Threats to and Sustainability of Ecosystems for Freshwater Mollusks

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Abstract — In North America, two groups of freshwater molluscs are most threatened by human activities and require ecosystem approaches to their sustainability. Prosobranch snails in the family Hydrobiidae are restricted to small spring systems and are limited by their relative immobility, dependence on highly oxygenated waters and use of gills. Many are narrow endemics of localized springs, which are altered by ground water depletion and surface water diversion and by changes in water quality such as nutrification and chemical pollution from non-point sources. Spring alteration can result in direct species extirpation. Conservation through threat assessment and abatement is recommended. Most rare and declining native mussels are Unionidae in riverine ecosystems. Their relative immobility, long lifespan, filter-feeding habits, and parasitic larval stage make them highly vulnerable to habitat disturbance. The major cause of their declines has been the fragmentation of river ecosystems through impoundments, channelization and other activities such as timber harvesting, which alter flow and sedimentation patterns. Fragmentation acts to increase the distance between mussel subpopulations and may have major consequences of the metapopulation structure of species, particularly rare species and those with narrow fish host requirements. As some populations are eliminated and dispersal distances are increased, demographic and genetic constraints will diminish the ability of local populations to respond to natural environmental disturbance as well as human-induced changes. Sustainable ecosystem management in river systems will require devising strategies to conserve mussel metapopulations.

INTRODUCTION

Lotic systems harbor a diverse array of species, including some of the most threatened (Allan and Flecker 1993). Those in the United States have been altered by humans in ways that often are detrimental to their native inhabitants. One consequence of this is that the native molluscan fauna in those systems has declined. We examine here ecological and life history characteristics of two groups of molluscs, prosobranch snails in the family Hydrobiidae and riverine bivalves in the family Unionidae, that have suffered declines due to human activities or appear to be threatened with declines in the future. Their distribution and life history characteristics render them vulnerable to human alteration of their habitats.

HYDROBIIDAE

The aquatic snail family Hydrobiidae is species rich and ranges worldwide. Many of the North American species occur as narrow endemics in one or a few small spring systems as living "fossils" that flourished during the Pleistocene (Deixis 1992, Taylor 1987). The systematic relationships of most North American species have only recently been addressed (Hershler 1984, 1985, 1989; Hershler and Landye 1988; Hershler and Longley 1986; Hershler and Sada 1987; Hershler and Thompson 1987; Taylor 1987; Thompson 1968, 1969), and many species remain undiscovered and undescribed (T. Frest, personal

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communication, R. Hershler, personal communication). Currently, 5 species have been listed as endangered (Federal Register 1991a, 1992), 10 are considered to merit listing as endangered or threatened, and 84 are under review for listing (Federal Register 1991b) (fig. 1).

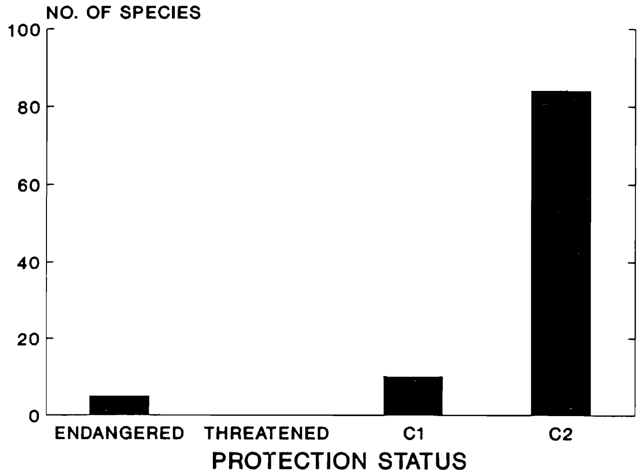

Figure 1.—Federal status toward listing of rare or declining snails of the family Hydrobiidae in the United States. Histogram shows number of species listed as endangered or threatened, number of candidate 1 species (species that merit listing) and number of candidate 2 species (species requiring further study to determine status).

Freshwater hydrobiids are indicators of artesian spring ecosystems with permanent, flowing, highly oxygenated waters (Ponder et al 1989). The waters may be highly mineralized, but must be relatively unpolluted. When hydrobiids occupy a significant portion of a spring system, it is an indication that the system is functioning and intact.

