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Freshwater Mussels of Virginia (Bivalvia: Unionidae): An Introduction to Their Life History, Status and Conservation

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ABSTRACT

With 77 species, the mussel fauna of Virginia is one of the most diverse in the United States. Fifty-four species or ~70% of the state's mussel fauna occurs in the rivers of the upper Tennessee River basin, especially in the Clinch and Powell rivers of southwestern Virginia. An additional 23 species reside in rivers of the Atlantic Slope, including the Potomac, Rappahannock, York, James and Chowan basins, and in the New River, a major tributary to the Ohio River. A total of 39 species or 51% of Virginia's mussel fauna is listed as federally endangered, state endangered or state threatened. Excess sediment, nutrients and various types of pollutants entering streams from agriculture and industries are the main drivers of imperilment. Freshwater mussels reproduce in a specialized way, one that requires a fish to serve as a host to their larvae, called glochidia, allowing the larvae to metamorphose to the juvenile stage. This extra step in their life cycle uniquely defines mussels among bivalve mollusks worldwide, in freshwater or marine environments, and adds significant complexity to their reproductive biology. Further, they utilize "lures" that mimic prey of fishes to attract their host. Mussels rely on their fish host to provide them with long-distance dispersal and nutrition while they are glochidia, which are small (<0.5 mm) ecto-parasites that attach and encyst on the gills and fins of fishes, typically taking weeks to months to metamorphose, excyst and then drop-away as similar-sized juveniles to the stream bottom where they grow into adults. Adult mussels are mostly sedentary animals living in the benthos, i.e., the bottom of streams and lakes, typically in mixed substrates of sand, gravel and fine sediments. Mussels generally filter suspended organic particles <20 μm from the water column but can also filter deposited particles through the shell-gap when burrowed in the benthos. Further, the adults of most species are long-lived, regularly living 25-50 years or longer in freshwater environments throughout North America. Conservation of freshwater mussels in Virginia will require citizens, non-governmental organizations, local, county, state and federal governments to apply their resources to five main areas: (1) water quality monitoring and regulation enforcement, (2) restoration of stream habitat, (3) restoration of mussel populations, (4) educating the public about the importance and status of mussels, and (5) monitoring and research to understand why mussels are declining and what are the best ways to protect them. Sustained long-term efforts in these five areas offers the greatest potential to conserve freshwater mussels throughout Virginia.

INTRODUCTION

With 77 documented species, the mussel fauna of Virginia is one of the most diverse in the United States — only the states of Alabama (178 species), Tennessee (129 species), Georgia (123 species), Kentucky (104 species) and Mississippi (84) have more species than Virginia (Neves et al. 1997; Paramalee and Bogan 1998; Williams et al. 2008). Virginia's mussel fauna spans two major geographic regions, the southwest region where rivers drain to the Mississippi River and ultimately to the Gulf of Mexico, and the eastern region where rivers drain to the Chesapeake Bay and ultimately to the Atlantic Ocean (Figure 1). The species occurring in these two regions generally are restricted to the major river basins of these areas. Hence, their distributions do not overlap and distinct morphological and biological differences exist between the regional faunas. These differences are in part due to the varied ecological and geological conditions that exist throughout Virginia, and the long-term separation of the Atlantic Slope and Mississippi River basin faunas.

Nationally, freshwater mussels are considered one of the most imperiled groups of animals in the country, with 213 species (72 %) listed as endangered, threatened, or of special concern (Williams et al. 1993). Virginia's fauna is no exception, with more than 50% of its species listed at the federal or state level (Figure 2) (Terwilliger 1991). Most of the endangerment is caused by habitat loss and destruction due to sedimentation, water pollution, dredging, and other anthropogenic factors (Neves et al. 1997). Many of these listed species occur in southwestern Virginia in the Clinch, Powell and Holston rivers, headwater tributaries to the Tennessee River (Figure 1). However, nearly all river systems in the state have mussel species of conservation concern. The rate of mussel imperilment in Virginia and nationally is increasing over time as populations of many species continue to decline and as additional species are listed as endangered by the federal government and state governments.

Population declines and the listing of many mussel species has prompted interest in their conservation (Freshwater Mollusk Conservation Society 2016). State and federal natural resource management agencies, including Virginia Department of Game and Inland Fisheries (VDGIF) and U.S. Fish and Wildlife Service (USFWS), various non-governmental organizations and universities are involved in improving water quality, stream habitat, and increasing abundance and distribution of mussels using population management techniques, such as out-planting hatchery-reared mussels back to native streams, and monitoring populations to determine their status and trends. For example, Virginia Tech, VDGIF and USFWS have been working together to raise mussels in hatcheries and release them to their native streams to build-up populations. Since 2004, this program has released thousands of mussels of numerous species to population restoration sites throughout Virginia.

Most mussels rely on fishes as hosts to metamorphose their larvae to juveniles, and therefore to complete their life cycle. This parasitic relationship uniquely defines

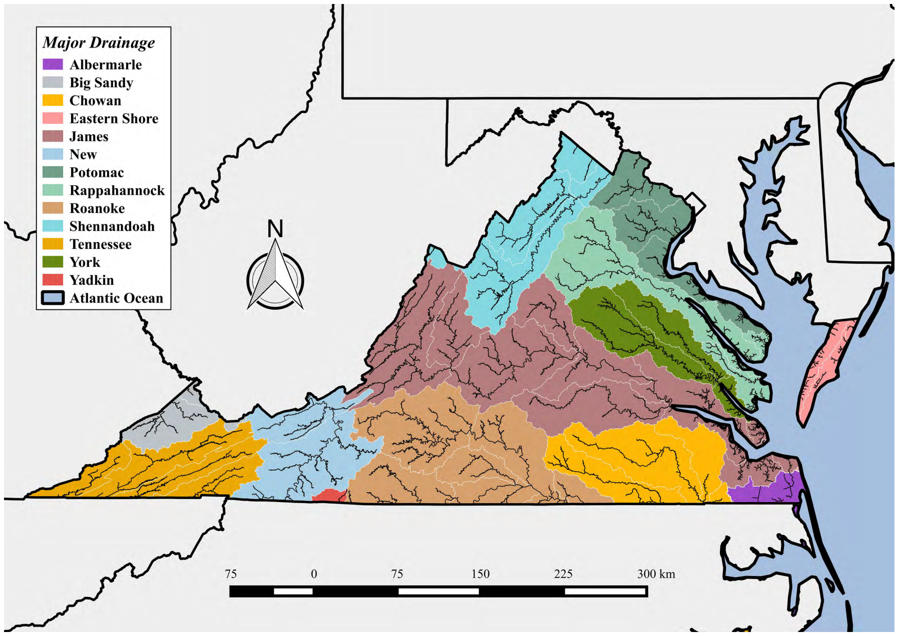

FIGURE 1. Major river drainages of Virginia. Map created by T. Lane, Virginia Tech.

