Freshwater Mussels
and the
Connecticut River Watershed

Chapter 2: Habitat and Distribution

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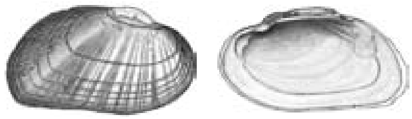


CHAPTER 2

Habitat and Distribution

To find mussels, it is important to first understand where they are likely to occur within a river, lake, or watershed. A species' distribution depends on its biology and habitat, distribution of its fish hosts, environmental constraints, and human influence. There are more than 20,000 miles of streams and hundreds of lakes in the Connecticut River watershed. It may seem daunting to describe the distribution of freshwater mussels within such a vast area. If elliptio were the only species, the task would be hard enough: it is ubiquitous and often abundant. Some species occupy a tiny fraction of available habitat, making it difficult to find them, characterize their habitat, or understand why they are rare. For example, the brook floater occurs discontinuously in fewer than 40 stream miles in the entire watershed. Distribution data provide a basis for insightful analysis about the species and habitats that are in greatest need of protection and what types of protection will be most effective.

People often feel a sense of pride when they learn that the fate of a species is intimately linked to the quality of the river flowing through their neighborhood. Distribution maps can unite towns that may never have known the other existed by creating a shared sense of responsibility to protect rare species and their critical habitats. For example, Otis, Massachusetts and Croyden, New Hampshire are among the handful of towns essential to the persistence of the brook floater, one of the most endangered species in the watershed.

I. GENERAL HABITAT

Freshwater mussels are found in permanent aquatic habitats such as streams, rivers, ponds, and lakes. Throughout North America, streams and rivers usually support the greatest diversity of mussels, perhaps because they provide a variety of habitat conditions, reliable flow, good water quality, and diverse fish communities. Species that live in flowing water usually prefer mud, clay, sand, gravel, and cobble substrates, and are more prevalent in areas with stable substrates. In contrast, mussels are usually less abundant in portions of rivers with constantly shifting sediments. Flowing water helps to maintain oxygen levels in the water and sediment. Flowing water also flushes sediments and other materials downstream, rather than allowing potentially harmful materials to accumulate and degrade conditions for some species of mussels.

Photo: The West Branch Farmington River in Otis, Massachusetts, supports one of the watershed's few brook floater populations. Ethan Nedeau

Mussels are usually sparse or absent in areas of rivers with bedrock and boulder substrates. This is the Rock Dam in Turners Falls, Massachusetts. Ethan Nedeau

Mussels can occur in water less than a few inches deep and even in areas that are frequently dewatered by fluctuating water levels; their ability to move vertically or horizontally in the sediment allows them to inhabit shallow areas. Highest mussel diversity and abundance is usually found in water less than 25 feet deep. Mussels are often abundant in depths greater than 50 feet in the Connecticut River where sunlight barely reaches the bottom, and divers have found elliptio in 122 feet of water at the bottom of the French King Gorge in the Connecticut River in Gill, Massachusetts (Sean Werle, University of Massachusetts, personal communication). These observations suggest that lack of sunlight, cold temperatures, and high pressure does not prohibit certain species from inhabiting deep water.

Mussels are often more abundant near banks than they are toward the middle of a river, especially stable banks on the outside of river bends. This phenomenon is more pronounced in rivers that transport high sediment loads or have prohibitively high water velocities toward the middle of the river. The insides of river bends tend to be depositional areas and have flow conditions that some riverine species do not prefer. Roots of riparian trees, large woody debris, and stable rocky substrates provide a stable refuge for many species of mussels and are often more prevalent near banks. Other areas of river channels that tend to support higher densities of mussels include areas with slow water flow and stable substrates, downstream ends of pools, protected side channels around islands, and downstream ends of islands.

Lake-dwelling species tend to be more tolerant of soft substrates (silt and sand), low dissolved oxygen, and warmer temperatures than stream-dwelling species. Mussels tend to be more abundant in shallow portions of lakes within the photic zone, which is the depth to which sunlight penetrates. In deep lakes that thermally stratify in the summer, mussels tend to be more abundant in the epilimnetic zone (warmer surface water) than the hypolimnetic zone (cold bottom water). Substrate in deeper areas of lakes tends to be a semi-liquid material called gyttja, which is a nutrient-rich sedimentary material consisting mainly of plankton, plant and

Table 2. General habitat requirements for freshwater mussels of the Connecticut River watershed.

Species	General Habitat
Dwarf Wedgemussel *Alasmidonta heterodon*	Small streams to large rivers; inhabits a variety of substrates and flow conditions. Never in lakes or ponds.
Triangle Floater *Alasmidonta undulata*	Small streams to large rivers; rarely in lakes; inhabits a variety of substrates and flow conditions.
Brook Floater *Alasmidonta varicosa*	Small streams and small rivers; mainly cold or coolwater habitats; inhabits sand, gravel, and cobble in riffles and runs. Never in lakes or ponds.
Alewife Floater *Anodonta implicata*	Small to large rivers and coastal lakes with anadromous (clupeid) fisheries; inhabits a variety of substrates and flow conditions.
Eastern Elliptio *Elliptio complanata*	Habitat generalist; abundant in most permanent aquatic habitats.
Yellow Lampmussel *Lampsilis cariosa*	Medium to large rivers and lakes; inhabits a variety of substrates and flow conditions.
Eastern Lampmussel *Lampsilis radiata*	Small to large rivers and lakes; mainly cool or warmwater habitats; inhabits a variety of substrates and flow conditions.
Tidewater Mucket *Leptodea ochracea*	Medium to large rivers and lakes; primarily coastal or within reach of anadromous fish; inhabits a variety of substrates and flow conditions.
Eastern Pondmussel *Ligumia nasuta*	Small to large rivers and lakes; primarily coastal or within reach of anadromous fish; inhabits a variety of substrates and flow conditions.
Eastern Pearlshell *Margaritifera margaritifera*	Small streams and small rivers; mainly coldwater habitats; inhabits a variety of substrates in riffles, runs, and pools.
Eastern Floater *Pyganodon cataracta*	Small to large rivers and lakes, including small ponds. Mainly cool or warmwater habitats; prefers lentic or depositional habitats.
Creeper *Strophitus undulatus*	Small streams to large rivers; inhabits a variety of substrates and flow conditions.

