the AME.

mous and catadromous species, as well as 6–8 mussel species. The Cumberland Basin and River Philip composites appear to be noteworthy deviations from the previously discussed pattern. Mussel diversity is relatively high, with eight species. Yet, these drainages host a relatively small number of obligate freshwater fish species. In some parts of the watershed, as few as 1–3 species of obligate freshwater fish are present, and there are never more than 10. This suggests that anadromous and catadromous fish may be important hosts for the glochidia produced within the mussel assemblages of these watersheds. A similar situation would appear to be present in the Mira River Composite of Nova Scotia where eight mussel species have been recorded. Numbers of strictly freshwater fish species are low, but overall fish diversity in this watershed is relatively high. The Lahave watershed is well populated, with 11–15 obligate freshwater fish species. That only four mussel species have been recorded in the drainage suggests that the area deserves further investigation.

Unfortunately, relatively little is known about glochidia – host fish relationships within the AME. Where host fish are known, with few exceptions (Wiles 1975; Hare and Frantsi 1974; Hare and Burt 1975; Cunjak and McGladdery 1991), these data have been collected from outside the AME. Frequently, information on the glochidia – host fish relationship has come from areas where freshwater fish assemblages are different than those in eastern Canada. In several cases only a subset of likely host fish have been identified to date (Nedeau et al. 2000; Kneeland and Ryhmer 2008). It is likely that a better understanding of glochidia–host relationships within the AME, as well as genetic data on specific mussel populations, will be needed to fully understand current zoogeographic patterns of AME unionoids.

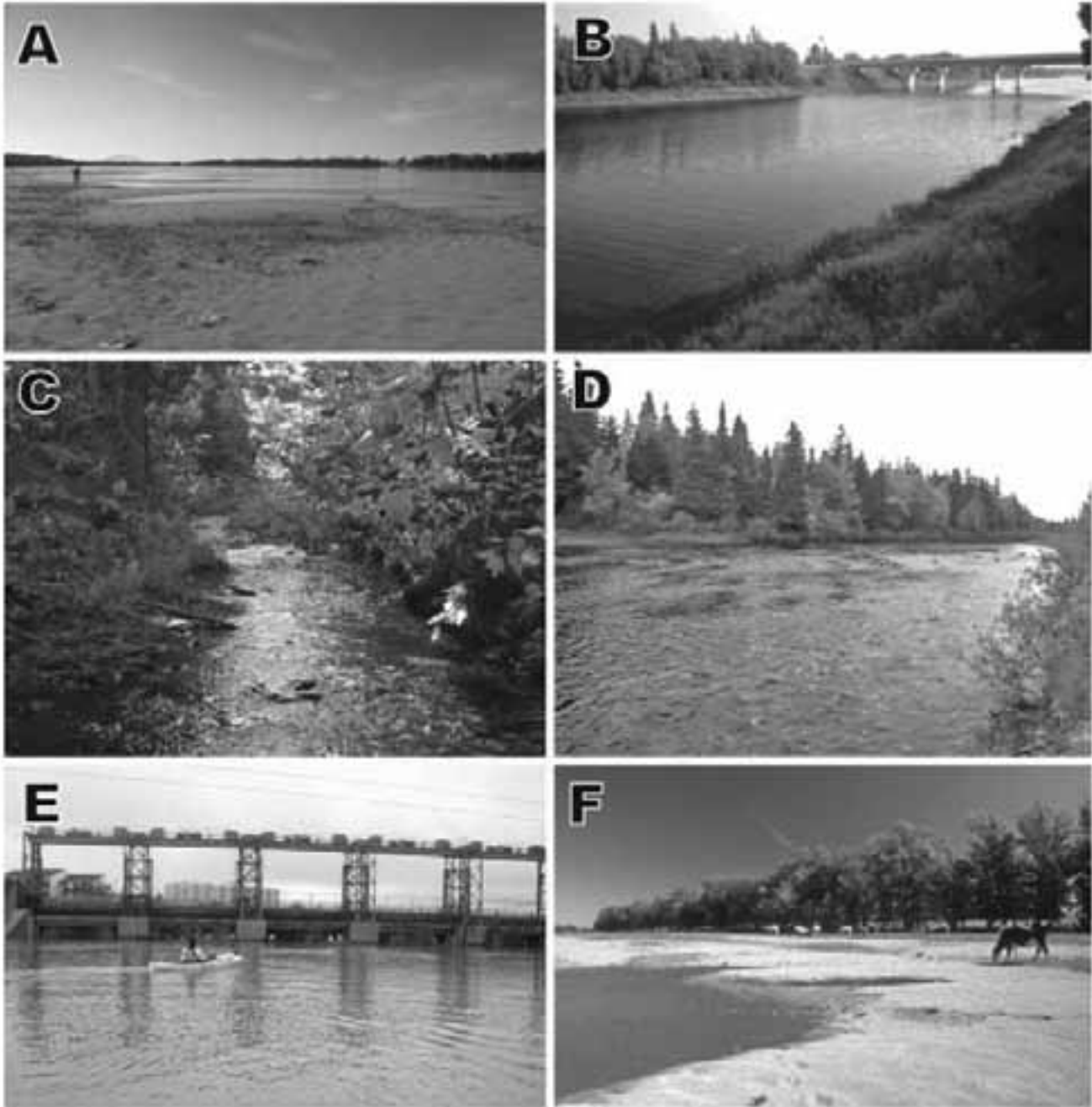
The 15 ecoregions that make up the AME are not concurrent with the drainages within the region. Although we have presented unionoid data by drainages because this makes biological sense, it may also be useful to consider unionid diversity by ecoregion for reasons of conservation management. Table 3 shows that 3 ecoregions in southern New Brunswick and northern Nova Scotia appear to be especially diverse in

Table 3. Number of mussel species by ecoregion (ecoregion number) within the Atlantic Maritime Ecozone.

Appalachians (117)	16
Northern New Brunswick Uplands (118)	6
New Brunswick Highlands (119)	3
Saint John River Valley (120)	8
Southern New Brunswick Uplands (121)	10
Maritime Lowlands (122)	11
Fundy Coast (123)	5
Southwest Nova Scotia Uplands (124)	6
Atlantic Coast (125)	7
Annapolis-Minas Lowlands (126)	8
South-central Nova Scotia Uplands (127)	7
Nova Scotia Highlands (128)	9
Cape Breton Highlands (129)	2
Prince Edward Island (130)	2
Îles de la Madeleine (131)	1

mussel species. These ecoregions contain the lower sections of several major river systems (high fish diversity, low slope, often significant alluvial deposits), hence their high mussel diversity. The Maritime Lowlands ecoregion of central and eastern New Brunswick, with 11 mussel species, is especially diverse because it contains both the Petitcodiac River and extensive areas of the species-rich lower Saint John River. Prince Edward Island and Îles de la Madeleine have few freshwater fishes and no large rivers. The former was isolated from the surrounding mainland relatively soon after glacial retreat and the latter was never connected to the mainland. Consequently, their mussel faunas are depauperate. Not surprisingly, two of the high-elevation ecoregions, which contain primarily small headwater streams, also have few mussel species. The Cape Breton Plateau, a flat, high-elevation plateau with few large water bodies, has only two mussel species. The New Brunswick Highlands, although higher in elevation, are more topographically varied and contain the headwaters of several large rivers as well as a number of lakes. Three species are known there: *M. margaritifera*, and two lake species common throughout the AME, *E. complanata* and *P. cataracta*. The ecoregion with the highest elevations in the AME, the Appalachians, is relatively unionoid-rich, with 16 species. The incongruity is due to the large size and broad classification of this ecoregion relative to others in the AME. In addition to extensive mountainous areas extending through the Gaspé Peninsula, it also contains sections of a number of large river systems that enter lowlands adjacent to the St. Lawrence River and estuary in the Mixedwood Plains Ecozone. The eight “spill-over” species identified in Group 4 are restricted to this ecoregion within the AME, but seven core species (with one exception all Groups 1 and 2) also occur here. One caution — while Table 3 reveals ecoregional species diversity, it does not reflect the occurrence of significant populations of endemics and disjuncts present in the Fundy Coast, South Central Nova Scotia Uplands, and Southwest Nova Scotia Uplands ecoregions.

Fig. 8. Habitat photos. (A) Lower Saint John River, near Oromocto, New Brunswick. (B) Bridge across the lower Canaan River, New Brunswick. (C) Kouchibouguac River, New Brunswick. (D) Kouchibouguacis River, New Brunswick. (E) Causeway dam across the Petitcodiac River, Moncton, New Brunswick. (F) Farming and river access to cattle, Saint John River, near Oromocto, New Brunswick.



Taxonomic diversity and species accounts

Family: Margaritiferidae

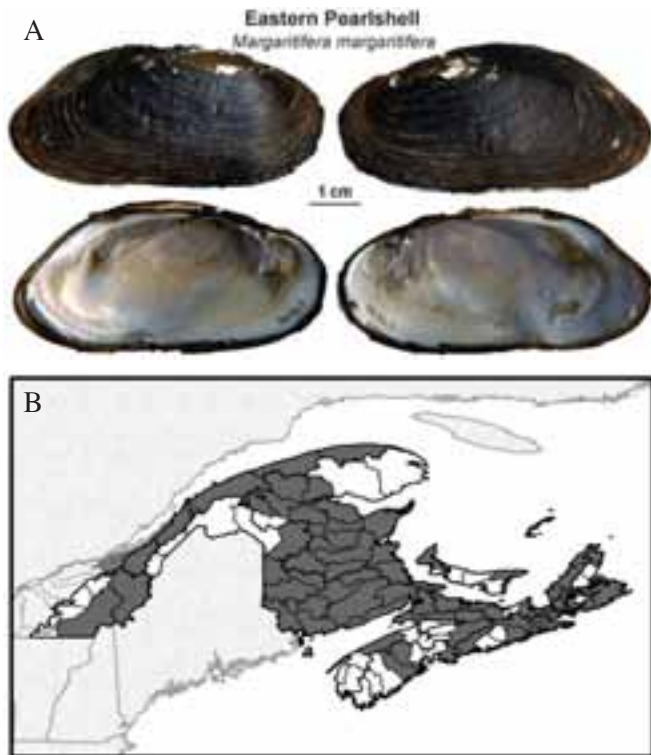
Eastern pearlshell

Margaritifera margaritifera (Linnaeus, 1758)

Distribution — The eastern pearlshell (Fig. 9A) is unique in that it is the only North America freshwater mussel with a holarctic distribution, including some European countries and

Russia. In North America, *M. margaritifera* occurs in the Atlantic Slope and Great Lakes – St. Lawrence River drainages. This mussel is also present in eight states along the Atlantic seaboard, from the coastal regions of Pennsylvania and Connecticut to Maine (NatureServe 2009). In Canada it occurs across the Canadian Atlantic region, where populations may represent the largest remaining stock of eastern pearlshells in the world. In Europe the *M. margaritifera* has become rare or extirpated in many countries.

Fig. 9. Eastern pearlshell (*Margaritifera margaritifera*). (A) External and internal view of shells from the South River, Nova Scotia. CMNML 92863. (B) Distribution map.



The pearlshell can be found in Newfoundland, Labrador, and much of southern Quebec on both sides of the St. Lawrence River. In the AME this species is found in rivers across New Brunswick and Nova Scotia, and is one of only two mussel species that occur on Prince Edward Island. In the Quebec portion of the AME, *M. margaritifera* occurs in the Eastern Townships (Estrie) region of southeastern Quebec in rivière au Saumon, near Sherbrooke. Small disjunct populations are also found in rivière Etchemin and in some Atlantic salmon rivers in the Bas-St-Laurent region (Fig. 9B).

Habitat — The eastern pearlshell typically inhabits small and medium-sized cold-water streams and rivers. It is not found in lakes but may occasionally occur in lake outlets. Contrary to other unionoid taxa, the eastern pearlshell can be found quite far upstream in the small, permanent, fast-running streams of watersheds. Usually bordered by a well-developed and shady riparian zone, sometimes these waterways are as little as 1.5 m wide. In North America, streams and rivers used by this species are typically characterized by low calcium carbonate levels (Clarke 1981a) and are especially well oxygenated, the latter a requirement of their salmonid hosts. This species commonly occurs in shallow sandy or gravel shoals, as well as in pools.

Reproduction and host fishes — By comparison with the glochidia of other freshwater mussels of the AME, the glochid-

ia of the eastern pearlshell are very small, measuring about 60–80 μm in shell length (Clarke 1981a; Wachtler et al. 2001). The glochidia are hookless and can be produced in astronomical numbers. Bauer (1987) reported a mean fecundity of 4 million glochidia per mature female annually for European populations of eastern pearlshells. This species is a short-term brooder, with females gravid during summer and early fall (Smith 1976; Clarke 1981a). In North America, known host fishes include the brook trout and the Atlantic salmon (Athearn and Clarke 1962; Smith 1976; Cunjak and McGladdery 1991), two fishes widespread in the AME. However, some streams in southern New Brunswick that have suffered severe declines or losses of salmon populations, and retain trout populations, appear to harbour nonreproducing populations of eastern pearlshells (Sabine, unpublished). This suggests that the Atlantic Salmon is the primary host species. The European brown trout (*Salmo trutta* Linnaeus) and the western Canadian rainbow trout (*Oncorhynchus mykiss* (Walbaum)), both introduced in some localities in the AME, are also confirmed hosts for this mussel (Smith 1976; Young et al. 1987).

Conservation status — In the United States, this mussel is either rare or at risk in most of the states where it is present (NatureServe 2009). Climate warming, which may reduce the number of cold-water streams in the AME, has the potential to affect the propagation of this long-lived species. The status of the eastern pearlshell is listed as secure in New Brunswick, but in Nova Scotia it is listed as sensitive because of the impact of acid rain and the reduction of Atlantic salmon in the southern part of the province (Metcalf-Smith and Cudmore-Vokey 2004). The species is listed as sensitive in Quebec (NatureServe 2009), where recent surveys show signs of decline and extirpation in some watersheds.

It is difficult to determine if this species is declining in the AME, since adult individuals are very long-lived and may persist for extended periods without reproducing, long after the host fish has been extirpated. The eastern pearlshell is one of the longest-lived animals on earth, with individuals between 100 and 200 years old reported (Bauer 1983, 1987; Mutvei and Westermarck 2001). Over the past 30–40 years, the drastic reduction of wild Atlantic salmon stocks may have impacted the eastern pearlshell, reducing or eliminating recruitment in some river systems. In some rivers of the Bay of Fundy drainage and Northumberland Strait only large individuals are observed, suggesting that recruitment in those rivers is extremely low or even nonexistent. However, the presence of young individuals with shell lengths <5 cm demonstrate successful reproduction for the species in some salmon rivers, such as the Rivière du Gouffre, located just across the St. Lawrence River estuary from the AME (Martel and McAlpine 2007). In 2007, juveniles were also found in the upper part of the rivière Etchemin and the rivière Matapédia (Paquet, unpublished data).

The impact of acid rain has not been evaluated for this species, which prefers oligotrophic soft-water habitats. It would

be useful to examine populations of eastern pearlshells remaining in regions of the AME, such as southwestern Nova Scotia, where the problem of acid rain has been particularly severe and where well over 50 rivers have lost their wild salmon stocks owing to acidification (Watt and Hinks 1999). In Europe this mussel has become rare or extirpated in many countries. Eastern Canada, and the AME in particular, may have among the largest remaining stocks of this species in the world (Young et al. 2001). It is therefore important that the conservation status of this mussel be carefully examined across the AME, as well as surrounding areas where the species occurs.

Family: Unionidae
Subfamily: Unioninae
[Tribe: Anodontini]

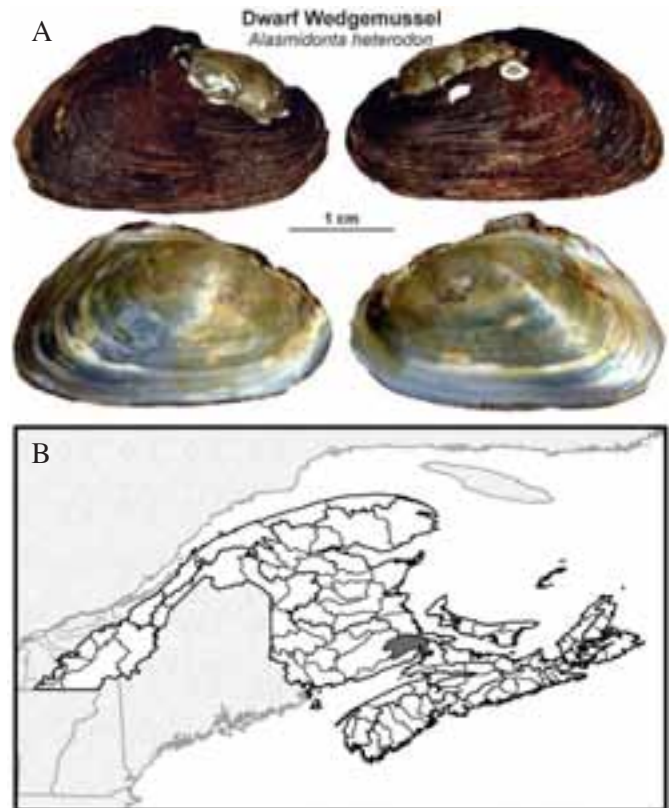
Dwarf wedgemussel
Alasmidonta heterodon (Lea, 1830)

Distribution — The dwarf wedgemussel (Fig. 10) is rare, with a disjunct distribution along the Atlantic Slope drainage. In the United States this mussel occurs in 12 states along the Atlantic coast region, from North Carolina to New Hampshire (Burch 1975; Clarke 1981a; Nedeau et al. 2000; NatureServe 2009). In Canada this mussel was known only in the Petitcodiac River Basin region of New Brunswick (Clarke 1981a, b; Hanson and Locke 1999; Fig. 11), but is now considered extirpated in Canada (COSEWIC 1999).