freshwater mussels among bivalve mollusks worldwide, both in freshwater and marine environments. The larvae and newly metamorphosed juveniles are very small, typically less than 0.5 mm long. Hence, these stages are considered weak links in the mussel life cycle, as they are susceptible to loss of host fishes, contaminants in streams, and physical disturbance of stream habitats. However, it is this interaction with fishes that makes mussels unique, and evolutionarily has given rise to some of the most complex and striking mimicry known in the natural world. For students of all ages, mussels are a fascinating portal to understanding streams and the incredible organisms that they contain. Thus, the purpose of this paper is to provide an introduction to the life history, status and conservation of freshwater mussels in Virginia.

METHODS

Occurrence of mussel species in the major river basins of Virginia was determined from publications, reports and personal communications with biologists. However, because mussel surveys and records from the Albemarle, Big Sandy, Eastern Shore and Yadkin basins are sparse to non-existent, species occurrences for these basins were not determined. A mussel species was considered extant in a basin if a live individual was recorded from 1985 to the present. Otherwise, it was considered extirpated or extinct. Species occurrences in the upper Tennessee River basin were determined for the Powell River from Ortmann (1918), Johnson et al. (2012), and Ahlstedt et al. (2016), for the Clinch River from Ortmann (1918), Jones et al. (2014), and Ahlstedt et al. (2016), for the North Fork Holston River from Ortmann (1918), Henley and Neves (1999), and Jones and Neves (2007), for the Middle Fork Holston River from Ortmann (1918),

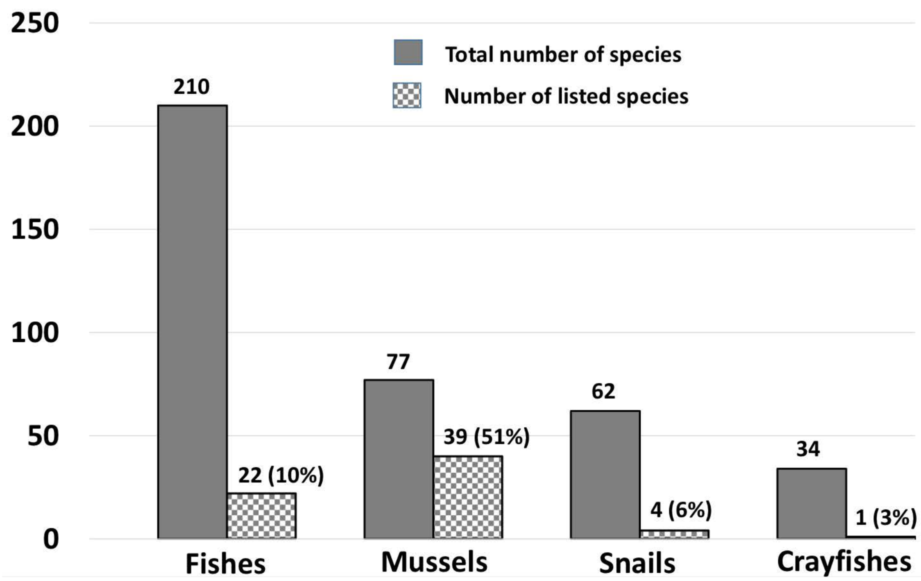

FIGURE 2. Number of species per major aquatic taxon in Virginia. Number of listed species includes species listed as federally endangered, federally threatened, state endangered, and state threatened.

Henley et al. (1999), and Henley et al. (2013), and for the South Fork Holston River from Ortmann (1918) and Pinder and Ferraro (2012). Species occurrences in the New River basin were determined from Pinder et al. (2002). Species occurrences in the major Atlantic Slope river basins were determined for the Roanoke, Chowan, James, York, Rappahannock, and Potomac (including its major tributary the Shenandoah River) river basins from Johnson (1970) and personal communication with VDGIF state malacologist Brian Watson. The legal status of listed species, including federally endangered (FE), federally threatened (FT), federal candidate species (FC), state endangered (SE), state threatened (ST) were accessed from VDGIF's database (last updated on July 18, 2014) and available online at: http://www.dgif.virginia.gov/wildlife/virginiatescspecies.pdf. The number and status of fishes in Virginia was obtained from Jenkins and Burkhead (1993), for snails from Johnson et al. (2013) and for crayfishes based on personal communication with B. Watson. The common and scientific names of freshwater mussels generally follow Turgeon et al. (1998).

RESULTS

A total of 77 mussel species are known from the major river basins of Virginia. Of these, three species (*Epioblasma haysiana*, *E. lenior*, and *Lexingtonia subplana*) and one sub-species (*E. torulosa gubernaculum*) are considered extinct range-wide, and four species (*Anodontoides ferrusacianus*, *Leptodea fragilis*, *L. leptodon*, and *Villosa fabalis*) are considered extirpated from the state, bringing the total extant species in Virginia to 69. From the total species known from the state, 25 are listed as FE, 32 as SE, and six as ST. Since most of the species listed as FE also are listed as SE, the total number of listed mussel species in Virginia is 39, or approximately 51% of the fauna (Figure 2).

The Powell, Clinch and forks of the Holston rivers form part of the upper Tennessee River basin (UTRB), and collectively contain a total of 54 mussel species known from the Virginia sections of these rivers (Table 1). This basin contains the highest diversity of mussel species in the state, especially the faunas of the Clinch and Powell rivers, with 53 and 47 known species, respectively. In the Virginia sections of the Holston, a total of 36 species are known from the North Fork, 22 species from the Middle Fork, and 14 species from the South Fork. Due to the extinction or extirpation of 7 species, a total of 47 species remain extant in the UTRB of Virginia. Again, most of these species occur in the Clinch and Powell rivers, with 46 and 37 extant species, respectively. From the total species known from the UTRB in Virginia, 23 are listed as FE, 29 as SE, and 3 as ST.