animal residues, and mud. The eastern floater is one of the few species that can thrive in gyttja because of its light thin shell and tendency to "float" on soft sediments. In a small lake in southeastern Massachusetts, mussel diversity and abundance declined precipitously at depths of 16-22 feet, roughly corresponding with the position of the epilimnion (Nedeau and Low 2008b), which is the dividing line between warm surface water and cold bottom water. The study estimated that more than 95 percent of habitat for three state-listed species occurred at depths less than 20 feet. Other studies have also documented low mussel abundance in deeper portions of lakes (Fisher and Tevesz 1958, Ghent *et al*. 1978, Strayer *et al*. 1981).

Freshwater mussels do not occur in small wetlands or ephemeral habitats such as headwater streams, swamps, bogs, or marshes. However, swamp and marsh-like habitats connected to larger aquatic habitats may support habitat generalists such as the eastern elliptio or eastern floater. Mussels are rarely found in high-gradient mountain streams that have flashy flows, rocky habitat (especially bedrock), and experience wintertime ice scour. Mussels usually do not inhabit small ponds unless they are connected to larger aquatic habitats that support mussels, or unless humans stocked mussels or host fish that were infected with glochidia.

II. HABITAT AND DISTRIBUTION IN THE WATERSHED

This section describes the distribution of mussels at different spatial scales (portions of a river, entire rivers, entire watersheds) in the Connecticut River watershed based on specific habitat requirements (Table 2) as well as biology, fish distribution, and other environmental constraints.

MAJOR HABITAT TYPES AND SPECIES ASSEMBLAGES

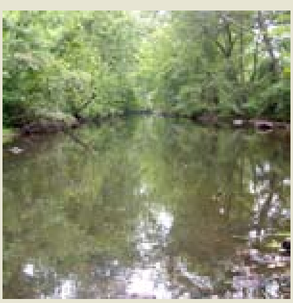
Large aquatic habitats that support freshwater mussels can be characterized according to major habitat features and the species (mussels and fish) that occur there. This simple classification can help to categorize watersheds and portions of rivers, and identify those areas most likely to support particular species. The major stream habitat types described below often overlap and some rivers exhibit features of two or more major habitat types.


Lower Salmon River, Connecticut

Large tidal river (LTR): LTR habitat includes the tidal freshwater portions of the lower Connecticut River and its coves almost to Windsor Locks, Connecticut. It extends into the mouths of major tributaries; the best examples are the lower Eightmile River and lower Salmon River. Aside from twice-daily tides, prominent habitat features include fairly deep water, fine sediments, and extensive submerged aquatic vegetation. Mussel species most characteristic of this habitat are the tidewater mucket, alewife floater, and eastern pondmussel. Other species consistently found in these habitats are the eastern elliptio, eastern lampmussel, and eastern floater; these three habitat generalists occur throughout the watershed. The fish community includes seasonally high abundances of anadromous species (such as American eel, river herring, and American shad), striped bass, and a suite of warmwater species such as yellow perch, white perch, carp, largemouth bass, smallmouth bass, bluegill, and spottail shiner.


Connecticut River, Massachusetts

Large southern river (LSR): LSR habitat includes the non-tidal portion of the mainstem Connecticut River from Windsor Locks, Connecticut, to southern New Hampshire. It extends into coves, oxbows, and large low-gradient tributaries such as the lower Farmington River and Westfield River. These rivers tend to be wide (75-200 meters), with fairly deep water, fine sediments, and fairly extensive floodplains (at least historically). Aside from the eastern elliptio that is highly abundant, the mussel species most characteristic of this habitat are the yellow lampmussel and alewife floater. The eastern floater, eastern lampmussel, tidewater mucket, and eastern pondmussel rarely occur in LSR portions of the Connecticut River mainstem, but these species do occur in tributaries. Prevalent fish include American eel, lamprey eel, American shad, river herring, striped bass, smallmouth bass, and a variety of other warmwater fish species. The Holyoke Dam, Turners Falls Dam, Vernon Dam (each on the Connecticut River), Rainbow Dam (Farmington River), and DSI Dam (Westfield River) influence this habitat and the distribution of fish.