Habitat — The dwarf wedgemussel lives in flowing stream and river systems with slow to moderate current (Clarke 1981a, b). It is not found in lakes. It prefers to inhabit the midstream or downstream sections of the watershed, being absent from the narrower, faster-running, upstream part of waterways. The species is found on various substrates, including mud, sand, and sometimes gravel (Clarke 1981a, b; Strayer and Ralley 1993).

Reproduction and host fishes — No detailed scientific studies were ever conducted on the reproductive biology of this species in Canadian waters before it was extirpated (Hanson and Locke 1999). We may never know with certainty what host fish(es) this unionoid used to disperse its glochidia in Canada. The species is a long-term brooder, the gravid period spanning at least the period from late August to the following early part of June (Clarke 1981a, b). Studies in the United States have shown that the mottled sculpin (*Cottus bairdi* (Girard)), tessellated darter (*Etheostoma olmstedi* Storer), and johnny darter (*Etheostoma nigrum* Rafinesque) are hosts in southern rivers (Michaelsen and Neves 1995). None of these fishes are found in the Petitcodiac River system. Locke et al. (2003) proposed the American shad (*Alosa sapidissima* (Wilson)) as a likely candidate fish for the now extirpated population of this mussel in the Petitcodiac River. The authors pointed to the confirmed occurrence of this anadromous fish in the Petitcodiac River before the Moncton causeway (Fig. 8E) was built, and to its

Fig. 10. Dwarf wedgemussel (*Alasmidonta heterodon*). (A) External and internal view of shells from the North River, New Brunswick. CMNML 30797. (B) Distribution map.

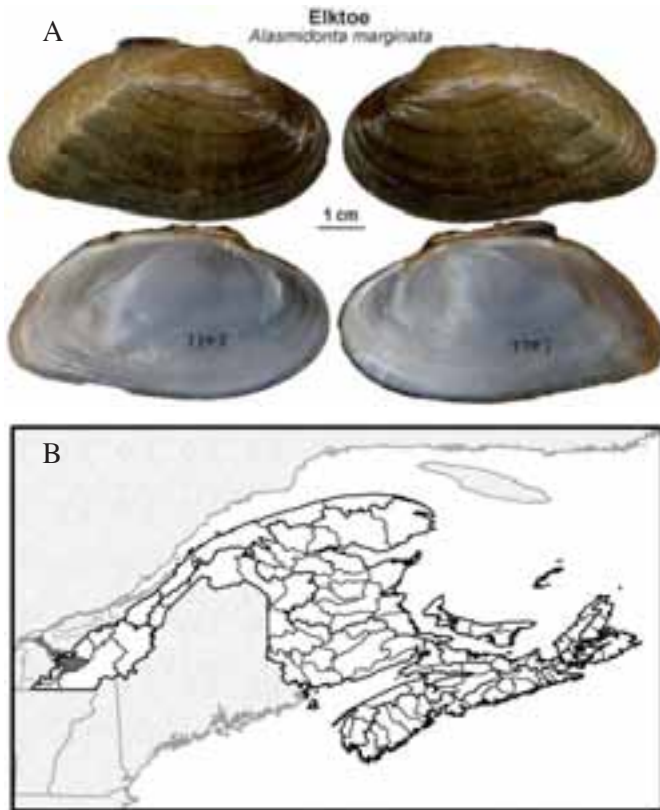


disappearance (with that of the mussel) following dam construction (Locke et al. 2003).

Conservation status — In the United States this mussel is a rare and inconspicuous species. It is listed as endangered or critically imperiled in nearly all of the 12 states where it has been reported along the Atlantic Coast, including all the New England states (Nedeau et al. 2000). In Canada it was listed as extirpated in 1999, after extensive surveys in the Petitcodiac River system failed to locate a single specimen (COSEWIC 1999; Hanson and Locke 2000). The last Canadian specimens of the dwarf wedgemussel were collected in 1967 by David Stansbery and are now in the Ohio State University Museum. The dwarf wedgemussel has the dubious distinction of being the first invertebrate to be officially extirpated from Canada. The extirpation of the dwarf wedgemussel from Canada is believed to have been caused by the loss of its host fish species from the Petitcodiac River when a causeway was constructed at the river mouth in 1968–1969 (Locke et al. 2003).

A recent federal report has concluded that recovery of the dwarf wedgemussel in Canada is not technically or biologically feasible at this time (Department of Fisheries and Oceans 2007).

Fig. 11. Elktoe (*Alasmidonta marginata*). (A) External and internal view of shells from Maitland River, Ontario (Mixedwood Plains Ecozone). CMNML 93191. (B) Distribution map.



Elktoe
Alasmidonta marginata Say, 1818

Distribution — The elktoe (Fig. 11A) is distributed in the Great Lakes (Lake Huron and Lake Ontario basins) — St. Lawrence River and the Mississippi drainages (Ohio–Mississippi, Cumberland, Tennessee, and Susquehanna River systems) (Burch 1975; Clarke 1981a; Parmalee and Bogan 1998; Williams et al. 2008). This mussel occurs in 24 states in the central and eastern United States (west of the Appalachian Mountains). It is rare in the nearby state of Vermont and has never been reported from Maine (Nedeau et al. 2000; NatureServe 2009).

In Canada, the elktoe is found in Ontario and Quebec. It occurs in southern, central, and eastern Ontario. It still occurs in some tributaries of the Ottawa River upstream of Ottawa, on the Ontario side of the river. It was recorded in the Outaouais region of the Ottawa River in 1882 and 1932 but has not been observed since. In Quebec the elktoe is a rare species. Historically, the elktoe had been observed in the St. Lawrence River, between Montreal and Quebec City (1863–1900). More recently, live specimens have been observed in the Centre-du-Québec region, outside the AME. Within the AME, a worn shell recently discovered in the rivière St François suggests that the species is present within the ecozone (Fig. 11B).

Habitat — The elktoe is a running-water species, preferring the riffle sections of mid-sized streams or small to medium-sized rivers. It is not found in lakes or impounded systems. The elktoe is usually deeply buried, displaying only a small portion of its shell above the substrate. The species preferred substrate is a gravel–sand mix, with the mussel sometimes occupying gravel patches between rocks.

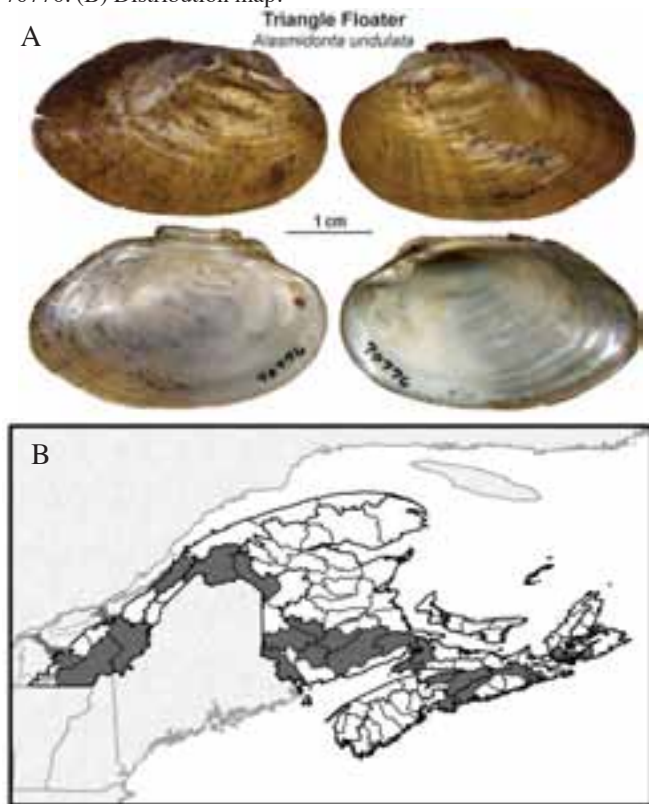
Reproduction and host fishes — The elktoe is a long-term brooder, with gravid females observed from July to June (Baker 1928; Clarke 1981a). Fertilization takes place in summer, and glochidia are held in the marsupial compartments until their release the following spring. Hermaphroditic individuals have occasionally been observed (van der Schalie 1970). Only a few fish species have been documented as hosts of glochidia of the elktoe based on natural infestations. Those present in the Quebec portion of the AME include the white sucker (*Catostomus commersonii* (Lacépède)), rock bass (*Ambloplites rupestris* (Rafinesque)) and shorthead redhorse (*Moxostoma macrolepidotum* (Lesueur)) (Howard and Anson 1922).

Conservation status — In the United States the elktoe has been declining over much of its range. It is listed as secure in only 5 of the 24 states where it occurs (NatureServe 2009), and is at risk or imperiled in many jurisdictions. In Canada, this mussel is considered vulnerable in Ontario (Metcalf-Smith and Cudmore-Vokey 2004; NatureServe 2009). In Quebec the elktoe has no legal conservation status, but unofficially it is listed as likely to be threatened or vulnerable and its rank is considered critically imperiled. A Canadian status report is in preparation. In the Centre-du-Québec region, threats to this species included degradation and destruction of aquatic habitats due to lack of riparian zones, siltation, and chemical pollution, all linked to intensive agriculture.

Triangle floater
Alasmidonta undulata (Say, 1817)

Distribution — The triangle floater (Fig. 12A) is found in the Atlantic Slope and adjacent lower Great Lakes – St. Lawrence River drainages (Burch 1975; Clarke 1981a). It occurs from Florida to the Canadian Maritime Provinces. In the United States, it is present in 19 eastern states (NatureServe 2009). In Canada, it is found in eastern Ontario, Quebec, New Brunswick, and Nova Scotia, (Clarke 1981a, b; Paquet, unpublished data). About half of this species range in Canada is restricted to the AME. It has a spotty distribution in a relatively small number of watersheds in New Brunswick and central Nova Scotia (Fig. 12B). In Quebec the species is primarily found in the St. Lawrence River drainage system outside of the AME. However, although the species appears to be absent from the Gaspé region, there are records of the triangle floater within the ecozone from several rivers in southwestern Quebec. It is never common or abundant where encountered in the AME, but as more intensive sur-

Fig. 12. Triangle floater (*Alasmidonta undulata*). (A) External and internal view of shells from Grand Lake, Nova Scotia. CMNML 70776. (B) Distribution map.



veys are carried out, the species will undoubtedly be found in more river systems. Although rarely abundant in Maine, it is found in nearly every watershed in that state (Nedeau et al. 2000).

Habitat — The triangle floater is most frequent in streams and rivers, but also occurs at low densities in lentic habitats such as lakes and ponds (Nedeau et al. 2000; Martel et al. 2006). Clarke (1981a, b) notes that in Canada the species occurs in rivers and lakes and reaches maximum size in outlet streams just below lakes. Although Ortmann (1919, cited in Clarke 1981b) states that this species avoids larger rivers and prefers smaller streams, in the AME it has been recorded mostly in large and medium-sized rivers. The species is most common where currents are steady but water is not rough. The occasional presence of this species in slack waters such as lakes is somewhat unusual in that all other Canadian species of *Alasmidonta* are strictly running-water dwellers. The triangle floater is found especially on sand or gravel bottoms (Clarke 1981a). Ortmann (1919, cited in Clarke 1981b) notes that this mussel lives mostly in a mixture of coarse or fine gravel with sand and mud, as well as sometimes embedded in mud between larger stones.

Reproduction and host fishes — The triangle floater is a long-term brooder, with gravid females observed from July

to the following June (Ortmann 1919, cited in Clarke 1981b; Clarke 1981a; Nedeau et al. 2000). Fertilization takes place in summer, and glochidia are released the following spring. A variety of fish have been documented as hosts for the triangle floater, including the following AME species: common shiner (*Luxilus cornutus* (Mitchill)), blacknose dace (*Rhinichthys atratulus* (Agassiz)), longnose dace (*Rhinichthys cataractae* (Valenciennes)), white sucker, pumpkinseed (*Lepomis gibbosus* (Linnaeus)), fallfish (*Semotilus corporalis* (Mitchill)), slimy sculpin (*Cottus cognatus* Richardson), and white perch (*Morone americana* (Gmelin)) (Watters et al. 1999; Kneeland and Rhymer 2008).

Conservation status — The triangle floater is not abundant in its range. In the United States this mussel is at risk or declining in many states (Williams et al. 1993; NatureServe 2009), including Maine, where it is listed as special concern (Nedeau et al. 2000). In a risk-factor analysis designed to identify the most imperiled freshwater mussel species in the Canadian lower Great Lakes drainage, Metcalfe-Smith et al. (1998b) placed this mussel in the category that included those species most at risk. In the AME, the triangle floater is listed as sensitive in Quebec and New Brunswick, but secure in Nova Scotia (Metcalfe-Smith and Cudmore-Vokey 2004). The species appears to be uncommon in the limited area in which it is known to occur in the AME, but its status here is in need of further study.

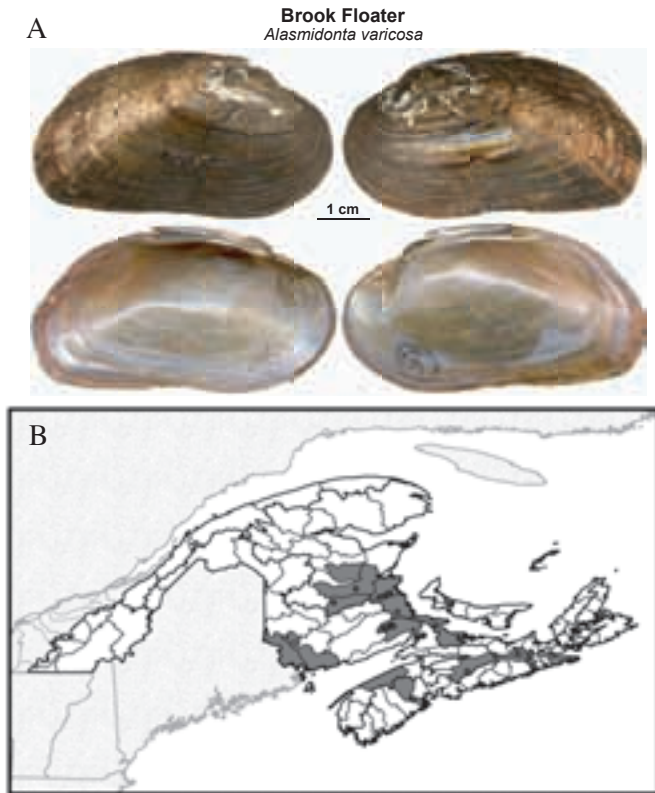
Brook floater

Alasmidonta varicosa (Lamarck, 1819)

Distribution — The brook floater (Fig. 13A) is restricted to the Atlantic Slope drainage of North America. In the United States this mussel occurs in 17 states along the Atlantic coast, from Georgia to Maine (NatureServe 2009). In Canada, the brook floater is found only in New Brunswick and Nova Scotia (Clarke 1981a, b; Metcalfe-Smith and Cudmore-Vokey 2004; Bredin and Martel 2009), where it has a limited, patchy distribution (Fig. 13B). In New Brunswick, recent freshwater mussel surveys have led to the discovery of brook floaters in the Petitcodiac, Miramichi, Kouchibouguacis (Fig. 8D), Bouctouche, Shediac, Scoudouc, Magaguadavic, and St. Croix river systems. This species appears to be less common in Nova Scotia, where it occurs in six river systems (Bredin and Martel 2009).

Habitat — This is a running-water species with specific habitat requirements; it occurs in moderate to rapidly flowing streams or rivers, often in riffles or rapids (Athearn and Clarke 1962). It prefers low-gradient rivers in the mid to lower reaches of watersheds (COSEWIC 2009). It is more common in small to mid-sized streams or creeks than in large rivers (Clarke 1981a, b) where it prefers rapids or riffles with moderate water currents. It is predominantly found on sandy shoals or in riffles with gravel bottoms (Athearn and Clarke 1962; Clarke

Fig. 13. Brook floater (*Alasmidonta varicosa*). (A) External and internal view of shells from outside the AME (Maryland, United States). CMNML 57542. (B) Distribution map.



1981a, b; Metcalfe-Smith and Cudmore-Vokey 2004; Bredin and Martel 2009).

Reproduction and host fishes — The brook floater is a long-term brooder, with gravid females found from August to May (Clarke 1981a, b). In Maine, Nedeau et al. (2000) state that the release of glochidia occurs from April to June, and possibly later into the summer. There is little field data available on host fishes in the wild, but experimental infections conducted in laboratories in the United States suggest that the following AME fishes could serve as hosts: blacknose dace, longnose dace, golden shiner (*Notemigonus crysoleucas* (Mitchill)), pumpkinseed sunfish, slimy sculpin, and yellow perch (*Perca flavescens* (Mitchill)) (Wicklowsky and Richards 1995; Nedeau 2008). In Canada, the only information on host fishes used by the brook floater is that of Beaudet (2006), collected in the Kouchibouguacis River, eastern New Brunswick, where the population of the brook floater is small (only 100–200 individuals). Beaudet (2006) reported only one glochidium of the brook floater on a single ninespine stickleback (*Pungitius pungitius* (Linnaeus)).

