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CONSERVATION AND COMMERCE: MANAGEMENT OF FRESHWATER MUSSEL (BIVALVIA: UNIONOIDEA) RESOURCES IN THE UNITED STATES

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ABSTRACT

The United States is blessed with the world's greatest diversity of freshwater mussels (Unionoidea), providing numerous ecological, scientific, and economic benefits to the nation. However, as a result of intense economic development in the 19th and 20th centuries, this fauna was subjected to habitat destruction, water pollution, and benign neglect that resulted in the loss of populations and species. Presently, about 35 mussel species are presumed extinct, 69 species are federally protected as endangered or threatened, and numerous other species are candidates for protection. Propagation of these endangered species is underway to expedite their recovery. In contrast to this sizable group of rare species, a small assemblage of ubiquitous species occurring in large rivers and reservoirs within the Mississippi River drainage supports a multi-million dollar commercial shell industry. Most shells are shipped to the Far East to provide beads for a thriving cultured pearl industry; however, exports in this decade peaked in 1995 and face an uncertain future. Harvest and management regulations are being unified in the Mississippi River in 1998 to conserve mussel resources from overexploitation, to resolve law enforcement problems among states, and to consider the exotic zebra mussel, *Dreissena polymorpha,* which now infests most commercially exploited unionid populations. In the next decade, the amount of attention given to conservation will decide the fate of this world-class mussel fauna.
Key words: unionoidea, conservation, freshwater, United States.

INTRODUCTION

The decline of species within the superfamily Unionoidea is of international scope, driven by habitat degradation and destruction in river systems that once teemed with an abundance of aquatic mollusks. To address this and other global-scale losses in biological diversity, the International Union for the Conservation of Nature (IUCN) began formalizing lists of endangered species in the early 1960s, to focus attention on the plight of rare species (Mace, 1995). The publication of Red Lists and Red Books by IUCN has promoted the formation of similar national lists of plants and animals in need of protection (Burton, 1984; Thomas & Morris, 1995). Although the focus on species only in such lists will not achieve the desired maintenance of biodiversity and ecological integrity, primarily because habitat loss is not addressed, species continue to be the units of extinction. Therefore, the development of practical strategies to achieve conservation goals and preserve biological diversity must make use of the flagship role played by species, so that public and legislative support can be mobilized for tangible benefits to both the species and their supporting ecosystems.

In a recent review of the global status of mollusks, Kay (1995) highlighted the current unprecedented rate of extinction of mollusks. From an admittedly incomplete data base of 1,130 taxa considered to be endangered, threatened, rare, or recently extinct, three possible explanations for the propensity of mollusks to become endangered were postulated. First, most of these species were essentially restricted to North America (United States), Australia and New Zealand, and Europe. These countries emerge seemingly as trouble spots only because of their more thorough biological inventories and monitoring programs. Thus, this apparent continental or national problem likely reflects a bias in available information. Second, most (98%) of the species are freshwater and terrestrial mollusks, with 61% from only nine families. Again, a possible reason for this phenomenon is the

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available data base on these taxonomic groups. Finally, life history traits shared by these designated families include k-selection, restricted distribution, and specialized habits and habitats. This commonality of biological traits is definitely correlated with endangerment, and describes the reason for declining status of most aquatic and terrestrial biota.

Of the 1,130 species identified as in trouble, 197 (17%) are bivalves and 158 (14%) of those species belong to the superfamily Unionoidea in the United States (Rosenberg, 1995). Because this taxon is recognized as the most endangered group of mollusks in the world, this paper will provide an assessment of the nearly 300 species and subspecies of freshwater mussels in the United States and discuss both conservation measures for the rare species and regulatory management for harvest of the abundant species. The management of this world-class resource has been a challenge for federal and state regulatory agencies; namely, to completely protect some species while allowing the exploitation of other species, often within the same river. My goal is to provide readers with an appreciation of the complexity of management issues, and to describe the conservation measures being implemented to recover rare species and to ensure the viability of all species.

CONSERVATION OF MUSSELS

Threatened and Endangered Species

An assessment of the fauna, flora, and ecosystems of the United States was recently completed to evaluate the state of the nation's environment (LaRoe et al., 1995). Of the roughly 300 species and subspecies of freshwater mussels in the United States, 69 (23%) are included on the federal Endangered Species List (Table 1). The Endangered Species Act (ESA) of 1973 was promulgated to protect a species in danger of extinction or endangerment throughout all or a significant portion of its range. The ESA also has a stated goal to protect the ecosystems that sustain those species considered to be endangered or

TABLE 1. Endangered and threatened species of freshwater mussels in the United States in 1998.