Life History and Ecological Characteristics

Hydrobiids are gill breathing and thus intolerant of drying or anaerobic conditions. Reproduction occurs annually or more often depending on water temperature (Deixis 1992, Hershler 1984, Mladenka 1992, Taylor 1987), and survivorship is estimated to be approximately one year (Mladenka 1992, T. Frest personal communication). They are found in flowing waters, often in thermal springs. The ecology of these snails in North America has received little study until recently (eg., Deixis 1992, Hershler 1984, Mladenka 1992, Reiter 1992). Here we examine ecological data for 59 species in the subfamilies Hydrobiinae and Littoridininae that have been reported as rare or threatened, or which occur in a narrow range in springs and their associated outflows. The sources of information consulted for each species are given in Appendix 1.

Of 59 species, most occur at only a single site and most of the remaining occur at only two or three sites (fig. 2). Occurrences represent single springs with no surface connection to other inhabited springs or parts of spring systems separated by more than 500 m of uninhabited waters. Because studies have not been conducted on gene flow among occurrences, it is not known whether an occurrence is the equivalent of a population.

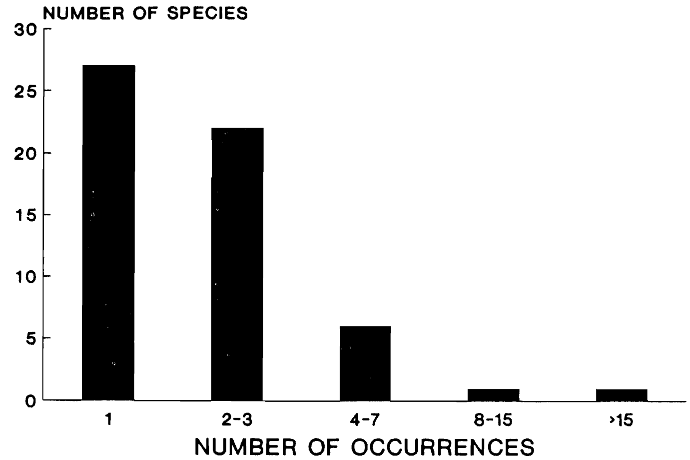

Figure 2.—Number of known occurrences per species of hydrobiid snails that are rare or threatened or have a narrow range of distribution.

Maximum occupied range was estimated in miles for 58 species as the greatest linear distance between two occupied points. Of those, 43% are known to occupy a range less than 0.1 mile, and less than 9% have a range greater than 10 linear miles (fig. 3).

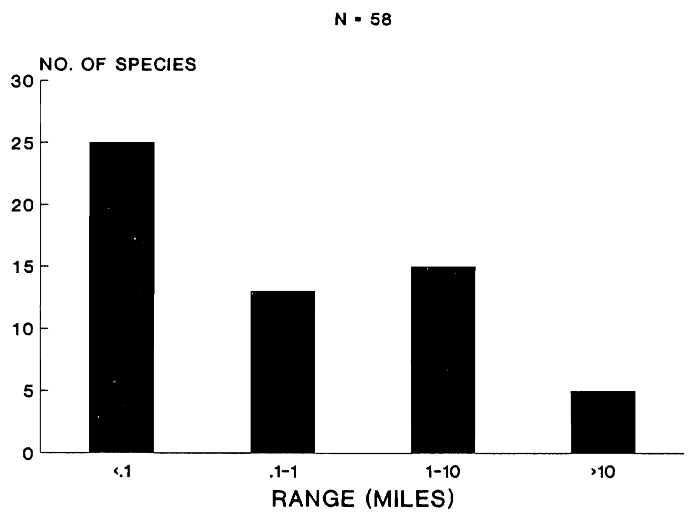

Figure 3.—Maximum occupied range per species (linear miles) of hydrobiids in the subfamilies Hydrobiinae and Littoridininae that are rare, threatened or have a narrow range of distribution.