Conservation status — In the United States, the brook floater is imperiled or critically imperiled in most states where it occurs (NatureServe 2009). It is officially listed as special concern in Maine and is endangered or threatened throughout the

rest of the New England states (Nedeau et al. 2000). Recent population estimates have revealed that New Brunswick supports most of the Canadian brook floater population (Bredin and Martel 2009). The species is uncommon to rare in Nova Scotia. COSEWIC has recently assessed the national status of the brook floater as special concern (COSEWIC 2009).

Alewife Floater

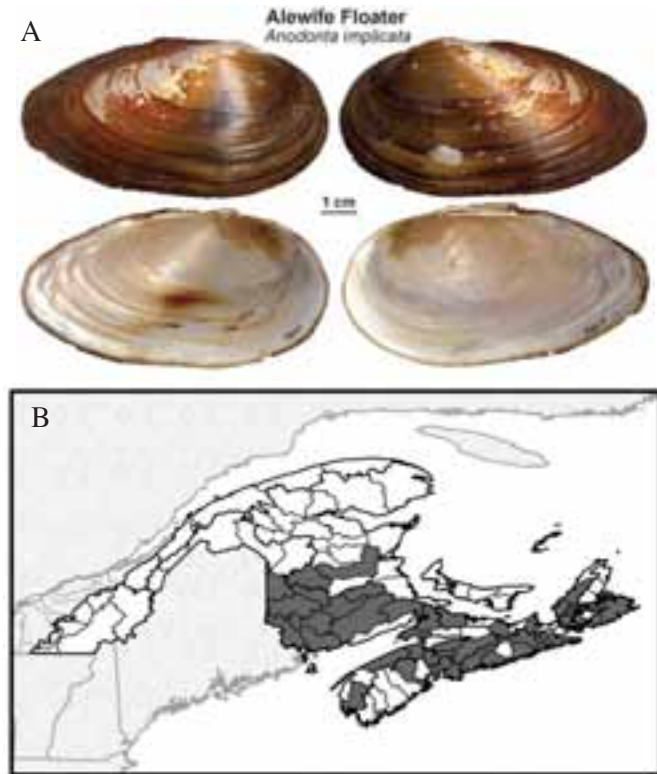
Anodonta implicata Say, 1829

Distribution — The alewife floater (Figs. 2A, B, and 14A) is restricted to the Atlantic Slope and adjacent Great Lakes – St. Lawrence River drainages, occurring from North Carolina to the Canadian Atlantic provinces (Burch 1975; Clarke 1981a; NatureServe 2009). In the United States, it is reported in 14 states from North Carolina to Maine. In Canada, this species occurs across most of New Brunswick and Nova Scotia, although like most AME freshwater mussels, it is not known to occur on Prince Edward Island (Clarke 1981a; Fig. 14B). Although the alewife floater has not been reported from the AME in Quebec, there are records from several Quebec rivers outside the AME, including the St. Lawrence River and two tributaries, the rivière St Charles and the Ottawa River. Most records are historic, although a few live or recently dead individuals have been found in the past decade (A. Paquet, unpublished data). In the rivière Matapédia and Restigouche, on the Gaspé Peninsula, this species has to date not been found, although the primary host, the alewife (*Alosa pseudoharengus* (Wilson)), is present.

Habitat — The alewife floater is restricted to coastal river, stream, and lake systems that can be reached by its primary anadromous host, the alewife. Like most *Anodonta* and *Pyganodon* species, the alewife floater thrives in both running-water and lake habitats. The species can be found on a variety of substrates, although it occurs principally in sand and gravel, and rarely on fine silt or muddy bottoms (Athearn and Clarke 1962; Clarke 1981a). Across the lower Saint John River system, New Brunswick, we have observed this species primarily on sandy bottoms.

Reproduction and host fishes — This floater is a long-term brooder, with gravid females observed from August until May–June of the following spring (Wiles 1975; Clarke 1981a). For a long time, the only confirmed host fish for this mussel was the alewife (Athearn and Clarke 1962; Davenport and Warmuth 1965). More recently, Nedeau et al. (2000) proposed that two other anadromous clupeid fishes, the American shad (*A. sapidissima*) and the blueback herring (*A. aestivalis* (Mitchill)), might also serve as suitable hosts. Working in Maine, Kneeland and Rhymer (2008) confirmed the presence of glochidia on the Blueback Herring and also reported alewife floater glochidia on the stripe bass (*Morone saxatilis* (Walbaum)). All four above-mentioned anadromous fishes are widespread in the AME.

Fig. 14. Alewife floater (*Anodonta implicata*). (A) External and internal view of shells from an unidentified lake near Sackville, New Brunswick. CMNML 72071. (B) Distribution map.



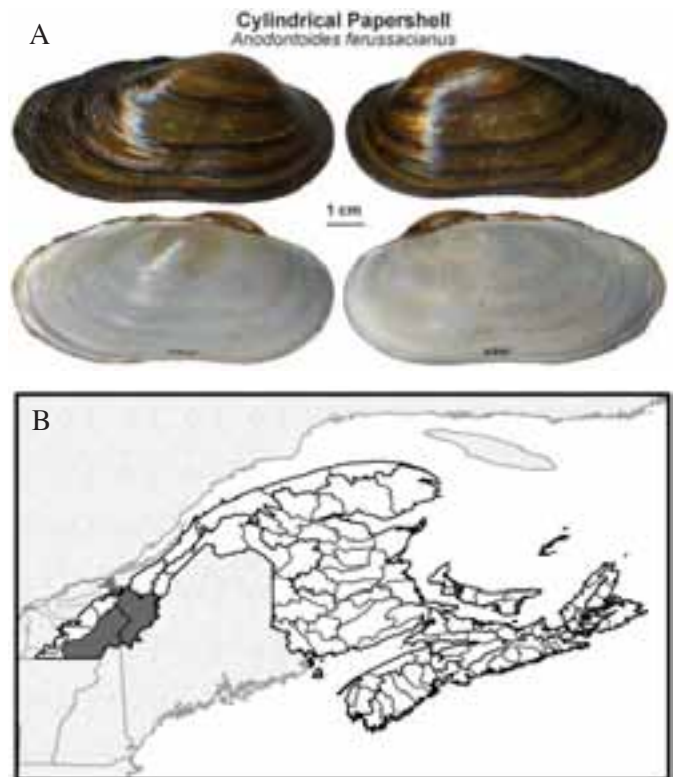
Conservation status — In the United States the alewife floater is critically imperiled in at least 5 of the 14 states where it occurs (NatureServe 2009). In New Brunswick and Nova Scotia the species is widespread (Fig. 14B) and often found at high densities. It is reported as secure in both provinces (Metcalf-Smith and Cudmore-Vokey 2004). In Quebec, the alewife floater is a very rare mussel; currently, it has no legal conservation status, but it is listed as likely to be designated threatened or vulnerable and is ranked in Quebec as critically imperiled. A status report is in preparation for that province.

Cylindrical papershell
Anodontoïdes ferussacianus (Lea, 1834)

Distribution — The cylindrical papershell (Fig. 15A) occurs in the Great Lakes – St. Lawrence River, Hudson Bay, and Mississippi (north of Tennessee) basin drainages (Burch 1975; Clarke 1981a; Parmalee and Bogan 1998). It is currently found in 22 central and eastern states in the United States (west of the Appalachian Mountains) (NatureServe 2009).

In Canada, the cylindrical papershell is widely distributed, occurring in Alberta, Saskatchewan, Manitoba, Ontario, and Quebec. In Quebec, it is found on either side of the St. Lawrence River from Montérégie to the Chaudière-Appalaches region and west in the Ottawa River drainage between Portage-du-Fort and Carillon. It also occurs as far north as the Saguenay – lac St. Jean region. Although its distribution in

Fig. 15. Cylindrical papershell (*Anodontoïdes ferussacianus*). (A) External and internal view of shells from Mile End Ponds, Montreal, Quebec (Mixedwood Plains Ecozone). CMNML 2335. (B) Distribution map.



Quebec is mostly outside the AME, there are observations of live specimens from the rivière Chaudière and its tributary, the bras St Victor, in Beauce County (Fig. 15B). This mussel has also been found in the AME Estrie region in lac Memphrémagog.

Habitat — The cylindrical papershell is usually found in quiet or slow-moving creeks, streams, or large rivers. It is able to tolerate impoundments and is found occasionally in unpolluted lakes. The preferred substrates are silt or mud, although it is sometimes found in sand or gravel (Clarke 1981a).

Reproduction and host fishes — The cylindrical papershell is a long-term brooder. Gravid females have been reported from August until May in Pennsylvania (Clarke 1981a). Several fish species have been shown to serve as hosts. These observations include lab-confirmed transformation of glochidia into juveniles from the bluegill (*Lepomis macrochirus* Rafinesque) and largemouth bass (*Micropterus salmoides* (Lacepède)) (Watters 1995; O'Dee and Watters 2000). Other fish species present in the Quebec portion of the AME may serve as hosts for this mussel. The sea lamprey (*Petromyzon marinus* (Linnaeus)) has been found with naturally occurring glochidia of the cylindrical papershell in the Great Lakes region (Wilson and Ronald 1967).

Conservation status — Where assessed in the the United States, the status of this mussel is listed as secure. Vermont, where the cylindrical papershell is considered critically imperiled, is an exception (NatureServe 2009). In Canada it is considered secure in Ontario and sensitive in Quebec (Metcalf-Smith and Cudmore-Vokey 2004).

Creek heelsplitter
Lasmigona compressa (Lea, 1829)

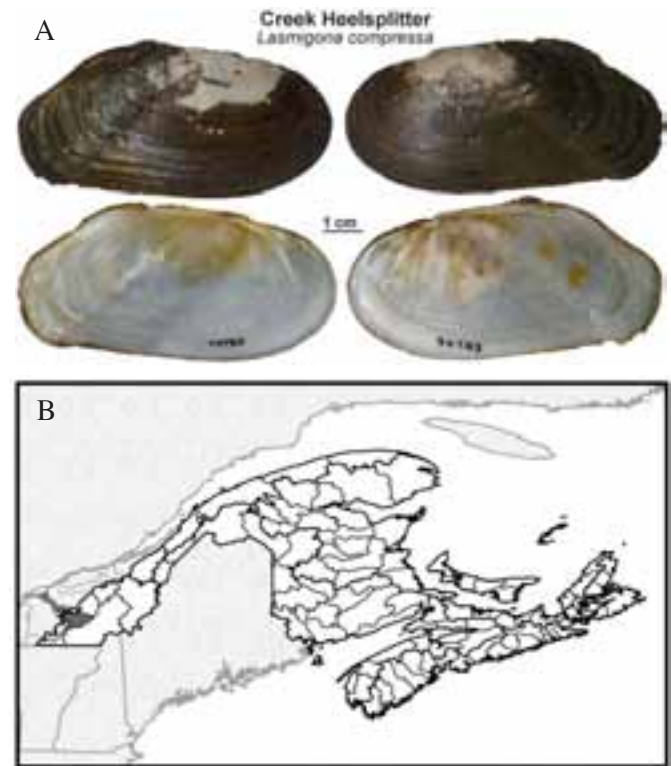
Distribution — The creek heelsplitter (Fig. 16A) is widely distributed in North America in the Atlantic Slope (Hudson River basin), Great Lakes – St. Lawrence River, Hudson Bay, and Mississippi drainages (upper Ohio – Mississippi River system) (Burch 1975; Clarke 1981a). The creek heelsplitter occurs in 15 central and eastern states in the United States (NatureServe2009), almost entirely west of the Appalachian Mountains. In Canada, the creek heelsplitter is present in Alberta, Saskatchewan, Manitoba, Ontario, and Quebec. The species is widespread in Ontario. Although widespread in central and southern Quebec, most of this distribution is outside the AME. In the Quebec portion of the AME the creek heelsplitter has been found only in the rivière St. François (Fig. 16B), the largest tributary of the St. Lawrence River.

Habitat — This mussel is principally found in creeks or small rivers; sometimes those too small or shallow to support other freshwater mussel species. It is only occasionally found in large rivers, and rarely in lakes (Clarke 1981a; Strayer and Jirka 1997; Metcalfe-Smith et al. 2005). This species thrives in various substrates, including sand, fine gravel, as well as mud (Clarke 1981a; Metcalfe-Smith et al. 2005).

Reproduction and host fishes — Unlike most unionids, the creek heelsplitter is generally hermaphroditic (van der Shalie 1970), although occasionally male individuals may be found (Ortmann 1911; Clifford 1991). According to Clarke (1981a) the breeding season of the creek heelsplitter lasts from August to June. Numerous fish species have been confirmed as potential hosts through laboratory experiments, and many of these fish occur in the Quebec portion of the AME, including the following: slimy sculpin, brook stickleback (*Culaea inconstans* (Kirkland)), smallmouth bass (*Micropterus dolomieu*), emerald shiner (*Notropis atherinoides* Rafinesque), mimic shiner (*Notropis volucellus* (Cope)), yellow perch, longnose dace and creek chub (*Semotilus atromaculatus* (Mitchill)) (Hove et al. 1995; McGill et al. 2002).

Conservation status — In the United States this mussel is listed as imperiled or critically imperiled in 6 of the 15 states where it occurs, including in adjacent Vermont (NatureServe 2009). In Canada, the status of the creek heelsplitter is considered to be secure in Ontario and sensitive in the province of Quebec (Metcalf-Smith and Cudmore-Vokey 2004; see also NatureServe 2009).

Fig. 16. (A) Creek heelsplitter (*Lasmigona compressa*). External and internal view of shells from outlet of Lac Philippe, Quebec (Mixed-wood Plains Ecozone). CMNML 70783. (B) Distribution map.



Flutedshell
Lasmigona costata (Rafinesque, 1820)

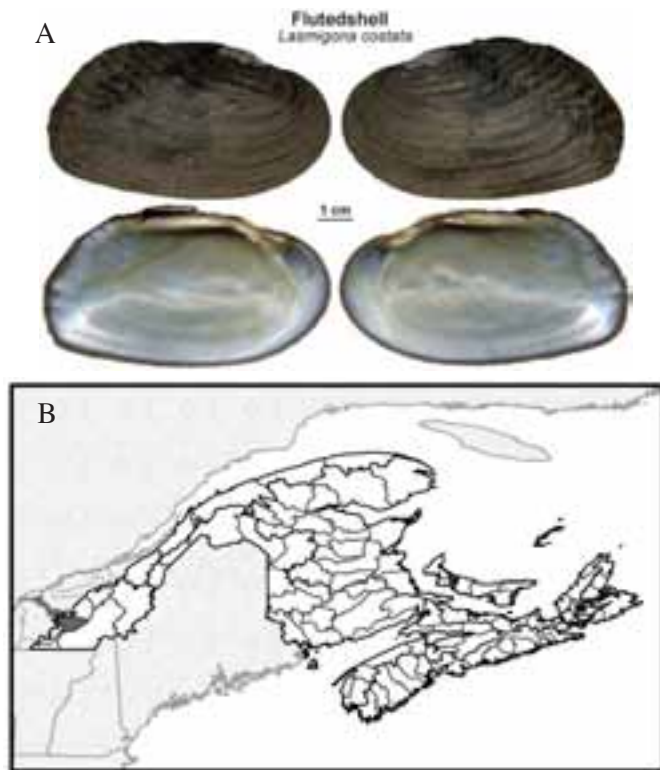
Distribution — The flutedshell (Fig. 17A) occupies a vast geographical range in North America, including the Great Lakes – St. Lawrence River drainage, some tributaries of the southern Hudson Bay drainage, as well as the Interior Basin drainage (including the entire Mississippi River system) (Burch 1975; Clarke 1981a; Parmelee and Bogan 1998). This mussel occurs in 22 states of the central and eastern United States, west of the Appalachian Mountains.

In Canada, the flutedshell occurs in Manitoba (Red River and Winnipeg River drainages) and is widespread in Ontario and in central and southern Quebec. In Quebec, the species is found in several tributaries on the northern side of the St. Lawrence River, but it is more widely distributed on the southern side of the drainage. The bulk of its distribution in the province of Quebec is outside the AME.

In the Quebec portion of the AME this species is found only in the rivière St. François (Fig. 17B), where it was the dominant mussel species recorded at several sites surveyed during 2002 and 2005.

Habitat — The flutedshell occurs in small to large rivers with slow to preferably moderately strong water current. It is also occasionally found in canals and lakes. This mussel prefers

Fig. 17. Flutedshell (*Lasmigona costata*). (A) External and internal view of shells collected from rivière Châteauguay, Quebec (Mixed-wood Plains Ecozone). CMNML 93401. (B) Distribution map.



coarse substrates such as coarse sand or gravel, although it is also occasionally found in mud.

