# Changing Perspectives on Pearly Mussels, North America's Most Imperiled Animals

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*Pearly mussels (Unionacea) are widespread, abundant, and important in freshwater ecosystems around the world. Catastrophic declines in pearly mussel populations in North America and other parts of the world have led to a flurry of research on mussel biology, ecology, and conservation. Recent research on mussel feeding, life history, spatial patterning, and declines has augmented, modified, or overturned long-held ideas about the ecology of these animals. Pearly mussel research has begun to benefit from and contribute to current ideas about suspension feeding, life-history theory, metapopulations, flow refuges, spatial patterning and its effects, and management of endangered species. At the same time, significant gaps in understanding and apparent paradoxes in pearly mussel ecology have been exposed. To conserve remaining mussel populations, scientists and managers must simultaneously and aggressively pursue both rigorous research and conservation actions.*

*Keywords: Unionidae, endangered species, spatial structure, food and feeding, life history*

**Pearly mussels (Unionacea) are among the most** fascinating, most widespread, and most endangered animals in fresh waters. They play important roles in freshwater ecosystems and are economically valuable for their shells and pearls. Recent research, fueled by concern over widespread extinctions and population declines, has produced valuable and even astonishing insights into the ecology, biology, and conservation needs of these animals. In this article, we review recent progress in pearly mussel research, identify promising directions for future research, and draw general lessons that may apply to other organisms. We omit one area of active research, the role of pearly mussels in ecosystems, because it has been reviewed elsewhere (Vaughn and Hakenkamp 2001).

Pearly mussels are large (2- to 30-centimeter) bivalves that live in the sediments of rivers, streams, and lakes worldwide (Bauer and Wächtler 2000). About 1000 species are known, 300 of which live in North America. These long-lived mussels—they may live for decades to centuries—have a bizarre life cycle. While most marine bivalves have a free-living larva, pearly mussels have a specialized larva, the glochidium, which is a parasite of fish (figure 1b).The need to place these larvae on the proper species of host has led to extraordinary adaptations to attract hosts, and this brief parasitic stage has lasting effects on adult mussel ecology. Juvenile mussels probably live for a few years buried in sediments before emerging to the sediment surface. Adult mussels are suspension feeders.

Pearly mussels are so abundant in many habitats (10 to 100 mussels per square meter, with a shell-free biomass of 5 to 100 grams dry matter per square meter; see photograph, figure 1c) that they must sometimes play important roles in particle processing, nutrient release, and sediment mixing, although these roles have not often been assessed (Vaughn and Hakenkamp 2001). Humans have gathered pearly mussels for their meat, pearls, and mother-of-pearl shells for millennia. Pearl fisheries were important sources of capital for developing rural economies in 19th-century North America (Claassen 1994). Later, in the early 20th century, the mother-of-pearl button industry (figure 1a) harvested huge numbers of

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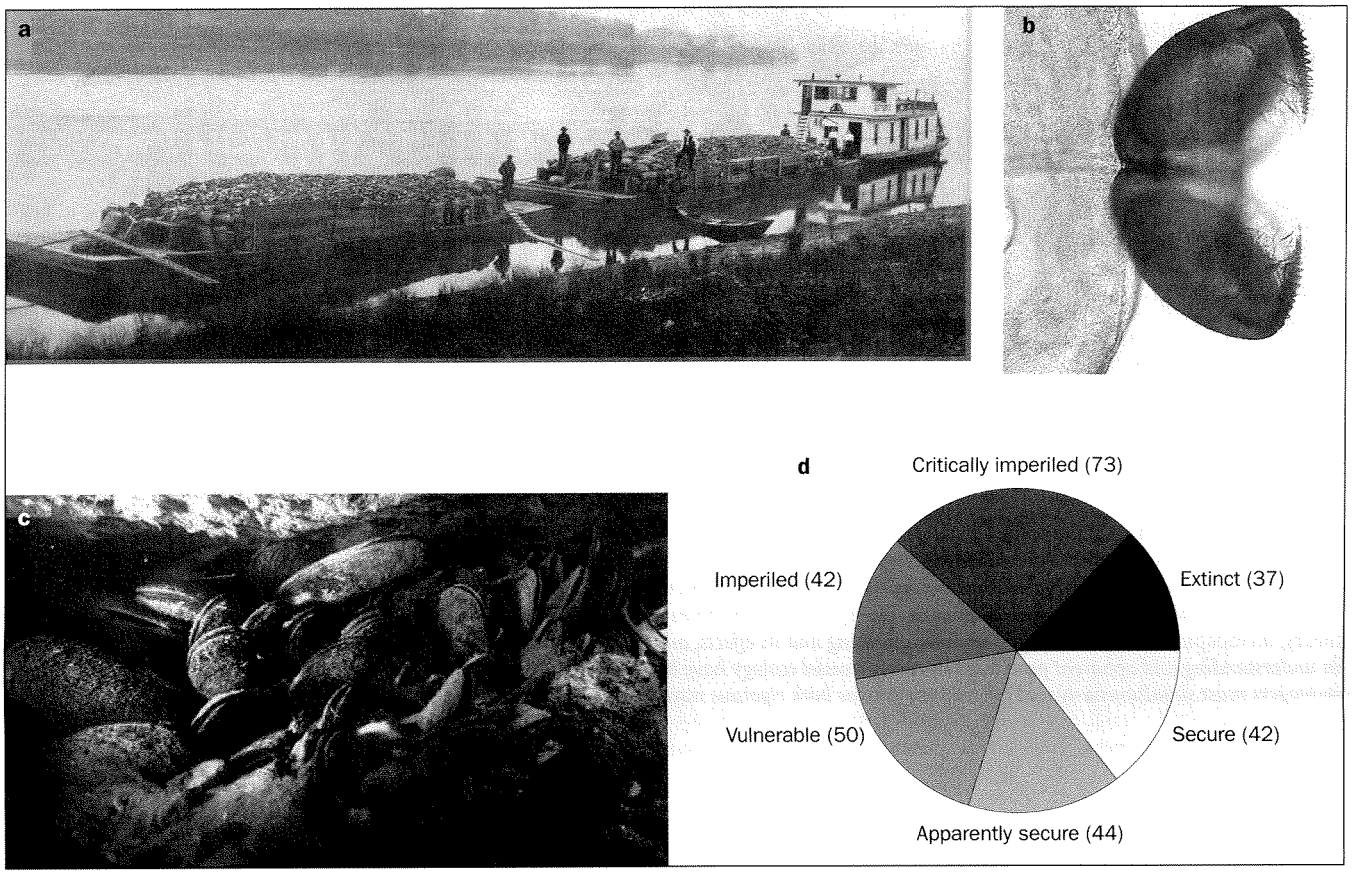