Alasmidonta atropurpurea	Cumberland elktoe	*Lampsilis subangulata*	shinyrayed pocketbook
Alasmidonta heterodon	dwarf wedgemussel	*Lampsilis virescens*	Alabama lampmussel
Alasmidonta raveneliana	Appalachian elktoe	*Lasmigona decorata*	Carolina heelsplitter
Amblema neislerii	fat threeridge	*Lemiox rimosus*	birdwing pearlymussel
Arkansia wheeleri	Ouachita rock pocketbook	*Margaritifera hembeli*	Louisiana pearlshell
Cyprogenia stegaria	fanshell	*Medionidus acutissimus*	Alabama moccasinshell
Dromus dromas	dromedary pearlymussel	*Medionidus parvulus*	Coosa moccasinshell
Elliptio chipolaensis	Chipola slabshell	*Medionidus penicillatus*	gulf moccasinshell
Elliptio steinstansana	Tar River spinymussel	*Medionidus simpsonianus*	Ochlockonee moccasinshell
Elliptoideus sloatianus	purple bankclimber	*Obovaria retusa*	ring pink
Epioblasma brevidens	Cumberlandian combshell	*Pegias fabula*	littlewing pearlymussel
Epioblasma capsaeformis	oyster mussel	*Plethobasus cicatricosus*	white wartyback
Epioblasma florentina curtisii	Curtis pearlymussel	*Plethobasus cooperianus*	orangefoot pimpleback
Epioblasma florentina florentina	yellow blossom	*Pleurobema clava*	clubshell
Epioblasma florentina walkeri	tan riffleshell	*Pleurobema collina*	James spinymussel
Epioblasma metastriata	upland combshell	*Pleurobema curtum*	black clubshell
Epioblasma obliquata obliquata	catspaw	*Pleurobema decisum*	southern clubshell
Epioblasma obliquata perobliqua	white catspaw	*Pleurobema furvum*	dark pigtoe
Epioblasma othcaloogensis	southern acornshell	*Pleurobema georgianum*	southern pigtoe
Epioblasma penita	southern combshell	*Pleurobema gibberum*	Cumberland pigtoe
Epioblasma torulosa gubernaculum	green blossom	*Pleurobema marshalli*	flat pigtoe
Epioblasma torulosa rangiana	northern riffleshell	*Pleurobema perovatum*	ovate clubshell
Epioblasma torulosa torulosa	tubercled blossom	*Pleurobema plenum*	rough pigtoe
Epioblasma turgidula	turgid blossom	*Pleurobema pyriforme*	oval pigtoe
Fusconaia cor	shiny pigtoe	*Pleurobema taitianum*	heavy pigtoe
Fusconaia cuneolus	finerayed pigtoe	*Potamilus capax*	fat pocketbook
Hemistena lata	cracking pearlymussel	*Potamilus inflatus*	Alabama heelsplitter
Lampsilis abrupta	pink mucket	*Ptychobranchus greenii*	triangular kidneyshell
Lampsilis altilis	finelined pocketbook	*Quadrula cylindrica strigillata*	rough rabbitsfoot
Lampsilis higginsii	Higgins eye	*Quadrula fragosa*	winged mapleleaf
Lampsilis perovalis	orangenacre mucket	*Quadrula intermedia*	Cumberland monkeyface
Lampsilis powelli	Arkansas fatmucket	*Quadrula sparsa*	Appalachian monkeyface
Lampsilis streckeri	speckled pocketbook	*Quadrula stapes*	stirrupshell
		Toxolasma cylindrellus	pale lilliput
		Villosa perpurpurea	purple bean
		Villosa trabalis	Cumberland bean

threatened in the United States. Scientists postulate that more than 500 species of plants and animals became extinct in the United States, primarily due to habitat loss and degradation (U. S. Fish and Wildlife Service, 1995). Unfortunately, some of the mussel species that are on the list are presumed extinct (Table 2). Soon after the law was implemented, 23 species of unionids were added to the list in 1976, in response to a petition to list all animals on the Appendix I list of the Conservation on International Trade in Endangered Species (CITES). Subsequent listing of mussel species has occurred sporadically, reflecting federal priorities, political climate, delays in the acquisition of sufficient data, and other requirements specified in the listing process (Fig. 1). The chronology of mussel species listed for federal protection, beginning in 1987, represents recognition of a backlog of species in need of protection, group listings of species within the same river, and the tenacity of the staff biologists responsible for preparing the documents needed to qualify particular species for protection.

Each mussel species on the endangered species list has a recovery plan prepared, which identifies the problems threatening the species and the actions needed to correct them. The plan summarizes our knowledge of the status, biology, and threats, and focuses on recovery actions essential to maintain existing populations and to re-establish sufficient historic populations so that the species can eventually be downlisted to threatened status or delisted. Because of the highly clustered, geographic distribution of federally listed species (Fig. 2), states such as Alabama and Tennessee are much more involved with recovery than other states. Recovery can involve natural increases in the abundance and range of a species due to improvements in habitat quality or availability, as well as human-assisted increases through habitat restoration, amelioration of threats, or artificial propagation. The goal is to implement those courses of action that will ultimately lead to the species' recovery. In the case of freshwater mussels, some species are in such critical condition that the only realistic goal at this time is to prevent extinction. These species in the "basket case" category are usually given highest priority so that the likelihood of near-term extinction may be reduced. Recovery of the remaining species is actively being pursued through improvements in physical habitat and water quality, as well as propagation through cooperative efforts between the U. S. Fish and Wildlife Service and the states where those species reside. Implementation of a recovery plan is a lengthy and difficult process, dependent less on biology than the human dimension to resource management. Without the support of numerous federal and state regulatory agencies, community leaders responsible for land management, and myriad other stakeholders, recovery would not be possible.

An evaluation of the number and distribution of protected species provides an effective means to identify watersheds in greatest need

TABLE 2. Species of freshwater mussels presumed extinct in the United States in 1998.

Alasmidonta mccordi	Coosa elktoe
Alasmidonta robusta	Carolina elktoe
Alasmidonta wrightiana	Ochlockonee arcmussel
Elliptio nigella	winged spike
Epioblasma arcaeformis	sugarspoon
Epioblasma biemarginata	angled riffleshell
Epioblasma flexuosa	leafshell
Epioblasma florentina florentina	yellow blossom
Epioblasma haysiana	acornshell
Epioblasma lenior	narrow catspaw
Epioblasma lewisii	forkshell
Epioblasma obliquata obliquata	catspaw
Epioblasma personata	round combshell
Epioblasma propinqua	Tennessee riffleshell
Epioblasma sampsonii	Wabash riffleshell
Epioblasma stewardsonii	Cumberland leafshell
Epioblasma torulosa gubernaculum	Green blossom
Epioblasma torulosa torulosa	tubercled blossom
Epioblasma turgidula	turgid blossom
Lampsilis binominata	lined pocketbook
Medionidus mcglameriae	Tombigbee moccasinshell
Pleurobema altum	highnut
Pleurobema avellanum	hazel pigtoe
Pleurobema bournianum	Scioto pigtoe
Pleurobema chattanoogaense	painted clubshell
Pleurobema flavidulum	yellow pigtoe
Pleurobema hagleri	brown pigtoe
Pleurobema hanleyianum	Georgia pigtoe
Pleurobema johannis	Alabama pigtoe
Pleurobema murrayense	Coosa pigtoe
Pleurobema nucleopis	longnut
Pleurobema rubellum	Warrior pigtoe
Pleurobema troschelianum	Alabama clubshell
Pleurobema verum	true pigtoe
Quadrula couchiana	Rio Grande monkeyface
Quadrula tuberosa	rough rockshell