The New River flows northwest from North Carolina, through southwestern Virginia, and into West Virginia, where it becomes the Kanawha River just upstream of Charleston, WV. This large, ancient river system has a depauperate mussel fauna of just 12 species (Table 2). Most of the fauna is derived from the Ohio River drainage system, with similarities to the UTRB. However, the pistogrip (*Tritogonia verucossa*), while widespread throughout its range, only occurs in Virginia in the New River. No species that occur in the basin are listed as FE but one species is listed as SE (*Lasmigona holstonia*) and two others as ST (*Lasmigona subviridis* and *T. verucossa*). Further, there are no known mussel species extinctions or extirpations from the basin.

The rivers of the Atlantic Slope of Virginia collectively contain a total of 24 mussel species (Table 3). All species known from the region remain extant, except *L. subplana*, which has not been collected alive in the upper James River basin for decades. The Chowan River basin, specifically its tributary the Nottoway River of Virginia, contains the highest diversity with 20 species, followed by the James River with 19 species. The Roanoke River system has 14 recorded species based on collections in the Virginia section of the Dan River. However, at least five additional species (*Alasmidonta varicosa*, *Elliptio congarea*, *E. fisheriana*, *E. lanceolata*, *Uniomerus carolinianus*) are known from the nearby section of the river and its tributaries in North Carolina. Thus, additional species may occur in the Virginia section of the river.

Two species listed as FE occur in Atlantic Slope rivers of Virginia, *Alasmidonta heterodon* remains extant in the Po River of the upper York River basin and in the Nottoway River, and *Pleurobema collina* is extant in several tributaries to the James River basin and in the Dan and Mayo rivers of the upper Roanoke River basin. Additionally, *Alasmidonta varicosa* (SE) occurs in Broad Run of the Potomac River basin, while *Fusconaia masoni* (ST) occurs in the James River and several river systems to the south and *L. subviridis* (ST) is more broadly distributed, known from all major Atlantic Slope river basins in the state.

TABLE 1. Scientific and common names of freshwater mussel species occurring in major tributaries to the upper Tennessee River basin in Virginia, where FE=federally endangered, SE=state endangered, ST=state threatened and - =no federal or state status, ✓=extant, *=very rare in river, X=known from the system but possibly extinct, EX=known from system but possibly extirpated, and NR=no records of species from river system.

Scientific Name	Common Name	Status	Powell	Clinch	Holston North Fork	Holston Middle Fork	Holston South Fork
Actinonaias ligamentina	Mucket	-	✓	✓	EX	✓	NR
Actinonaias pectorosa	Pheasantshell	-	✓	✓	✓	✓	✓
Alasmidonta marginata	Elktoe	-	✓*	✓*	EX	✓	EX
Alasmidonta viridis	Slippershell	SE	NR	✓*	✓*	EX	EX
Amblema plicata	Threeridge	-	✓	✓	EX	NR	NR
Anodontoides ferrusacianus	Cylindrical papershell	-	EX	NR	NR	NR	NR
Cumberlandia monodonta	Spectaclecase	FE, SE	✓*	✓	NR	NR	NR
Cyclonaias tuberculata	Purple wartyback	-	✓	✓	✓*	✓	NR
Cyprogenia stegaria	Fanshell	FE, SE	EX	✓	NR	NR	NR
Dromus dromas	Dromedary pearlymussel	FE, SE	✓	✓	NR	NR	NR
Elliptio crassidens	Elephantear	SE	✓*	✓*	EX	NR	NR
Elliptio dilatata	Spike	-	✓	✓	EX	✓	EX
Epioblasma brevidens	Cumberlandian combshell	FE, SE	✓	✓	EX	NR	NR
Epioblasma capsaeformis	Oyster mussel	FE, SE	✓	✓	EX	NR	NR
Epioblasma florentina aureola	Golden riffleshell	FE, SE	NR	✓	NR	EX	EX
Epioblasma haysiana	Acornshell	-	X	X	X	NR	NR
Epioblasma lenior	Narrow catspaw	-	X	X	NR	NR	NR
Epioblasma torulosa gubernaculum	Green blossom	FE, SE	X	X	X	NR	NR
Epioblasma triquetra	Snuffbox	FE, SE	✓*	✓	EX	NR	NR

TABLE 1. Continued.

Scientific Name	Common Name	Status	Powell	Clinch	Holston		
					North Fork	Middle Fork	South Fork
Fusconaia cor	Shiny pigtoe	FE, SE	✓*	✓	✓	EX	NR
Fusconaia cuneolus	Finerayed pigtoe	FE, SE	✓	✓	✓	NR	NR
Fusconaia subrotunda	Longsolid	-	✓	✓	EX	NR	NR
Hemistena lata	Cracking pearlymussel	FE, SE	EX	✓	NR	NR	NR
Lampsilis abrupta	Pink mucket	FE, SE	NR	✓	NR	NR	NR
Lampsilis fasciola	Wavyrayed lampmussel	-	✓	✓	✓	✓	✓
Lampsilis ovata	Pocketbook	-	✓	✓	✓	✓	NR
Lasmigona costata	Flutedshell	-	✓	✓	✓	✓	✓
Lasmigona holstonia	Tennessee heelsplitter	SE	✓	✓	✓*	✓	NR
Lemiox rimosus	Birdwing pearlymussel	FE, SE	✓*	✓	EX	NR	NR
Leptodea fragilis	Fragile papershell	ST	EX	EX	NR	NR	NR
Leptodea leptodon	Scaleshell	FE	NR	EX	NR	NR	NR
Ligumia recta	Black sandshell	ST	✓*	✓	NR	EX	NR
Medionidus conradicus	Cumberland moccasinshell	-	✓	✓	✓	✓	✓
Pegias fabula	Littlewing pearlymussel	FE, SE	EX	✓*	✓*	EX	EX
Plethobasus cyphyus	Sheepnose	FE, SE	✓	✓	NR	NR	NR
Pleurobema cordatum	Ohio pigtoe	SE	NR	✓	NR	NR	NR
Pleurobema oviforme	Tennessee clubshell	-	✓*	✓	✓	✓	✓
Pleurobema rubrum	Pyramid pigtoe	SE	NR	✓	NR	NR	NR

TABLE 1. Continued.