Substrates occupied by each of 50 species were grouped into seven substrate types. Species in the Littoridininae were most often reported on vegetation, including algal mats and on soft substrates, such as mud and flocculent, but they were reported also on fine substrates such as silt and sand and on tufa (fig. 4). Species in the Hydrobiinae were reported from the same substrates as Littoridininae and also from wood, from stones, including pebbles and cobble, and from boulders and bedrock. It is not clear whether substrate associations reflect particular substrate preferences or hydrologic regimes of the occupied springs and spring runs, which in turn influence substrate availability. Mladenka (1992) showed experimentally that *Pyrgulopsis bruneauensis* (subfamily Hydrobiinae) preferred gravel and sand to silt.

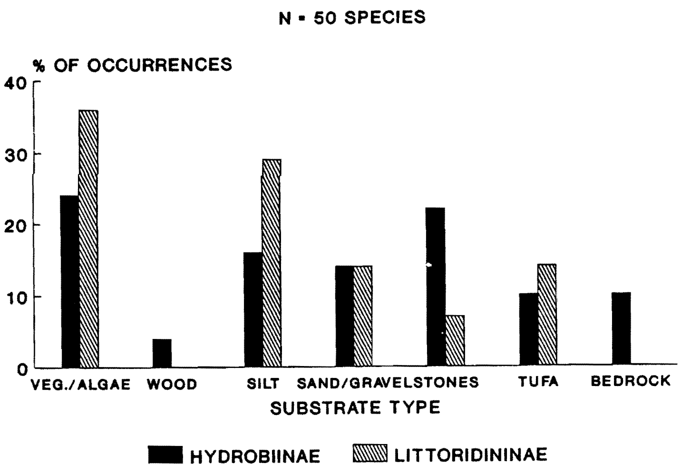

Figure 4.—Reported substrates at occurrences of hydrobiid snails in the subfamilies Hydrobiinae (N = 50 occurrences) and Littoridininae (N = 27 occurrences).

The extreme endemism of the species surveyed, as measured by the number of occurrences and occupied range, suggests that they may be extremely vulnerable to human disturbance. Threats to viability were assessed or identified for 53 species (fig. 5). When more than one threat was identified for a species, the two most prominent threats were tabulated. Decrease in water quantity, due to aquifer depletion or surface water diversion, was identified as a threat for 33 species, with many of those species threatened by both aquifer depletion and surface water diversion. Declines in water quality, due to habitat destruction (from impoundment, dredging or cattle trampling), or pollution (nutrient or chemical), was identified as a threat for 21 species. Recreation, such as swimming or hot spring bathing, was identified as a threat for 10 species. A study by Reiter (1992) suggests that recreation may not be as severe a threat as a change in water quantity or quality. He found that swimmers at a spring in Florida displaced *Aphaostracon monas* from a small area favored by both swimmers and snails, but the snails repopulated the area following the swimming season. For 2 species, no threats were identified in threat assessment procedures.

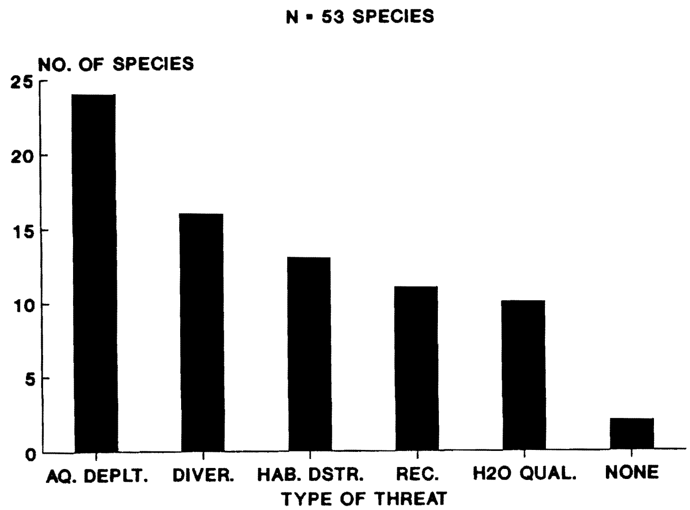

Figure 5.—Reported threats to snails in the family Hydrobiidae. AQ DEPLT = aquifer depletion, DIVER = water diversion, HAB DSTR = habitat destruction, REC = recreation, H2O QUAL = water quality, NONE = no threats found.