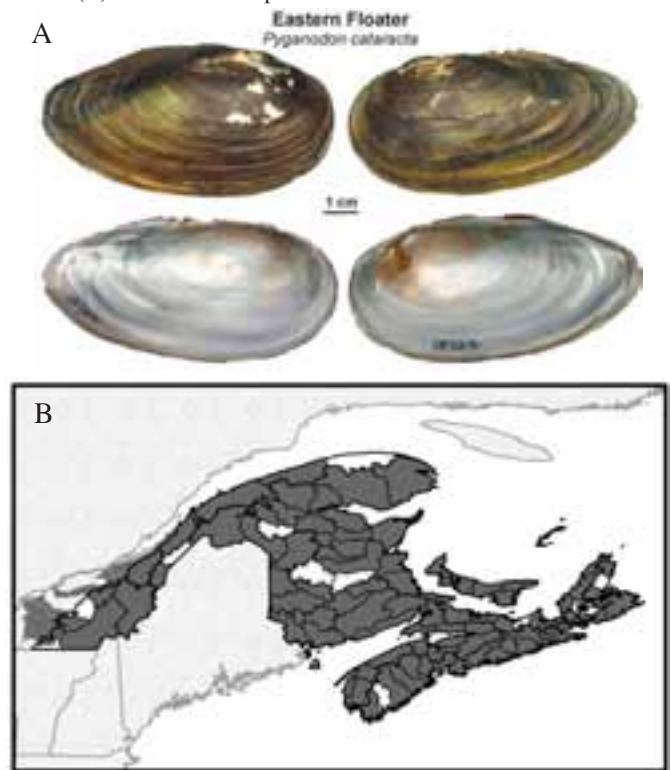
Reproduction and host fishes — Like many mussels in the AME, the flutedshell is a long-term brooder. In Michigan, Baker (1928) reported gravid females from August through the following May. Clarke (1973) also observed gravid females in August in the Canadian Interior Basin. A variety of fish species have been shown to serve as hosts, of which seven occur in the Quebec portion of the AME, including lab-confirmed transformation into juveniles on the goldfish (*Carassius auratus* (Linnaeus)), common carp (*Cyprinus carpio* Linnaeus), pumpkinseed, smallmouth bass, longnose dace, yellow perch, and creek chub (*Semotilus atromaculatus* (Mitchill)) (Hove et al. 1994; Watters et al. 1998, 2005).

Conservation status — In the United States, the flutedshell is listed as secure or apparently secure in 9 of the 22 states where it occurs, but is at risk in the nearby state of Vermont (NatureServe 2009). In Canada, this species has been evaluated as may be at risk in Manitoba, sensitive in Quebec, and secure in Ontario (Metcalf-Smith and Cudmore-Vokey 2004).

Eastern Floater
Pyganodon cataracta (Say, 1817)

Distribution — The eastern floater (Fig. 18A) is primarily found in the Atlantic Slope and the lower Great Lakes – St.

Fig. 18. Eastern floater (*Pyganodon cataracta*). (A) External and internal view of shells from Baird Brook, Nova Scotia. CMNML 13722. (B) Distribution map.



Lawrence River drainages, although a small portion of its range occurs in the Gulf of Mexico drainage (Burch 1975; Clarke 1981a). In the United States, this mussel is common along the Atlantic coast, and is found in 20 states from Georgia to Maine. Collection records suggest the eastern floater is among the most common freshwater mussels in eastern Canada, occurring abundantly in all four provinces of the AME (Fig. 18B).

Habitat — The eastern floater inhabits a wide range of freshwater habitats. It is common in lakes and permanent ponds, particularly ponds directly connected to a lake or a river system. It also occurs in riverine environments, including creeks and streams of various sizes, as well as rivers, particularly those with slow-moving waters. The eastern floater lives on a variety of substrates but is most commonly found on soft, oozy mud, where it is often the only unionid found, or sand (Athearn and Clarke 1962; Clarke 1981a). Like most unionoids, the eastern floater occurs most abundantly in shallow waters. It also occurs at low densities in the deeper parts of lakes or rivers where sediments are often very fine and muddy and not suitable for species with thick shells. *Pyganodon* spp. typically have thin, light-weight shells that literally float in the bottom mud, hence the name “floaters”.

Reproduction and host fishes — This mussel is a long-term brooder, with brooding females observed from July or August to the following spring (Clarke 1981a; Nedeau et al. 2000).

Few studies have been conducted to determine suitable hosts for the eastern floater. Beudet (2006) showed that in a small pond adjacent and connected to the Kouchibouguacis River, New Brunswick, glochidia of the eastern floater occurred on 5 of the 12 fish species collected: common shiner, blacknose dace, creek chub, threespine stickleback (*Gasterosteus aculeatus* Linnaeus), and ninespine stickleback. In Nova Scotia, Wiles (1975) observed attachment of eastern floater glochidia on pumpkinseed sunfish, yellow perch, and white sucker. In the eastern United States, Gray et al. (1999) confirmed metamorphosis in the lab on rock bass. The eastern floater, like other *Pyganodon* spp., seems to be a host generalist (Watters 1994).

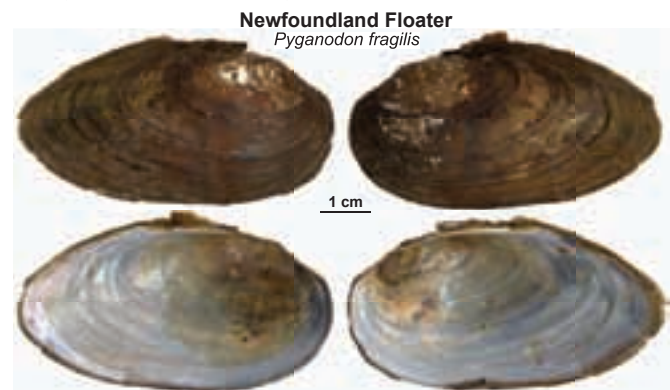
Conservation status — In the United States, the eastern floater is considered secure or apparently secure (NatureServe 2009), including in the New England region. The species is widespread and abundant across eastern Canada and is listed as secure in the four provinces that make up the AME (Metcalf-Smith and Cudmore-Vokey 2004). It has been proposed that the wide distribution and abundance of the eastern floater in eastern Canada and Maine is linked to high environmental tolerance and low host-fish specificity (Nedeau et al. 2000; Metcalf-Smith and Cudmore-Vokey 2004).

Newfoundland Floater

Pyganodon fragilis (Lamarck, 1819)

Distribution — The taxonomy of the Newfoundland floater (Fig. 19) is poorly understood; the mussel has been recognized as both species (Turgeon et al. 1998; Metcalf-Smith and Cudmore-Vokey 2004) and subspecies (*P. cataracta fragilis*) (Clarke and Rick 1963; Clarke 1981a). Our understanding of genetic variation in *Pyganodon* spp., as well as any differences in adult anatomy and glochidial morphology in the AME, is still incomplete. According to Clarke (1981a) and other sources (NatureServe 2009), the Newfoundland floater is restricted to the Atlantic Slope and adjacent Great Lakes – St. Lawrence River drainage. Information currently available would suggest that this mussel does not occur in the United States, but is confined to eastern Canada. Because the taxonomy of this mussel is unresolved, details on its Canadian distribution must therefore be interpreted with caution, and we have chosen not to map this species. Clarke (1981a) stated that this mussel occurs principally in Newfoundland but that specimens exhibiting characteristics intermediate between the Newfoundland floater and the eastern floater are common throughout northern Nova Scotia, New Brunswick, and eastern Quebec. Hoeh (1990) suggested that typical *P. fragilis* may be restricted to Newfoundland and Labrador and confirmed the genetic distinctness of material from Newfoundland. However, on the basis of allozyme electrophoresis and internal anatomical structure of the stomach, Kat (1984) found *Pyganodon* populations in Nova Scotia that he identified as *P. fragilis*, and which were differentiated from New Jersey and Delaware *P. cataracta*. Hanlon and Smith (1999) made a specific search for the

Fig. 19. Newfoundland floater (*Pyganodon fragilis*). External and internal view of shells from Well's Gully, Whitbourne, Newfoundland (Boreal Shield Ecozone). CMNML 45770.



Newfoundland Floater in Maine, where the species has been reported, and concluded that historical records were based on misidentified *P. cataracta* (see also Nedeau et al. 2000). Recent molecular studies on northeastern North American *Pyganodon* spp. propose divergent views regarding the distinction between the Newfoundland floater and the eastern floater (Cyr 2007; Cyr et al. 2007; Stanton 2008). Cyr (2007) and Cyr et al. (2007) studied the taxonomy and distribution of *Pyganodon* species in northeastern North America, primarily across Quebec, using mitochondrial DNA and adult shell morphology. They concluded that *P. fragilis* is a distinct genotype, with both male and female mitochondrial genomes distinct from those of its nearest sibling species, the eastern floater. Thus, Cyr et al. (2007) support the validity of the Newfoundland floater as a distinct taxon. They also suggest that the species is more widespread than previously believed (e.g., Clarke 1981a) and is common in Quebec, occurring on the Gaspé Peninsula, Anticosti Island, and in the eastern portion of the Saguenay region. Nedeau et al. (2000) also suggested that the Newfoundland floater may occur across many regions of New Brunswick and Nova Scotia. Stanton (2008), comparing mitochondrial and genomic DNA between the Newfoundland floater and the eastern floater, reached a different conclusion. Focusing primarily on populations from the Canadian Atlantic region, including Newfoundland, New Brunswick, and Nova Scotia, she concluded that the Newfoundland floater is not sufficiently genetically distinct from the eastern floater to warrant species status. Stanton (2008) proposed synonymizing the Newfoundland floater and the eastern floater, noting that the latter has nomenclatural priority.

Our recommendation at this point is to distinguish forms of the floaters of the “*Pyganodon cataracta* group”, as either *P. cataracta* form *cataracta*, or *P. cataracta* form *fragilis*, depending on shell morphology, including details of umbo morphology (with reference to double-looped for eastern floater vs. single-looped for Newfoundland floater; see Clarke 1981a, as well as Nedeau et al. 2000, for morphological details). This approach allows one to retain information during this current period of taxonomic uncertainty, may contribute

to a better understanding of the significance of morphological variation within the genus, and also recognizes the possibility of distinct genotypes.

Habitat — The Newfoundland floater has been reported from lakes and permanent ponds, as well as streams and rivers. Like other *Pyganodon* spp. of eastern Canada, this mussel is typically found in silt or mud, sometimes in sand, and less frequently in gravel (Clarke 1981a).

Reproduction and host fishes — This mussel has not been the subject of any reproductive study, and no information is available on the host fish or fishes involved in its life cycle. As is the case for other *Pyganodon* spp. for which reproduction is known, it is possible that many host fish species are involved in the larval development and dispersal of the Newfoundland floater's glochidia. Nedeau et al. (2000) suggested that it may have a similar reproductive period and use the same hosts as the eastern floater.

Conservation status — The conservation status of the Newfoundland floater is unknown, although Williams et al. (1993) list this species status as currently stable in North America. Metcalfe-Smith and Cudmore-Vokey (2004) include the Newfoundland Floater as one of the 54 species of freshwater mussels occurring in Canada, while also acknowledging the taxonomic uncertainty surrounding this species.

Giant floater

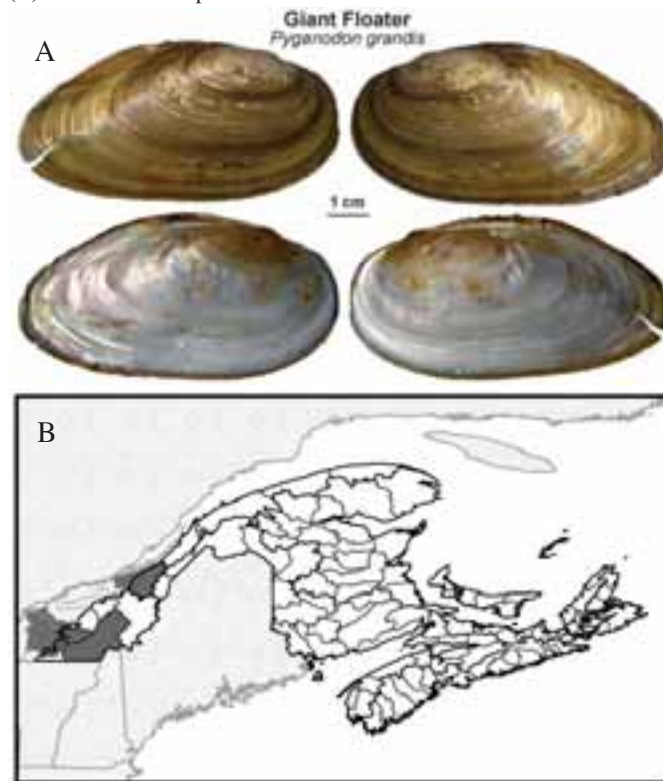
Pyganodon grandis (Say, 1829)

Distribution — The giant floater (Fig. 20A) has one of the most extensive geographical ranges among North American freshwater mussels. It occupies the Great Lakes – St. Lawrence River and Hudson Bay drainages and occurs throughout the Mississippi drainage (Burch 1975; Clarke 1981a; Parmelee and Bogan 1998). It has been recorded in 32 states in the central and eastern United States west of the Appalachian Mountains (NatureServe 2009).

In Canada the giant floater is also widespread, occurring in Alberta, Saskatchewan, Manitoba, Ontario, Quebec, and the Northwest Territories (McKenzie River) (Clarke 1981a). In Quebec its distribution is mostly outside the AME. However, there are historical records of the giant floater in lac Waterloo and lac Memphrémagog (Fig. 20B), and more recently molecular methods have confirmed that the species is present in the rivière St. François and rivière Noire (Cyr et al. 2007). It may occur elsewhere in the Quebec portion of the AME. Many *Pyganodon* specimens recently found in the region could not be identified to species using morphological criteria alone owing to the erosion of the umbo or beak sculpture of specimens.

Habitat — The giant floater occurs in permanent ponds, lakes, and rivers of various sizes. The species reaches its highest numbers and greatest shell size in areas with little or no cur-

Fig. 20. Giant floater (*Pyganodon grandis*). (A) External and internal view of shells from Magog, Quebec. CMNML 2415. (B) Distribution map.



rent, such as the backwaters of rivers, lakes, ponds, and reservoirs. It is also occasionally found in rivers with moderate flow and sometimes even rough waters (Strayer and Jirka 1997). Although this mussel occurs on all types of substrates, it is most abundant on mud (Clarke 1981a). Like other *Pyganodon* spp., the giant floater has a light and inflated shell, which allows it to remain on top of soft substrates, such as silt or mud. It has been recorded in water to 6 m depth.

Reproduction and host fishes — This species is normally dioecious, although hermaphroditic individuals have been reported (van der Schalie and Locke 1941). The brood period of the giant floater is lengthy, extending from August to May for some southern populations (Baker 1928) as well as from July to the following June in Alberta (Jensen and Hanson 1991). Much shorter brood periods are also suggested, with Lewis (1985) reporting the release of glochidia in September from a lake in the Laurentians. The extensive geographic distribution of *P. grandis* in North America may be due, in part, to its ability to adapt to a wide diversity of host fishes. Transformation from glochidia to juveniles in the laboratory has been confirmed for the following fish species known to occur in the Quebec portion of the AME: blacknose dace, creek chub, common shiner, blacknose shiner, golden shiner, banded killifish (*Fundulus diaphanus* (Lesueur)), bluntnose minnow (*Pimephales notatus* (Rafinesque)), brook stickleback, rock bass, pumpkinseed,

yellow perch, johnny darter, and goldfish (Tucker 1928; Penn 1939; Trdan and Hoeh 1982; Watters et al. 2005).

Conservation status — The giant floater is rather tolerant of polluted waters and habitat degradation. It is a host generalist with numerous fish species capable of serving as hosts for the glochidia. Both factors contribute to the maintenance of stable populations of this mussel in Canada and the United States. This mussel is abundant over most of its North American range. In the United States, the giant floater is listed as secure in 18 of the 32 states where it has been reported (NatureServe 2009). In Canada it is secure in most provinces where it occurs (Metcalf-Smith and Cudmore-Vokey 2004; NatureServe 2009).

Creeper

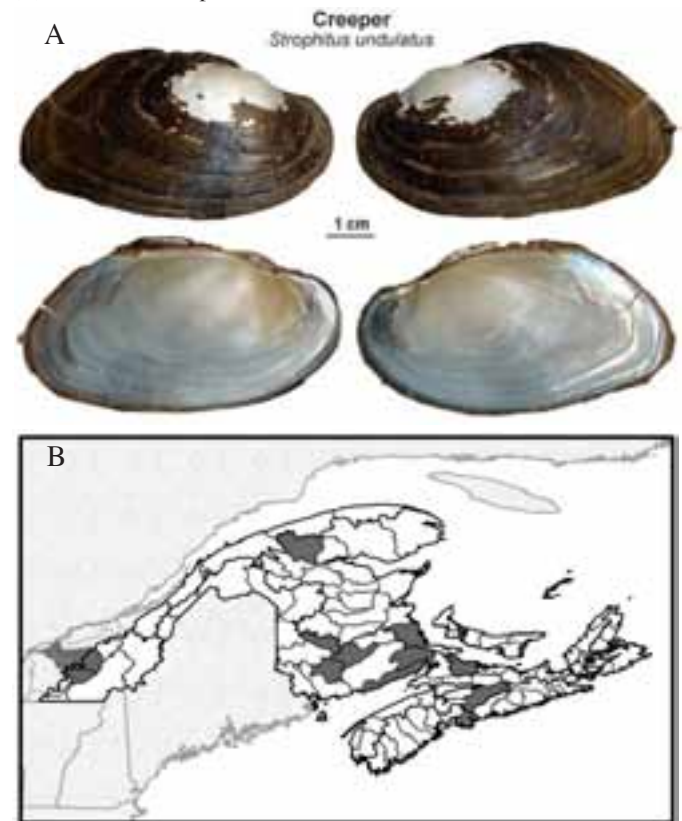
Strophitus undulatus (Say, 1817)

Distribution — The creeper (Fig. 21A) is one of the most widely distributed freshwater mussels in North America, occurring in all four major continental drainages; the Atlantic Slope, Great Lakes – St. Lawrence River, Hudson Bay, and the Mississippian drainages (Burch 1975; Clarke 1981a; Parmelee and Bogan 1998). In the United States it is widely distributed, occurring in 38 states (east and west of the Appalachian Mountains). In Canada, the creeper is found in Nova Scotia, New Brunswick, Quebec, Ontario, Manitoba, and Saskatchewan (Clarke 1981a). However, there are few confirmed records for Maritime Canada, with specimens in museums representing localities scattered throughout the AME. The few recent records of creepers from the Maritimes include collections from the Shediac River, Westmorland County, New Brunswick, where the species was also reported by Athearn (1961), and from Vickery Lake, Cumberland County, Nova Scotia (Fig. 21B). Recent surveys in Quebec show that the creeper occurs throughout the southern part of the province on either side of the St. Lawrence River, but most of this distribution is outside the AME. Within the Quebec portion of the AME, the creeper occurs in the rivière St. François, and there is an old record from lac Matapédia on the Restigouche River system.