Scientific Name	Common Name	Status	Powell	Clinch	Holston		
					North Fork	Middle Fork	South Fork
Pleuronaia barnesiana	Tennessee pigtoe	-	✓*	✓	✓	✓	EX
Pleuronaia dolabelloides	Slabside pearlymussel	FE, SE	✓*	✓	✓	✓	NR
Potamilus alatus	Pink heelsplitter	-	✓*	✓	NR	NR	NR
Ptychobranchus fasciolaris	Kidneyshell	-	✓	✓	✓	✓	NR
Ptychobranchus subtentum	Fluted kidneyshell	FE, SE	✓	✓	✓	✓	EX
Quadrula cylindrica strigillata	Rough rabbitsfoot	FE, SE	✓	✓	EX	NR	NR
Quadrula intermedia	Cumberland monkeyface	FE, SE	✓	EX	EX	NR	NR
Quadrula pustulosa	Pimpleback	ST	✓*	✓	NR	NR	NR
Quadrula sparsa	Appalachian monkeyface	FE, SE	✓*	✓*	NR	NR	NR
Strophitus undulatus	Creeper	-	✓*	✓*	✓*	NR	NR
Toxolasma lividum	Purple lilliput	SE	EX	✓*	✓*	NR	NR
Truncilla truncata	Deertoe	SE	✓*	✓*	NR	NR	NR
Villosa fabalis	Rayed bean	FE, SE	NR	EX	EX	NR	NR
Villosa iris	Rainbow mussel	-	✓	✓	✓	✓	✓
Villosa trabalis	Tennessee bean	FE, SE	EX	✓	EX	NR	NR
Villosa vanuxemensis	Mountain creekshell	-	✓	✓	✓	✓	✓
TOTAL SPECIES KNOWN (54)			47	53	36	22	14
TOTAL SPECIES EXTANT (47)			37	46	20	17	7

TABLE 2. Scientific and common names of freshwater mussel species occurring in the New River basin of Virginia, where SE=state endangered, ST=state threatened and -=no state status, ✓=extant.

Scientific Name	Common Name	Status	New
Actinonaias ligamentina	Mucket	-	✓
Alasmidonta marginata	Elktoe	-	✓
Cyclonaias tuberculata	Purple wartyback	-	✓
Elliptio complanata	Eastern elliptio	-	✓
Elliptio dilatata	Spike	-	✓
Lampsilis fasciola	Wavy-rayed lampmussel	-	✓
Lampsilis ovata	Pocketbook	-	✓
Lasmigona holstonia	Tennessee heelsplitter	SE	✓
Lasmigona subviridis	Green floater	ST	✓
Tritogonia verucossa	Pistol-grip	ST	✓
Pyganodon grandis	Floater	-	✓
Utterbackia imbecillis	Paper pondshell	-	✓
TOTAL SPECIES KNOWN (12)			12
TOTAL SPECIES EXTANT (12)			12

DISCUSSION

Complexity of the mussel life cycle and traits of vulnerability

Freshwater mussels reproduce in a specialized way, one that requires a fish to serve as a host to their larvae, called glochidia, allowing the larvae to metamorphose to the juvenile stage. This extra step in their life cycle uniquely defines mussels among bivalve mollusks worldwide, in freshwater or marine environments, and adds significant complexity to their reproductive biology. Eggs of female mussels are fertilized internally by sperm released by males into the water and taken in during siphoning. The embryos then develop or "brood" in the gills of the female until becoming mature glochidia. Depending on the species, mussel glochidia brood in the gills of females during either winter or summer. Winter-brooders typically spawn in late summer to early fall, brood their larvae through the winter and then release glochidia the following spring and summer. Summer-brooders typically spawn in spring to early summer, and then brood and release their glochidia in the same summer period. Once mature, female mussels release glochidia out into the water, where they must attach and encyst on a suitable host fish for the transformation of larvae to juvenile mussels. Mussels rely on their fish host to provide them with long-distance dispersal and nutrition to metamorphose to juveniles while they are glochidia, which are small (<0.5 mm) ecto-parasites that attach and encyst on the gills and fins of fishes, typically taking weeks to months to metamorphose, excyst and then drop-away as similar-sized juveniles to the stream bottom where they grow into adults. However, for several species, including Green floater (*Lasmigona subviridis*), Creeper (*Strophitus undulatus*), and Paper pondshell (*Utterbackia imbecillis*), the glochidia can

Table 3. Scientific and common names of freshwater mussel species occurring in major Atlantic Slope river basins of Virginia, where FE=federally endangered, SE=state endangered, ST=state threatened and - =no federal or state status, ✓=extant, X=known from the system but possibly extinct, EX=known from system but possibly extirpated, and NR=no records of species from river system. Roanoke=1, Chowan=2, James=3, York=4, Rappahannock=5, and Potomac=6.

Scientific Name	Common Name	Status	1	2	3	4	5	6
Alasmidonta heterodon	Dwarf wedgemussel	FE, SE	NR	✓*	EX	✓	EX	EX
Alasmidonta undulata	Triangle floater	-	✓	✓	✓	✓	✓	✓
Alasmidonta varicosa	Brook floater	SE	NR	NR	✓	NR	NR	✓
Elliptio complanata	Eastern elliptio	-	✓	✓	✓	✓	✓	✓
Elliptio congaraea	Carolina slabshell	-	NR	✓	NR	✓	NR	NR
Elliptio fisheriana	Northern lance	-	NR	✓	✓	✓	✓	NR
Elliptio lanceolata	Yellow lance	-	NR	✓	✓	✓	✓	NR
Elliptio roanokensis	Roanoke slabshell	-	✓	✓	NR	✓	NR	NR
Fusconaia masoni	Atlantic pigtoe	ST	✓	✓	✓	NR	NR	NR
Lampsilis cariosa	Yellow lampmussel	-	✓	✓	✓	✓	NR	✓
Lampsilis cardium/ovata	Pocketbook	-	NR	NR	NR	NR	NR	✓
Lampsilis radiata	Eastern lampmussel	-	NR	✓	NR	✓	NR	✓
Lasmigona subviridis	Green floater	ST	✓	✓	✓	✓	✓	✓
Leptodea ochracea	Tidewater mucket	-	✓	✓	✓	✓	✓	✓
Lexingtonia subplana	Virginia pigtoe	-	NR	NR	X	NR	NR	NR
Ligumia nasuta	Eastern pondmussel	-	NR	✓	✓	✓	NR	✓
Pleurobema collina	James spinymussel	FE, SE	✓	NR	✓	NR	NR	NR
Pyganodon cataracta	Eastern floater	-	✓	✓	✓	✓	✓	✓

TABLE 3. Continued.