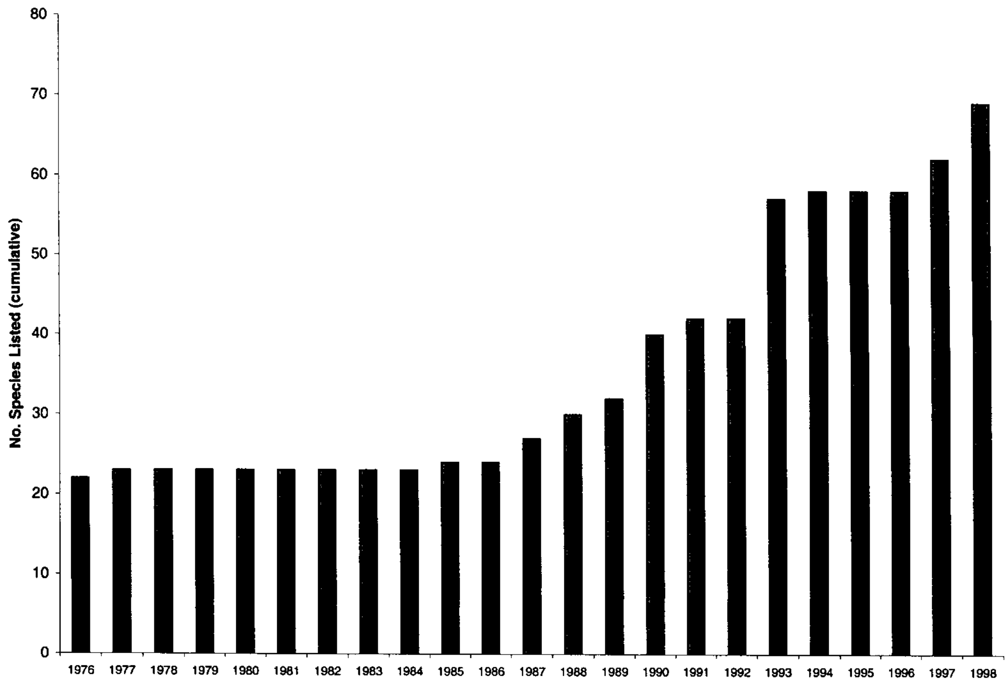

FIG. 1. Chronology of freshwater mussel species listed under the federal Endangered Species Act, 1976–1998.

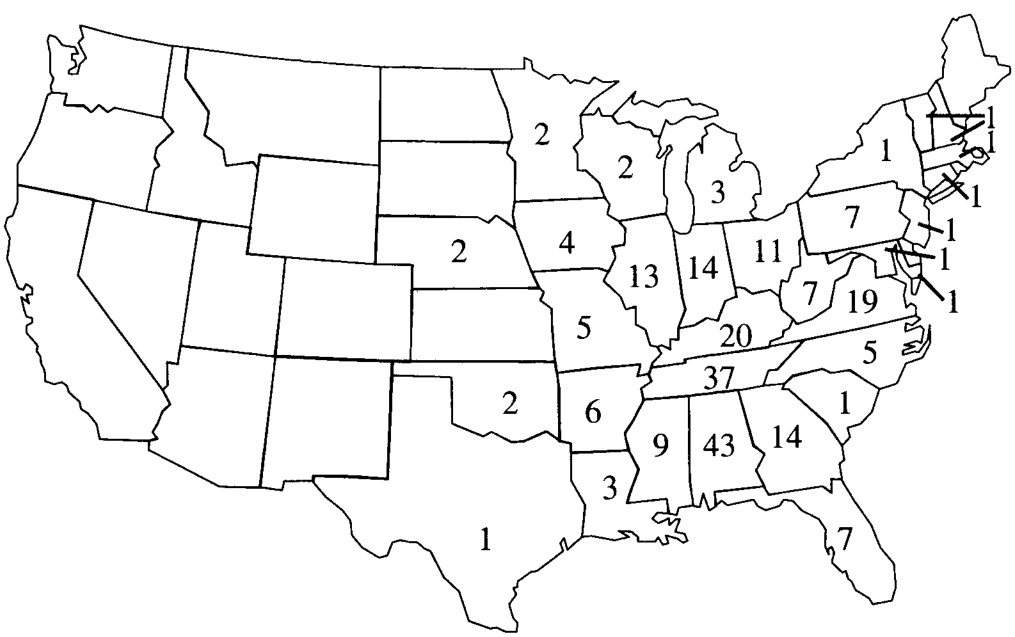

FIG. 2. Numbers of federally endangered and threatened species of freshwater mussels in the various states.

of conservation efforts. As with most endangered or threatened species, the principle cause for their decline and endangerment is cumulative habitat alteration and destruction. The Tennessee River system provides an excellent case study and one of the best-documented descriptions of molluscan changes from anthropogenic manipulations of a large river. Therefore, the next section will describe the effects of habitat alteration over the last 60 years.

Tennessee River Case Study

The Tennessee River drainage in the southeastern U.S. includes watersheds in seven states: Tennessee, Virginia, North Carolina, Georgia, Alabama, Mississippi, and Kentucky. Within this river system of roughly 105,000 km^2 is the richest fish and mussel fauna for its size of any temperate river system in the world (Starnes & Ethnier, 1986). The 224 taxa of native fishes and 91 taxa of mussels were widespread in habitats ranging from headwater streams to small natural lakes and the mainstream river. Because the species richness of mussels often is correlated with the diversity and abundance of their host fishes, environmental alterations could directly affect mussel populations and indirectly affect long-term viability through effects on host fishes. Thus, the ecosystem's biotic and ecological integrity was vulnerable to large-scale changes from human intervention.

