A State-of-the-Unionids Address

Richard J. Neves

*U.S. Fish and Wildlife Service, Virginia Cooperative Fish and Wildlife Research Unit, Virginia Polytechnic Institute and State University, Blacksburg**

Abstract. The freshwater mussel fauna of the United States is in serious trouble. Of the 297 species and subspecies recognized, 21 species (7%) are presumed extinct, 42 (15%) are federally listed as endangered or threatened, and 69 (23%) are candidates for federal protection. The highly diverse endemic mussel fauna of the southeastern United States is in greatest jeopardy, with depressed population levels today reflecting transgressions to rivers decades earlier. Reservoir construction and hydrologic changes documented in rivers such as the upper Mississippi, upper Ohio, Tennessee, and Cumberland rivers have been particularly disruptive to big-river species. Our knowledge of the biology and ecological requirements of most species is limited, and fish hosts are known for fewer than 70 species. We lack, therefore, the essential information and tools to recover declining populations. The next 10 years will be the most significant bottleneck yet for this fauna, with chronic perturbations now intensified by the zebra mussel invasion. An extinction spasm is inevitable, with or without the ecological synergism of human manipulation and the zebra mussel. Greater effort to educate and muster public support is essential for the conservation of riverine ecosystems; otherwise, a cascade of extirpations and extinctions of invertebrates will imprecate the 21st century.

Introduction

The freshwater mussel fauna (Unionacea) of North America consists of a diverse assemblage of about 297 species and subspecies (Turgeon et al. 1988), distributed principally throughout the Mississippi River drainage and river systems in eastern North America. Although the higher classification of these taxa has not been resolved, most malacologists tentatively recognize two families, three subfamilies, and about 49 nominal genera of unionids. Regions of endemism and high species diversity occur mainly in the southeastern United States, including the Ohio, Tennessee, Cumberland, and Mobile drainages, and other rivers to the Gulf of Mexico and South Atlantic.

The wholesale destruction of freshwater mollusks and other fauna by dams and pollution was reported in the late 19th and early 20th centuries (Lewis 1868, Ortmann 1909), although previous reports of environmental degradation began to appear in the early 19th century. The especially diverse assemblage of river snails (Pleuroceridae) and mussels in the eastern United States was being jeopardized by unabated development and industrialization. Although habitat loss and alteration in rivers were decried by aquatic biologists, the environmental conscience of the nation remained dormant at that time.

The first coordinated effort to recognize rare molluscan taxa in North America was a symposium convened in 1968 by the American Malacological Union. This attempt to assemble a preliminary list of rare and endangered mollusks documented that the freshwater mollusks of streams and rivers were in the greatest danger of extirpation and extinction. The precarious future of the mussel fauna was evident—33 rare and endangered species and 8 presumed extinct species in the Mississippi and St. Lawrence river systems (Stansbery 1970) and about 61 nominal taxa considered to be rare and endangered in Gulf Coast drainages (Athearn 1970). Conclusions from the symposium were that (1) conservation measures by regulatory agencies were long overdue and (2) research on all aspects of rare species was essential to maintain and restore declining populations.

In 1971 a conference on unionids updated the preliminary list of rare and endangered mussels in the United States (Jorgensen and Sharp 1971). In the proceedings of that symposium, Stansbery (1971)

* The Virginia Unit is jointly supported by the United States Fish and Wildlife Service, Virginia Department of Game and Inland Fisheries, Wildlife Management Institute, and Virginia Polytechnic Institute and State University.

identified 11 species of *Dysnomia* (= *Epioblasma*) that became extinct in the 20th century. All of them inhabited riffles and shoals of large rivers, habitats nearly eliminated by impoundments and navigational locks and dams in the Mississippi River basin. In addition to these extinct species, another 120 nominal taxa were listed as rare or endangered. It was readily apparent that many of the unionid species were in precipitous decline, due principally to habitat destruction. The current list of extinct species has grown to about 21 species, as judged by recent surveys and the consensus of experts (Table 1). All molluscan nomenclature is according to Turgeon et al. (1988).

Protection of rare invertebrates in the United States was legislated first in the Endangered Species Preservation Act of 1969. This legislation redefined "fish and wildlife" to include mollusks and crustaceans and amended the Lacey Act to prohibit interstate and foreign commerce of these invertebrate groups. However, no species were identified for protection. Passage of the Endangered Species Act of 1973 and subsequent amendments provided the mechanism for official recognition and protection of invertebrate fauna nationwide. The first freshwater mussels were listed in June 1976; 23 U.S. species were designated as endangered. Another 19 species have been added to the list since then, such that 40 mussels are endangered and 2 are threatened in the United States at this time (Table 2). In November 1991, the U.S. Fish and Wildlife Service for possible addition to the federal List of Endangered and Threatened Wildlife [Federal Register published a list of vertebrate and invertebrate taxa native to the United States that are being considered 56(225), 21 November 1991]. On this candidate list are 70 extant species and 4 species that are likely extinct (Table 3). These lists continue to lengthen as status surveys and data compilation confirm the limited distribution and rarity of many localized and endemic species.

Table 1. Species of freshwater mussels in the United States presumed to be extinct.