Fort River, Massachusetts

Small southern lowland river (SSLR): SSLR habitat includes small to medium-sized tributaries from southern Connecticut to southern New Hampshire. Streams range in size from less than five meters wide up to 75 meters wide. These areas are usually transitional between larger habitats (LTR and LSR) and smaller upland habitats (SUR) and therefore provide tremendous habitat diversity. All mussel species have the potential to occur in SSLR habitats; species most characteristic include the dwarf wedgemussel, triangle floater, creeper, and eastern pondmussel. Areas near the transition between LTR/LSR and SSLR may include species such as the alewife floater, tidewater mucket, and yellow lampmussel. Areas near the transition between SSLR and SUR may include the eastern pearlshell and brook floater. The eastern elliptio, eastern lampmussel, and eastern floater almost always occur in SSLR habitats. SSLR habitats are usually accessible to anadromous species such as river herring, American eel, and lamprey eels. Other common fish species include smallmouth bass, white sucker, fallfish, stocked trout (brown, rainbow, and brook), redbreast sunfish, brown bullhead, tessellated darter, blacknose dace, longnose dace, and common shiner.


Connecticut River, New Hampshire

Large northern river (LNR): LNR habitat is physically similar to LSR habitat, with wide channels (75-200 meters), deep water, fine sediments, and fairly extensive floodplains (at least historically). Submerged aquatic vegetation is often abundant in shallow areas that receive ample sunlight. Large northern rivers without these habitat characteristics (such as the White River, Ammonoosuc River, and Sugar River) fall under the SUR description. LNR habitat mainly occurs in the Connecticut River between the Bellows Falls Dam and North Stratford, New Hampshire, including its coves and backwaters. It extends into low-gradient portions of large tributaries upstream to the fall line, including the Black River, Ottauquechee River, and Johns River. Species characteristic of this habitat include the dwarf wedgemussel, triangle floater, creeper, and eastern lampmussel. The eastern elliptio and eastern floater also occur here. LNR habitats lack four species that occur in LSR and LTR: alewife floater, tidewater mucket, yellow lampmussel, and eastern pondmussel. Dominant fish species include smallmouth bass, largemouth bass, white sucker, walleye, yellow perch, sunfish, tessellated darter, chain pickerel, and common shiner.


Sandy Brook, Connecticut

Small upland river (SUR): SUR habitat is the most common stream habitat in the Connecticut River watershed but supports the lowest diversity of mussels. These streams tend to have a fairly high gradient; confined channels with a variety of riffles, pools, and runs; cool water temperatures; and forested uplands. Rocky substrates—particularly gravel, cobble, boulder, and bedrock—are typical of SUR habitats; depositional areas with finer substrates tend to be less prevalent. These rivers tend to have lower nutrient levels and higher acidity than other rivers. The environmental conditions described are more important than stream size; many large tributaries (e.g., White River, Ammonoosuc River, Deerfield River, Passumpsic River, Sugar River, Millers River) fall into this category because their rocky conditions and steep gradients preclude mussels that might otherwise prefer rivers of that size. Of all the major habitat types, SUR habitats are most likely to support few or no mussels due to challenging environmental conditions. Mussel species that may be found in SUR habitats include the eastern elliptio, eastern pearlshell, triangle floater, creeper, brook floater, and sometimes the dwarf wedgemussel. Dominant fish species include trout (brook, brown, and rainbow), Atlantic salmon, blacknose dace, longnose dace, slimy sculpin, white sucker, redbreast sunfish, and fallfish.


Sunapee Lake, New Hampshire
Midge Eliassen

Lakes and Ponds: Lakes in the Connecticut River watershed are poorly surveyed. In general, seven species may occur in lakes. Three species (tidewater mucket, eastern pondmussel, and alewife floater) have a coastal affinity and are usually restricted to southern lakes that have (or once had) a direct unimpeded connection to rivers with anadromous fish populations. Three species (eastern elliptio, eastern floater, and eastern lampmussel) tend to be more widely distributed in lakes. Most northern oligotrophic (nutrient-poor) lakes are likely to support the eastern elliptio and eastern floater. The triangle floater is also infrequently found in lakes and impoundments, but since few of these habitats have been surveyed in the watershed, its lake distribution is not well understood. Lakes contribute little to the number of species in watersheds because all lake species also occur in rivers. A large proportion of a watershed's mussel diversity and biomass may reside in lakes if the primary rivers provide poor mussel habitat. Mussel densities are often higher in lakes than in rivers.

Watershed-wide Patterns

Of the 12 species that occur in the Connecticut River watershed, eight have a broad geographic range (though discontinuous for some species). Of these, six are considered host generalists: eastern elliptio, eastern lampmussel, eastern floater, triangle floater, brook floater, and creeper. Five of these species (all but the brook floater) are the most widespread species in the watershed. Two mussel species—dwarf wedgemussel and eastern pearlshell—with a broad geographic range are host specialists but their hosts are widely distributed. The brook floater and dwarf wedgemussel are rare; their rarity is not easily explained because their host fish are far more widely distributed than they are, and their preferred habitats are prevalent throughout the Connecticut River watershed.

Four of the 12 species that occur in the watershed are confined to southern areas: yellow lampmussel, tidewater mucket, eastern pondmussel, and alewife floater. The alewife floater is a habitat generalist but a host specialist and its distribution is tied to the distribution of alewife, blueback herring, and American shad. The tidewater mucket and eastern pondmussel are habitat generalists within small to large coastal rivers and lakes (Strayer 1987, Nedeau *et al.* 2000). The yellow lampmussel is currently confined to the lower Connecticut River mainstem, suggesting a connection to migratory fish, but its distribution in other northeastern watersheds suggests otherwise. For example, it is found in upper portions of the Penobscot River watershed in Maine and the Susquehanna River in New York (Nedeau *et al.* 2000, Strayer and Fetterman 1999). The rarity of these species—particularly yellow lampmussel and tidewater mucket—is probably related more to human influence (habitat modification and pollution) than to specific habitat requirements or host fish. This is because these species occur mainly downstream of the watershed's largest cities where pollution has been the most acute.