Habitat — Although the creeper occurs primarily in streams and small rivers, it is also found in large rivers, river impoundments, and lakes (Clarke 1981a; Strayer and Jirka 1997; Nedeau et al. 2000, 2008). Several authors report that lake outlets in particular can provide prime habitat for this species (Clarke 1981a; Nedeau et al. 2000), and in Vermont, the creeper is most common in lakes and ponds (Fitchtel and Smith 1995). The species is found primarily in sand, silty sand, or sand and gravel.

Reproduction and host fishes — This mussel is a long-term brooder, with gravid females observed from summer to the following spring (Clarke 1981a). Early research suggested that glochidia of this species could complete their develop-

Fig. 21. Creeper (*Strophitus undulatus*). (A) External and internal view of shells from Shinimicas River, Nova Scotia. CMNML 20508. (B) Distribution map.



ment within the marsupial compartments of the female's gills, without use of a host fish (Lefevre and Curtis 1911). More recent research shows that creeper glochidia do require attachment to a host fish for metamorphosis and transformation into juveniles (Wicklow and Beisheim 1998; Gray et al. 2002). A wide variety of fish species have been shown to serve as hosts, many of which occur in the AME. These include Atlantic sturgeon (*Acipenser oxyrinchus* Mitchell), brook trout, fathead minnow (*Pimephales promelas* Rafinesque), creek chub, fallfish, golden shiner, common shiner, slimy sculpin, longnose dace, and yellow perch (Hove 1995; Hove et al. 1997; Wicklow and Beisheim 1998; Gray et al. 1999; Watters et al. 1999; Gray et al. 2002). Larval two-lined salamanders (*Eurycea bislineata* (Green)), widespread throughout the New Brunswick and Quebec portions of the AME, may also serve as hosts (Wicklow and Beisheim 1998).

Conservation status — Although populations of the creeper are considered stable across North America (Williams et al. 1993), it is listed as imperiled or critically imperiled in about 10 states in the United States. It is present but not abundant in Maine (Nedeau et al. 2000) and is considered a species of special concern in that state. Metcalf-Smith and Vokey (2004) report that the creeper is considered sensitive in Quebec and may be at risk in Nova Scotia. In New Brunswick there is insufficient

data to determine conservation status. Further field study of the creeper in the AME is required to fully evaluate this species status in the ecozone.

Family: Unionidae
Sub-family: Ambleminae
[Tribe: Pleurobemini]

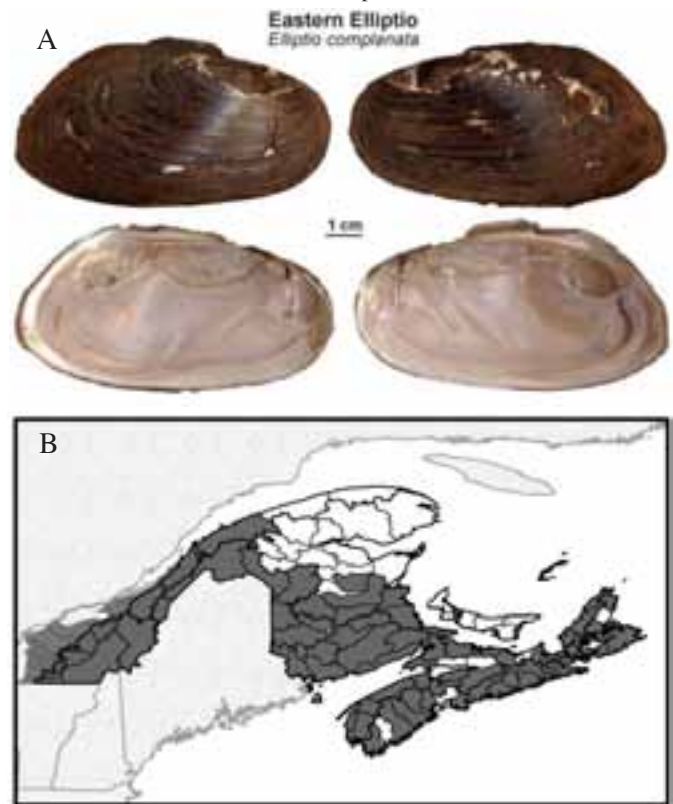
Eastern elliptio
Elliptio complanata (Lightfoot, 1786)

Distribution — The eastern elliptio (Fig. 22A) occurs in the Atlantic Slope, Great Lakes – St. Lawrence River, Hudson Bay, and Mississippian drainages (Burch 1975; Clarke 1981a; Parmelee and Bogan 1998). In the United States it is present in 23 states (NatureServe 2009), being especially prevalent immediately east and west of the Appalachian Mountains. In Canada, it is found in Ontario, Quebec, New Brunswick, and Nova Scotia (Clarke 1981a, b; Fig. 15A). It is the most widespread and abundant freshwater mussel in eastern Canada (Metcalf-Smith and Cudmore-Vokey 2004). This species ranges from southeastern Ontario (Lake Ontario basin) to northern Lake Superior and the southern James Bay basin, southern and central Quebec, and east across most of the AME (Clarke 1981a) where it is an ecologically dominant species. This is the sole mussel species that has been recorded on Îles de la Madeleine (Fig. 22B).

Habitat — The eastern elliptio lives in a variety of lake types and small to medium-sized streams, as well as large river systems in either soft or hard waters. It occurs on bottoms that range from clay or mud, through sand, gravel, or cobble. Typically, this species is most abundant in lakes or large river systems, thriving in shallow waters of 0.3–7 m in depth. It is usually not found in the deep part of lakes or rivers, especially if the sediment is soft.

Reproduction and host fishes — This is one of the few short-term brooders in the AME region. Females are gravid from late spring to midsummer (Clarke 1981a), with all glochidia released by late summer. Wiles (1975) found fully developed glochidia in females for only 5–6 weeks in June and July in Nova Scotia. The AME fishes on which glochidia of the eastern elliptio have been known to attach include the yellow perch, banded killifish, lake chub (*Couesius plumbeus* (Agassiz)), creek chub, and brook stickleback (Wiles 1975; Watters 1994; Beaudet 2006). Recently, Kneeland and Rhymer (2008) observed the glochidia of the eastern elliptio on 13 species of fishes in Maine (however, no metamorphosis confirmed). The authors reported that among the most common hosts were the white perch, yellow perch, banded killifish, pumpkinseed sunfish, and smallmouth bass. Because the eastern elliptio is so widespread and often abundant in lake systems, it is not surprising that numerous fish species act as effective hosts for its glochidia.

Fig. 22. Eastern elliptio (*Elliptio complanata*). (A) External and internal view of shells from the Shinimika River, Nova Scotia. CMNML 45779. (B) Distribution map.



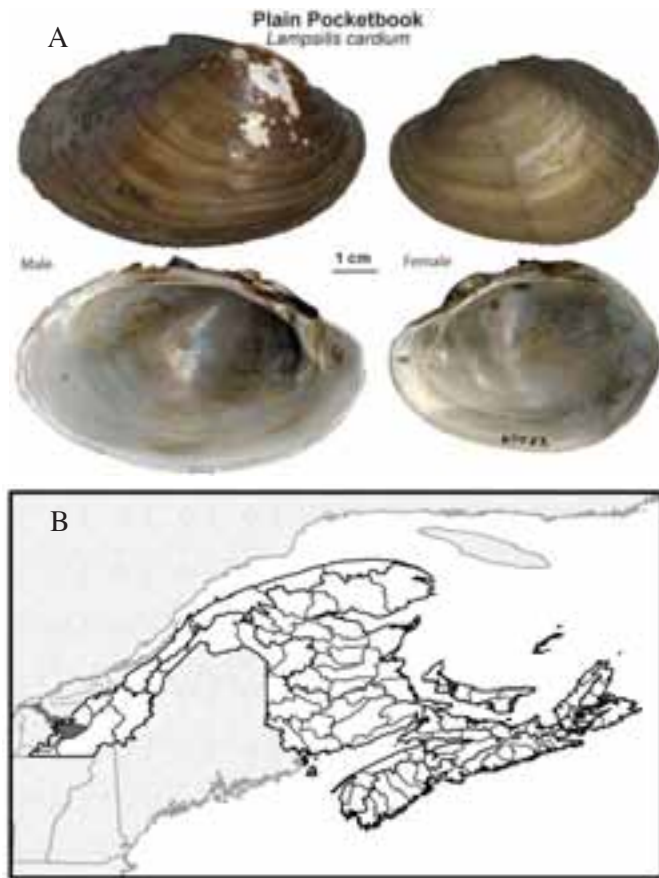
Conservation status — In the United States, the eastern elliptio is listed as secure in most jurisdictions where it is found (NatureServe 2009). It is listed as secure in all provinces where it occurs in the AME region: Quebec, New Brunswick, and Nova Scotia (Metcalf-Smith and Cudmore-Vokey 2004). Paterson (1985) recorded eastern elliptio densities of about 16 individuals/m² in Morice Lake, New Brunswick. The species can be very abundant; in Belleisle Bay, in the lower reach of the Saint John River, densities of 10–60+ individuals/m² at water depths of 1–4 m are commonly observed (Martel, pers. obs.). Similar densities occur in numerous places across the AME. With its widespread distribution and abundance, this species undoubtedly plays an important ecological function in AME river and lake ecosystems.

Family: Unionidae
Sub-family: Ambleminae
[Tribe: Lampsilini]

Plain pocketbook
Lampsilis cardium Rafinesque, 1820

Distribution — The plain pocketbook (Fig. 23A) is widely distributed in North America, occurring in the Great Lakes – St. Lawrence River, Hudson Bay (Assiniboine – Red – Winnipeg – Nelson River system), and upper Mississippi River

Fig. 23. (A) Plain pocketbook (*Lampsilis cardium*). External and internal view of shells collected from St. Lawrence River, Pte-aux-Trembles, Quebec (Mixedwood Plains Ecozone). CMNML 67052. (B) Distribution map.



drainages (Parmelee and Bogan 1998). In the United States it is found in 24 central and eastern states (west of the Appalachian Mountains) (NatureServe 2009). In Canada the plain pocketbook is present in Saskatchewan (Assiniboine River), Manitoba, Ontario, and Quebec. In southern Quebec this species is common in tributaries on either side of the St. Lawrence River. Although most of its distribution in Quebec is outside the AME, it does occur in the ecozone in the rivière St. François, where many small concentrations of individuals have been found (Fig. 23B).

Habitat — The plain pocketbook is found in slow to fast-flowing waters in both small streams and large rivers. It occurs on a variety of substrates, including gravel, sand, or mud.

Reproduction and host fishes — The plain pocketbook is a long-term brooder. Gravid females are found from August to July of the following summer (Baker 1928). At onset of breeding, the female plain pocketbook displays elaborate mantle flaps that mimic a small fish. These flaps serve as a lure, attracting potential host fishes to the female mussel prior to release of glochidia. The mantle is even equipped with an imitation eye

spot and flaps that mimic dorsal spines or fins. Transformation from glochidia to juveniles in the laboratory has been confirmed for the following host fish species known to occur in the Quebec portion of the AME: banded killifish, pumpkinseed, smallmouth bass, and yellow perch (Coker et al. 1921; Lefevre and Curtis 1921; Waller et al. 1985; O’Dee and Watters 2000; Watters et al. 2005; Draxler et al. 2006).

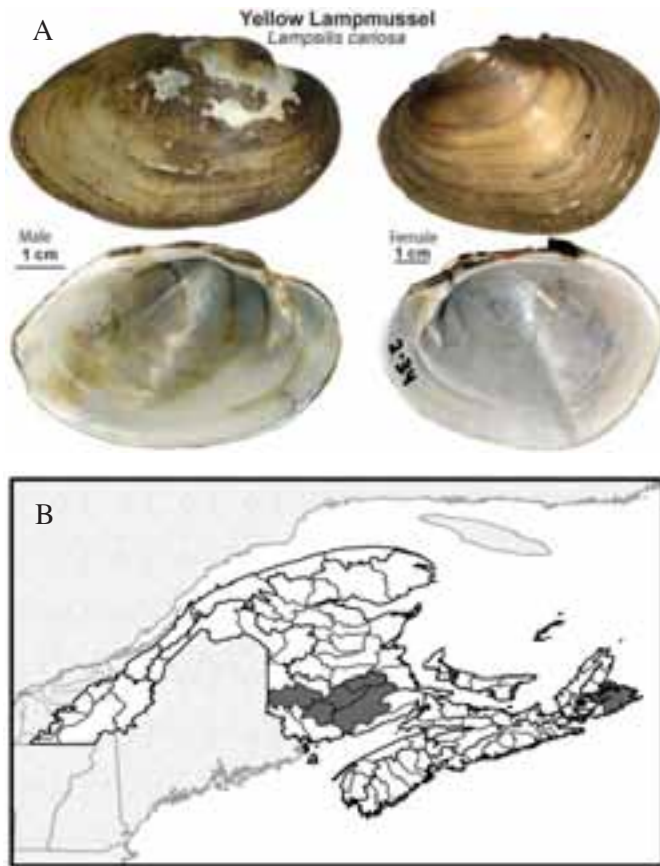
Conservation status — In the United States the plain pocketbook is apparently stable or secure in only 10 of the 24 states where it occurs (NatureServe 2009). In Canada this mussel is considered secure in both Manitoba and Ontario, but sensitive in the province of Quebec (Metcalf-Smith and Cudmore-Vokey 2004).

Yellow Lampmussel
Lampsilis cariosa (Say, 1817)

Distribution — The yellow lampmussel (Figs. 2E, F, and 24A) is a rare to uncommon mussel in North America. It occurs primarily along the Atlantic Slope, with a tiny portion of its range in the Great Lakes – St. Lawrence River drainage. In the United States, it occurs in 15 states east of the Appalachian Mountains, from Georgia to Maine (Williams et al. 1993; NatureServe 2009). Strayer and Jirka (1997) report that the yellow lampmussel is also found in northern New York, west of the Appalachian Mountains, in the St. Lawrence River system. In Canada, *L. cariosa* has been confirmed to occur in only two disjunct regions, both in the AME: the Sydney River, Nova Scotia (Mira River Composite), and the Saint John River and tributaries, New Brunswick (Fig. 24B). Clarke and Rick (1963), recorded the yellow lampmussel from the Sydney River in 1962. Although they believed this to be the first Canadian report, there is an earlier record from the Saint John River system (Matthew and Stead 1903). There is evidence that the species range in the lower Saint John River system may have decreased over the past century (Sabine et al. 2004). In Quebec there are two historic records of the yellow lampmussel from the rivière St. François and rivière Nicolet, 20–30 km downstream of the AME boundary (Athearn 1952). Considering the possibility of confusion or hybridization with *L. cardium*, and the lack of recent records for Quebec, additional survey effort is required to determine the current status of the yellow lampmussel in that province. The presence of this species in the St. Lawrence River drainage in New York (Strayer and Jirka 1997) suggests that there is potential for the species to occur in Quebec.

Habitat — Clarke (1981a) states that the yellow lampmussel is predominantly a river species that prefers rather swift currents on shoals or in riffles and occurs principally on sandy bottoms. However, in the lower reaches of the Saint John River, the species is most commonly found in areas of slow current. Here, the low gradient and tidal nature of the river has resulted in the formation of extensive sand bars, largely devoid of aquatic vegetation (Fig 8A, F). This habitat appears

Fig. 24. Yellow lampmussel (*Lampsilis cariosa*). (A) External (right valve) and internal (left valve) view of a male specimen from the Sydney River, Nova Scotia. CMNML 71133. External (left valve) and internal (right valve) view of a female specimen from the same river. CMNML 93785. (B) Distribution map.



to offer exceptionally favorable conditions for this species (Sabine et al. 2004). Nedeau (2008) also reported that shallow sand bars were the most favorable habitat for the yellow lampmussel in the Connecticut River watershed. In Blacketts Lake, a reservoir on the Sydney River where Nova Scotia yellow lampmussel populations seem to be most dense, this mussel occurs primarily on sandy, silt-free substrates with a low density of aquatic plants (White 2001; Davis et al. 2004). In the AME, this species has been recorded in water depths up to 5 m (Sabine et al. 2004).