Scientific name	Common name
Alasmidonta mccordi Athearn, 1964	Coosa elktoe
Alasmidonta robusta Clarke, 1981	Carolina elktoe
Alasmidonta wrightiana (Walker, 1901)	Ochlocknee arc-mussel
Epioblasma arcaeformis (I. Lea, 1831)	sugarspoon
Epioblasma biemarginata (I. Lea, 1857)	angled riffleshell
Epioblasma flexuosa (Rafinesque, 1820)	leafshell
Epioblasma florentina florentina (I. Lea, 1857)	yellow blossom
Epioblasma haysiana (I. Lea, 1834)	acornshell
Epioblasma lenoir (I. Lea, 1843)	narrow catspaw
Epioblasma lewisii (Walker, 1910)	forkshell
Epioblasma obliquata perobliqua (Conrad, 1836)	white catspaw
Epioblasma personata (Say, 1829)	round combshell
Epioblasma propinqua (I. Lea, 1857)	Tennessee riffleshell
Epioblasma sampsonii (I. Lea, 1861)	Wabash riffleshell
Epioblasma stewardsoni (I. Lea, 1852)	Cumberland leafshell
Epioblasma torulosa gubernaculum (Reeve, 1865)	green blossom
Epioblasma torulosa torulosa (Rafinesque, 1820)	tubercled-blossom
Epioblasma turgidula (I. Lea, 1858)	turgid blossom
Medionidus mcglameriae van der Schalie, 1939	Tombigbee moccasinshell
Pleurobema bournianum (I. Lea, 1840)	Scioto pigtoe
Quadrula tuberosa (I. Lea, 1840)	rough rockshell

Table 2. List of federally protected mussel species in the United States in 1992.

Scientific name	Common name
Alasmidonta heterodon (I. Lea, 1829)	dwarf wedgemussel
Arkansia wheeleri Ortmann & Walker, 1912	Ouachita rock-pocketbook
Cyprogenia stegaria (Rafinesque, 1820)	fanshell
Dromus dromas (I. Lea, 1834)	dromedary pearlymussel
Elliptio steinstansana R. I. Johnson & Clarke, 1983	Tar spinymussel
Epioblasma florentina curtisi (Utterback, 1916)	Curtis pearlymussel
Epioblasma florentina florentina (I. Lea, 1857)	yellow blossom
Epioblasma florentina walkeri (Wilson & H. W. Clark, 1914)	tan riffleshell
Epioblasma obliquata obliquata (Rafinesque, 1820)	catspaw
Epioblasma obliquata perobliqua (Conrad, 1836)	white catspaw
Epioblasma penita (Conrad, 1834)	southern combshell
Epioblasma torulosa gubernaculum (Reeve, 1865)	green blossom
Epioblasma torulosa torulosa (Rafinesque, 1820)	tubercled blossom
Epioblasma turgidula (I. Lea, 1858)	turgid blossom
Fusconaia cor (Conrad, 1834)	shiny pigtoe
Fusconaia cuneolus (I. Lea, 1840)	fine-rayed pigtoe
Hemistena lata (Rafinesque, 1820)	cracking pearlymussel
Lampsilis abrupta (Say, 1831)	pink mucket
Lampsilis higginsii (I. Lea, 1857)	Higgins eye
Lampsilis powellii (I. Lea, 1852)	Arkansas fatmucket
Lampsilis streckeri Frierson, 1927	speckled pocketbook
Lampsilis virescens (I. Lea, 1858)	Alabama lampmussel
Lemiox rimosus (Rafinesque, 1820)	birdwing pearlymussel
Margaritifera hembeli (Conrad, 1838)	Louisiana pearlshell
Obovaria retusa (Lamarck, 1819)	ring pink
Pegias fabula (I. Lea, 1838)	little-wing pearlymussel
Plethobasus cicatricosus (Say, 1829)	white wartyback
Plethobasus cooperianus (I. Lea, 1834)	orange-foot pimpleback
Pleurobema collina (Conrad, 1837)	James spinymussel
Pleurobema curtum (I. Lea, 1859)	black clubshell
Pleurobema gibberum (I. Lea, 1838)	Cumberland pigtoe
Pleurobema marshalli Frierson, 1927	flat pigtoe
Pleurobema plenum (I. Lea, 1840)	rough pigtoe
Pleurobema taitianum (I. Lea, 1834)	heavy pigtoe
Potamilus capax (Green, 1832)	fat pocketbook
Potamilus inflatus (I. Lea, 1831)	inflated heelsplitter
Quadrula fragosa (Conrad, 1835)	winged mapleleaf
Quadrula intermedia (Conrad, 1836)	Cumberland monkeyface
Quadrula sparsa (I. Lea, 1841)	Appalachian monkeyface
Quadrula stapes (I. Lea, 1831)	stirrupshell
Toxolasma cylindrellus (I. Lea, 1868)	pale lilliput
Villosa trabalis (Conrad, 1834)	Cumberland bean

Table 3. Species of freshwater mussels proposed as candidates for federal protection (published in Federal Register, November 1991).