Freshwater mussel assemblages (used here to refer to species composition) in the Connecticut River and its tributaries follow predictable patterns. Mainstem assemblages vary with proximity to tidal influence and distance from the mouth. Tributary assemblages depend on proximity to tidal influence, location of the tributary within the larger Connecticut basin, stream size, and landscape features such as topography and geology. Several points can be made about the distribution of freshwater mussels on a watershed scale (Table 3, Figure 4):

- Highest numbers of species occur in tributaries of varying sizes in the southern half of the watershed. Thirty-six percent of major tributaries or mainstem segments support more than five species, and 71 percent of these are in Connecticut and Massachusetts.
- Minor tributaries and many major tributaries in Vermont and New Hampshire support very low numbers of species. Of major tributaries with five or fewer species, 70 percent are in Vermont and New Hampshire.
- All segments of the Connecticut River support fairly high numbers of species or endangered species that may be uncommon in nearby tributaries.
- The number of species in the three portions of the mainstem Connecticut River are comparable (lower (CT) = 8, middle (MA) = 7, upper (NH/VT) = 8) but only four species overlap: eastern elliptio, alewife floater, eastern floater, and eastern lampmussel.
- No single waterbody contains all species known from the watershed; rivers with the highest number of species include the Farmington River (11), Connecticut River (11), and Salmon River (10).
- Lakes are not well surveyed. Watersheds with lakes probably have at least two species (eastern elliptio and eastern floater) even if these have not been found in the principal rivers and therefore are not listed in Table 3.

Table 3. Species and habitats within major segments of the Connecticut River and its major tributaries. A major tributary is defined as having a drainage area larger than 30 square miles. Watersheds with the most recent and complete mussel data are shaded; those rivers not shaded have not been well surveyed and additional species might occur there. Species abbreviations are comprised of the first letter of the genus and species name, for example, MM = *Margaritifera margaritifera* (eastern pearlshell). See Table 2 (page 15) for these names.

	Species													Stream
Tributary or Segment	MM	EC	AU	AV	AH	PC	AI	SU	LN	LO	LR	LC	#Taxa	Habitats
Farmington River (CT/MA)	x	x	x	x	x	x	x	x	x	x	x		11	LSR, SSLR, SUR
Connecticut River (All)	x	x	x		x	x	x	x	x	x	x	x	11	ALL
Salmon River (CT)	x	x	x	x		x	x	x	x	x	x		10	LTR, SSLR, SUR
Mill River (Northampton, MA)	x	x	x		x	x	x	x	x		x		9	SSLR, SUR
Fort River (MA)	x	x	x		x	x	x	x	x		x		9	SSLR, SUR
Mill River (Hatfield, MA)	x	x	x		x	x	x	x	x		x		9	SSLR, SUR
Eightmile River (CT)	x	x	x	x		x	x	x	x		x		9	LTR, SSLR, SUR
Lower Connecticut River (CT)		x	x			x	x		x	x	x	x	8	LTR, LSR
Chicopee River (MA)	x	x	x	x		x	x	x			x		8	LSR, SSLR, SUR
Ashuelot River (NH)	x	x	x		x	x	x	x			x		8	SSLR, SUR
Bachelor Brook (MA)		x	x	x		x	x	x	x		x		8	SSLR, SUR
Upper Connecticut River (NH/VT)	x	x	x		x	x	x	x			x		8	LSR, LNR, SUR
West River (VT)	x	x	x	x		x		x			x		7	SSLR, SUR
Westfield River (MA)	x	x	x			x	x	x			x		7	LSR, SSLR, SUR
Scantic River (CT/MA)	x	x	x			x	x	x			x		7	SSLR, SUR
Middle Connecticut River (MA)		x	x			x	x			x	x	x	7	LSR
Black River (VT)		x	x		x	x		x			x		6	LNR, SUR
Johns River (NH)		x	x		x	x		x			x		6	SUR
Mill River (Amherst, MA)	x	x	x			x			x				5	SSLR, SUR
Ottauquechee River (VT)		x			x	x		x			x		5	LNR, SUR
Stony Brook (CT)		x	x		x	x		x					5	SSLR, SUR
Sugar River (NH)	x	x		x		x		x					5	SUR
Mascoma River (NH)	x	x	x			x		x					5	SUR
Upper Ammonoosuc River (NH)	x	x	x			x		x					5	SUR
Millers River (MA)		x	x			x	x	x					5	SUR
Deerfield River (MA/VT)	x	x				x	x						4	SUR
Passumpsic River (VT)	x	x				x		x					4	SUR
Nulhegan River (VT)	x	x	x			x							4	SUR
Sawmill River (MA)	x	x				x							3	SSLR, SUR
Cold River (NH)		x				x							2	SUR
Mattabesset River (CT)		x				x							2	SSLR, SUR
Stevens River (VT)		x				x							2	SUR
Williams River (VT)		x									x		2	SUR
Israel River (NH)	x												1	SUR
White River (VT)		x											1	SUR
Ompompanoosuc River (VT)		x											1	SUR
Wells River (VT)						x							1	SUR
Ammonoosuc River (NH)													0	SUR
Fall River (MA)													0	SUR
Hockanum River (CT)													0	LTR, SSLR, SUR
Indian Stream (NH)													0	SUR
Little Sugar River (NH)													0	SUR
Mill Brook (VT)													0	SUR
Mohawk River (NH)													0	SUR
Oliverian Brook (NH)													0	SUR
Saxtons River (VT)													0	SUR
Waits River (VT)													0	SUR
Total	22	35	24	7	11	33	17	23	10	5	20	3		