Documented watershed-scale changes began in the 1930s when the Tennessee Valley Authority (TVA) was established by Congress in 1933 to produce electricity, control flooding, and improve navigation in the Tennessee River Valley. With these goals in mind, the TVA proceed to build 36 multi-purpose dams, with nine of these on the mainstem Tennessee River. The effects of these dams on aquatic fauna, both in the impoundments and in downstream tailwaters were immediate (Yeager, 1993). The chain of reservoirs on the Tennessee River essentially eliminated free-flowing river reaches, causing much more dramatic changes in the mussel fauna than in the fish fauna (Starnes & Etnier, 1986). Obligatory riverine species began to decline and disappear within the impoundments. Along with the gradual loss of many unionids (Isom, 1969), there was a concurrent increase in resident lentic-tolerant species and a few species that invaded the new reservoirs. These invasive species, either by host fish immigration or through the initiative of commercial harvesters, eventually formed large populations that became the focus of a commercial shell industry in Tennessee and Kentucky. It appears that only one fish species became extinct in the Tennessee River (Starnes & Etnier, 1986), whereas 30 species of mussels became extinct or were extirpated from the river (Neves et al., 1997). Perhaps the refugia for fishes were the lower portions of large, free-flowing tributaries that remained unimpounded and allowed populations of so-called "big river" fishes to survive. The sedentary and more vulnerable mussel species were unable to escape as a population, during the relatively brief period of inundation. The current status of the 91 native unionoid species of the Tennessee River is as follows: 10 extinct, 20 extirpated, 24 endangered, 9 relic, and 28 stable at this time. Thus, a diverse riverine fauna was replaced by a depauperate, lentic-tolerant assemblage of species as a result of increased sedimentation, minimal flow, loss of host fishes, reduced dissolved oxygen, and other hydrologic changes typical of newly constructed reservoirs.

Downstream of these dams, similar biotic changes were underway. The TVA dams were constructed with water intake structures low on the dam to increase hydropower efficiency (Krenkel et al., 1979). From the hypolimnion, the cold water discharges drastically altered the seasonal temperature regime in tailwaters. Because short-term brooders (subfamily Ambleminae) require warm summer temperatures to initiate gametogenesis, spawning, glochidia release, and the presence of warm-water fishes to serve as hosts, unionid populations experienced reproductive failures (Heinricher & Layzer, 1999). Long-term brooders (subfamily Lampsilinae) also were negatively affected by the low water temperature's effects on reproductive biology and host fishes, such that declines in mussel populations occurred over several decades. Senescent mussels still reside below many of these dams as reminders of the biological cost to improve standards of living for residents of the valley. The richest fauna of freshwater mussels became, in roughly five decades, a shell of its former self.

Water Quality Management

Water pollution in rivers became a major problem to mussels in U.S. rivers since the late 1800s. Lewis (1868), Smith (1899), and Ortmann (1918) recorded the damage to mussel beds resulting from industrial wastes, sewage, and myriad chemicals dumped into public waterways. Nearly every major river in the U.S. experienced acute or chronic pollution events during the twentieth century, resulting in precipitous declines in its mussel fauna.

Much of the improvement in water quality over the last 25 years has been derived principally from improvements in municipal wastewater discharges (Smith et al., 1987). The investment of roughly $300 billion in the construction and operation of wastewater treatment plants has produced noticeable improvements in some rivers and only slight improvements in others (USEPA, 1984, 1994; Smith et al., 1987). The environmental stress and altered characteristics and functions of streams caused by exploitative users and modifications are obviously reflected in the status of freshwater fisheries (Judy et al., 1984). Undoubtedly, what causes stress to the fish community also has an adverse effect on the mussel community through host fish availability and their similar physiological requirements for survival. More than 50% of the nation's rivers have fish communities adversely affected by turbidity, high temperature, toxins, and low dissolved oxygen (USEPA, 1994). Roughly 40% of perennial streams are affected by low flow, siltation, bank erosion, and channelization. Annual sediment loads in major rivers range from 111 million to 1.6 trillion metric tons, with roughly 75% deposited in river beds, reservoirs, or flood plains. Although improvements in water quality have occurred, there is still the need for an integrated policy to protect and enhance water quality to sustain societal benefits (Water Environment Federation, 1992).

Although the mussel fauna in many rivers continues to decline from marginal to unsuitable habitat conditions, the restoration of rivers that serve as historic habitat for federally protected and other mussel species has been underway since about 1970. The U.S. is home to more than 5.1 million kilometers of streams and rivers. Early laws, such as the River and Harbors Act of 1899, were promulgated to prevent further degradation of rivers from refuse disposal, while others, such as the Water Pollution Control Act of 1948, attempted to abate water pollution. However, effective environmental legislation began with the National Environmental Policy Act of 1970. Its goal was to prevent or eliminate damage to the environment and biosphere, to enrich our understanding of ecological systems and natural resources of national importance, and to bring society into harmony with nature. This was a tall order to fill, in a nation bent on sustaining its gross national product and stature in the global economy. Environmental protection became a national priority, which led to further legislation to improve the quality of our land and water resources. A flurry of environmental legislation followed to address various national concerns, but the Clean Water Act of 1972 became the most significant law to maintain and restore rivers and streams long abused by effluent discharges. The goal of this Act is "to restore and maintain the chemical, physical, and biological integrity of the Nation's water". One of its specific objectives is to allow for the protection and enhancement of fish, shellfish, and wildlife through the elimination of harmful pollutants discharged into national waterways. National standards and regulations to promote clean water were established. As a result, there are numerous success stories over the last 25 years of rejuvenated rivers with recoveries of native fauna, due largely to this single piece of legislation (National Research Council, 1992; Becker & Neitzel, 1992).

Current degradation in water quality of our national waterways stems mostly from deleterious management practices on the landscape. In 1970, the major problem was point-source discharges of effluents from a variety of sources. Today, nonpoint source pollution is the leading cause of impairment (USEPA, 1994). Rivers continue to be plagued by elevated levels of bacteria and silt, derived primarily from agriculture and municipal wastewater treatment plants. Nitrate concentrations continue to be high in surface waters downstream of agricultural areas, whereas elevated levels of ammonia and phosphorus occur primarily downstream of urban areas (Mueller et al., 1995). Because half of all citizens receive their drinking water from surface water supplies (Mueller et al., 1995), public health is also at issue and a motivating force to continue the national focus on improving water quality, particularly in rivers degraded by sediment and nutrients derived from agriculture. If agricultural pollution can be reduced, then nearly every river of present or historic significance for unionids will become suitable for restoration of its native fauna.