***Figure 1. (a) Barges loaded with mussel shells collected for pearl buttons (Arkansas, early 20th century) (Coker 1919). (b) A glochidium (larva) of* Strophitus undulatus. *(c) A dense bed of* Cumberlandia monodonta. *(d) Conservation status of the pearly mussels of North America (Master et al. 2000). The number in parentheses is the number of species in each category. Photographs: (b, c) Courtesy of Chris Barnhart, Southwest Missouri State University.***

mussels from American rivers (13 million kilograms of shells from Illinois in 1913 alone), depleting mussel beds in the large rivers of the Midwest (Claassen 1994). More recently, a regionally significant mussel fishery has provided shells to be used as nuclei for producing cultured pearls in oysters, and North American mussels are now also being used to produce cultured pearls.

Overharvesting, widespread habitat destruction, pollution, land-use change, and exotic species introductions have caused many mussel populations to decline or disappear. Pearly mussels are among the most imperiled of all organisms in North America (figure 1d) and elsewhere around the world. This desperate conservation situation has spurred intensive research into mussel biology and ecology (figure 2), which has both led to much greater understanding and exposed interesting paradoxes and key gaps in knowledge.

## What do pearly mussels eat?

Although it might seem odd to be asking this question more than a century after the first study of mussel feeding, recent research has questioned the portrayal of pearly mussels as exclusively suspension feeders on phytoplankton. Early studies of mussel feeding were based on analyses of gut contents, a method that has three weaknesses: (1) Material in mucus-bound gut contents is difficult to identify and quantify; (2) material found in the gut may pass undigested out of the mussel, not contributing to its nutrition; and (3) examination of the gut contents offers limited insight into the mechanisms and behaviors by which mussels acquire food. Modern studies suggest that pearly mussels feed on more than just algae and may obtain food by means other than suspension feeding.

It has been known for some time that pearly mussels capture more than phytoplankton from the water column; their guts also contain small animals, protozoans, and detritus. Recent studies show that mussels can capture and assimilate bacteria as well (Silverman et al. 1997), a potentially important source of food in many fresh waters. Mussel species from streams and rivers are about 10 times more efficient than those from ponds and lakes at capturing bacteria. Another potential source of food for mussels is dissolved organic matter. Early studies showing that pearly mussels could take up simple organic compounds were largely discounted because such labile compounds are rarely abundant in nature. Nevertheless, recent work on other bivalves (e.g., Roditi et al. 2000) suggests that dissolved organic matter may be a significant source of nutrition.

Pearly mussels may also get food from sources other than suspended particles. Many marine bivalves use their foot to sweep edible material from the sediment (pedal feeding) or siphon food from the sediment surface (deposit feeding). It is now known that juvenile pearly mussels can pedal feed (Yeager et al. 1994), although researchers still do not know how the ability to pedal feed varies across species, over the lifetime of a single mussel, or with the relative availability of food in the water column and in the sediment. Raikow and Hamilton (2001), studying a stream that was labeled with $^{15}N$, suggested that even adult mussels may deposit feed. The subject of suspension feeding versus deposit feeding by pearly mussels deserves more scrutiny, as it affects scientific understanding of food availability for mussels and of the role of mussels in food webs.