Scientific Name	Common Name	Status	1	2	3	4	5	6
Pyganodon grandis	Floater	-	✓	✓	✓	✓	✓	✓
Pyganodon implicata	Alewife floater	-	✓	✓	✓	✓	✓	✓
Strophitus undulatus	Creeper	-	✓	✓	✓	✓	✓	✓
Uniomerus carolinianus	Florida pondhorn	-	NR	✓	NR	NR	NR	NR
Utterbackia imbecillis	Paper pondshell	-	✓	✓	✓	✓	✓	✓
Villosa constricta	Notched rainbow	-	✓	✓	✓	NR	NR	NR
TOTAL SPECIES KNOWN (24)			14	20	19	17	12	16
TOTAL SPECIES EXTANT (23)			14	20	17	17	11	15

metamorphose to the juvenile stage inside the gill of the female parent mussel without parasitizing a host fish (Lefevre and Curtis 1911; Howard 1915; Barfield and Watters 1998; Cliff et al. 2001; Dickinson and Seitman 2008).

Many mussel species have elaborate adaptations to attract their fish hosts. To facilitate attachment of glochidia to their hosts, mussels have evolved highly modified mantle tissues to serve as lures or they produce packets called conglutinates that contain glochidia (Barnhart et al. 2008). Mantle lures and conglutinates closely resemble and mimic prey of fish, such as worms, insect larvae and pupae, leeches, crayfish and even other fish. This mimicry is among the most complex and striking known in the natural world! For example, the mantle lure of the Cumberlandian combshell (*Epioblasma brevidens*) mimics insect larvae and that of oyster mussel (*E. capsaeformis*) is brightly colored blue (Figure 3, photographs A and B); both lures attract their fish host and then capture them like a "venus flytrap" to infest their glochidia directly on fish (Jones et al. 2006a). Mantle lures of other mussels may resemble legs of aquatic insects, such as the lure of Mountain creekshell (*Villosa vanuxemensis*) or that of a large insect larvae, such as the lure of Wavy-rayed lampmussel (*Lampsilis fasciola*) (Figure 3, photographs C and D). Perhaps even more remarkable than these mantle lures, are conglutinates of the kidneyshell (*Ptychobranchus fasciolaris*) that resemble larvae of the black fly (Simuliidae), and conglutinates of the fluted kidneyshell (*P. subtentum*) that resemble pupae (Figure 4, photographs A and B) (Jones et al. 2006b). Conglutinates of the creeper (*Strophitus undulatus*) encase triangular shaped glochidia within individual compartments that are kinetically released by contact with host fish (Watters et al. 2002) and conglutinates of the dromedary pearlymussel (*Dromus dromas*) mimic freshwater leaches (Figure 4, photographs C and D) (Jones et al. 2004). All of these mussels live in rivers of Virginia.

Adult mussels are mostly sedentary, living in the benthos, i.e., the bottom of streams and lakes, typically in mixed substrates of gravel, sand, and silt. Mussels generally filter suspended organic particles <20 µm from the water column to eat but can also filter deposited particles through the shell-gap when burrowed in the benthos (Strayer et al. 2004). Further, the adults of most species are long-lived, regularly living 25-50 years or longer in freshwaters throughout North America (Haag and Rypel 2011). The kidneyshell (*Ptychobranchus fasciolaris*) has been aged to as old as 85 years in the upper Clinch River, Virginia (Henley et al. 2002). Because they are long-lived, their population growth rates tend to be slow, and stable population sizes are sustained by modest to low levels of annual recruitment by juveniles. Collectively, these life history traits, such as dependency on fish to metamorphose their larvae, a small sensitive juvenile stage, filter-feeding, and long-lived benthic-dwelling adults, make mussels vulnerable to various natural and anthropogenic impacts, including severe floods and droughts, habitat alteration from dams, various types of pollution entering rivers and streams, sedimentation from agriculture and urban environments and many other factors (Neves et al. 1997; Strayer et al. 2004).

Distribution and diversity of mussels in Virginia

With 77 species, the mussel fauna of Virginia is one of the most diverse in the United States. However, due to the varied physiography of the state, including the Appalachia Mountains to the west, the rolling hills of the central Piedmont, and the flat coastal plain of the east, Virginia's mussel fauna has a complex distribution and

FIGURE 3. Mantle-lure displays of female mussels: (**A**) Cumberlandian combshell (*Epioblasma brevidens*), Clinch River, Hancock County, Tennessee (Photo by J. Jones); (**B**) Oyster mussel (*Epioblasma capsaeformis*), Clinch River, Hancock County, Tennessee (Photo by N. King, Virginia Tech); (**C**) Mountain creekshell (*Villosa vanuxemensis*), Clinch River, Russell County, Virginia (Photo by T. Lane, Virginia Tech); (**D**) Wavy-rayed lampmussel (*Lampsilis fasciola*), Nolichucky River, Hamblen County, Tennessee (Photo by T. Lane, Virginia Tech).

origins. Mussel diversity is not evenly distributed throughout the state, with a major phylo-geographic break occurring between rivers of the UTRB of western Virginia and those draining the Atlantic Slope. The faunas of these two regions are quite different in their species compositions. Because the rivers of these two geographic areas flow in different directions, those of the former into the Mississippi River valley (=Interior Basin) and ultimately to the Gulf of Mexico, and those of the latter to the Atlantic Ocean, the evolutionary histories and the sources or origins of these faunas are quite different. Further, the rivers of Virginia flow through varied gradient, geology, soils, and vegetative cover, creating a range of environmental conditions suitable to mussel growth and survival. Hence, Virginia's rivers have given rise to a unique mussel fauna, one that contains some of the rarest freshwater species in the country, and is in need of continued scientific study and conservation.

Of course, a majority (70%) of the state's mussel fauna resides in rivers of the UTRB, especially the Clinch and Powell rivers. Several factors account for the high species diversity of this region. First, Virginia as a whole was not glaciated during the last ice-age more than 20,000 years ago. Both terrestrial and aquatic biota were