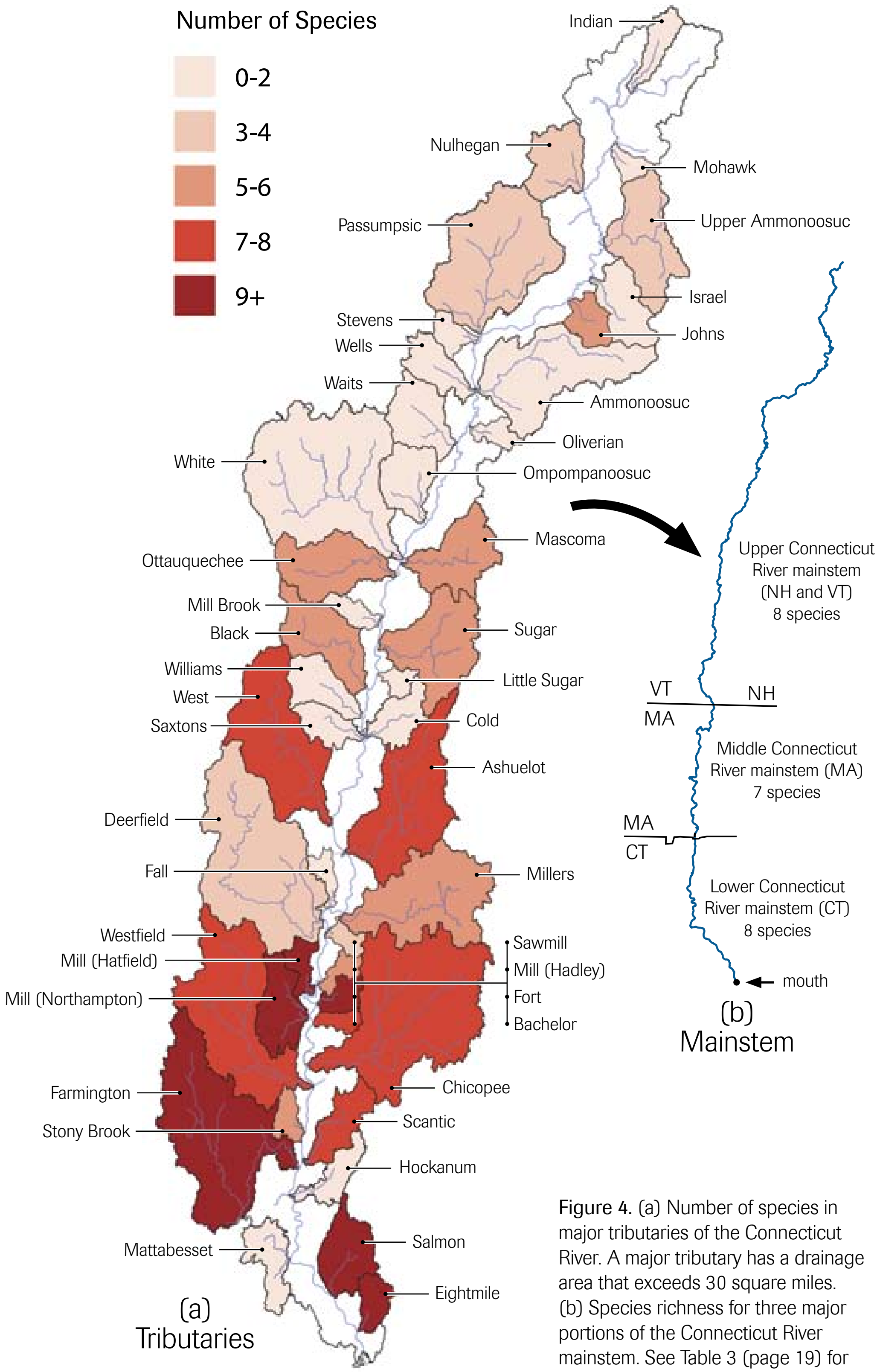


Figure 4. (a) Number of species in major tributaries of the Connecticut River. A major tributary has a drainage area that exceeds 30 square miles. (b) Species richness for three major portions of the Connecticut River mainstem. See Table 3 (page 19) for numeric data.

The broad flat valley of the Pioneer Valley in Massachusetts was once the bottom of Lake Hitchcock, a massive lake that formed as glaciers retreated from southern New England. Streams that now flow through these ancient lakebed soils have many characteristics that freshwater mussels prefer, and therefore these streams have some of the most diverse freshwater mussel communities in the entire watershed. Patrick Zephyr

Two factors explain much of the natural variation in mussel distribution at a watershed scale. The first is proximity to the ocean. Four species are restricted to southern portions of the watershed. The yellow lampmussel only exists in the mainstem Connecticut River from Windsor Locks, Connecticut, upstream to the Turners Falls Dam in Massachusetts. The tidewater mucket is currently known from the Connecticut River and three of its tributaries in Connecticut. The alewife floater and eastern pondmussel frequently occur in small lowland rivers in Connecticut and southern Massachusetts, and less frequently in lakes. These four species contribute largely to the higher diversity observed in the southern part of the watershed.