Ecosystem Sustainability

Species on public land and on private land designated for conservation offer some degree of long-term protection of ecosystems (Crumpacker et al. 1988). The number of occurrences for 59 hydrobiids was tallied by land ownership (fig. 6), multiple owners of any single occurrence were each counted as an owner. The greatest number of occurrences were on federal lands managed by the Bureau of Land Management (BLM) with private owners having the second greatest number. However, most of the occurrences on BLM lands were attributed to over 100 occurrences of *Pyrgulopsis bruneauensis* in springs along less than 10 miles of a water course (Mladenka 1992), a concentration of occurrences that has not been reported for other North American hydrobiids. If these are clustered as a single occurrence, 85 of the reported occurrences, or 65%, are on public lands or private conservation lands, 44 (33%) are on private lands other than those with a conservation interest and 3 (2%) are on tribal lands. Springs in western states are frequently in private ownership, often as inholdings or adjacent to large tracts of public land, while in Florida many are in the State Park system (Florida Natural Areas Inventory 1992).

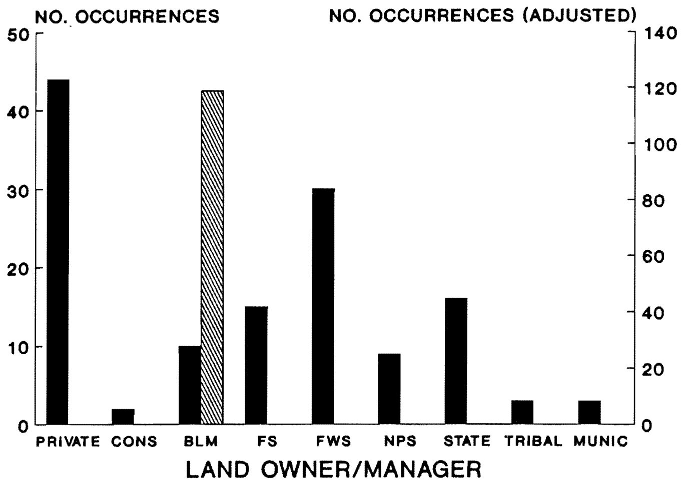

Figure 6.—Land owner or management agency of sites where hydrobiid snails in this study occur. When more than one owner was reported for a species occurrence, each owner was counted. The hatched bar shows the number of occurrences on BLM land without adjustment for the close clustering of over 100 occurrences of a single species. PRIVATE = private land with no formal protection status, CONS = private land with protection status, BLM = Bureau of Land Management; FS = USDA Forest Service, FWS = Fish & Wildlife Service, NPS = National Park Service, MUNIC = municipal ownership or control.

Recommendations for Ecosystem Sustainability

Most freshwater hydrobiids that have been reported as rare or threatened, or which occupy a narrow range, occur in one or a few artesian springs and their associated outflows (figs. 2 and 3). The aquifer source and hydrology of most of the spring systems is not well understood and because of this, hydrobiid ecosystems tend to be defined in reference to the surface waters of the host springs and outflows. When several springs are in close proximity to one another and have one or more hydrobiid species in common, they tend to be treated as a single system for management purposes (Deixis 1992; Federal Register 1991, 1992; Mladenka 1992). Hydrobiid-occupied springs are spatially small ecosystems, which is an advantage for management toward sustainability.

However, conservation and management planning needs to begin at a level higher than single spring ecosystems. For instance, a few spring systems, such as the Ash Meadows system in Nevada (Hershler and Sada 1987) and the Cuatro Cienegas system in Coahuila, Mexico (Hershler 1984, 1985) are quite large with several endemic species in various subsets of springs within the large system. In such cases, management needs to begin with the entire spring system. Artesian springs, especially those in arid environments, are analogous to islands in a sea of dry land that is inhospitable to aquatic species (Ponder et al. 1989). Striking regional species radiations have been demonstrated for both fishes (Soltz and Naiman 1978) and hydrobiids (Ponder et al. 1989, Thompson 1968). This argues for management perspectives that are at regional or large ecosystem levels rather than at the level of single isolated springs.

In many instances, springs are components of larger riverine ecosy-tems, though hydrologically distinct from them. Two examples of this are the Gila River ecosystem in southwestern New Mexico, which is a riverine ecosystem with eight known spring ecosystems occupied by hydrobiids (Mehlhop 1992 and unpublished data, Taylor 1987), and the middle Snake River with numerous associated springs (Deixis 1992, Federal Register 1992). In those situations, spring management must be a special target of management plans for larger ecosystems.