Reproduction and host fishes — The yellow lampmussel is a long-term brooder (Clarke 1981a; Bogan and Alderman 2004), although the limits of the breeding season are not known for the AME. During breeding, the female of the yellow lampmussel displays elaborate mantle flaps, which resemble a minnow, complete with eye spot and tail. Glochidia for this species have been reported on the white perch in the Sydney River in July (Davis et al. 2004). Wick and Huryn (2002) and Wick (2006) note successful transformation in the laboratory on yellow perch and white perch for yellow

lampmussels from rivers in Maine. Kneeland and Rhymer (2008), using molecular techniques to identify glochidia on the gills of wild fish in Maine, found numerous yellow lampmussel glochidia on natural populations of white perch in June and July and on smallmouth bass.

Conservation status — The yellow lampmussel has been listed as threatened in the United States by the American Fisheries Society (Williams et al. 1993) and as endangered globally by the International Union for the Conservation of Nature (Bogan 1996b). In the United States this mussel is at great risk and is listed as extirpated, critically imperiled, or imperiled in 11 of the 15 states where it occurs (NatureServe 2009). It is rare and has been declining over much of its range, including Maine (Nedeau et al. 2000) and other states along the Atlantic coast (Nedeau 2008).

Although further work is needed to estimate densities and overall abundance of the yellow lampmussel in New Brunswick, recent evidence indicates the presence of a significant population of this species in the lower Saint John River system (Sabine et al. 2004). The Nova Scotia population is apparently healthy and shows signs of recent recruitment (White 2001; Davis et al. 2004). The species is listed as special concern in Canada (COSEWIC 2004). Metcalfe-Smith and Cudmore-Vokey (2004) report a conservation status of sensitive for New Brunswick and may be at risk for Nova Scotia. Fisheries and Oceans Canada (2009) has produced a conservation management plan for the yellow lampmussel in Canada.

Eastern Lampmussel

Lampsilis radiata radiata (Gmelin, 1791)

Distribution — The eastern lampmussel (Figs. 2G, H, 4A, and 25A) is widespread across the northeastern United States and eastern Canada. It occurs in both the Atlantic Slope and Great Lakes – St. Lawrence River drainages (Burch 1975; Clarke 1981a). In the United States this mussel occurs in 16 states, primarily east of the Appalachian Mountains, from South Carolina to Maine. In Canada the eastern lampmussel occurs in Nova Scotia, New Brunswick, Quebec, and Ontario. In spite of this wide distribution, the species is not known from Prince Edward Island, most of the Gaspé Peninsula (one record; four well-preserved valves from Douglstown, near Gaspé, at the mouth of the rivière St. Jean), northern New Brunswick, and southwestern Nova Scotia (Fig. 25B).

Habitat — The eastern lampmussel is one of the more common and ecologically dominant unionoid species in eastern Canada. The species occupies a wide range of freshwater habitats, occurring in small to large river systems and lakes of various sizes. Although this mussel prefers gravel or sand bottoms, it is also occasionally found in silty or muddy bottoms.

Reproduction and host fishes — The species is a long-term brooder. During breeding, the female displays swollen, pig-

Fig. 25. Eastern lampmussel (*Lampsilis radiata radiata*). (A) External and internal view of shells from Darlings Lake, New Brunswick. CMNML 31084. (B) Distribution map.

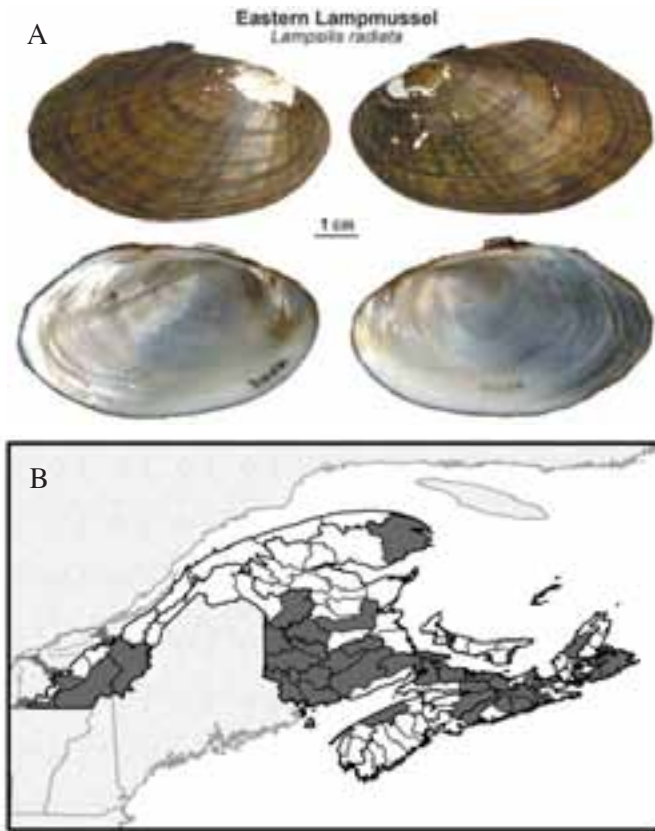
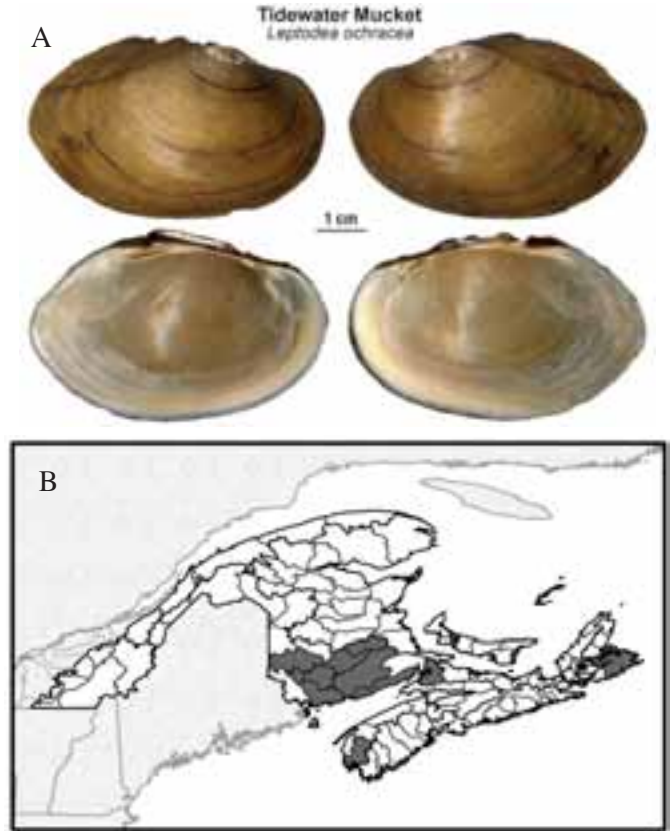


Fig. 26. Tidewater mucket (*Leptodea ochracea*). (A) External and internal view of shells from Saint John River, New Brunswick. CMNML 93781. (B) Distribution map.



mented, mantle flaps with margins bordered by a series of fleshy lobes. Below these lobes, where the shell usually protrudes from the sediment, a pair of 1–3 cm marginal mantle digitations extend (Fig. 2G). The peach–orange, ocre, or pale brown digitations contract rhythmically to attract potential host fishes. It is believed this behavior mimics worm or insect prey. Fish species occurring in the AME that have been recorded as hosts elsewhere include four warm-water species: smallmouth bass, pumpkinseed, white perch, and yellow perch (Tedla and Fernando 1969; Watters 1994). In a study conducted in three major watersheds in Maine, Kneeland and Rhymer (2008) reported that the yellow perch was the most common host fish for the glochidia of the eastern lampmussel. The yellow perch is abundant and widespread in the AME and may be an important host for this mussel in the ecozone. Figure 4A illustrates the hookless glochidia of this species.

Conservation status — In the eastern United States this mussel is listed as at risk in 6 of the 16 states where it occurs (NatureServe 2009). The species is common throughout most of its range in eastern Canada, including the AME. It is listed as secure in Quebec and New Brunswick but sensitive in Nova Scotia (Metcalf-Smith and Cudmore-Vokey 2004). In the neighbouring state of Maine, it is also secure (Nedeau et al. 2000).

Tidewater mucket
Leptodea ochracea (Say, 1817)

Distribution — The tidewater mucket (Figs. 2C, D, and 26A) is restricted to coastal regions in the Atlantic Slope drainage, from the Savannah River in Georgia to Cape Breton, Nova Scotia (Clarke 1981a). In the United States it occurs in 14 states, including adjacent Maine. In Canada this mussel is restricted to the AME, occurring in southern coastal New Brunswick and several scattered regions of Nova Scotia (Fig. 26B). The tidewater mucket was first reported from the Maritimes by Athearn (1961) at localities in New Brunswick, and subsequently, in Nova Scotia (Athearn and Clarke 1962; Clarke and Rick 1963; Price 1968).

Habitat — The tidewater mucket typically inhabits coastal freshwater habitats. The species occurs primarily in quiet waters, often in the lower tidal portions of rivers, on mud or sand bottoms (Clarke 1981a; Johnson 1970). In the eastern United States, this mussel occurs on a variety of substrates, including silt, sand, gravel, cobble, and even clay (Nedeau et al. 2000, 2008). It is often found in association with the yellow lampmussel in Maine, Nova Scotia, and New Brunswick (Nedeau et al. 2000; White 2001; Sabine et al. 2004), although it is not as limited to sand substrates as is the latter

species. Although typically a species of coastal drainages, the tidewater mucket may occur well inland, including behind significant impoundments, such as the Mactaquac Dam on the Saint John River.

Reproduction and host fishes — This mussel is a long-term brooder, although details of its reproductive period are unknown. There has been very little research conducted on the host fish of the tidewater mucket. Nedeau et al. (2000) noted that anadromous fish are lacking from some of the Maine lakes where the tidewater mucket occurs, indicating that non-anadromous hosts may be involved. Kneeland and Rhymer (2008) found that in Maine, among the 20 fish species sampled in three watersheds, the white perch was by far the most common host on which glochidia of the tidewater mucket occurred, followed by the banded killifish (see also Wick 2006). Both the white perch and the banded killifish are widespread in Nova Scotia and southern New Brunswick.

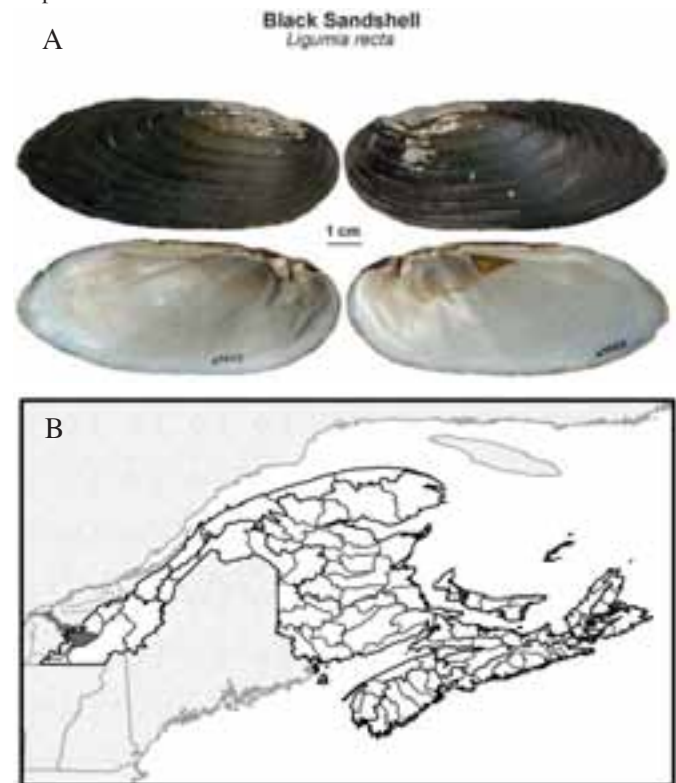
Conservation status — In the United States this mussel is listed as at risk (imperiled or critically imperiled) in 11 of the 14 states where it occurs (NatureServe 2009). In Maine it is considered a threatened species (Nedeau et al. 2000). The tidewater mucket has also been listed as a species of special concern for North America (Williams et al. 1993). Strayer and Jirka (1997) predict that the presence of the zebra mussel may soon lead to the extirpation of this species from New York. In Canada its status has yet to be formally assessed, and various informal status ranks seem to be contradictory. Metcalfe-Smith and Cudmore-Vokey (2004) list the tidewater mucket as secure in New Brunswick and sensitive in Nova Scotia, while NatureServe (2009) lists this species as vulnerable for New Brunswick and critically imperiled for Nova Scotia. Recent field studies have shown the species to be widely distributed in southern coastal New Brunswick, where it is locally abundant in portions of the Saint John River system.

Black sandshell
Ligumia recta (Lamarck, 1819)

Distribution — The black sandshell (Fig. 27A) occurs in the Great Lakes – St. Lawrence, Mississippi, and parts of the Hudson Bay drainages (Clarke 1981a; Parmelee and Bogan 1998). In the United States it occurs in 26 central and eastern states in drainages west of the Appalachian Mountains. In Canada the black sandshell occurs in Saskatchewan, Manitoba, Ontario, and Quebec. In Quebec this mussel occurs mostly outside the AME, primarily in the St. Lawrence River and both its north- and south-shore tributaries. The black sandshell is recorded from the AME on the basis of two isolated live mussels observed during recent MRN – Faune du Québec surveys on the rivière St François, Quebec (Fig. 27B).

Habitat — The black sandshell is a running-water species, although Clarke (1981a) states that this mussel can sometimes

Fig. 27. (A) Black sandshell (*Ligumia recta*). External and internal view of shells from St. Lawrence River, Pte-aux-Trembles, Quebec (Mixedwood Plains Ecozone). CMNML 67053. (B) Distribution map.



occur in large lakes. It is typically found in medium-sized and large rivers, preferring moderate to strong water currents. Preferred substrates include fine gravel, firm sand, and sometimes mud.

Reproduction and fish hosts — The species is a long-term brooder. Gravid females can be found from July to August to the following summer (Surber 1912; Ortmann 1919; Coker et al. 1921). Metamorphosis of black sandshell glochidia to juveniles have been confirmed in the laboratory on the following fish species known from the Quebec portion of the AME; rock bass, banded killifish, pumpkinseed, white perch, and yellow perch, (Steg and Neves 1997; Hove et al. 1994; Watters et al. 1999; Khym and Layzer 2000). Natural infestations of the black sandshell have also been shown to occur on the American eel (*Anguilla rostrata* (Lesueur)) (Coker et al. 1921).

Conservation status — In the United States, the black sandshell is listed as imperiled or critically imperiled in 17 of the 26 states where it occurs (NatureServe 2009), including nearby Vermont and New York. In Canada the status of the black sandshell is listed as sensitive (Metcalfe-Smith and Cudmore-Vokey 2004) or vulnerable (NatureServe 2009) in both Ontario and Quebec.

Hickorynut

Obovaria olivaria (Rafinesque, 1820)

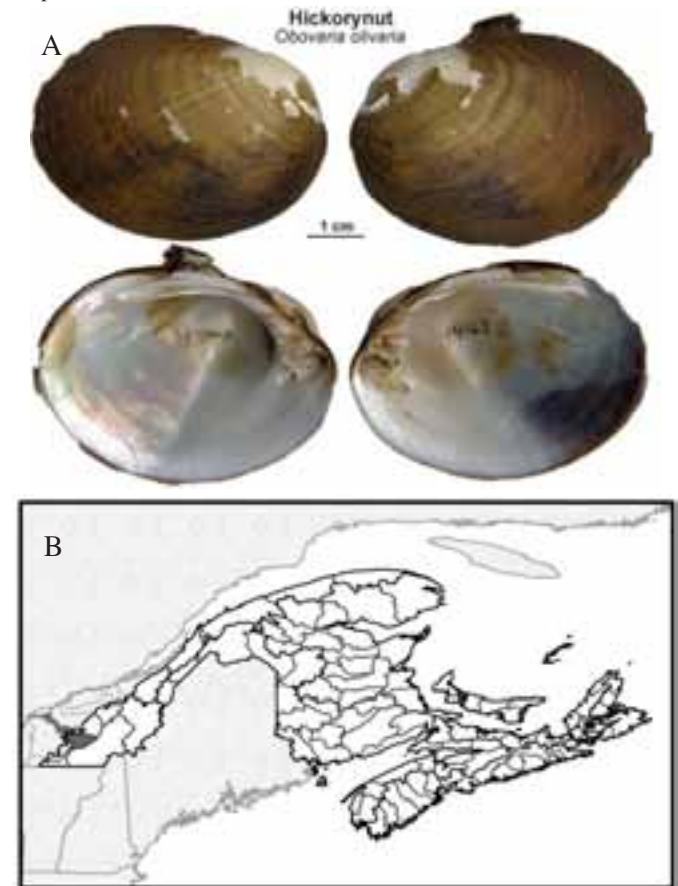
Distribution — The hickorynut (Fig. 28A) occurs in the Great Lakes – St. Lawrence and Mississippi drainages (River system) (Burch 1975; Clarke 1981a; Parmelee and Bogan 1998). In the United States this mussel occurs in 19 central and eastern states west of the Appalachian Mountains. In Canada this mussel is found only in Ontario and Quebec. Prior to the introduction of the zebra mussel in 1985–1986 it occurred in Lake St. Clair, Lake Erie, and Lake Ontario. The hickorynut has declined drastically in Ontario and is now critically imperiled in that province (Metcalf-Smith et al. 1998a, b; NatureServe 2009). Recent surveys indicate that Quebec (outside the AME) contains most of the remaining Canadian populations of this mollusc (Martel and Picard 2005; Martel et al. 2006). Within the AME in Quebec, all records of the hickorynut are from the rivière St François (Fig. 28B), where a few live individuals have been found during recent surveys.