The second factor that contributes to watershed-wide patterns of mussel distribution is the combination of geology and topography. Streams flowing through low-gradient valleys with alluvial (river-deposited) or glacial outwash soils tend to support a higher number of species than streams flowing through more confined, high-gradient valleys with rocky soils. Much of the lower Connecticut River has a broad flat valley whose soils were deposited by rivers and post-glacial lakes, including Lake Hitchcock that once stretched from present-day Rocky Hill, Connecticut, to Bath, New Hampshire and far up many tributaries. Tributaries that now flow through these alluvial and lakebed soils before reaching the Connecticut River possess many attributes that are favorable to mussels and fish: ample fine sediment, stable hydrology, strong groundwater influence, naturally rich in nutrients, and diverse habitat. There are fewer natural dispersal barriers in many of these rivers, and proximity to the Connecticut River is important for maintaining fish diversity and migration between neighboring watersheds.

In contrast, much of the upper Connecticut River has a narrow valley with steep sides and rocky soils. Tributaries in the upper valley tend to be shallow, with rocky substrates, flashy flows, nutrient-poor acidic water, and abrasive conditions. These conditions often extend all the way to the confluence with the Connecticut River, leaving no room for mussels to inhabit these watersheds. Nearly all tributaries in the northern watershed that support high species

TWO VERY DIFFERENT NEIGHBORS


Johns River

The Israel River (top) and Johns River (bottom) are small neighboring watersheds only seven miles apart in northern New Hampshire. The Israel River supports almost no freshwater mussels; fewer than five individual animals (all eastern pearlshell) have been found in it or its tributaries. The Johns River, the smaller of the two rivers, supports six species and densities as high as 100 animals per square meter. Why are these rivers so different? Aerial photographs provide clues. The Israel River is a highly dynamic river with fast water, rocky substrates, and moderate to severe bank erosion near its confluence with the Connecticut River. Sandy point bars are evident on the insides of all its river bends (arrows), indicating a high degree of erosion and sedimentation. The large alluvial fan, or sediment deposit, at the mouth of the river is another clue about its harsh environmental conditions. The Johns River flows through a broad wetland area before entering the Connecticut River; these wetlands help to slow its flow and create a fairly deep and stable stream channel. No alluvial fan exists at the mouth of the Johns River because its sediment load was captured and dispersed in wetlands further upstream. In many ways, the lower Johns River resembles the SSLR habitats of southern watershed. Conditions found in the Johns River are somewhat rare in the upper Connecticut River watershed, which why the upper watershed supports so few mussels in its tributaries. Aerials: USDA-Natural Resources Conservation Service

A short portion of tiny Hop Brook (left), a tributary of the Fort River in Massachusetts, supports more mussel species than many of the largest tributaries of the northern Connecticut River combined. Paul Stream (right), a small tributary located in northern Vermont, is typical of high-gradient northern tributaries that support few or no mussel species. Ethan Nedeau

richness join the Connecticut River in a broad portion of the valley (e.g., Black River and Johns River), or have lengthy low-gradient reaches somewhere in the watershed (e.g., Sugar River, Ashuelot River). Mussels are scarce and largely absent from most high-gradient rivers in New Hampshire and Vermont (Fichtel and Smith 1995, Ferguson 1999, Nedeau 2006b, 2006c).

Within Rivers and Tributary Watersheds

The distribution of mussels within individual rivers or tributary watersheds also follows fairly predictable patterns. The overall watershed context (described above) is important because it largely determines the pool of potential species. For example, a large southern tributary that provides potential for LSR, SSLR, and SUR assemblages is very different from a small northern tributary that only provides potential for SUR assemblages, even though portions of these rivers might have similar depths, substrates, thermal regimes, and upland characteristics.

The best (i.e., high number of species) freshwater mussel locations in the Connecticut River watershed have mostly been in low-gradient stream reaches with relatively deep water and stable flows. All of these locations included the SSLR assemblage but were transitional with other assemblages, particularly LSR and SUR. The only species that has not been found in such a location is the yellow lampmussel, which only occurs in a few locations in the mainstem Connecticut River that support a low diversity of species (Nedeau 2005a). This may be largely due to human influence and an unnaturally restricted distribution rather than a unique habitat preference, since the yellow lampmussel occurs in high-diversity assemblages (among

The Salmon River in East Haddam, Connecticut. This tidal portion of the Salmon River is downstream of the Leesville Dam and near Salmon Cove. It exhibits features of LTR, SSLR, and SUR habitats. Nine mussel species occur together in this location, including the only known location in the entire Connecticut River watershed where tidewater muckets and eastern pearlshell co-occur. Ethan Nedeau

SUR species) in Maine and the upper Susquehanna in New York (Strayer and Fetterman 1999, Nedeau *et al.* 2000).

No species have habitat requirements so unique that they would not occur in the same place as other species. There are many examples where every species that occurs in a tributary (even very large tributaries) occupy the same areas of a stream. There are three examples where nine species have been found within one mile of each other in one river—the Farmington River and Salmon River in Connecticut and the Fort River in Massachusetts (Nedeau 2005b, Nedeau 2005c, Nedeau 2008). Locations with such high diversity are rare because they require a unique combination of stable habitat, diverse fish assemblages, minimal human disturbance, and are within the geographic range of a large number of species. Humans have altered many of those potential locations by building dams or destroying habitat.