Scientific name	Common name
Alasmidonta arcula (I. Lea, 1838)	Altamaha arc-mussel
Alasmidonta atropurpurea (Rafinesque, 1831)	Cumberland elktoe
Alasmidonta raveneliana (I. Lea, 1834)	Appalachian elktoe
Alasmidonta varicosa (Lamarck, 1819)	brook floater
Alasmidonta wrightiana (Walker, 1901)	Ochlocknee arc-mussel
Amblema neislerii (I. Lea, 1858)	fat threeridge
Anodonta californiensis I. Lea, 1852	California floater
Cumberlandia monodonta (Say, 1829)	spectaclecase
Cyprogenia aberti (Conrad, 1850)	western fanshell
Disconaias salinasensis (Simpson, 1908)	Salina mucket
Elliptio sp.	Waccamaw lance pearlymussel
Elliptio judithae (Clarke, 1986)	Neuse slabshell
Elliptio lanceolata (I. Lea, 1828)	yellow lance
Elliptio marsupiobesa Fuller, 1972	Cape Fear spike
Elliptio nigella (I. Lea, 1852)	winged spike
Elliptio shepardiana (I. Lea, 1834)	Altamaha lance
Elliptio spinosa (I. Lea, 1836)	Altamaha spinymussel
Elliptio waccamawensis (I. Lea, 1863)	Waccamaw spike
Elliptoideus sloatianus (I. Lea, 1840)	purple bankclimber
Epioblasma biemarginata (I. Lea, 1857)	angled riffleshell*
Epioblasma brevidens (I. Lea, 1831)	Cumberlandian combshell
Epioblasma capsaeformis (I. Lea, 1834)	oyster mussel
Epioblasma haysiana (I. Lea, 1834)	acornshell*
Epioblasma lewisii (Walker, 1910)	forkshell*
Epioblasma metastriata (Conrad, 1840)	upland combshell
Epioblasma othcaloogensis (I. Lea, 1857)	southern acornshell
Epioblasma propinqua (I. Lea, 1857)	Tennessee riffleshell*
Epioblasma torulosa rangiana (I. Lea, 1839)	northern riffleshell
Epioblasma triquetra (Rafinesque, 1820)	snuffbox
Fusconaia escambia Clench and Turner, 1956	narrow pigtoe
Fusconaia masoni (Conrad, 1834)	Atlantic pigtoe
Lampsilis altilis (Conrad, 1834)	fine-lined pocketbook
Lampsilis australis Simpson, 1900	southern sandshell
Lampsilis binominata Simpson, 1900	lined pocketbook
Lampsilis cariosa (Say, 1817)	yellow lampmussel
Lampsilis fullerkati R. I. Johnson, 1984	Waccamaw fatmucket
Lampsilis perovalis (Conrad, 1834)	orange-nacre mucket
Lampsilis rafinesqueana Frierson, 1927	Neosho mucket
Lampsilis subangulata (I. Lea, 1840)	shiny-rayed pocketbook
Lasmigona sp.	Barrens heelsplitter
Lasmigona decorata (I. Lea, 1852)	Carolina heelsplitter
Lasmigona holstonia (I. Lea, 1838)	Tennessee heelsplitter
Lasmigona subviridis (Conrad, 1835)	green floater
Leptodea leptodon (Rafinesque, 1820)	scaleshell
Lexingtonia dolabelloides (I. Lea, 1840)	slabside pearlymussel
Margaritifera marrianae R. I. Johnson, 1983	Alabama pearlshell
Medionidus acutissimus (I. Lea, 1831)	Alabama moccasinshell
Medionidus parvulus (I. Lea, 1860)	Coosa moccasinshell
Obovaria rotulata (Wright, 1899)	round ebonyshell
Pleurobema clava (Lamarck, 1819)	clubshell
Pleurobema decisum (I. Lea, 1831)	southern clubshell
Pleurobema furvum (Conrad, 1834)	dark pigtoe
Pleurobema georgianum (I. Lea, 1841)	southern pigtoe
Pleurobema oviforme (Conrad, 1834)	Tennessee clubshell
Pleurobema perovatum (Conrad, 1834)	ovate clubshell
Pleurobema pyriforme (I. Lea, 1857)	oval pigtoe
Pleurobema rubellum (Conrad, 1834)	Warrior pigtoe
Pleurobema rubrum (Rafinesque, 1820)	pink pigtoe
Pleurobema verum (I. Lea, 1860)	true pigtoe
Popenaias popei (I. Lea, 1857)	Texas hornshell
Potamilus amphichaenus (Frierson, 1898)	Texas heelsplitter
Ptychobranchus greenii (Conrad, 1834)	triangular kidneyshell
Ptychobranchus jonesi (van der Schalie, 1934)	southern kidneyshell
Ptychobranchus occidentalis (Conrad, 1836)	Ouachita kidneyshell
Quadrula cylindrica strigillata (Wright, 1898)	rough rabbitsfoot
Quincuncina mitchelli (Simpson, 1896)	false spike
Simpsonaias ambigua (Say, 1825)	salamander mussel
Toxolasma lividus (Rafinesque, 1831)	purple lilliput
Toxolasma pullus (Conrad, 1838)	Savannah lilliput
Truncilla cognata (I. Lea, 1860)	Mexican fawnsfoot
Villosa choctaensis Athearn, 1964	Choctaw bean
Villosa fabalis (I. Lea, 1831)	rayed bean
Villosa ortmanni (Walker, 1925)	Kentucky creekshell
Villosa perpurpurea (I. Lea, 1861)	purple bean

* Presumed extinct (category 3A).

Traits of Vulnerability and Threats

The decline, extirpation, or extinction of numerous taxa can be attributed to ecological and biological traits that make unionids particularly vulnerable to anthropogenic impacts. The life cycle of unionids contains a larval stage (glochidium) that is an obligate parasite on the gills or fins of fishes. Gravid female mussels release these glochidia either individually from their marsupial gills or as clusters (conglutinates) through the excurrent aperture. Estimates of fecundity range from about 75,000 to 3.5 million, depending on the species and the size of the female (Surber 1912, Coker et al. 1921, Yeager and Neves 1986). The glochidia of all unionids, except the salamander mussel (*Simpsonaias ambigua*), parasitize fishes, but the intensity of infestation is typically low (Coker et al. 1921, Trdan 1981). Despite the tremendous fecundity of females, few glochidia come into contact with suitable hosts during this critical stage in the life cycle. Contact between glochidia and host(s) is a low-probability event, promoted by the respiratory and feeding behaviors of fishes (Dartnall and Walkey 1979, Neves et al. 1985) and the behavioral characteristics of some mussel species (Chamberlain 1934, Davenport and Warmuth 1965, Kraemer 1970). Despite these adaptations to facilitate host contact, host specificity of some degree is seemingly the rule rather than the exception for most mussel species that have been studied (Table 4). Host fishes have been identified, with various degrees of certainty, for 33 genera and about 65 species of mussels (Hoggarth 1992). Host specificity is particularly evident among the short-term brooders that release glochidia or conglutinates in summer. Another 16 genera of mussels, mostly monotypic, have no fishes implicated as hosts.

Narrow host specificity would seemingly entail reproductive costs, restricting geographic range and wasting glochidia that attach to unsuitable hosts. The obvious advantage of eurytopic parasitism is, for whatever reason, secondary to natural selection for specificity among diverse assemblages of sympatric short-term brooders. Although the database on host fish identifications is partial but growing, the seemingly greater degree of host specificity within regions of endemism would argue for competition for fish hosts and resultant specificity. As a consequence, these mussel species may be particularly vulnerable to a reproductive bottleneck because of host fish availability. As new fish hosts and degrees of specificity are determined in laboratory experiments, the vulnerability of rare mussel species to reproductive failure, as a result of host fish declines, can be assessed.