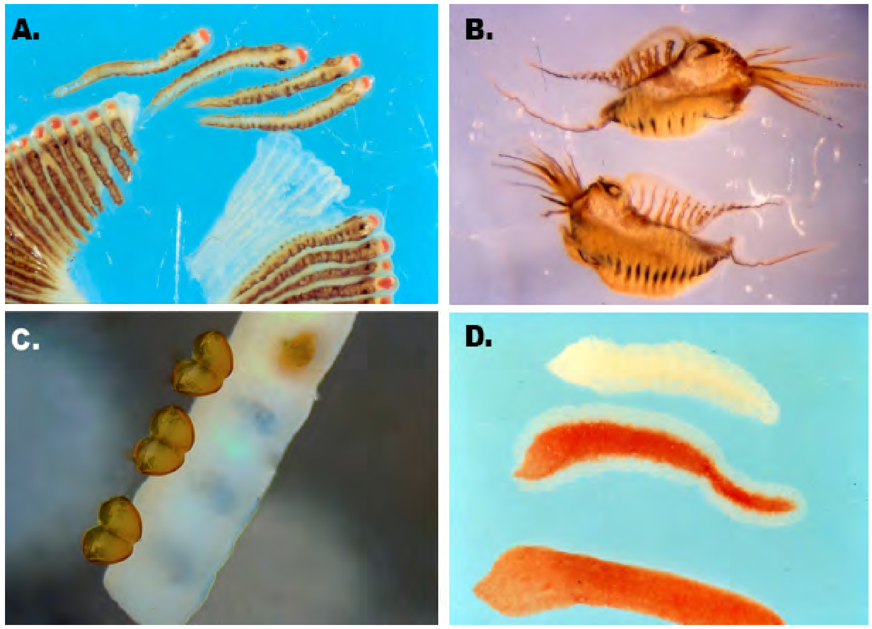

FIGURE 4. Conglutinates of female mussels: (**A**) Kidneyshell (*Ptychobranchus fasciolaris*) Clinch River, Hancock County, Tennessee; (**B**) Fluted kidneyshell (*Ptychobranchus subtentum*), Clinch River, Russell County, Virginia; (**C**) Creeper mussel (*Strophitus undulatus*) Clinch River, Hancock County, Tennessee (Photo by T. Lane, Virginia Tech); (**D**) Dromedary pearlymussel (*Dromus dromas*), Clinch River, Hancock County, Tennessee. Photographs A and B originally published by Jones et al. 2006 and D by Jones et al. 2004.

therefore not destroyed by massive ice sheets that covered large sections of North America north of Virginia. The UTRB served as a glacial refuge area for mussels, fishes and many other aquatic species. Second, the UTRB is connected to and is a part of the Mississippi River basin fauna, which is naturally diverse and where many species are widely distributed throughout its tributary streams and ecoregions. The interconnected nature of this river valley promotes high fish host diversity for mussels. For example, the Clinch River alone contains more than 120 species of fish (Jenkins and Burkhead 1993). High host-fish diversity in turn promotes high mussel diversity (Watters 1994). Third, the rivers of the UTRB in Virginia mostly flow through the Valley and Ridge physiographic province, where geologic rock strata are predominately limestone-based and rich in calcium and other minerals, which enhances shell growth and survival of mussels. These rivers also contain abundant and high quality habitat for mussels. Shoals are shallow areas in streams where cobble, gravel and sand substrate collect and remain stable over time. This type of habitat is critical to mussels because they need it to burrow into to protect themselves during floods, and to feed and reproduce effectively in stream environments. Thus, the UTRB's excellent habitat and its connection to the rich aquatic fauna of the Mississippi River basin have acted together to sustain a high diversity of mussels and fishes.

In contrast, mussel diversity in the New River of Virginia is low, with only twelve species recorded. This basin lies between the UTRB and rivers of the Atlantic Slope and has faunal elements of both. For example, the Tennessee heelsplitter (*Lasmigona holstonia*) is native to the Tennessee River basin but now occurs in two tributaries, upper Big Walker Creek and upper Wolf Creek, Bland County (Pinder et al. 2002). Although most of the species that occur in this river originated from streams of the Mississippi River valley, the green floater (*Lasmigona subviridis*) and the eastern elliptio (*Elliptio complanata*) are of Atlantic Slope origin (Clarke 1985; Johnson 1970). The latter species has been recently documented in Claytor Lake, Pulaski County and is considered introduced in the last ten years (B. Watson, VDGIF pers. comm.). The New River was not glaciated but for millennia it has been isolated from the Ohio River and hence the much richer aquatic fauna of the Mississippi River basin by Kanawha Falls, located just upstream of Charleston, West Virginia. These large falls are 20 to 30 feet high and span the river, blocking upstream migration of fish hosts; therefore, preventing many mussel species from colonizing the river above the falls. Of the 89 fish species known from the New River in Virginia, only 46 species are considered native, the remainder having been introduced over the last 50 to 100 years (Jenkins and Burkhead 1993). Hence, its low mussel diversity is mirrored by low native fish diversity. The majority of the New River basin drains the Blue Ridge physiographic province, where geologic rock strata are predominately crystalline based (granite and gneiss) and poor in minerals, including calcium. Mussel shells often appear eroded and of poor quality in the river, indicating shell growth is compromised by the naturally soft water of the basin. Despite ample shoal habitat, mussel abundance is low, further indicating growing conditions are not ideal.

The mussel fauna of the Atlantic Slope contains numerous species unique to the region. Many species that occur here have no direct analogue to species occurring in the Mississippi River basin. For example, *Elliptio complanata* is widely distributed from Florida to New Brunswick and is one of the most abundant species on the Atlantic Slope. However, it does not occur naturally in the Mississippi River basin nor is there a taxonomic equivalent to it in this basin. Mussels such as dwarf wedgemussel (*Alasmidonta heterodon*), yellow lance (*Elliptio lanceolata*), tidewater mucket (*Leptodea ochracea*), James spinymussel (*Pleurobema collina*) and other species also are unique to the Atlantic Slope. Further, a phylogeographic break occurs in the mussel fauna north and south of the James River basin (Johnson 1970). North of this river the fauna contains less species and most are not endemic to the northern half of the Atlantic Slope, i.e., they also occur in the James River basin and south of it. However, the river contains several species such as *P. collina*, Atlantic pigtoe (*Fusconaia masoni*), and notched rainbow (*Villosa constricta*) where the northern limit of their range is the James River (Fuller 1973; Hove and Neves 1994; Eads et al. 2006). To the south, these species and many others are unique to the southern half of the Atlantic Slope. This half of the region contains more mussel species, suggesting that colonization of the Atlantic Slope has occurred from the southern fauna and then moved northward through time. Streams of the Atlantic Slope in Virginia contain excellent habitat for mussels, flowing through varied geology of the Valley and Ridge, Blue Ridge, Piedmont Plateau, and

Coastal Plain physiographic provinces. Habitat in these creeks and rivers can range from rocky-bottom shoals typical of montane streams, sandy-bottom streams of the Piedmont, and the organic-rich, almost swamp-like conditions of the lower Coastal Plain. Mussel populations can reach high abundance in all of these habitat types, especially the ubiquitous *E. complanata*.