Most spring ecosystems examined in this survey are best sustained through threat analysis and control. Systems that are highly degraded with marginal hydrobiid populations probably cannot be restored without large financial expenditure and may not be worthy of investment if other, more naturally functioning spring ecosystems can be protected. Systems such as Torreon Spring in New Mexico, which has been impounded to an extent that the hydrobiid *Pyrgulopsis neomexicana* occupies less than 1 m^2 of its former range, is an example of an ecosystem that is no longer functional in its natural state (personal observation). The following recommendations for sustaining spring ecosystems for hydrobiids use a threat assessment and control approach.

1) Identify all springs in the landscape with hydrobiid snails and prioritize them for conservation.
2) Monitor and maintain water quantity in priority spring ecosystems.
3) Monitor and maintain water quality in priority spring ecosystems.
4) Identify and assess the need to abate other threats to ecosystem sustainability.
5) Quantitatively monitor occupied hydrobiid habitats within the targeted springs. In spring ecosystems with co-occurring hydrobiids, monitor relative numbers.

Monitoring will be the most time consuming action in sustaining many spring ecosystems. In most instances, it need not be elaborate, but it must be repeatable and occur at a frequency that will indicate decline in the parameters being monitored.

Hydrobiids are minute and easily overlooked by an untrained observer. To avoid investing in spring ecosystem management in lower priority spring systems, it is important to survey all springs and seeps in a large landscape (e.g., a National Forest and adjacent lands with similar landscape features). Primary threats to hydrobiid-occupied springs should then be identified and management actions prioritized based on assessments of species rarity, population size, degree of threat and amenability of threats to control measures.

Surface water diversion is readily detected and easily monitored. However, protection of surface waters alone is insufficient for many of the spring ecosystems. There are a large number of species for which ground water depletion has been identified as a major threat (fig. 5). Monitoring and protection of ground water flows for those systems is probably the single most important management need. This requires assessing the uses and regulation of the spring aquifer, for which depth and size are most often unknown. A long term monitoring program that roughly estimates water quantity at a spring may be an inexpensive, but adequate means of detecting ground water depletion.

For spring ecosystems that are a high priority for conservation, water quality should be measured initially to obtain baseline water quality data. The subsequent frequency of monitoring will vary with degree of threat. Results of this survey suggest that recreation is a threat to spring ecosystems only if spring outflows are altered substantially or if chemicals are added to the system. For instance, a hot spring in New Mexico is used for recreational bathing upstream from one of only two populations of a hydrobiid, and the population is maintained by flows of 0.3 cm and less over the snail substrate. While the probability of diversion or chemical pollution appears low, the consequences of such threats could be great.

Monitoring the snails themselves provides both a measure of the impacts of identified threats and a means of detecting unanticipated threats. Hydrobiid snail populations are difficult and costly to estimate, and methods used at one spring system may not be applicable to others (personal observation, T. Frest, personal communication). However, population stability can be estimated by monitoring the surface area occupied or the boundary of occupation. This needs to be done at approximately the same time of year due to seasonal population fluctuations generally associated with birth and death events. When hydrobiids co-occur in a spring, they usually cannot be distinguished with certainty without some disturbance to the population. However, some minimal monitoring is desirable to confirm that species proportions remain relatively stable.

UNIONIDAE

The unionid mussel fauna of North American freshwater is the most diverse in the world but is highly threatened. There have been major declines of mussel populations and species diversity in North American over the last century. Of the 283 species of native North American mussels, 131 species, or approximately 40%, are threatened with extinction: 17 species are presumed extinct, 44 species are actually listed as threatened or endangered, and 70 species are federal candidates for listing (Neves 1993, Master 1993) (fig. 7). Furthermore, all federally listed unionids are declining. There are no listed species with populations that are being maintained or increasing (Neves 1993).