Table 4. Genera of freshwater mussels with fish species implicated as hosts of their glochidia.

Mussel genus	No. species	Number with known hosts	Number fish hosts
Actinonaias	2	1	12
Alasmidonta	9	3	9
Amblema	3	1	13
Anodonta	15	6	42
Anodontoides	2	1	2
Arcidens	1	1	5
Cyclonaias	1	1	2
Cyprogenia	2	1	1
Elliptio	31	3	8
Ellipsaria	1	1	3
Epioblasma	15	3	8
Fusconaia	13	3	13
Glebula	1	1	2
Lampsilis	32	6	21
Lasmigona	7	3	16
Lemiox	1	1	1
Leptodea	3	1	1
Ligumia	3	2	7
Margaritifera	4	3	14
Medionidus	6	1	4
Megalonaias	2	1	18
Obovaria	6	1	1
Plethobasus	3	1	1
Pleurobema	31	3	12
Potamilus	6	3	2
Ptychobranchus	5	1	5
Quadrula	20	6	17
Simpsonaias	1	1	1*
Strophitus	3	1	4
Toxolasma	8	3	6
Truncilla	4	2	2
Uniomerus	5	1	1
Villosa	18	2	10
Total	263	65	264

* Amphibian host.

The seemingly inefficient reproductive cycle, with its obligate fish host, seems to be a weak link in population recruitment. Susceptibility of glochidia and fish hosts to polluted water, altered temperature regimes below impoundments, and the chance encounter between glochidium and host can lead to recruitment failures in some years and relic populations dominated by only old cohorts. Similarly, the fish faunas of many rivers have changed significantly as a result of impoundments, forage and sport species introductions, channelization, snag removal, and other permanent changes in the chemical and physical environment. Any factor that limits survival of the glochidium or decreases the abundance and species composition of the fish fauna is likely to be detrimental to co-dependent mussel populations. The millions of years of co-evolution between mussels and fishes cannot be reprogrammed to accommodate the rapid settlement of North America. Unfortunately, our knowledge of host fish requirements for most species is too incomplete to correlate changes in fish fauna with those of the unionids.

Naiades are considered reliable indicators of water pollution because they are sedentary and filter particulate matter from the water column. Early on, chemical pollution was suspected to cause the decline and disappearance of mussels from sections of waterways with industrial discharges (Lewis 1868, Ortmann 1909, Baker 1928). Declines in mussel populations correlated with industrial development have been reported throughout North America, but few studies have demonstrated a cause-effect relationship. In most instances, the combined effects of numerous contaminants and induced physiological stresses are the ultimate cause for acute or chronic mortality in a population. Siltation will degrade water quality and substratum, clog gills, reduce feeding efficiency and growth, and eventually smother mussels if sufficient accumulation occurs (Ellis 1936, Marking and Bills 1979, Kat 1982). Numerous field studies have implicated siltation and sedimentation from farming, mining, and other land-use practices in the decline of stream populations of unionids (Ellis 1931, Coon et al. 1977). Similarly, mortality from toxic spills and chronic lethality of polluted waters are well documented (Cairns et al. 1971). Although mussels can avoid short-term doses of toxic chemicals by valve closure, they cannot tolerate chronic exposure to contaminated water. Dosing with heavy metals, chlorine, ammonia, or other industrial and municipal effluents is lethal to most invertebrate taxa, particularly the early life stages, as judged by available bioassay results (Rand and Petrocelli 1985).

In a review of contaminant effects on mussels, Havlik and Marking (1987) noted that although the uptake, storage, and elimination of contaminants has been studied, few data are available on toxicity levels. In general, adult mussels are not suitable bioassay organisms because they can close their valves and avoid or reduce exposure to experimental dosing. However, glochidia and juveniles are suitable for toxicity testing, and larval forms are usually more sensitive than adults of the same species to toxicants. Recent studies have demonstrated their sensitivities to contaminants, relative to standard bioassay organisms such as the zooplankter *Ceriodaphnia dubia* and the fathead minnow, *Pimephales promelas*. Johnson (1990) and Jacobson (1990) used glochidia and juvenile mussels to determine the toxicity of various contaminants and established protocols for testing these early life stages. In general, glochidia and juvenile mussels are among the most sensitive bioassay organisms used in standard toxicity testing (Goudreau et al. 1993). Because no freshwater bivalves are used routinely in bioassays to set effluent standards, and because the early life stages of mussels seem to be sensitive indicators of toxicants, their use as bioassay organisms probably would identify acceptable limits of contaminants for most riverine mollusks.

Unionids may be the longest-lived freshwater invertebrates, with life spans ranging to about 100 years (Hendelberg 1960, Neves and Moyer 1988). Riverine populations of heavy-shelled species grow slowly and reach maximum ages greater than those of thin-shelled lentic species (Grier 1922, Stansbery 1961). Owing to slow growth and immobility, recolonization of impacted river reaches is a protracted process, attained through a combination of passive dispersal of adults downstream and dispersal of newly metamorphosed juveniles by infested host fishes. Establishment of stable, self-sustaining populations, therefore, requires decades of immigration and recruitment, even for common riverine species that typically occur at high densities. Population stability is maintained by numerous, slow-growing cohorts that contribute new year-classes of variable strengths (Neves and Widlak 1987). This extremely slow rate of population growth and attainment of carrying capacity makes recovery of decimated populations extremely difficult, even when habitat is ideal for recolonization. Similarly, translocations of adults for recovery are fraught with problems and require a long-term commitment of funds and effort to evaluate success (Sheehan et al. 1989).