A determination of existing water quality problems in each river is critical to prioritizing recovery actions in watersheds with endangered species. Using this knowledge and the known effects of degrading physical and chemical factors on survival of unionid populations, and the life history and ecology of each species, a team of natural resource specialists can plan an effective recovery of the fauna to accommodate current conditions that limit natural recovery. As judged by current trends in ambient water quality at the state and national levels, and the level of effort and expenditures to achieve adequate water quality in most river systems, I believe that sufficient suitable habitat soon will be available to recover many federally endangered mussel species. The availability and suitability of habitat in rivers for endangered mussel species is sufficient to initiate recovery actions now for most species. Thus, the bottleneck to recovery of endangered and threatened mussels is less an issue of habitat now as it is the biological traits of disjunct residual populations and the cost to achieve recovery. Low density, population isolation, and reproductive failure are the key biological factors in preventing natural recovery of these rare species, whereas required financial commitments impede the implementation of recovery plans.

Zebra Mussels

A brief overview of conservation of mussel resources in the U.S. would not be complete without mention of the exotic zebra mussel, which now threatens many mussel species in large rivers and reservoirs of the eastern U.S. From an establishment in Lake St. Clair in 1986 (Hebert et al., 1989), the zebra mussel quickly swept through the Great Lakes in five years and entered the Mississippi River system in 1991 through the Illinois River (Whitney et al., 1995). The trail of devastation to native unionoids in the Great Lakes is well documented (Nalepa & Schloesser, 1993), and now a similar scenario is being displayed in rivers with numerous commercial vessels, infested with zebra mussels and serving as vectors of dispersal. Although quantification of the mortality being suffered by native mussels in rivers is incomplete (Hunter et al., 1997), severe mortality at sites in the Ohio River is now confirmed, and various levels of mortality in the Mississippi and Illinois rivers have been reported (Tucker, 1994; Ricciardi et al., 1998). As of 1998, the zebra mussel is confirmed in at least 19 states and more than 100 lakes throughout this region of infestation (Amy Benson, USGS, Gainesville, Florida, pers. comm.). The zebra mussel continues to spread to new waterways through principally anthropogenic means, and the worst fears of malacologists are being fulfilled. The continued existence and recovery of rare unionids in mainstem rivers is undoubtedly in jeopardy, and implementation of a national strategy to address this exotic species and other serious threats is long overdue.

COMMERCIAL HARVEST OF MUSSELS

Shell Buttons

Although the exploitation of freshwater mussels for making pearl buttons dates back to at least 1800 (Coker, 1919), a thriving industry did not develop until John Boepple set up his button business in Iowa in 1891. Species of mussels used to manufacture buttons had to meet the following requirements: white nacre, iridescent, solid crystalline structure, smooth surfaces, uniform thickness, and adequate size and shape to yield several buttons blanks (Coker, 1919). Using these criteria, commercial harvesters exploited such species as washboard (*Megalonaias nervosa*), yellow sandshell (*Lampsilis teres*), mucket (*Actinonaias ligamentina*), black sandshell (*Ligumia recta*), and ebonyshell (*Fusconaia ebena*) because of their localized abundance and excellent shell quality. The ebonyshell was the preferred species because it possessed all of the traits needed to produce top quality buttons.

As the industry expanded in production and geographic range, from the mainstem Mississippi River into major tributaries such as the Ohio River, overexploitation of mussel beds and preferred species mandated that other species be harvested to meet the demand for shells. By the late 1890s, a "shell rush" to supply the button industry swept through the Mississippi River Valley (Table 3). Although harvest records are incomplete, the extent of exploitation was intense (Claassen, 1994). As mussel beds became depleted and resource abundance declined, the market value of shells increased, stimulating further intensive and extensive harvest in old and new river reaches. The insatiable demand for buttons in the burgeoning manufactured clothing industry created an influx of new harvesters and reexploitation of new and old mussel beds, as less desirable species became acceptable.

The frenzied harvest made use of various techniques to collect the mussels from shallow and deep water areas of lakes and rivers. Hand collecting, clam tongs, pitchforks, rakes,

TABLE 3. Tons of mussel shells harvested for button production in selected years from the Mississippi River Valley, 1898–1944.

Year	Tons of Shell
1898	3,641
1899	23,824
1908	38,133
1912	55,671
1929	27,176
1933	30,146
1937	26,993
1941	17,381
1944	20,300

and dredges were commonly used, but brailing was the predominant technique used in rivers. The standard brail bar was about 4 m long, with crowfoot hooks attached by chains to the bar. The crowfoot hooks were constructed of galvanized wires in various hook-design configurations, with four prongs and a bulbous tip on each prong to prevent mussels from slipping off the hook. The brail bar and attached hooks, suspended on a rope, was bounced along the river bottom as the boat drifted downstream. When the hook moves across a gaped mussel, the mussel closes on the hook and is pulled from the substratum. After several minutes of dragging the hooks, the brail is brought to the surface to remove attached mussels. This basic brail design and method of brailing is still in use in the Mississippi River basin, although surface-supplied air diving is much more common today.

Harvested mussels were brought ashore to shell camps where they were steamed open in large vats. It was at this stage that natural pearls were discovered and sought in the cooking vats and mussel meats. Quality pearls fetched a handsome reward from local jewelers. The shells were sorted, meats were discarded, and specimens were taken to the factories where the button blanks were cut, drilled, polished, and processed for shipment to garment factories in the eastern U.S. In its heyday, the button industry consisted of more than 100 factories and tens of thousands of workers (Claasen, 1994). However by the early 1940s the availability of plastic buttons, zippers, automated button sewing machines, strong detergents and other advancements spelled the demise of this once lucrative but resource-damaging venture. Except for small businesses working specialty buttons from shells into the 1960s, the once thriving button industry perished by the late 1940s.