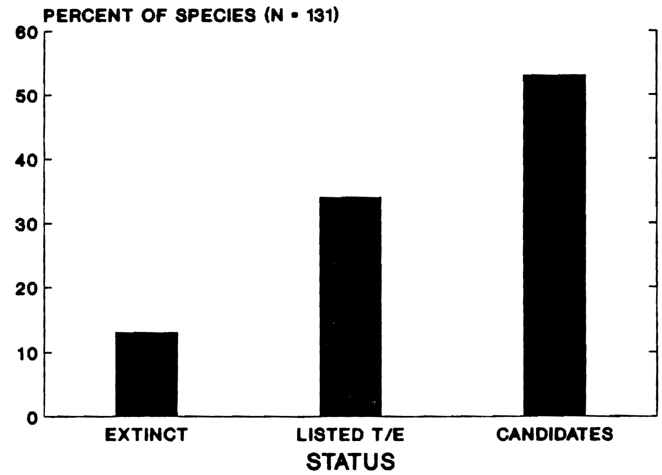

Figure 7.—Status of unionid mussels in the United States. N = 131. LISTED T/E = listed by the federal government as threatened or endangered, CANDIDATES = candidates for federal listing.

Unionid Characteristics

Freshwater mussels possess a suite of traits that make them highly vulnerable to habitat disturbance (table 1). Mussels have a complicated life history. The larval stage of freshwater mussels (glochidia) are temporary, obligate parasites on the gills or fins of fish. Many mussel glochidia can survive only on a narrow range of fish species hosts (Way 1988). Contact with an appropriate fish host and the location where young mussels are shed from the host is largely due to chance and only juveniles that reach a favorable habitat survive (Neves & Widlak 1987). Because only larvae can move between patches and juvenile survival is low, the potential rates of colonization are low. Reproductive maturity is not reached until age 6, most species live greater than 10 years, and some species live as long as 90 years (Haskin 1954, Imlay 1982, McMahon 1991). Once mature, adult mussels exhibit high survivorship (>80%) (McMahon 1991). However, adult mussels are sedentary; movements are

Table 1. — Life history characteristics of the Unionidae. Modified from McMahon (1991).

Life span	< 6 > - 100 yr
Age at maturity	6 - 12 yr
Strategy	Iteroparous
Fecundity	200,000-17,000,000
Reprod. efforts/year	1
Juvenile size	50 - 400 um
Rel. juvenile survivorship	Very low
Rel. adult survivorship	High
Larval habitat	Obligate parasite on fish

seasonal and on a scale of a few to an estimated maximum of 100 meters (Green et al. 1985). Therefore, unlike many stream organisms such as fish and aquatic insects (Townsend 1989), adult mussels have no refugia from disturbance events in streams. In addition, their filter-feeding habits make them especially vulnerable to sedimentation and chemical pollution events.

Threats and Causes of Decline

Species associations, species richness, metapopulation structure, and densities and population size structure of individual species are all potentially impacted by forest management practices. In addition, any effects on fish communities may ultimately affect mussels as well. Watters (1992) recently found high correlation between fish distribution and diversity and mussel distribution and diversity.

One major cause of mussel declines has been the fragmentation of river drainages through impoundments, channelization and other activities, such as timber-harvesting, which alter flow and sedimentation patterns. Declines in mussel species for various river drainages and the disturbance factor associated with these declines are shown in Table 2.

Timber harvesting operations can have significant effects on both stream water quantity and quality. The influence of catchment vegetation on stream discharge is dependent on a large number of variables, many of which are site-specific. However, in general, removal of forest vegetation increases stream runoff (Campbell and Doeg 1989). Increased flows have the potential to alter the distribution of sediment through scour, flushing, and deposition of newly eroded materials from the banks. Increased flows also have the potential to activate the bed. Bedload movement will wreak havoc on the survival of many mussels, particularly juveniles (Young and Williams 1983). Erosion caused by increased flows at one location results in deposition of this material further downstream. This "zone of aggradation" results in an increased width/depth ratio of that portion of the channel. As width/depth ratios increase the potential for bedload transport also increases. Thus, increased flows cause habitat loss through both sediment deposition and increased bed mobility. In the long term, higher base flow levels and shorter periods between peak flood periods will decrease habitat complexity by preventing the formation of islands, establishment of macrophyte beds, etc. (Frissell 1986). Stabilized sediments, sand bars, and low flow areas, are all preferred unionid habitats (Hartfield and Ebert 1986, Payne and Miller 1989, Stern 1983, Way et al. 1990). It is around these "complex" areas that most mussel beds, and indeed the highest diversity of stream fauna, are found.