While the species compositions of the UTRB, New River, and Atlantic Slope rivers are distinct from each other, species exchanges have occurred among these basins over time. These exchanges have taken place over millennial to contemporary timescales, and are most likely the result of natural stream capture events between basins and from humans introducing host fishes naturally infected with mussel glochidia. There are a suite of species considered native to the Atlantic Slope of Virginia and other east coast states that have very recognizable Interior Basin (namely, UTRB, New, upper Ohio River) forms or analogues; for example, *Alasmidonta varicosa* (=*Alasmidonta marginata*), *Fusconaia masoni* (=*Fusconaia flava*), *Ligumia nasuta* (=*Ligumia recta*), *Lampsilis siliquoidea* (=*Lampsilis radiata*), and *Villosa constricta* (=*Villosa vanuxemensis*). These species are morphologically diverged enough from their Interior Basin counterparts and distributed widely enough on the Atlantic Slope to suggest that faunal exchanges occurred through stream captures millennia ago. Further, given the ubiquitous and widespread nature of these species throughout the Interior Basin, the direction of the exchange likely was from this basin to the Atlantic Slope. *Lampsilis ovata* is native to the Mississippi River valley but its presence and now common occurrence in the Potomac River system indicates a recent introduction. The species is restricted to just this basin on the Atlantic Slope and Johnson (1970) states that it was first introduced here through the Shenandoah River from fish stockings conducted in the late 1800s. The New River has at least three species that are not native to the system, *Lasmigona subviridis* and *Elliptio complanata* originating from the Atlantic Slope, and *L. holstonia* from the UTRB. Other species likely introduced to the system include *Lampsilis ovata* and *L. fasciola*. How and when these species came to the basin is unknown, but similarly, fish stockings and stream captures offer the best explanations.

Over ecological time, species exchanges and dispersal of mussels from one basin to another is seemingly a rare but natural process. More recently, humans have been responsible for introducing species outside their known ranges. Effects on the native or receiving fauna are unknown, but in most cases, it appears that the introduced species is simply incorporated into the native mussel assemblage with minimal consequences. However, research is needed to determine how such introductions can negatively affect native species through competition and hybridization. For example, genetic techniques could be used to determine if hybridization is occurring between *L. ovata* and *L. cariosa* in the Potomac River. Negative consequences potentially are greatest between closely related species that possibly can interbreed and compete for fish hosts and habitat.

Mussel Taxonomy and Cryptic Species Diversity

Within the freshwater mussel order Unionoida, the families Unionidae and Margaritiferidae contain the species that occur throughout Virginia, North America and even in other regions of the world (Table 4). In Virginia, the spectaclecase (*Cumberlandia monodonta*) is the only representative of the Margaritiferidae, while all other species in the state belong to the Unionidae. For North American species, the

TABLE 4. Scientific classification of freshwater mussels, including all sub-families, tribes, and genera known from Virginia. Classification scheme is based on Campbell et al. (2005). The number of species in each genera is in parentheses; total is 77 species.

Kingdom:	Animalia	Tribe:	Pleurobemini
Phylum:	Mollusca	Genera:	Cyclonaias (1)
Class:	Bivalvia		Fusconaia (4)
Order:	Unionoida		Hemistena (1)
Family:	Margaritiferidae		Lexingtonia (1)
Genera:	Cumberlandia (1)		Plethobasus (1)
Family:	Unionidae		Pleurobema (4)
Sub-family:	Ambleminae		Pleuronaia (2)
Tribe:	Lampsilini		Uniomerus (1)
Genera:	Actinonaias (2)	Tribe:	Quadrulini
	Amblema (1)	Genera:	Quadrula (4)
	Cyprogenia (1)		Tritogonia (1)
	Dromus (1)	Sub-family:	Anodontinae
	Elliptio (7)	Genera:	Alasmidonta (5)
	Epioblasma (7)		Anodontoides (1)
	Lampsilis (5)		Lasmigona (3)
	Lemiox (1)		Pegias (1)
	Leptodea (3)		Pyganodon (3)
	Ligumia (2)		Strophitus (1)
	Medionidus (1)		Utterbackia (1)
	Potamilus (1)		
	Ptychobranchus (2)		
	Toxolasma (1)		
	Truncilla (1)		
	Villosa (6)		

Unionidae is divided into two subfamilies, the Anodontinae and Ambleminae, with the later subfamily further subdivided in three tribes, Quadrulini, Lampsilini, and Pleurobemini (Campbell et al. 2005). Key mussel life history and anatomical traits are reflected in these taxonomic groups. For example, the Quadrulini and Pleurobemini mussels generally are summer brooders, whereas the Lampsilini and Anodontinae mussels generally are winter brooders. Lampsilini mussels in the genera *Epioblasma*, *Lampsilis*, and *Villosa* have complex mantle lures and those in the genera *Dromus*, *Cyprogenia*, and *Ptychobranchus* produce intricate conglutinates that mimic invertebrate prey of fishes (Jones and Neves 2002; Jones et al. 2004; Jones et al. 2006a; Jones et al. 2006b; Barnhart et al. 2008). Species in the Lampsilini are considered some of the most anatomically advanced species in North America. Quadrulini and Pleurobemini mussels have rudimentary mantle lures or none at all, and generally release simple conglutinates. The Anodontinae mussels have large triangular shaped glochidia with hooks at the tip of each valve, which allows the glochidia of these species to attach to and metamorphose on a wide variety of fish hosts (Clarke 1981; Clarke 1985; Hoggarth 1999). Thus, each of these four taxonomic groups of mussels have life history and anatomical features that uniquely defines them.

While 77 mussel species currently are known from Virginia, the recognized taxa and species names are likely to change over time. For example, a recent molecular genetics study conducted by Lane et al. (2016) showed that purple bean (*Villosa perpurpurea*) and Cumberland bean (*V. trabalis*) in the UTRB are the same species. Since the latter scientific name has priority it was unchanged but the authors changed the common name to "Tennessee bean" (see Table 1). Further mussels in the genus *Elliptio* on the Atlantic Slope are not well understood genetically and taxonomically. The shell shape and color of these species are phentotypically variable. Many of the currently recognized species in this genus look quite similar in their shell morphology, prompting biologists to question the taxonomic validity of some *Elliptio* species. The lanceolate *Elliptio* mussels on the Atlantic Slope of Virginia previously included four nominal species: *E. angustata*, *E. fisheriana*, *E. lanceolata*, and *E. producta.* Recently, Bogan et al. (2009) used mitochondrial DNA sequence analysis to show that only *E. fisheriana* and *E. lanceolata* actually occur in the state. At least in Virginia, the other two lanceolate species were shown to be genetically the same species as *E. fisheriana*. These finding reduced the number of recognized taxa in the state from 80 to 77.