Cultured Pearls

During the boom and bust of the shell button industry, researchers in Japan were attempting to implant bead nuclei into oysters to produce cultured spherical pearls. As early as the 1920s, tons of pigtoe mussels were being shipped to Japan annually to provide the raw material for bead nuclei (Claassen, 1994). By the 1950s, the U.S. became the exclusive source of raw shell for Japan's booming cultured pearl industry. Thus, the mussel populations in the Mississippi River system had only a brief reprieve from exploitation. During this second "shell rush", the lower Tennessee River became an important source of shell. Reservoirs constructed by TVA in the 1940s became repopulated and colonized by several species that were highly sought because of their thick shell, white unstained nacre, and large size. Such species as the washboard, threeridge (*Amblema plicata*), mapleleaf (*Quadrula quadrula*), and Ohio pigtoe (*Pleurobema cordatum*) were abundant and of excellent quality. Shell harvesting in reservoirs as well as in free-flowing rivers became widespread in the Mississippi, Ohio, Tennessee, Cumberland, and other rivers in the central United States.

The resurgence of musseling initially focused on rivers and mussel beds underexploited or unexploited during the intense harvest earlier this century for the pearl button industry. A flotilla of brail boats explored and exploited mussel beds in the Tennessee, Mississippi, Cumberland, Ohio, Wabash, Missouri, and other rivers with commercial stocks of mussel species. In addition to the traditional method of brailing for mussels, diving came into practice in the 1960s. Underwater harvest by surface-supplied air diving began amid a flurry of controversy, but allowed a new suite of harvesters to ply their trade particularly in reservoirs. The competition and controversies between these two user groups (brailers vs. divers) is still unresolved, but the efficiency and selective harvest by divers cannot be denied.

Harvesters sell their catch typically alive, to buyers representing companies of the Shell Exporters Association (Table 4). This nonprofit corporation was chartered in 1994 "to advance the interest in research, environmental protection, and the commercial markets which concern the freshwater mussel". Nearly all of the mussel harvest is passed through one of these companies for process-

TABLE 4. Members of the Shell Exporters Association (SEA) that export mussel shells in United States.

James Peach American Shell Company, Inc. 4805 Old Hickory Blvd. Hermitage, Tennessee 37076 Phone 1-800-251-9372 1-800-248-3064 (205) 359-4345	Nelson Cohen P.O. Box 235 Terre Haute, Indiana 47808-0235 Phone 1-800-222-6436 FAX (812) 234-6198
Butch Ballenger Mississippi Valley Shell Company, Inc. 2579 Stewart Road Muscatine, Iowa 52761 Phone 1-800-882-2526 (319) 264-5883 FAX (319) 264-2053	Tennessee Shell Company, Inc. Highway 70E P.O. Box 647 Camden, Tennessee 38320 Phone 1-800-835-0964 (901) 584-7747 FAX (901) 584-8043
Robert Leasure Leasure Shell Company, Inc. 2612 Jackson, No. 4 Bradford, Arkansas 72020 Phone (501) 523-5028	Peggy Linley Hudson Shell Company, Inc. P.O. Box 965 Decauter, Alabama 35602 Phone (205) 353-6944 FAX (205) 353-2793
Lonnie Garner U.S. Shell Company, Inc. Route 1, Box 323 Hollywood, Alabama 35752 Phone (205) 437-9784	

ing. As in earlier times, the live animals are steamed open in large cookers, passed through rotators to remove the meats, sorted by species and size, and then bagged for shipment via containers to their overseas destination.

The methods of commercial harvest of freshwater mussels have not changed appreciably in the last 30 years. Underwater divers are the principal harvesters, although brailing is still conducted in large rivers and where diving is prohibited (Kentucky). Because there are no safety regulations required of musselers, most divers work alone using principally hookah rigs of imaginative but unsafe design. Exploitation of the mussel resource remains a competitive venture, and to avoid the "tragedy of the commons," management is by restrictive regulations. Most states have no restriction on the number of harvesters for either in-state or out-of-state residents, with higher license fees for non-resident musselers. However, when shell prices are high, the license fees often are recouped during the first day of harvest.

Foreign demand for shell regulates the level of effort and number of people who participate in today's shell industry. An evaluation of the numbers of licenses sold in key states, such as Tennessee and Kentucky, shows a direct correlation between demand (price) and number of licenses sold. When prices are high, part-time divers venture out in summer to supplement their income. When prices are low, only the full-time, hardy musselers continue to ply their trade, even in winter.

The decade of the 1990s has seen a tremendous upheaval in the shell business. Shell exports have exhibited a steady decline since 1993 (Table 5). In the early 1990s, high demand for shell by Japan and other Asian markets created employment and income opportunities for musselers of all ages. John boats dotted the surface of numerous reservoirs and rivers with sought-after species, such as washboards and threeridges. The industry, with an estimated value of $50 million, stimulated local economies in rural towns along these waterways. However, the shell business fell on hard times beginning in 1996 when a major die-off of Akoya pearl oysters occurred in Japan. This mortality, combined with declining value of the yen and the booming Chinese pearl culture industry, has drastically reduced the demand for shell. For the last two years (1997–1998), the shell harvest

TABLE 5. Export of freshwater mussel shells and shell products from the United States to Asian countries, from October 1992–December 1997.

Year	Exported Shell (×1000 kg)*
1992	1,535
1993	6,263
1994	5,352
1995	3,565
1996	2,574
1997	1,329

*Data compiled from LEMIS (U.S. Fish and Wildlife Service)

has been minimal, and most musselers have sought employment elsewhere.

FRESHWATER MUSSEL MANAGEMENT

Management of the freshwater mussel resources in the United States has historically been the responsibility of the states, whereas shell exports are regulated and monitored by the law enforcement branch of the U.S. Fish and Wildlife Service. Shell export records are cataloged in the Law Enforcement Management Information System (LEMIS) of the U.S. Fish and Wildlife Service, and data are retained for the most recent 5–6 year period (Table 5). Nearly all shell exports were destined for Japan, to be processed into beads for the pearl oyster industry.