Road-building activities and low water crossings associated with logging can lead to the development of "headcuts", or migrating knickpoints in the channel remote from areas of actual modification. Headcuts result in severe bank erosion, channel widening, and depth reduction and can have devastating effects on the mollusc fauna (Hart 1993).

Stream organisms, including mussels, have evolved in rivers that experience seasonal low-flow and high-flow periods (Meador and Matthews 1992). Fluctuating flows, especially if there will be lower flows for long periods of time, will result in the stranding of many mussels. Unlike fish species which can move rapidly in and out of microhabitats with changes in water levels, mussels move very slowly and are unable to respond to sudden drawdowns. Even if stranding doesn't actually kill a mussel, desiccation and thermal extremes will cause physiological stress and may reduce reproductive potential (McMahon 1991).

Fluctuating flows also mean that transport of particulates will vary. Depending on the flow schedule and the materials normally transported in the water column, there is the potential for loss of organics which are the food base for mussels.

Flow alteration not only has the potential to profoundly affect the stream fauna, but riparian fauna as well. Flood waters that normally recharge soils and aquifers may be rapidly exported

Table 2. — Reported loss of unionid mussel species from rivers and factors contributing to the losses.

Drainage	% Species Lost	Major Factor in Decline	Source
Upper Tennessee River	36%	Impoundments, sedimentation	Starnes and Bogan (1988)
Middle and Lower Tennessee R. sedimentation	13%	Impoundments, channelization,	Starnes and Bogan (1988)
Tombigbee River at Epes, AL	68%	Impoundment	Williams et al. (1992)
Stones River, TN	40%	Impoundment	Schmidt et al. (1989)
Upper Stones River, TN	25%	Gravel dredging, water quality	Schmidt et al. (1989)
Sugar Creek, IN	20%		Harmon (1992)
Illinois River, IL	51%	Impoundments, channelization, sedimentation	Starret (1971)
Kankakee River, IL	25%	Siltation	Suloway (1981)
Kaskaskia River, IL	38%	Siltation (80% reduction in numbers of individuals)	Suloway et al. (1981)
Vermillion River, IL	40%		Cummings (1991)
Embarras River, IL	39%		Cummings (1991)
Little Wabash River, IL	24%		Cummings (1991)

downriver. Lowered water tables may cause shrinkage of the riparian corridor and shifts in terrestrial species composition (Allan and Flecker 1993, Smith et al. 1991).

Mussels are most successful where water velocities are low enough to allow sediment stability but high enough to prevent excessive siltation (Salmon and Green 1983, Way et al. 1990). Thus, well-oxygenated, coarse-sand and sand-gravel beds comprise optimal habitat (McMahon 1991). Sediment deposition not only removes or moves habitat, but also clogs mussel siphons (i.e. smothers them) and interferes with feeding and reproduction (Dennis 1984, Aldridge et al. 1987). In addition, because mussels are sedentary filter-feeders, they are particularly sensitive to changes in water quality (Havlik and Marking 1987).

Demographic Consequences

Because of this dependence on the appropriate substrate and flow conditions, freshwater mussels are already naturally patchily distributed in rivers. Fragmentation acts to increase patchiness and to increase the distance between patches. These effects may have major consequences for the metapopulation (i.e. local or subpopulations connected by infrequent dispersal) structure of mussel species, particularly rare species and those with narrow fish-host requirements (Vaughn 1993). As some subpopulations are eliminated and dispersal distances are increased between other subpopulations, demographic and genetic constraints will diminish the ability of mussels to respond to even natural stochastic events much less human-induced environmental change (Wilcox 1986, Murphy et al. 1990).

Forest Management Strategies

Managing forests to maintain fully functional riverine ecosystems is the best way to protect unionid populations in National Forests. Best land-use practices should strive to maintain an uncut riparian corridor at least as wide as the predicted 100 year channel meander (Boon et al. 1992). Forest managers should seek to minimize the use of biocides and encourage selective logging rather than clear-cutting whenever possible. Disturbances such as low-water crossing which were thought to have temporary effects are now known to have long-term detrimental effects on mussel populations through the formation of migrating headcuts. Managing forests from an ecosystem perspective must include long-term monitoring of unionid populations.