Habitat — The hickorynut is normally found in large rivers with moderate to strong currents, often with mid-river sand bars. In comparison to other riverine freshwater mussels, the hickorynut prefers deep water. It is commonly found on sand, mixed sand, or gravel bottoms at depths of 2 m or more (Clarke 1981a; Cummings and Mayer 1992; Parmelee and Bogan 1998; Martel and Picard 2005; Martel et al. 2006). For this reason, SCUBA diving is the preferred survey method for the species (Martel et al. 2006).

Reproduction and host fishes — This species is a long-term brooder with females gravid from August to June of the following summer (Surber 1912; Ortmann 1919; Baker 1928). In the wild, glochidia of the hickorynut mussel have only been identified from the shovelnose sturgeon (*Scaphirhynchus platyrhynchus* Rafinesque), a fish not present in Canada (Coker et al. 1921). However, metamorphosis from glochidium to juvenile has been confirmed in the laboratory on the lake sturgeon (*Acipenser fulvescens* (Rafinesque)) (Brady et al. 2004), which occurs in all Quebec rivers where this mussel has been observed. The freshwater drum (*Aplodinotus grunniens* Rafinesque) has also been mentioned as a host fish for this mussel Clarke (1981a).

Conservation status — The hickorynut is a rare mussel in many regions in North America. In the United States it is secure in only 2 of the 19 states where it has been recorded, and it is imperiled or extirpated in the remaining states, including the nearby state of New York (NatureServe 2009). Its national status is currently being assessed by COSEWIC (Zanatta et al., in preparation) and a provincial status report is also in preparation for Quebec. Currently, it has no legal conservation status in Quebec, but it is listed as likely to be designated threatened or vulnerable, and it is ranked as imperiled. In populations of

Fig. 28. (A) Hickorynut (*Obovaria olivaria*). External and internal view of shells from Ottawa River, MacLaren's Landing, Ontario (Mixedwood Plains Ecozone). CMNML 14163. (B) Distribution map.



this species in Quebec tributaries, such as rivière St François, little or no recruitment is evident (Paquet, unpublished data), suggesting that the future of the hickorynut in the AME is very uncertain.

Ecosystem functions and ecosystem services

Unionoid mussels fulfill a number of important functions and services in freshwater ecosystems, including the lakes and rivers of the AME. The discussion below outlines some of these functions and services. Vaughn et al. (2008) provide a more detailed review of freshwater mussel ecosystem services and functions and food web ecology. Vaughn and Spooner (2006) demonstrate that at the patch scale there is a positive correlation between the abundance of freshwater mussels and the abundance of other macroinvertebrates. Such results support the important role that freshwater mussels play in enhancing and maintaining species richness and freshwater ecosystem function. Still, much research remains to be done to better understand the role these organisms play in freshwater ecosystems (Strayer et al. 1999; Vaughn and Hakenkamp 2001).

Cleaning up the water: filter feeding, including eating bacteria

Freshwater mussels are natural “biofilters” (Strayer et al. 1999). They can filter large amounts of water, up to 300 mL h⁻¹ mg⁻¹ dry weight (Paterson 1984). The volume of water filtered by an average, mid-sized mussel has been conservatively estimated at 0.5–1.0 L/h (Vaughn et al. 2008), although clearance rates in the range of 2–3+ L/h have also been recorded (Kryger and Riisgard 1988). This filtering process results in the extraction of large numbers of planktonic particles from the water column, including phytoplankton, small zooplankton (e.g., rotifers), and coliform and other bacteria, as well as detritus (Vaughn and Hakenkamp 2001; Vaughn et al. 2008). Where densities of freshwater mussels are high, as commonly observed in the AME, the proportion of the total available water volume that is filtered can be significant. It can sometimes equal, or even exceed, the daily stream discharge (Welker and Walz 1998). Through this process, freshwater mussels increase water clarity and play a role in removing bacteria from the water column (Vaughn and Hakenkamp 2001).

Mixing and oxygenation of sediments

The horizontal and vertical movement of freshwater mussels through sediment contributes to the mixing or loosening of bottom substrates (McCall et al. 1979; Zimmerman and de Szalay 2007). This process, which can aptly be called the “earthworm effect”, significantly increases water content and oxygen concentration within the sediment (Nedeau 2008). This enhances aerobic processes by microorganisms. Thus, mussel activity at the water–sediment interface, including the normal probing or digging effect of the powerful muscular foot, can significantly increase benthic productivity and biodiversity of freshwater communities (Sephton et al. 1980). Spooner and Vaughn (2006) demonstrated experimentally that the presence of freshwater mussels increased the density of other invertebrates in the surrounding sediments and on live mussel shells and also increased the abundance of periphyton. The ecosystem services provided to the surrounding invertebrate community by crawling and burrowing mussels remains an area of research largely unexplored. Contrary to our native freshwater mussels, the invasive dreissenid mussels do not mix or oxygenate the sediments. These immobile, byssally-attached, bivalves typically cover and smother the bottom. They produce large quantities of pseudofeces and in this way render the underlying sediment largely anoxic, especially when they are present at high density.

Benthic biomass and P and N sink

Mussels can represent 90–95% of the living biomass of benthic communities in lakes and rivers (Negus 1966; Strayer et al. 1999; Martel et al. 2004b; Nedeau 2008). They may occur at densities exceeding 100 adults/m², and numbers may sometimes be as high as 400 mussels/m² (Nedeau 2008; Martel, pers. obs). With so many mussels filtering water, their tissues, feces, and pseudofeces constitute an important sink in aquatic

ecosystems for phosphorous (P), nitrogen (N), and carbon (C). In this way, freshwater mussels provide nutrients to rooted macrophytes, microorganisms, deposit-feeding meiofauna, and other macroinvertebrates (Nalepa et al. 1991; Strayer et al. 1999). This P, N, and C source also enhances benthic biodiversity and organic productivity, including that of juvenile and adult fishes.

Creation of microhabitats and modification of the physical structure of the bottom

Live or dead freshwater mussel shells on the bottom create a natural hard substrate, a microhabitat, which numerous organisms can exploit (Becket et al. 1995; Strayer et al. 1999; Vaughn and Hakenkamp 2001; Spooner and Vaughn 2006; Nedeau 2008). Small invertebrates, including epizoic microinvertebrates, amphipods, isopods, crayfishes, and small-bodied fishes, can be found on both live and dead mussel shells, and both inside and outside the shell, increasing biodiversity.

In large rivers where the substrate is dominated by silt or mud, dense unionid mussel beds can modify the hydraulic roughness of the bottom. This creates favorable bottom conditions for organisms seeking shelter from strong water currents (Strayer et al. 1999; Vaughn and Hakenkamp 2001).

Food source for wildlife

Freshwater mussels provide an important protein source for some wetland vertebrates, particularly muskrat (Hanson et al. 1989), but also otter, raccoon, mink, turtles, and various birds (Fuller 1974, cited in McMahon and Bogan 2001; Nedeau 2008). Juvenile mussels may serve as food for fishes, such as sturgeons, redhorse, suckers, and sunfishes.

Stressors affecting freshwater mussels

Humans have abused North American freshwater ecosystems, especially since the onset of the industrial era in the nineteenth and twentieth centuries. We have consistently underestimated and undervalued wetland faunal diversity (Karr 1991). It is therefore not surprising, that the decline of freshwater mussels is caused primarily by the destruction or degradation of freshwater habitats, including declines in water quality. Increasingly, the introduction of invasive nonindigenous species has played a role (Bogan 1993; Ricciardi et al. 1998). Also important is the manner in which adjacent terrestrial ecosystems, through which water in mussel habitats necessarily passes, are managed (Karr 1991). The following paragraphs detail interrelated environmental stressors that are linked to the decline of the Canadian freshwater mussel fauna, including that of the AME region.

Loss of riparian zone adjacent to wetlands, lakes, and rivers

The area of vegetation adjacent to a wetland or body of water, the riparian zone, contributes greatly to a healthy union-

oid community. Removal of the riparian zone has been directly linked to the catastrophic decline of freshwater mussels and their host fishes (Morris and Corkum 1996; Vaughn 1997; Poole and Downing 2004). In addition to creating transition or ecotone habitats, the root systems of riparian zone plants stabilize the soil at the water edge. This significantly reduces silt runoff during heavy rains and snowmelt, thus contributing to water quality (Watters 1995). Water retention by riparian zone vegetation may reduce the impact of severe drought on mussels through the gradual release of ground water. The presence of an extensive riparian zone adjacent to any stream, river, or lake can significantly reduce the impact of floods and rainstorms through water absorption via root systems (Watters 2000). Streamside woodland zones also create shaded habitats nearshore and contribute woody debris to lakes and streams. This creates shelter and microhabitats for aquatic fauna, including mussels and fishes. *Margaritifera margaritifera*, for example, lives in small to mid-size rivers where its trout and salmon hosts find shelter and shade along the riverbanks (Fig. 8C).

Human activities near waterways, including cottage development, agriculture, forestry, and road construction, often alter the riparian zone. Loss of the riparian zone can dramatically affect the temperature regime of surface waters near shore. It can also lead to the release into the water of large amounts of sediment and excessive nutrients. A healthy and wide band of natural vegetation bordering a creek, stream, or lake will help absorb or filter herbicides or pesticides that would otherwise be rapidly transported to the water during snowmelt or rainfall.

Since the riparian zone is such an important component of aquatic ecosystems, particularly in forested landscapes, all provinces in the AME have legislation and policies designed to protect it. Nonetheless, riparian retention zones are sometimes too small or narrow to protect water quality. Degradation, or even loss, of riparian zones remains a problem in areas of the AME. The situation is particularly critical in agricultural, suburban, and industrial areas, or where cottage development occurs near creeks, streams, or rivers.

Water pollution: point source and nonpoint source

Freshwater mussels do not occur in highly polluted waters. These organisms require reasonably good to very good water quality for their survival (Clarke 1981a; Williams et al. 1993). Water pollutants may leach into a wetland from a widespread area, or even originate from releases into the atmosphere. Toxic chemicals and other pollutants, whether from a point source or non-point source, can have deleterious effects on native freshwater mussels (Bogan 1993; Williams et al. 1993).

In lakes, streams, and rivers of the AME, water pollutants originate in runoff from urbanized, industrial, and agricultural regions, including golf courses and peat moss operations (George et al. 2001). Such runoff often contains fertilizers, pesticides, animal waste, and pharmaceuticals. In the AME industries such as pulp mills introduce numerous toxic substances to freshwater ecosystems, many of which can travel

long distances downstream. Other pollutants impacting mussels include industrial by-products such as PCBs. Sex change has been documented in freshwater mussels in the St. Lawrence River owing to pharmaceutical drugs present in human effluent (Blaise et al. 2003).

High siltation

Erosion, and the ensuing silt loads, present a serious stressor to freshwater mussels. Large amounts of sediment can be put into suspension during road construction or repair, housing development, forestry operations, and especially agriculture. These impacts can be felt far downstream. A significant factor that contributes to siltation is the removal or alteration of the riparian zone. Sediments dispersed into waterways eventually settle, covering the bottom of rivers and lakes, and suffocating freshwater mussels and damaging fish habitat. High siltation and smothering of river beds have been identified as a leading cause in the decline of mussels and their host fishes in American rivers (Anderson et al. 1991; Bogan 1993; Watters 1995; Vaughn 1997; Watters 2000; Poole and Downing 2004).

Historical logging and log drives

In many AME rivers, historic logging has scoured river bottoms and eroded river banks. This has produced rivers that are wider and shallower than they were prior to logging. Examples include the St. Marys River, Nova Scotia, and the Kouchibouguac River, New Brunswick. Although this activity occurred generations ago, the impacts on mussels is still being felt. The transportation of logs via the river commonly resulted in the downstream migration of bed load and consequently, the loss of habitat (substrate). Moreover, in the shallow-water situations produced, ice now commonly freezes to the substrate. In spring, during ice-out, any mussels present and their habitat are scoured away. Log drives also severely impacted habitat of host fishes in AME rivers.

Dams, dykes, and causeways: rivers in peril

The construction of a dam, or a causeway (Fig. 8E), even of small size, produces significant changes in the hydrology, sedimentation, physical-chemical limnology and biology of a river (Baxter 1977). Dams dramatically influence the abundance and diversity of freshwater mussels (Watters 1996; Parmelee and Bogan 1998; Watters 2000; Nedeau 2008; Williams et al. 2008). The environmental and water-quality degradation that follows dam construction includes changes in water-flow patterns, seasonal temperature regimes, phosphate and nitrogen budgets and phytoplankton and zooplankton productivity. The impacts of dams can be so severe that freshwater mussel populations may be eliminated entirely from the impounded section of a river, or severely reduced considerable distances downstream (Vaughn and Taylor 1999).

The impoundment of a river causes a sudden shift from shallow to deep, lake-like, water conditions upstream of the dam. Only those freshwater mussel species capable of living in

lake-like ecosystems can survive; river-dwelling mussels are quickly eliminated. Because river systems harbour a greater diversity of mussels than lake environments (McMahon and Bogan 2001), impoundments normally result in a loss of mussel diversity. Studies have shown that following impoundment, the diversity of freshwater mussels can decrease by 60% or more (Suloway et al. 1981; Williams et al. 1993).

Dams modify the seasonal temperature regimes over the impoundment bed (Baxter 1977). Near-bottom temperatures above a dam remain cold, even during warm summer months, creating a habitat similar to the hypolimnion found in deep lakes. The cooler temperatures produced can even extend downstream if the water going through the dam originates from the bottom of the structure, as is the case with some hydroelectric dams. Such changes to the natural seasonal temperature cycle can severely impair the seasonal growth, feeding, and reproductive cycle of freshwater mussels (Tippit et al. 1997). River-adapted mussels cannot live in such environments (Watters 2000). Moreover, dams can also effect the aquatic environment downstream by releasing water from the surface of the reservoir during the summer. This can occur when the surface water is warmer than the thermal tolerance of cold-water fish in downstream areas (Nedeau et al. 2000).

The construction of dams, dykes, or causeways also affects sedimentation rates in river systems. Siltation upstream of the structure may increase significantly (Watters 2000). Increasing siltation rates change the substrate quality of the river bottom and smother benthic organisms, including mussels. High siltation can be detrimental to even the most tolerant lake-adapted freshwater mussels, although some species survive in such situations.

Stocks of host fishes may be reduced following impoundment, affecting the freshwater mussel–fish linkage (Williams et al. 1993; Watters 1996, 2000). River-adapted fishes may be extirpated upstream of the dam owing to habitat alteration. Even small dams can reduce the movement and dispersal of host fishes (Watters 1996). In the AME dam construction has been particularly detrimental to anadromous fishes (Locke et al. 2003), such as American shad, alewife, and Atlantic salmon. Fish ladders often perform poorly and do not allow sufficient numbers of fish to pass above the dam to maintain stocks. Where the movement of anadromous fish is impeded, freshwater mussels that depend on these fish are eventually extirpated. Such may have be the case for the *A. heterodon*, formerly present in the Petitcodiac River system, New Brunswick (Fig. 8E; Locke et al. 2003).

Impoundments can result in an increase in habitat for some lake-adapted mussel species. However, impoundment management practices can offset these partial gains. Rapid water-level reductions or drawdowns occur during normal dam operation and maintenance. These occur both above and below the structure, especially hydropower dams. Such activity can cause massive mussel mortality owing to desiccation and increased predation when mussels are stranded (Burlakova and Karatayev 2007). Such mortality is most prevalent where mussels

occupy the shallow, near-shore areas most exposed to fluctuations in water level (Parmelee and Bogan 1998; Nedeau et al. 2000). This is the case behind the Mactaquac Dam on the Saint John River, where impoundment has created extensive habitat for the tidewater mucket and alewife floater. These species are uncommon or less common in upstream sections of the river, yet appear to suffer high mortality rates during midsummer drawdowns (D. Sabine, pers. obs.).

Several river systems, notably the Saint John River in New Brunswick, and Magog River in Quebec, and perhaps the Sis-sibou, Tusket, and Mersey rivers in Nova Scotia, have been extensively altered by dams. While impoundments are also scattered among a number of other rivers in the AME, the majority of AME waterways are not currently dammed. However, small-scale dams associated with historic mills or log drives were at one time present on most AME river systems. While most of these dams are now gone, the consequences are still being felt where riverbeds and hydrology have been changed. How these dams might have affected current mussel distribution is unknown. In the AME, *A. heterodon*, *A. varicosa*, and *M. margaritifera* are all species adapted to running-water environments, and have probably been those most affected by impoundments. The installation of even a small dam or dyke across a river or stream modifies the entire hydrology and ecology of the waterway and makes it impossible for these mussels to survive.

Notwithstanding the detrimental impact that impoundments may have on mussels, *L. cariosa* in the Sydney River, Nova Scotia, is thought to have benefited from an increase in habitat owing to the construction of a dam in 1902 (COSEWIC 2004). Although predominantly a river species, this mussel is sometimes found in still waters or lake-like environments. However, it is also likely that other unionoid species present in the Sydney River system at the time were negatively impacted by this impoundment.