Like other fish and wildlife resources, the state fish and wildlife agencies should manage freshwater mussels to benefit the residents of their respective states, while assuring conservation of the resource for future generations. Although mussels occur in most rivers and lakes, from western tributaries of the Mississippi River to the East Coast of the United States, not all states allow commercial harvest (Fig. 3). Because of the paucity of viable mussel populations, law enforcement costs, and other factors, some states with commercial species, such as Indiana, West Virginia, Ohio, and Mississippi, do not permit commercial harvest. Complete protection of all species prevents possible violations of the Endangered Species Act through the incidental take of federally listed or state-protected species. Only 14 states allowed commercial harvest in 1997 and only in designated waters (Parrott, 1998). Texas was technically open to shell harvest, but a reduction in minimal daily catch to 25 lb of live mussels or 12 lb of shell essentially precluded commercial musseling. Shell harvests are tightly regulated by the state agencies through permit and harvest reports required of both musselers and shell buyers according to the regulations of state-issued licenses. Each state specifies the species that can be harvested, minimum size limits, open and closed areas, season and time of day, method of capture, and other limitations to prevent overharvest and ensure continued reproduction of harvested species. Unfortunately, harvest regulations are not uniform and vary considerably from state to state (Table 6). Therefore, musselers who travel among states to work must be cognizant of each state's regulations, as violations of state law by ignorance or intent are treated the same.

The mussel resources in the upper Mississippi River are effectively managed by an Upper Mississippi River Conservation Committee (UMRCC), consisting of representatives from Minnesota, Wisconsin, Iowa, Illinois, and Missouri. These five states are working towards unifying management regulations for harvested species in the upper Mississippi River. Although some differences in growth rates occur among mussel subpopulations within various navigation pools of the river, standardized harvest regulations would be biologically sound, facilitate compilation of harvest data for stock assessment, and simplify law enforcement within and among states. An extension of this UMRCC effort to the lower river as well would promote holistic resource management based on biological factors rather than on political boundaries that often interfere with management of widespread species.

State of Tennessee

Because roughly half of the shells exported from the United States are harvested in Tennessee, I will showcase this state's management of the resource. The extent of commercial harvest, number of endangered species, presence of mussel sanctuaries and other factors in Tennessee cover the range of conflicts faced by most states in the management and conservation of freshwater mussels. In 1995, 3881 tons of mussels were harvested in Tennessee, with a wholesale market value of nearly $15 million. Over 90% of these mussels were obtained from Kentucky Lake, touted as perhaps the most productive reservoir for mussels in the nation. Commercial species are abundant in the lake, and the quality of shell is excellent and commands a high price.

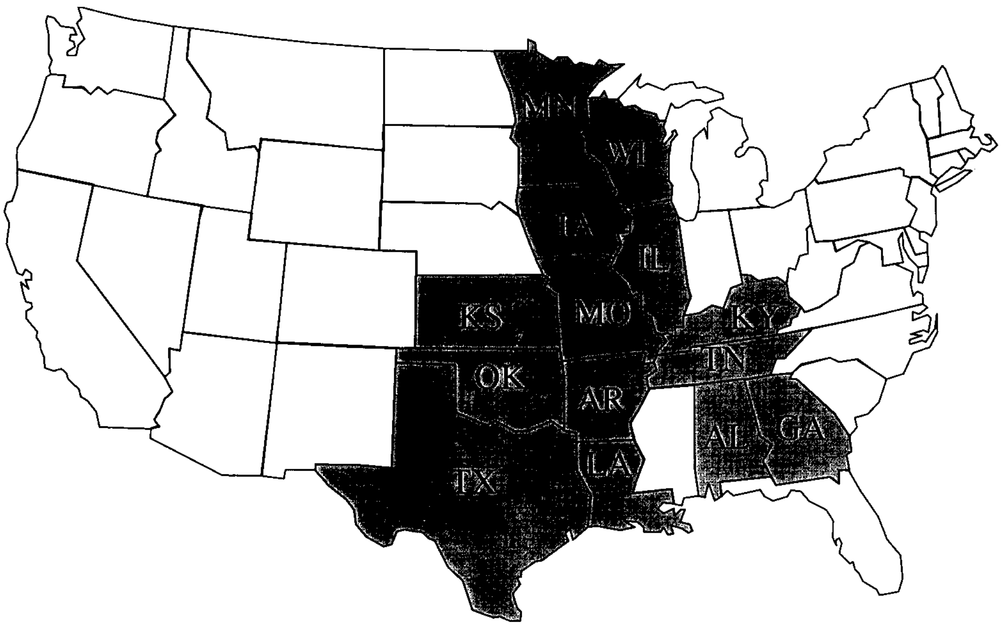

FIG. 3. States that allowed commercial harvest of freshwater mussels in 1997.

TABLE 6. Summary of commercial harvest regulations for freshwater mussels in the United States.

State	No. Species Harvestable	Size Limits[1] (inches)	Season	Methods[2]
Alabama	13	1 ¾–4	year-round	H,B,R,D
Arkansas	16	2 ¼–4	year-round	H,B,D
Georgia	0	>4	4/1–8/31	H,D
Illinois	11	2 ½–4	4/11–8/31	H,B,D
Kansas	4	2 ¾–3	4/1–9/30	H,B,D
Kentucky	4	2 ⅜–3 13/16	year-round	B
Iowa	7	3–4	4/1–8/31	H,B,D
Minnesota	1	2 ¾	5/16–8/31	H,D
Oklahoma	7	2 ¾–4	year-round	H,B,R,D
Missouri	3	2 ¾–4	4/1–8/31	H,B,D
Tennessee	11	2 ⅜–3 ¾	year-round	H,B,D
Wisconsin	5	2 ¾–4	4/1–8/31	H,B,D
Louisiana	4	2 ¾–4	5/20–9/30	H,D
Texas	6	2 ½–4	year-round	H,B,D

[1]Each species has a specific minimum size limit
[2]H = Hand-collecting; B = Brail; D = Dive; R = Rake