Our knowledge of the biology and ecology of this faunal group in the United States is expanding but remains grossly inadequate. The first lesson learned by field biologists is that all mussel species are not created equal. Although species may look alike, live in similar habitats, and seemingly respond to the same environmental cues, they are as different biologically as species in any other family of animals. We tend to be lumpers in our explanations of requirements for poorly studied taxa, and splitters for genera with better-studied species. Studies that generate even minimal data dramatically change our willingness to extrapolate on the previously unknown. Information on habitat suitability, physiological requirements or tolerance limits, and responses to environmental cues is so incomplete that we are forced to apply results of few studies to all species. For example, by default and for regulatory purposes, the LC_{50} of copper to *Amblema plicata plicata* in the Mississippi River is applied to *Epioblasma* spp. in the Tennessee River. This speculative extrapolation among species, particularly for physiological requirements and sensitivities to contaminants, is a sad indictment of our limited knowledge of species biology and likely jeopardizes the survival of pollution-sensitive species. More biological studies on a greater variety of species would greatly benefit this faunal group. My hope is that no one species—such as the fairly ubiquitous and lacustrine paper pondshell, *Anodonta imbecillis*—becomes the "standard mussel" by which all mussels are judged by water quality and regulatory agencies at the federal and state levels. We need sufficient testing to identify those species with sensitivities at least representative of the assemblages they will be used to protect.

Exotic Species

This status review would not be complete without mention of exotic species, particularly other bivalves, that have invaded inland waterways. The Asian clam, *Corbicula fluminea*, has co-occurred with Interior Basin naiades for more than 20 years now, and evidence for the potential competitive interactions between this clam and native mussels is contradictory. Of greatest concern are substratum space and food utilization by Asian clams and juvenile mussels, particularly in streams where either of these requisite resources may be limited. Invasion of the zebra mussel, *Dreissena polymorpha*, poses a much more omninous threat, as judged by reports of biofouling of naiades in the Great Lakes (Schloesser and Kovalak 1991, Hunter and Bailey 1992). The zebra mussel has ravaged mussel populations in Lake St. Clair and western Lake Erie and is poised to do untold harm to mussel populations in our major rivers and reservoirs. The zebra mussel will likely be on the epitaph of many rare mussel species that get pushed beyond the brink of extinction by its biofouling presence. Other mussel species will require federal protection after the zebra mussel does its damage and achieves some equilibrium population level in our streams. Whatever the consequences, unionids will be on the losing side of this molluscan war for survival.

Matters of Habitat

The decline, extirpation, and extinction of freshwater mussel species is almost totally driven by habitat loss and degradation. Anthropogenic changes to rivers that sustain diverse molluscan assemblages have been well documented. The upper Mississippi River is deteriorating hydrologically and ecologically, with pools suffering the same fate as most shallow reservoirs, namely, inputs of sediments, nutrients, and affiliated contaminants (Fremling and Claflin 1984). Of the 50 or so species of mussels collected in this river reach prior to the 9-ft channel construction project, roughly 32 species remain (Fuller 1980). The mussel assemblage in the upper Ohio River experienced similar changes from navigation projects. Although the diversity of this mussel fauna, reported to be at least 37 species from historic collections, has not changed appreciably, there has been a dramatic 41% change in species composition this century (Taylor 1989). *Epioblasma* spp. and other species once widespread but now federally endangered are being replaced by anodontines and other impoundment-tolerant species. The dynamic changes in the mussel fauna of both rivers will be evidenced by declining diversity, altered species composition, and lowered abundance of some species attributed to chronic degradation of habitat suitability for the indigenous species.

From Europe to America

Because Europe had a historically depauperate mussel fauna of roughly 15 species, studies of and changes to that fauna were more numerous. A recent assessment of the decline of the freshwater pearl mussel, *Margaritifera margaritifera*, a long-lived resident of headwater trout streams, has correlated eutrophication, specifically nitrate concentration, with mortality rates of adult mussels in 11 rivers (Bauer 1988). Mortality of juvenile mussels (ages 0–20) was linked to BOD levels, leading to the hypothesis that young mussels can only develop in sediment of low organic content. Although the causal mechanisms for juvenile mortality are unknown, anoxia, predator abundance, and contaminants are possible factors. In Sweden the postulated cause for decline of the pearl mussel is lowered host fish abundance because of acidification. In essence, any factor that reduces the spawning stock of adults, survivability of juveniles, or abundance of hosts will eventually diminish population size and jeopardize its continued existence.

Most of the U.S. mussel species reside in higher-order warmwater rivers with a variety of anthropogenic impacts, depending on geographic region and land-use patterns. The reported correlation between the decline of pearl mussels and water pollution in Europe is probably valid worldwide, but evidence to support this cause and effect relationship is principally anecdotal and unquantified. For example, most headwater tributaries of the upper Cumberland and upper Tennessee rivers are experiencing precipitous declines in unionids. The extensive coal mining in these watersheds over the past 50 years may be coincidental to faunal declines, but sufficient indirect evidence is available to demonstrate negative effects of coal mining operations to survival and recruitment in mussel populations (Anderson 1989, McCann and Neves 1992). There is rarely a smoking gun, only fresh dead and weathered valves of mussels that were alive and well when sampled previously. The same scenario is played out in rivers with unsafe point-source discharges; mussels decline or disappear for suspected but unsubstantiated causes. The short-term economic gains of private industry are allowed to supersede the long-term viability of our faunal heritage and water quality for all downstream user groups. Only when a federally listed species is part of the faunal assemblage will regulatory agencies be receptive to requests for greater scrutiny of permits and violations of effluent standards. Typically, the response is too little and too late for those species intolerant to water quality degradation. The entire practice of effluent discharge to receiving streams is a sad indictment of our willingness to sanction treatment of waste, partial in most cases, and to accept degraded water quality for purely economic reasons.

Protection of Rivers

The assault on U.S. rivers, begun during the mid-19th century, accelerated dramatically in the 1930s to provide for water supply, navigation, flood control, and electricity. Because extensive biological inventories of river systems were never conducted, the degree of faunal loss or decline is unknown (Schindler 1989). Of the original 5.2 million km of rivers in the contiguous United States, only 42 free-flowing rivers greater than 200 km remain (Benke 1990). In 1982 the National Rivers Inventory was completed to identify streams or river reaches of high quality with potential for special protection. Only 2% of the 5.2 million km of streams qualified for inclusion in the inventory.