The eastern elliptio (*E. complanata*) is widely distributed in Virginia from mountain to coastal plain streams. Hence, the shape and color of its shell can be quite variable depending on local stream conditions. Over 180 species names for *E. complanata* were synonymized by Johnson (1970) because the species was excessively over-described by earlier taxonomists, in part due to its highly variable shell morphology. In addition, *Elliptio congarea*, *E. roanokensis*, and *Uniomerus tetralasmus* all can resemble *E. complanata*; therefore, research is needed to determine the taxonomic validity of these three species in the Virginia portion of their ranges.

The taxonomy of Virginia pigtoe (*Lexingtonia subplana*) in the upper James River basin also has been questioned by biologists. Is this species simply a morphological variant of *Fusconaia masoni* which it closely resembles? Possibly, but Ortmann (1914) and Fuller (1973) have argued that it is a valid species because only the outer two gills are charged in gravid females, versus four charged gills in gravid females of *F. masoni*. Similarly, the shell morphology of Tennessee clubshell (*Pleurobema oviforme*) and Tennessee pigtoe (*Pleuronaia barnesiana*) in the UTRB are nearly indistinguishable but females of the former have two charged gills and those of the later four charged gills. These two similar looking species are genetically distinct based on DNA sequences (Campbell et al. 2005). The Virginia pigtoe was last collected alive in lower Craig Creek in Botetourt and Craig counties (Gerberich 1991). Thus, the taxonomic validity of *L. subplana* should not be discounted until scientific data become available to dispute Conrad's (1836) original description and Ortmann's (1914) observations on its gravid condition.

Conservation of mussels in Virginia

Conservation of freshwater mussels in Virginia will require citizens, non-governmental organizations, local, county, state and federal governments to apply their resources to five main areas: (1) water quality monitoring and regulation enforcement,

(2) restoration of stream habitat, (3) restoration of mussel populations, (4) educating the public about the importance and status of mussels, and (5) monitoring and research to understand why mussels are declining and what are the best ways to protect them (Freshwater Mollusk Conservation Society 2016). Sustained long-term efforts in these five areas offer the greatest potential to conserve freshwater mussels throughout the state.

The federal Clean Water Act (CWA) of 1972 and applicable water laws of Virginia govern water quality monitoring and enforcement in the state; the rules and regulations of these laws can be obtained by conducting a key word internet search (e.g., CWA 1972). Especially for those streams in Virginia with important mussel resources, such as in the Powell, Clinch, and Holston rivers of the UTRB and the James and Nottoway rivers of the Atlantic Slope, it is imperative that good water quality be maintained so mussel populations can survive long-term (Jones et al. 2014; Price et al. 2014; Zipper et al. 2014).

Stream restoration is one of the best ways to improve water quality and habitat conditions, especially in tributaries to main rivers. Tributary streams are vital arteries contributing to the health of a river. If they are clogged by excessive sediments from stream-bank erosion for example, habitat quality will decline in the main river where mussels are most diverse and abundant. Hence, projects that create riparian corridors filled with trees, shrubs and grasses can go a long way toward controlling sediment erosion, and in turn, help protect mussels. Fencing out cattle and other livestock from streams and their respective riparian corridors is especially effective in improving the health and condition of streams important to mussels.

Restoration of mussel populations by stocking hatchery-reared or translocated mussels is now technically feasible and the quickest way to boost population size of imperiled species or those lost via toxic spills or other anthropogenic impacts (Carey et al. 2015). To alleviate the immediate risk of extinction, population restoration will play a critical role in mussel conservation. In Virginia, three hatcheries currently produce mussels for restoration purposes: the Freshwater Mollusk Conservation Center at Virginia Tech in Blacksburg, the VDGIF Aquatic Wildlife Conservation Center near Marion, and the U.S. Fish and Wildlife Service's Harrison Lake National Fish Hatchery near Charles City. Collectively, these mussel hatcheries have produced thousands of mussels of more than two dozen species and that have subsequently been stocked in Virginia river's, including the Powell and Clinch of the UTRB, and on the Atlantic Slope in the upper James and Nottoway.

Environmental outreach to K-12 students is critical to increasing awareness and respect for streams and freshwater mussels in future generations. In 2010 the VDGIF stocked several thousand mussels at Cleveland Islands on the Clinch River, Russell County. Biologists invited more than a dozen students from Cleveland Elementary School to attend and participate in stocking and searching for mussels at the event. The students learned about what mussels do in streams and had a great time wading into the river to help stock them. Read about the event at: http://www.fws.gov/endangered/map/ESA_success_stories/VA/VA_story2/index.html. Events like these directly connect kids with nature and can make lasting impressions on them to increase their appreciation for mussels and the importance of healthy streams.

Monitoring and research to understand mussel population trends

Monitoring rare and endangered mussel species is critical to determining if their populations are declining, stable, or increasing over time. Assessing population trends is an important first step in understanding the reasons for declines, such as identifying various sources of industrial, agricultural and urban pollution. Therefore, when considering the traits that make mussels vulnerable, they make ideal organisms to monitor how contaminants in freshwater systems might influence their population trends. Because mussels are considered one of the most imperiled animal groups in the United States, state and federal natural resource agencies are initiating population monitoring programs for species of conservation concern in selected river and stream locations (Strayer et al. 2004). Long-term monitoring programs in the Clinch and Powell Rivers are good examples (Johnson et al. 2012; Jones et al. 2014; Ahlstedt et al. 2016). Since mussels are filter feeders and relatively immobile, they can uptake and accumulate toxins from the environment into their vital organs, including the foot, gonads, digestive gland and kidney. Thus, focused research efforts to concurrently monitor trends in population abundance, contaminants in stream networks, toxin accumulation in vital organs, and the transport, fate and toxicity of chemicals in the aquatic environment are needed to protect mussels in rivers and streams throughout Virginia. In addition, research is needed to understand the roles of excess fine sediments and nutrients, disease, altered temperature regimes, and fish host availability on mussel reproduction and survival. Finally, several areas and watersheds in Virginia have not been surveyed for mussels, including Dismal Swamp of the Albemarle basin, Levisa and Russell forks of the Big Sandy River basin, the Ararat River of the Yadkin basin, and freshwater streams of the Eastern Shore (Figure 1). Surveys in these areas may add new species and records of occurrence for freshwater mussels in Virginia.

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