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Appendix 1. Species of snails in the family Hydrobiinae included in this study and the sources of information used.

Apachecoccus arizonae	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Landye 1973, Taylor 1987
Aphaostracon asthenes	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Aphaostracon monas	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Aphaostracon pycnus	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Aphaostracon theiocrenetus	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Aphaostracon xynoelictus	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Cincinnatia helicogyra	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Cincinnatia mica	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Cincinnatia monroensis	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Cincinnatia parva	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Cincinnatia ponderosa	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Cincinnatia vanhyningi	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Cincinnatia wekiwae	FL	Florida Natural Areas Inventory 1993, Thompson 1984
Pyrgulopsis aardahli	CA	California Natural Heritage Division 1993, Hershler 1989
Pyrgulopsis bacchus	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988
Pyrgulopsis bruneauensis	ID	Idaho Conservation Data Center 1993, Mladanka 1992
Pyrgulopsis chupaderae	NM	National Museum Natural History collections, Mehlhop (personal observation), Taylor 1987
Pyrgulopsis conicus	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988
Pyrgulopsis crystalis	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Pyrgulopsis davisi	TX	Taylor 1987, Texas Parks & Wildlife Department 1993
Pyrgulopsis deserta	AZ, UT	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Utah Natural Heritage Program 1993
Pyrgulopsis erythopoma	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Pyrgulopsis fairbanksensis	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Pyrgulopsis gilae	NM	Mehlhop (1992, personal observation), Taylor 1987
Pyrgulopsis glandulosus	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988
Pyrgulopsis isolatus	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Pyrgulopsis merriami	NV	Nevada Natural Heritage Program 1993
Pyrgulopsis metcalfi	TX	Taylor 1987, Texas Parks & Wildlife Department 1993
Pyrgulopsis montezumensis	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Landye 1973
Pyrgulopsis morrisoni	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988
Pyrgulopsis nanus	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Pyrgulopsis neomexicanus	NM	Federal Register 1991a, Taylor 1987
Pyrgulopsis nevadensis	NV	Nevada Natural Heritage Program 1993
Pyrgulopsis n. sp.	NM	Mehlhop (1992, personal observation)
Pyrgulopsis owenensis	CA	California Natural Heritage Division 1993, Hershler 1989
Pyrgulopsis pecosensis	NM	Mehlhop (1992), Landye 1973, Taylor 1987
Pyrgulopsis pisteri	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Pyrgulopsis perturbata	CA	California Natural Heritage Division 1993, Hershler 1989
Pyrgulopsis roswellensis	NM	Mehlhop (1992), Landye 1973, Taylor 1987
Pyrgulopsis simplex	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Landye 1973
Pyrgulopsis solus	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988
Pyrgulopsis thermalis	NM	Mehlhop (1992), Taylor 1987
Pyrgulopsis thompsoni	AZ, MX	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Landye 1973
Pyrgulopsis trivialis	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Landye 1973
Tryonia adamantina	TX	Taylor 1987, Texas Parks & Wildlife Department 1993
Tryonia alamosae	NM	Landye 1973; Mehlhop, P. personal observation, New Mexico Natural Heritage Program 1993, Taylor 1987
Tryonia angulata	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Tryonia brunei	TX	Taylor 1987, Texas Parks & Wildlife Department 1993
Tryonia cheatumi	TX	Taylor 1987, Texas Parks & Wildlife Department 1993
Tryonia elata	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Tryonia ericae	NV	Hershler and Sada 1987, Nevada Natural Heritage Program 1993
Tryonia gilae	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Landye 1973, Taylor 1987
Tryonia kosteri	NM	Landye 1973, Mehlhop, P. 1992, New Mexico Natural Heritage Program 1993, Taylor 1987
Tryonia margae	CA	Hershler 1989
Tryonia quitobaquitae	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988
Tryonia rowlandsi	CA	Hershler 1989
Tryonia salina	CA	Hershler 1989
Tryonia stocktonensis	TX	Taylor 1987, Texas Parks & Wildlife Department 1993
Yaquicoccus bernardinus	AZ	Arizona Heritage Data Management System 1993, Hershler and Landye 1988, Taylor 1987