Roughly 30% of the United States is federally owned and under the jurisdiction of the Bureau of Land Management, Forest Service, or National Park Service. However, most of this land and inclusive streams is in the West or in high-gradient areas with headwater streams that lack mussels. Thus, despite the significant landmass owned by the federal government and commitments by responsible federal agencies to secure protection of streams on federal lands, there will be negligible effects on freshwater mussels.

Legislation establishing national river parks was passed in the early 1960s to protect rivers and riparian corridors, but only four rivers have been granted such status. The Wild and Scenic Rivers Act of 1968 provided a mechanism to identify and protect river reaches by prohibition of federal approval or assistance on water projects that would adversely affect them. However, the legislation provided inadequate protection of these rivers against private development (Goldfarb 1984). Of the 119 river reaches (15,000 km) designated as wild and scenic, fewer than 1,600 km occur east of the Mississippi River. Once again, the hot spots of molluscan diversity have been missed by the legislative web.

Conservation groups such as the Izaac Walton League, American Rivers, The Nature Conservancy, and Sierra Club are spearheading the fight to save important rivers of aesthetic as well as biological value. The efforts of these publicly supported organizations will provide the best chance of protecting rare aquatic mollusks and their habitats in quality rivers. Protection of big-river habitats and associated fauna, because of significant alterations and water quality degradation, will be one of the greatest challenges facing agency biologists with multiple-use management goals for rivers.

Water Quality Protection

Recent assessments of water quality in North American rivers provide a mixed prognosis for surface waters (Smith et al. 1987, Becker and Neitzel 1992, Patrick 1992). The sequence of federal laws to protect surface waters began with the River and Harbors Act of 1899 to curb refuse disposal; however, the Water Pollution Control Act of 1948 was the first law intended to abate water pollution and to assign responsibility to the individual states. Subsequent amendments to the Act in 1956 and 1961 provided construction grants for wastewater treatment plants and provided research funds to study pollution effects and to develop improved methods of effluent treatment. A series of federal laws was passed in the 1960s to address interstate waters principally and to strengthen the original Water Pollution Control Act. Creation of the Environmental Protection Agency in 1970 and passage of the Clean Water Act of 1972 set the stage for the regulations and water standards we have today. Goals of the Clean Water Act were to allow for the protection and enhancement of fish, shellfish, and wildlife; provide conditions suitable for recreation in surface waters; and eliminate the discharge of pollutants in U.S. waters. These noble goals and those of the Clean Water Act of 1977 established the National Pollution Discharge Elimination System and effluent standards for point-source discharges. The system has been in force for about 15 years and, for the most part, seems to be working well.

Results from two nationwide water sampling networks indicate widespread decreases in fecal coliform bacteria and lead but increases in nitrate, chloride, arsenic, and cadmium concentrations (Smith et al. 1987). These water quality changes seem to reflect changing technologies in society for sewage treatment, highway maintenance, gas consumption, fertilizer application, and coal combustion. Analyses of water quality detect acute and chronic problems passing downstream, but sediments are the long-term storehouses of toxicity. For mollusks and other benthos, contaminants in sediments are and will be a problem for years to come.

In a detailed analysis of three river systems, Patrick (1992) concluded that water quality attributes such as dissolved oxygen, BOD, and ammonia levels have decreased, but concentrations of nitrates have tended to remain the same or have increased. The possible correlation between nitrogenous compounds (especially nitrate) and declining mussel populations needs further evaluation, as judged by European studies (Bauer 1988). According to Smith et al. (1987), fertilizer application rates increased 68% between 1970 and 1981 to bolster farm production. Nitrates from fertilized acreage, greater livestock densities, feedlots, and atmospheric deposition have increased nutrient loading to East Coast and Gulf Coast rivers and estuaries. Total nitrogen trends now seem to be more related to nonpoint-source than point-source effluents (Smith et al. 1987). Agriculture is the most prominent of nonpoint sources of pollutants and is calculated to affect more than two-thirds of the nation's river basins (USEPA 1984). Agriculture, although an industry, has had few regulations imposed for runoff control, and most programs are voluntary. An expansion of programs to mitigate nonpoint pollution from agriculture is long overdue.

The time is rapidly approaching when nonpoint-source pollution from agriculture, road systems, golf courses, parking lots, and other land uses, debilitating to water quality but not sewered and treated, will be our greatest problem. With human population growth and suburbanization, more fields and forests are converted to residential areas of high runoff potential. We observe frequent modifications of our hometown landscapes and receiving waterways from additional roadways, shopping malls, housing developments and other intrusions caused by conventional economic development. Similarly, pesticide use has increased steadily, principally because we as consumers demand perfect produce in the marketplace. Consumer standards for goods and services have promoted increases in soil erosion, fertilizer and pesticide use, and the landscape necrology induced by our prodigal and profligate life styles.

Future Outlook

There is no hope of returning to pristine ecosystems and little hope of maintaining the biodiversity that exists today. The power of humans to degrade the natural world is awesome; the capability to reconstitute it later is mythical (Lindburg 1992). Flagrant egocentrism, benign neglect, and lack of reverence for all life forms have resulted in a world of perpetual change, occurring too quickly for evolution to keep pace and too extensively for biologists to impede most extirpations and extinctions. Mussel biologists seethe at the thought of sacrificing a mussel bed to a development project. Large beds may serve as critical nodes in the reproductive network throughout a river. These keystone beds of recruitment and stability are particularly critical to sustainability of some populations. Each link lost in a chain of mussel beds for a river may be the one most crucial for reproduction, recruitment, and stability of particular species or the entire assemblage. Judgements made by regulatory agencies in the permit review process are, therefore, crucial; mistakes in underestimating project or effluent impacts can be irreconcilable for rare species, to the extreme that the final resting places of species are in cabinets of museum collections.