This reservoir has received such intense shellfishing pressure over the last 20 years that mussels are harvested soon after attaining legal size. This is particularly evident for the highly sought washboard and threeridge. Quantitative sampling of the populations of commercial species in Kentucky Lake during 1995 yielded the following percentages of legal-size mussels per species: ebonyshell (14%); threeridge, pigtoe, mapleleaf (5%); and washboard (2%). Thus, most large animals have been harvested, and populations consist mostly of age classes below the legal size limits. Most mussels are cropped soon after reaching legal size, and sub-legal animals are undoubtedly handled and sized by divers, resulting in disturbance to these and other species collected incidental to sought-after specimens. Studies by the Tennessee Wildlife Resources Agency indicate that most commercial species require 12–16 years to attain legal size (Hubbs & Jones, 1996). Because the larger species (washboard, threeridge) are at maximum exploitation levels, the more abundant smaller-size species are being harvested more intensely to meet the demand for shells. In recent years, the demand for large beads to produce large pearls by the South Pacific pearl companies has intensified the harvest of large, thick-shelled species; other populations of washboard and threeridge in Tennessee and elsewhere, therefore, have experienced higher exploitation rates.

To orchestrate Tennessee's mussel management program, a shell tax of 1.45 cents/lb of mussel shell is charged to buyers. Revenues of nearly $99,000 in 1995 were used to monitor harvest, implement law enforcement, and conduct surveys and research to improve the status of commercial stocks. During spot-checks of harvesters, seven specimens of the federally endangered orangefoot pimpleback (*Plethobasus cooperianus*) were taken from musselers at the shell camp. This species, and the white wartyback (*Plethobasus cicatricosus*), resemble several tubercled species that were allowed to be harvested: purple wartyback (*Cyclonaias tuberculata*), pimpleback (*Quadrula pustulosa*), and wartyback (*Quadrula nodulata*). Thus, the inclusion of look-alikes on the commercial list resulted in the incidental take of an endangered species. To resolve this problem, TWRA removed these tubercled species from the commercial list in 1996. These three species comprised less than 1% of harvested mussel in Tennessee, so removal from the list did not create an economic hardship to the shell industry. Protection of the orangefoot pimpleback, white wartyback, and other tubercled species by this regulation change reduces the incidental take of rare species, especially by harvesters unskilled in shell identification.

Sanctuaries

Although commercial harvest of mussels is allowed in the Mississippi, Tennessee, Cumberland, and Duck rivers in Tennessee, certain areas are designated as sanctuaries (Table 7), and all other water bodies are off limits to harvesting. These refugia have extensive populations of endangered and other species, and provide relatively undisturbed conditions for reproduction, recruitment, and population stability. The sanctuaries in the upper Tennessee River system, such as the Duck, Clinch, and Powell rivers, are critical to indigenous species residing in habitats that have not been altered significantly or destroyed by development projects.

TABLE 7. Mussel sanctuaries in Tennessee closed to commercial harvest.

River	River Mile Limits
Tennessee	140.0–141.5
Tennessee	201.9–206.7
Tennessee	465.9–471.0
Tennessee	520.0–529.9
Tennessee	416.5–424.7
Powell	55.0–115.6
Clinch	151.9–202.1
Duck	105.6–head
Cumberland	262.9–265.5
Cumberland	284.1–284.8
Cumberland	292.5–313.5
Hiwassee	53.5–65.9

Comprehensive Management

Because of the dual responsibilities of states where commercial harvest is legal, the various tools of resource managers must be effectively implemented to protect endangered species and regulate harvest of commercial species. Survey and monitoring of mussel populations and annual harvest records provide the information needed to assess population trends and to ensure that overharvest does not deplete the resource. Basic biological information for each species, such as reproductive period, host fish, growth rates, recruitment, age at first reproduction, longevity, and other factors, is essential to address questions on minimum size limits to maintain sustainable harvest on a species-by-species basis. Although changes in demand for the various species, driven by shell quality, thickness, bead size, and other factors have varied greatly over the last 20 years, management has continued on a biological basis rather than on an economic one. Neither mussel size limits nor total allowable harvest are modified to accommodate drastic fluctuations in the price of shell from year to year. Supply and demand for shell dictate harvest levels. Under this management strategy, the mussel resources in Tennessee and other states have been managed with sufficient success, such that no commercial species has been jeopardized by inappropriate harvest regulation. The evidence of overharvest and depletion of mussel populations during the pearl button era has not sullied the present management regime of commercial species, nor has incidental take of rare species been shown to jeopardize the continued existence of those species. In my opinion, periodic episodes of illegal harvest are the only potentially damaging activities that reduce the effectiveness of current mussel resource management. The occasional poaching of shells from sanctuaries or closed areas, harvest of undersize shell or non-legal species, and the incidental take or habitat destruction of endangered species are all breaches to effective management. These management violations are the responsibility of state and federal law enforcement agencies authorized to enforce harvest regulations. Therefore, a balance of efforts to manage mussel populations and the mussel harvesters is essential to protect the resource and ensure long-term sustainability.

There is one additional management issue that I feel needs to be addressed by the appropriate states. A few states still allow the harvest of a variety of non-commercial species for the purpose of sale to biological supply companies. From conversations with colleagues in various states, it is apparent that modern-day market hunters can ravage a stream of its mussels and jeopardize those populations through overharvest. Although these species are unprotected by law, the destruction of viable populations for the financial gain of an unscrupulous few is unacceptable. The commercial shell industry can provide biological supply houses with all the specimens they need without resorting to the decimation of non-commercial species residing in small streams. In those states where such professional collectors can still operate, it is imperative that the regulatory agency introduce legislation to prevent indiscriminate collecting of live mussels. There is certainly adequate documentation in our nation's past, such as the cases of the bison and the Carolina parakeet, to demonstrate that unregulated harvest can result in the extinction or extirpation of species that once were abundant. With so many U.S. mussel species in a precarious condition, whether legally protected or in need of protection, the looting of state-owned resources must be reduced if comprehensive wildlife management for all species is to be the goal of natural resource agencies in the twenty-first century.

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