All mussel habitats that fall somewhere in between the "best" (low-gradient stream reaches with relatively deep water and stable flows) and "worst" (high-gradient and rocky headwater streams) may or may not be inhabited by mussels and diversity will vary. There is no general trend applicable to all watersheds—mussel distribution in specific locations will depend on habitat types and the species that could occur in that watershed. Natural features that influence mussel distribution are stream size; geology and soils; topography; number and proximity of lakes, ponds, tributaries, and wetlands (which can stabilize flows); groundwater influence; water chemistry; and many of the habitat features described in this chapter.

Diversity is usually highest in lower and middle reaches of a watershed, especially in areas transitional between major habitat types. The most striking example is in the lower Salmon River near the Leesville Dam, where the river undergoes a short transition from a shallow upland river to a large tidal river. Nine species occupied a portion of the river less than a quarter-mile long. This is the only place in the entire Connecticut River watershed where the eastern pearlshell (an SUR species) and tidewater mucket (an LTR species) co-occur (Nedeau 2005c). There are several instances of diverse mussel populations in upper portions of watersheds whose middle or lower portions are less diverse, and the mussel community within these high-diversity areas often includes the brook floater (e.g., Chicopee River watershed, Sugar River, Salmon River, Farmington River).

Strong source populations can influence the distribution of a species within a waterbody. Source populations exhibit traits such as a higher population density, even age structure, consistent recruitment, and high adult survival. Source populations tend to be self-sustaining and resilient to some of the problems that plague low-density populations, and have the potential to spread into nearby habitats that might not seem optimal for the species. This may be due to high reproductive output and a large number of infected host fish that emigrate to new areas. The presence, number, and distance between source populations of any species will greatly influence their distribution and viability within a watershed, and their ability to recover from disturbance. Likewise, a lack of nearby source populations, or poor connectivity with source populations, may be the most important reason why mussels are absent from portions of rivers with otherwise ideal habitat. Identifying and protecting source populations is one of the most important challenges to freshwater mussel conservation in the Connecticut River watershed.

When species that are not predicted to occur in a river are discovered, this usually provides valuable insight into habitat preference for the species. Biologists are continually tweaking their understanding of species as they explore new habitats and find species in unexpected places. In some cases, the presence of species in a river where they are not predicted to occur is due to human intervention, such as habitat modification or stocking. For example, the alewife floater occurs in the Ashuelot River upstream of several impassable dams and far beyond the reach of its migratory fish hosts (Nedeau 2004a). Since the mid-1990s, shad have been transported, via truck, from the Connecticut River in Massachusetts and placed in the Ashuelot River to provide a small sport fishery. Some shad must have been infected with glochidia of the alewife floater. The juveniles found the Ashuelot River to their liking and grew into adults. Elsewhere, the eastern floater has been introduced into many small man-made ponds either purposefully (by stocking mussels) or accidentally (by stocking host fish that were infected with glochidia).

III. DISTRIBUTION AND HUMAN BIAS

There is no information on the distribution and condition of mussel populations prior to human disturbance. Humans have lived in the watershed for thousands of years, and European colonization that began 400 years ago ushered in a period of unprecedented destruction of aquatic, riparian, and upland habitats. No rivers in the watershed were untouched by the myriad threats that humans wrought. Humans have greatly altered the distribution of freshwater mussels in the watershed, although no native mussels have been altogether eliminated. Analyses of natural distribution patterns are no longer possible. Any apparent patterns and variation must be interpreted cautiously, weighing natural causes and potential human influence.

Some of the more interesting questions about mussel distribution relate to why species are, or are not, in a particular location. Answers to these questions are often biased by incomplete information and subjective interpretations of habitat and history. When species that are predicted to occur in a river or specific location are not known to occur, there are three possible explanations:

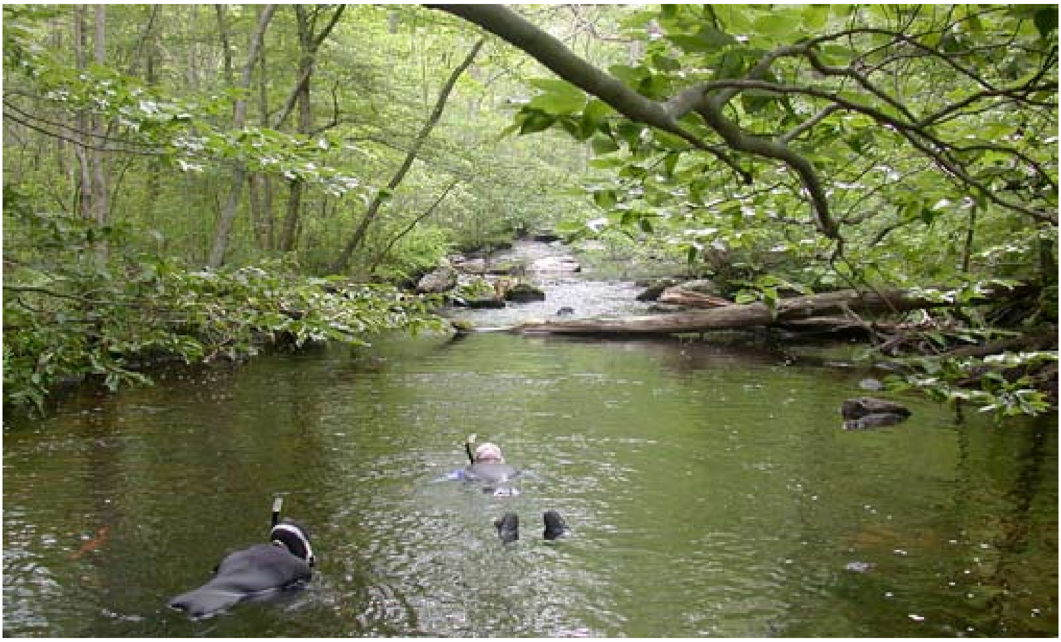
1. It has not been discovered yet or historic populations have not been rediscovered.
2. Our understanding of its habitat and potential distribution was incorrect.
3. The species has been eliminated.