Introduction of invasive dreissenid mussels

The introduction of two species of invasive dreissenid mussels to the North American Laurentian Great Lakes during 1986–1992 has led to the large-scale extirpation of native freshwater mussels from the region (Nalepa et al. 1996; Schloesser et al. 1996). Originally from the Caspian Sea region, both dreissenid bivalves entered the Great Lakes via the discharge of ballast water of transoceanic cargo ships (Hebert et al. 1991). The life cycle of these species is similar to that of other marine bivalves in that a free-swimming planktonic veliger larval stage is produced. The veliger settles on any hard substrate, including the shells of live unionoids (Mackie 1991). Live unionoid mussels may become covered by hundreds, even thousands (up to 10 000), of dreissenid mussels. Unionoids have little chance of survival, as this type of bio-fouling impedes their filter feeding, locomotion, and reproduction (Haag et al. 1993). Ricciardi et al. (1996), working in the St. Lawrence River near Montreal, demonstrated that infestations as low as ca. 10 adult zebra mussels per live unionid

may eventually lead to the death of the native mussel. Laboratory study has also shown that *D. polymorpha* can select and ingest the best food particles from the plankton available, and in this way out-compete native mussels for food (Baker and Levinton 2003). In eastern Canada *D. polymorpha* has swiftly extirpated native freshwater mussels from both large (Ricciardi et al. 1996) and small (Martel et al. 2001) river systems.

Although yet to be observed in the AME, there is a danger that dreissenid mussels may be introduced into the ecozone (Martel et al. 2004a). They are easily transported by barges, pleasure boats, and boat trailers. A probable first point of entry for this exotic species into the AME is the Saint John River. The upper reaches of this system are located very close to waterways near Quebec City, an area already colonized by *Dreissena*. Smallmouth bass and muskellunge (*Esox masquinongy* Mitchell), both introduced into the Saint John River, are becoming popular for sport fishing tournaments, attracting fishermen with their boats from outside the AME. Boats and fishing gear present a potential source of *Dreissena* introduction to the region.

Also, the water chemistry of the Saint John River (Cunjak and Newberry 2005) meets requirements for reproduction that elsewhere in North America has led to rapid growth and severe fouling by dreissenids (Ramcharan et al. 1992; Jokela and Ricciardi 2008). The Saint John system has the richest freshwater mussel fauna of Atlantic Canada, including mussel species restricted to the region and (or) of conservation concern. The impact of dreissenid mussels on the native freshwater mussels of the Saint John River system would be devastating (Martel et al. 2004a). Many lakes in the Quebec portion of the AME also have favorable water chemistry for the establishment and proliferation of dreissenid mussels. Concerted efforts, including improving public awareness and education, should be made to ensure that dreissenid mussels are never introduced into the Saint John or other river or lake systems in the AME.

Introduction of predatory sport fishes

The long-standing tradition of introducing nonindigenous piscivorous fish into lake and river systems across much of eastern Canada has had an unknown impact on populations of freshwater mussels. Piscivorous fish are top predators that forage heavily on small-bodied fishes, including minnows, chubs, daces, and others (Chapleau et al. 1997; Whittier et al. 1997; Findlay et al. 2000), many of which are hosts to native freshwater mussels. One such fish, introduced over much of the AME, is the smallmouth bass. Over the past century this fish has been purposely introduced to dozens of lakes and connecting river systems in southern Nova Scotia, southern and western New Brunswick, and in the eastern townships of Quebec and has been implicated in the loss or severe decline in minnow assemblages (Whittier et al. 1997; Findlay et al. 2000; Jackson 2002). It may have had a significant impact on the reproduction and recruitment ability of unionoid mussels in the northeast (Nedeau et al. 2000; Nedeau 2008). The smallmouth

bass has very recently been introduced into the headwaters of the Miramichi River system (Miramichi Lake), New Brunswick, where it may constitute a threat to wild stocks of Atlantic salmon (A. Curry, pers. comm. to A.L.M., 2009) and native freshwater mussels, including *M. margaritifera* and *A. varicosa*. The chain pickerel (*Esox niger* Lesueur), another highly piscivorous non-native fish, now occurs across much of the southern part of the ecozone with unknown effects. The impact on freshwater mussels of the recent introduction to the Saint John River of the muskellunge, a large fish that feeds heavily on smaller native fishes, is likewise unknown (Stocek et al. 1999). This latter species in particular should be of concern to those monitoring mussel populations in the large mussel-rich Saint John River system. Unfortunately, the introduction of nonindigenous piscivorous sport fishes into lake and river systems continues across Canada, including in the AME. Available information on the long-term ecological consequences of predatory sport-fish introductions clearly suggests that such activity negatively impacts local biodiversity.

Destruction of fish habitats and fish stocks

Freshwater mussels depend on native host fishes to reproduce. The decline of resident or migratory fish populations therefore can dramatically impact the dispersal and recruitment ability of mussels. The decline in diversity and abundance of fish populations may result from pollution, introduction of non-native predatory fishes, overfishing, dam construction, or habitat loss. Because host fishes are highly mobile and use different types of habitats during their life cycle, host depletion can originate in an area remote from the mussel population. In the AME the decline of Atlantic salmon stocks may have reduced the recruitment success of *M. margaritifera*. This mussel is very long-lived, and adults may therefore still be present in a river system even though recruitment has ceased as host fishes have disappeared. Unfortunately, empirical data that might resolve this question is still lacking for the AME.

Large woody debris (LWD) is a natural component of lakes and rivers bordered by a mature riparian zone. Beaches, areas near cottages or where boats are used, are often cleared of LWD (Martel et al. 2004b). Although scientific studies on the effect of LWD on freshwater communities have not focused on mussels, it is known that fish greatly benefit from the presence of LWD. Large woody debris is an important source of shelter for fishes, providing microhabitats, protection from predation and competition, and shelter from water currents (Slaney and Zaldokas 1997). Thus, LWD may indirectly benefit freshwater mussel populations, whose larvae depend on fishes for metamorphosis and dispersal (Martel et al. 2004b). The relationship between the loss of LWD, fish habitat, and the decline of freshwater mussels needs to be examined.

Acid precipitation

Environmental studies conducted in Scandinavia and Canada reveal that acid rain, especially emissions of nitrous and sulfur oxides, negatively impact freshwater ecosystems.

Prevailing winds exacerbate the problem of acid rain in the AME. The region receives much of its atmospheric pollution and acid rain from the oil and coal power plants, ore smelters, and automobiles of major cities across eastern Canada and the northeastern United States. In lake and river systems underlain with largely granitic rock, such as southern Nova Scotia, buffering capacity is low or lacking. In these areas acidification of soil and fresh water has led to ecological damage. Doka et al. (1997) demonstrated a positive correlation between the diversity of aquatic organisms and the pH of water, with the lowest diversity observed in the most acidic waterways. When the pH drops below 6.0, the diversity and abundance of living organisms begins to decline (Doka et al. 1997).

The calcium carbonate crystals that make up the mussel shell are subject to natural abrasion and chemical erosion. This is especially the case in the region of the shell that is the oldest, the umbo. Chemical erosion is especially noticeable in areas where water is soft or slightly acidic. Although the umbo is commonly eroded in mussels, this is greatly amplified when acid rain has reduced the pH of the water. Where acidic waters promote chemical erosion of the shell, mussel soft tissue may become exposed, leading to mortality.

Atmospheric transportation of acid rain, coupled with low soil buffering capacity, has led to the acidification of numerous lakes and rivers in the AME. In over 50 southeastern Nova Scotia rivers, the fish host for *M. margaritifera*, the Atlantic salmon (Cunjak and McGladdery 1991), has been entirely lost or has seriously declined owing to acidification (Watt and Hinks 1999; Atlantic Salmon Federation, available from <http://asf.ca> [accessed 19 April 2009]). Unfortunately, lack of data makes it difficult to be certain of the impact of acid rain on native freshwater mussel communities. In AME regions where water acidification is most severe, such data is urgently needed.

Climate warming

Climate change studies show that the annual mean temperature of the earth's atmosphere is rising (Environment Canada, www.ec.gc.ca). In northeastern North America, including the AME, predicted changes in temperature patterns and annual precipitation will impact the freshwater fauna and flora of the region. Climate change may influence AME freshwater mussel distribution and abundance directly, as well as indirectly via changes in regional host-fish assemblages (Nedeau 2008). Variations in climate may have an effect on various aspects of freshwater mussel biology, including filter-feeding processes, the timing of the annual reproductive cycle, and the timing and success of the mussel–fish linkage (Nedeau 2008). This may influence annual recruitment of sensitive species adapted to specific annual temperature or flow regimes.

Harvest of freshwater mussel shells by humans

In some mussel species, secretion of an iridescent nacre inside the shell can produce natural, usually irregularly shaped, pearls. Over the past centuries, the search for fresh-

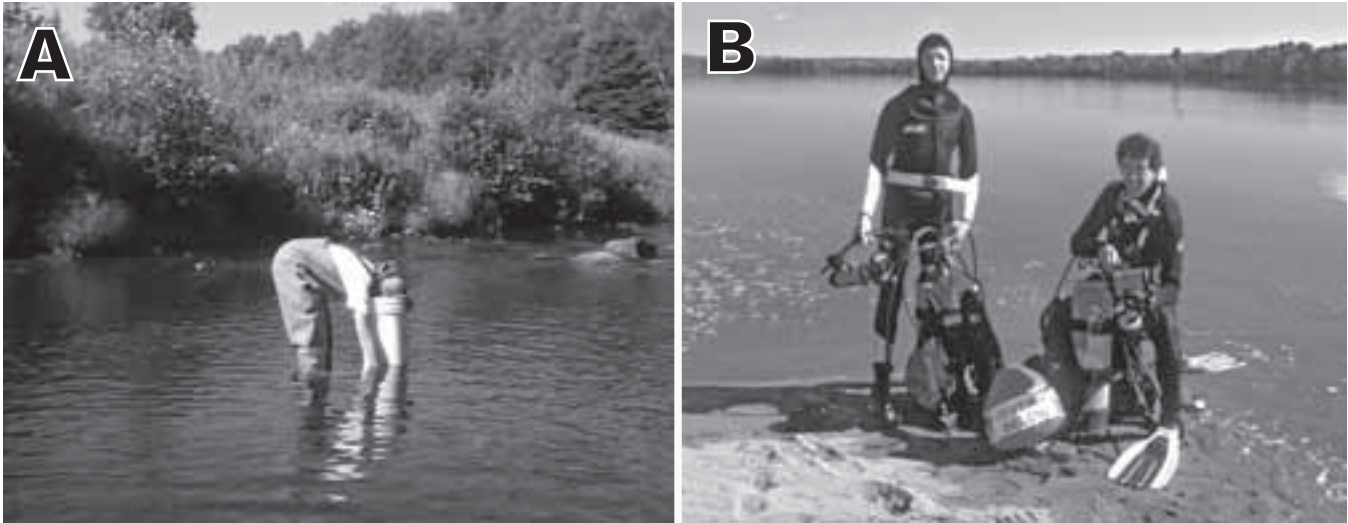
water pearls in *M. margaritifera* has contributed to the decline of European populations of this species (Young et al. 2001). Some harvest of natural pearls from this mussel occurred in the early 1900s in Atlantic salmon rivers in the Charlevoix area, Quebec (Jocelyn Gilbert, Baie St. Paul, Quebec, pers. comm. to A.P., 2008). Even where pearls are present in a mussel population, they are rare and now of little or no economic value. Most importantly, pearl collection necessitates killing large numbers of these long-lived animals. Nonetheless, this has not dissuaded a recent misguided suggestion that native freshwater mussels in New Brunswick be seeded for pearl production (Anonymous 2001, 2002). Historical information indicates that during the latter half of the 19th century some local, noncommercial, pearl harvest of *M. margaritifera* occurred in New Brunswick, and perhaps parts of Nova Scotia (Ganong 1889). Bailey (1887) also reported shell beads of local manufacture produced from unionids in a prehistoric native aboriginal grave on the Tobique, northern New Brunswick. However, there is nothing to suggest that native harvest of freshwater mussels in the AME was extensive.

In the United States, native Americans treasured the natural pearls that were occasionally found inside freshwater mussels, and also made tools, utensils, small bowls, and ornaments from the mussel shell (Parmelee and Bogan 1998; Williams et al. 2008). In the early 1890s, Europeans immigrants in the east-central United States initiated a successful and lucrative pearl button industry, harvesting thousands of tons of thick-shelled mussel species each year (Parmelee and Bogan 1998; Williams et al. 2008). This mussel-based nacre button industry ended in the early 1960s with the severe decline of harvestable mussels and the introduction of plastic buttons. However, thick-shelled mussel species continue to be commercially harvested in parts of the United States for the production of nacre shell beads that are used in the Asian cultured marine pearl industry (Parmelee and Bogan 1998). Such harvest has not occurred in Canada, because of a lack of high-density populations of suitable thick-shelled mussels. Anthony and Downing (2001) point out that these historic and contemporary commercial harvests in the United States are market-driven and carried out with a disregard for the life history and ecology of mussels.

Freshwater mussels as environmental indicators

Freshwater mussels are recognized as useful environmental indicators when conducting long-term studies of change in aquatic systems (Green et al. 1985). However, so far, they have been little used this way in the AME. Mussels are relatively large invertebrates that are easy to locate in the field, and are generally ubiquitous. The 19–20 species occurring in the AME reflects a relatively modest diversity, and identification is not difficult with available field guides, photographic plates, and identification keys (e.g., Clarke 1981a; Oesch 1984; Cummings and Mayer 1992; Nedeau et al. 2000; Metcalfe-Smith et al. 2005).

Fig. 29. Survey methods for freshwater mussels. (A) In shallow water, using a handmade view bucket; Kouchibougaucis River, New Brunswick. (B) Scuba-diving to conduct an underwater survey in the lower Saint John River, near Oromocto, New Brunswick.



Their sedentary habits also make them ideal for long-term studies of environmental change, and they have been widely used to monitor levels of toxins in freshwater systems (Green et al. 1985, 1987; Hinch and Stephenson 1987). The lipid-rich soft tissue of unionoids combined with their filter-feeding habit and longevity make them ideal for the latter purpose (Hinch and Stephenson 1987). The continuous growth of the mussel shell also allows the valves to be sectioned and analyzed for certain heavy metals or natural isotopes. In this way, shells deposited in natural history museums can be used as environmental archives (Carell et al. 1987; Mutvei and Westermark 2001) and environmental change over time inferred (Carell et al. 1987; Mutvei and Westermark 2001).

Freshwater mussels are sensitive to the loss of ecosystem integrity within their habitat. Watters (1992) has shown a direct and positive correlation between the diversity of freshwater mussels and that of fishes found in a watershed. Clarke (1981a) notes that the disappearance of freshwater mussels from mildly polluted habitats may not be a direct result of poor water quality. Host fishes may be more susceptible to low oxygen or pollutant levels than the mussels, but when hosts disappear or become rare, freshwater mussels cannot reproduce or disperse. Long-term monitoring of freshwater mussels can thus yield information on the local fish community and the quality of freshwater habitats.

For all of these reasons freshwater mussels are a useful group to target when conducting qualitative or quantitative surveys in lake or river systems.

General conclusions and conservation recommendations

The AME region has a unique Canadian freshwater mussel assemblage

Of the 55 Canadian species of native freshwater mussels,

19–20 species (36%) occur, or have occurred, in the AME. A quarter of the AME fauna is found nowhere else in Canada.

Freshwater mussels have many stressors and have declined in the AME

Although historical field surveys are few, when recent surveys are compared to museum collections and the older literature, there is evidence that the freshwater mussel fauna of the AME has declined over the past century. However, this decline does not appear to have been as dramatic as that observed during the same time in the more industrialized parts of central North America, including the Laurentian Great Lakes and tributaries. Among the primary environmental stressors that have affected the AME freshwater mussel fauna are the construction of dams and dikes, water pollution, siltation, and local declines in host fishes. Research is still needed to determine the impact of nonindigenous fish introductions on the AME freshwater mussel fauna.

AME freshwater mussel fauna is dependent on the fish fauna of the ecozone

Freshwater mussels are dependant upon fishes for the development and dispersal of their specialized larvae. Long-term conservation of mussels in the AME therefore depends on the conservation of the native freshwater fishes. Clarke (1981a) states that “high mussel diversity also indicates high fish diversity, and implies good fishing”. His comment summarizes the freshwater mussel–fish connection and can help the public appreciate that various elements of biodiversity are interconnected.

Freshwater mussels are good environmental indicators

Freshwater mussels in the AME display qualities that make them especially suitable for monitoring environmental change in river and lake systems; large size, easy visibility, moderate

diversity, long lives, sedentary habits, and generally straightforward identifiability are all contributors. When combined with their links to fish and fish habitat, freshwater mussels clearly have a role as river sentinels in the ecozone.

Further monitoring and surveys are needed

The long-term conservation of freshwater mussels depends on knowledge of species status, distribution, and diversity. Protocols for carrying out freshwater mussels surveys (Fig. 29) and for their long-term monitoring have been developed (Strayer et al. 1997; Vaughn et al. 1997; Nedeau et al. 2000; Strayer and Smith 2003; Nedeau 2008) but need to be more widely applied in the AME. It is important that such programs produce voucher specimen collections that can be deposited in permanent, public collections. These collections will provide the essential tools for future reference in evaluating species status and trends, as well as for assessing environmental change over time, and geographically.

Scientific research is required

Research on the taxonomy, life history, population genetics, and environmental relations of freshwater mussels in the AME is required. Only with such information can the protection and long-term conservation of this unique fauna be ensured. There is an urgent need for data on the impact of acid rain on freshwater mussel populations in those AME regions where acidification is most severe. We agree with Strayer and co-workers (2004) who state that “to conserve remaining mussel populations, scientists and managers must simultaneously and aggressively pursue rigorous research and conservation actions”.

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