Humanity will dictate policy on mollusk survival in the 21st century. Therefore, it would behoove us to affect human conscience and behavior sufficiently to instill value to invertebrate species and the messages that they send us on environmental quality. Public education through mass media is our most effective route. As spokespersons for the mussel fauna, we must argue their case based on sheer numbers in decline and their utility as indicators of environmental degradation. Water quality and the biological integrity of river systems are essential to the health, economic prosperity, and long-term survival of humans.

Unless and until the legislative mandates and management policies throughout North America are balanced to enhance and conserve as well as develop and exploit riverine ecosystems, the loss of mussel species will be the first wave of modern extinctions to characterize our superficial concern for species living in the turbulence of our downstream wake.

Literature Cited

Anderson, R.M. 1989. The effect of coal surface mining on endangered freshwater mussels (Mollusca: Unionoidea) in the Cumberland River drainage. M.S. thesis, Tennessee Technological University, Cookeville. 82 pp.

Athearn, H.D. 1970. Discussion of Dr. Heard's paper. Malacologia 10(1):28–31.

Baker, F.C. 1928. Freshwater Mollusca of Wisconsin. Part II. Pelecypoda. Bulletin of the Wisconsin Geological and Natural History Survey 70(2):1–495.

Bauer, G. 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in central Europe. Biological Conservation 45(4):239–254.

Becker, C.D. and D. A. Neitzel. 1992. Water quality in North American river systems. Battelle Press, Richland, Washington. 304 pp.

Benke, A. C. 1990. A perspective on America's vanishing streams. Journal of the North American Benthological Society 9:77–88.

Cairns, J., J. S. Crossman, K. L. Dickson, and E. E. Herricks. 1971. The recovery of damaged streams. Association of Southeastern Biologists Bulletin 18:79–106.

Chamberlain, T. K. 1934. The glochidial conglutinates of the Arkansas fanshell, *Cyprogenia aberti* (Conrad). Biological Bulletin 66:55–61.

Coker, R. E., A. F. Shira, H. W. Clark, and A. D. Howard. 1921. Natural history and propagation of fresh-water mussels. Bulletin of the U.S. Bureau of Fisheries 37:77–181.

Coon, T.G., J.W. Eckblad, and P. M. Trygstad. 1977. Relative abundance and growth of mussels (Mollusca: Eulamellibranchia) in pools 8, 9, and 10 of the Mississippi River. Freshwater Biology 7:279–285.

Dartnall, H.J.G., and M. Walkey. 1979. The distribution of glochidia of the swan mussel, *Anodonta cygnea* (Mollusca), on the three-spined stickleback, *Gasterosteus aculeatus* (Pisces). Journal of Zoology (London) 189:31–37.

Davenport, D., and M. Warmouth. 1965. Notes on the relationship between the freshwater mussel *Anodonta implicata* Say and the alewife *Pomolobus pseudoharengus* (Wilson). Limnology and Oceanography (Supplement) 10:74–78.

Ellis, M.M. 1931. Some factors affecting the replacement of the commercial fresh-water mussels. U.S. Bureau of Fisheries Economic Circular 7:1–10.

Ellis, M.M. 1936. Erosion silt as a factor in aquatic environments. Ecology 17(1):29–42.

Fremling, C.R., and T.O. Claflin. 1984. Ecological history of the Upper Mississippi River. Pages 5–24 *in* J. G. Wiener, R.V. Anderson and D.R. McConville, eds. Contaminants in the Upper Mississippi River: Proceedings of the 15th Annual Meeting of the Mississippi River Research Consortium. Butterworth Publishers, Boston, Massachusetts.

Fuller, S.L.H. 1980. Freshwater mussels (Mollusca: Bivalvia: Unionidae) of the upper Mississippi River: Observations at selected sites within the 9-foot navigation channel project for the St. Paul District, United States Army Corps of Engineers, 1977–1979. Volume I. Final report, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania. 175 pp.

Goldfarb, W. 1984. Water law. Butterworth Publishers, Boston, Massachusetts.

Goudreau, S., R.J. Neves, and R.J. Sheehan. 1993. Effects of wastewater treatment plant effluents on freshwater mollusks in the upper Clinch River, Virginia, U.S.A. Hydrobiologia 252(3):211–230.

Grier, N.M. 1922. Observation on the rate of growth of the shell of lake dwelling fresh water mussels. American Midland Naturalist 8(6):129–148.

Havlik, M.E., and L.L. Marking. 1987. Effects of contaminants on naiad mollusks (Unionidae): a review. U.S. Fish and Wildlife Service Resource Publication 164. 20 pp.

Hendelberg, J. 1960. The fresh-water pearl mussel, *Margaritifera margaritifera* (L.). Report of the Institute of Freshwater Research Drottningholm 41:149–171.

Hoggarth, M.A. 1992. An examination of the glochidia-host relationships reported in the literature for North American species of Unionacea (Mollusca: Bivalvia). Malacology Data Net 3(1–4):1–30.

Hunter, R.D. and J.F. Bailey. 1992. *Dreissena polymorpha* (zebra mussel): colonization of soft substrata and some effects on unionid bivalves. The Nautilus 106(2):60–67.

Jacobson, P.J. 1990. Sensitivity of early life stages of freshwater mussels (Bivalvia: Unionidae) to copper. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg. 162 pp.

Johnson, I.C. 1990. Proposed guide for conducting acute toxicity tests with the early-life stages of freshwater mussels. Final report. U.S. Environmental Protection Agency, EPA contract number 68–024278.

Jorgensen, S.E., and R.W. Sharp, eds. 1971. Proceedings of a symposium on rare and endangered mollusks (naiads) of the U.S. U.S. Fish and Wildlife Service, Twin Cities, Minnesota. 79 pp.

Kat, P.W. 1982. Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia: Unionidae). Malacological Review 15(1–2):199–127.