Often the first two explanations are discounted and analysis focuses on why a species has been eliminated. It can sometimes take a tremendous amount of time and effort to find rare species in a waterbody, and not finding them does not mean they are absent (Strayer and Smith 2003). One cannot demonstrate absence—any claim of absence is conditional on effort expended, survey conditions, and how the survey was designed. In some cases, there is doubt that historic records were accurate and whether a species ever existed in a waterbody. This may be due to misidentifications, poorly kept records, or confusion about how nomenclature has changed.

Arthur Clarke surveyed much of the mainstem Connecticut River and published an article in the journal *The Nautilus* titled, "Unionidae of the upper Connecticut River: a vanishing resource" (Clarke 1986). In the article he stated that no live freshwater mussels occurred in a 100-mile portion of the Connecticut River from the First Connecticut Lake and Lake Francis downstream to the mouth of the Ammonoosuc River, and that from Hartland to the Massachusetts border, the fauna had been reduced to a single species. He cited the effects of dams and pollution from the pulp and paper industry as probable causes. He concluded the article with the statement, "*Clearly the mussel fauna of the whole Connecticut River now survives in only a very few remnant communities. Conservationists and government agencies are urged to help in reversing this unfortunate trend toward extinction.*"

Similar reports created a sense of urgency to protect and restore aquatic ecosystems and to extend state and federal protections to non-game species such as mussels. This resulted in support for conducting basic surveys, especially for species that were considered on the brink of extinction. In recent years, large populations of species once considered eliminated (or nearly so) have been found throughout the Connecticut River and many of its tributaries. The three largest populations of dwarf wedgemussels in the world, including large populations of five other species, are now known to occur in the portion of the Connecticut River that Clarke said was nearly devoid of mussels only 25 years ago. Though it is tempting to credit this and other such examples (there are many) to recovery, it is more likely that original surveyors lacked the resources, time, or training to survey these waters thoroughly. Even as recently as 2005, dwarf wedgemussels were thought to have been eliminated from the Connecticut River in between the Wilder Dam and Fifteen Mile Falls, but SCUBA surveys in 2005 and 2006 documented what is perhaps one of the three largest populations in the world in an 18-mile mile portion of the river (Nedeau 2005d, 2006d).

There are several possible reasons why new populations are being discovered and historic populations are being rediscovered. There is a greater amount of funding for professional surveyors and a greater need to document rare species to fulfill objectives of state and federal endangered species laws. Survey equipment and techniques are much improved and more widely available, especially SCUBA for surveying in deep water. Biologists have a better understanding of habitat requirements of each species and where to look for them. Conditions are now healthier for surveyors, especially cleaner water and less concern for bacterial pathogens and toxins. Few people would have dared to spend countless hours looking for freshwater mussels in the Connecticut River at a time when it was considered America's best-landscaped sewer.



Ethan Nedeau and Carson Mitchell survey mussels in the Jeremy River in Connecticut, a tributary of the Salmon River. Careful surveys are essential for finding and protecting rare species. Paul Low

Our understanding of freshwater mussel distribution in the Connecticut River watershed is a work in progress; a goal of producing this publication is to raise awareness and compel people to survey new areas and contribute to conservation.

IV. SUMMARY

- Mussels occur in most large permanent aquatic habitats, including streams, rivers, lakes, and ponds. All 12 of the watershed's species occur in rivers but only seven of these may also occur in lakes and ponds.
- Rivers with stable substrates, stable flow, low-gradient reaches with relatively deep water, ample fine sediment, and diverse fish populations support the greatest number of species.
- Each of the major habitat types described in this chapter support regionally-important mussel assemblages, but the greatest number of species occur in SSLR habitats in the southern half of the watershed, and in rivers that provide characteristics of more than one habitat type (such as LTR-SSLR, LSR-SSLR, and SSLR-SUR).
- Thirty-six percent of major tributaries or mainstem segments support more than five species, and 71 percent of these are in Connecticut and Massachusetts. Of major tributaries with five or fewer species, 70 percent are in Vermont and New Hampshire.
- Three rivers with the highest diversity include the Farmington River (CT and MA; 11 species), Connecticut River (entire; 11 species), and Salmon River (CT; ten species).
- Analyses of natural distribution patterns are no longer possible because of four centuries of human influence that has eliminated species from portions of their native range.
- Recent surveys have discovered new populations and rediscovered populations once thought to be eliminated. Yet most of the watershed has not been surveyed and it is likely that populations of endangered species are awaiting discovery and protection.