Kraemer, L.R. 1970. The mantle flap in three species of *Lampsilis* (Pelecypoda: Unionidae). Malacologia 10(1):225–282.

Lewis, J. 1868. Remarks on the mollusks of the Valley of the Mohawk. American Journal of Conchology 4:241–245.

Lindburg, D.G. 1992. People, millennium arks, and the future of wildlife. Zoo Biology 11:137–138.

Marking, L.L., and T.D. Bills. 1979. Acute effects of silt and sand sedimentation on freshwater mussels. Pages 204–211 *in* J. L. Rasmussen, ed. Proceedings of the UMRCC symposium on Upper Mississippi River bivalve mollusks. UMRCC, Rock Island, Illinois. 270 pp.

McCann, M.T., and R.J. Neves. 1992. Toxicity of coal-related contaminants to early life stages of freshwater mussels in the Powell River, Virginia. Final report. U.S. Fish and Wildlife Service, Asheville, North Carolina. 92 pp.

Neves, R.J., L.R. Weaver, and A.V. Zale. 1985. An evaluation of host fish suitability for glochidia of *Villosa vanuxemi* and *V. nebulosa* (Pelecypoda: Unionidae). American Midland Naturalist 113(1):13–19.

Neves, R.J., and J.C. Widlak. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. American Malacological Bulletin 5(1):1–7.

Neves, R.J., and S.N. Moyer. 1988. Evaluation of techniques for age determination of freshwater mussels (Unionidae). American Malacological Bulletin 6(2):179–188.

Ortmann, A.E. 1909. The destruction of the fresh-water fauna in western Pennsylvania. Proceedings of the American Philosophical Society 48:90–110.

Ortmann, A.E. 1918. The nayades (freshwater mussels) of the upper Tennessee drainage with notes on synonymy and distribution. Proceedings of the American Philosophical Society 57:521–626.

Patrick, R. 1992. Surface water quality: have the laws been successful? Princton University Press, Princeton, New Jersey. 198 pp.

Rand, G.M., and S.R. Petrocelli. 1985. Fundamentals of aquatic toxicology. Hemisphere Publishing Corporation, New York. 666 pp.

Schindler, D.W. 1989. Biotic impoverishment at home and abroad. Bioscience 39:426.

Schloesser, D.W. and W.P. Kovalak. 1991. Infestation of unionids by *Dreissena polymorpha* in a power plant canal in Lake Erie. Journal of Shellfish Research 10:355–359.

Sheehan, R.J., R.J. Neves, and H.E. Kitchel. 1989. Fate of freshwater mussels transplanted to formerly polluted reaches of the Clinch and North Fork Holston rivers, Virginia. Journal of Freshwater Ecology 5(2):139–149.

Smith, R.A., R.B. Alexander, and M.G. Wolman. 1987. Water-quality trends in the nation's rivers. Science 235:1607–1615.

Stansbery, D.H. 1961. The naiades (Mollusca, Pelecypoda, Unionacea) of Fishery Bay, South Bass Island, Lake Erie. Sterkiana 5:1–37.

Stansbery, D.H. 1970. Eastern freshwater mollusks (I): the Mississippi and St. Lawrence River systems. Malacologia 10(1):9–22.

Stansbery, D.H. 1971. Rare and endangered freshwater mollusks in eastern United States. Pages 5–18 *in* S. E. Jorgensen and R. W. Sharp eds. Proceedings of a symposium on rare and endangered mollusks (naiads) of the U.S. U.S. Fish and Wildlife Service, Twin Cities, Minnesota.

Surber, T. 1912. Identification of the glochidia of freshwater mussels. United States Bureau of Fisheries Document Number 771:1–10.

Taylor, R.W. 1989. Changes in freshwater mussel populations of the Ohio River: 1,000 BP to recent times. Ohio Journal of Science 89(5):188–191.

Trdan, R.J. 1981. Reproductive biology of *Lampsilis radiata siliquoidea* (Pelecypoda: Unionidae). American Midland Naturalist 106(2):243–248.

Turgeon, D.D., A.E. Bogan, E.V. Coan, W.K. Emerson, W.G. Lyons, W.L. Pratt, C.F.E. Roper, A. Scheltema, F.G. Thompson, and J.D. Williams. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. American Fisheries Society Special Publication 16, Bethesda, Maryland. 277 pp.

USEPA. 1984. Report to Congress: nonpoint source pollution in the U.S. EPA. Office of Water Program Operations, Washington, D.C.

Yeager, B.L., and R.J. Neves. 1986. Reproductive cycle and fish hosts of the rabbit's foot mussel, *Quadrula cylindrica strigillata* (Mollusca: Unionidae) in the upper Tennessee River drainage. American Midland Naturalist 116(2):329–340.

Editor's Note

Since this paper was presented (October 1992), an additional 14 species of freshwater mussels have been added to the federal Endangered Species List (see table below). This brings the total number of federally endangered mussel species to 56, or 19% of the North American fauna.

Epioblasma metastriata (Conrad, 1840)	upland combshell
Epioblasma othcaloogensis (I. Lea, 1857)	southern acornshell
Epioblasma torulosa rangiana (I. Lea, 1839)	northern riffleshell
Lampsilis altilis (Conrad, 1834)	fine-lined pocketbook
Lampsilis perovalis (Conrad, 1834)	orange-nacre mucket
Lasmigona decorata (I. Lea, 1852)	Carolina heelsplitter
Medionidus acutissimus (I. Lea, 1831)	Alabama moccasinshell
Medionidus parvulus (I. Lea, 1860)	Coosa moccasinshell
Pleurobema clava (Lamarck, 1819)	clubshell
Pleurobema decisum (I. Lea, 1831)	southern clubshell
Pleurobema furvum (Conrad, 1834)	dark pigtoe
Pleurobema georgianum (I. Lea, 1841)	southern pigtoe
Pleurobema perovatum (Conrad, 1834)	ovate clubshell
Ptychobranchus greenii (Conrad, 1834)	triangular kidneyshell