Of this complex mix of materials that pearly mussels acquire, what is actually required and assimilated? Stable isotope analyses of mussels taken from nature and from captive-rearing studies are beginning to offer some insight into this difficult question. Nichols and Garling (2000) showed that unionaceans in a small river were omnivorous, subsisting mainly on particles less than 28 micrometers in diameter, including algae, detritus, and bacteria. Bacterially derived carbon was apparently the primary source of soft-tissue carbon. However, bacteria alone cannot support mussel growth, because they lack the necessary long-chain fatty acids and sterols and are deficient in some amino acids. Bacteria may supplement other food resources, provide growth factors (e.g., vitamin $B_{12}$), or be the primary food in habitats such as headwater streams, where phytoplankton is scarce. Juvenile mussels have been most successfully reared in the laboratory on diets containing algae high in polyunsaturated fatty acids (Gatenby et al. 1997). Thus, it appears that the unionacean diet in nature may consist of a mixture of algae, bacteria, detritus, and small animals, and that at least some algae and bacteria may be required as a source of essential biochemicals. Scientists are still a long way from knowing precisely what constitutes the unionacean diet or being able to quantitatively assess the quality or quantity of mussel food in a given habitat.

Nevertheless, it appears that pearly mussels may sometimes be food limited in nature. A preliminary experimental study showed that mussel growth declined at high population densities (Kat 1982). Further, the zebra mussel invasion caused the density and body condition of pearly mussels to decline, consistent with food limitation (Strayer 1999a). Identifying the extent and severity of food limitation of mussel populations is an important research challenge. Mussel feeding is a complicated, dynamic process that may vary across environments, species, and life stages and have important consequences for mussel populations.

## The secret life of pearly mussels

Like the mousy Walter Mitty, pearly mussels (sometimes disparaged as "living rocks") would hardly seem likely to have a secret life. Yet recent studies have uncovered astonishing adaptations that allow the mussels to place glochidia on fish hosts and have revealed significant variations in mussel life history. These studies provide the basic information needed to understand the evolution of the group and guide conservation efforts.

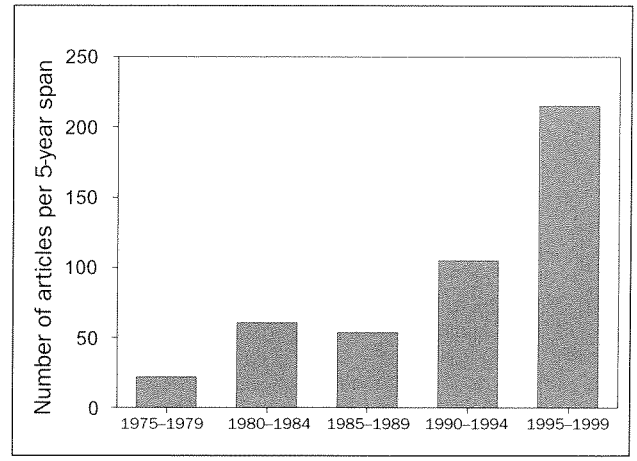


***Figure 2. Number of peer-reviewed scientific articles referring in their title or abstract to unionacean mussels, 1975–1999. Data from Web of Science (30 March 2004; http://isi10.isiknowledge.com/portal.cgi/wos).***

Perhaps the most remarkable life-history discovery of the last 10 years is that mussels have a wide variety of behavioral and morphological adaptations to facilitate transmission of glochidia to hosts. At least three strategies have been identified (Haag and Warren 2003). Gravid females of some species display moving lures that mimic fish or invertebrates. These lures readily elicit attacks from fish (figure 3), resulting in glochidial infections (Haag and Warren 2000). Most lures are modifications of the mantle margin, but in four species from the southeastern United States, glochidia are released in two large, minnow-like structures tethered to the female by a long, mucous tube that serves as a "fishing line" (Haag et al. 1995). In other species, females release glochidia in packages that mimic worms, insect larvae, larval fish, or fish eggs (figure 3; Jones and Neves 2002). Fish readily attack these "conglutinates" (figure 3; Haag and Warren 2003). Both of these strategies are employed by mussels that use only a few species of fish as hosts and probably reduce the transmittal of glochidia to unsuitable fish by mimicking prey items of specific fish (Haag and Warren 2000). A third strategy, documented mostly for host generalists, involves the release of glochidia in large, mucous webs that entangle fish less discriminately. These adaptations indicate a close evolutionary link between mussel life-history traits and host-fish use. Host attraction is an active area of research and will probably reveal additional mechanisms by which mussels increase the chance of placing their glochidia on their hosts.

Mussel life histories vary more among and within species than textbook accounts would suggest. It now appears that sexuality may not be fixed in all species. Some mussels can change from males to females as they age (Downing et al. 1989)

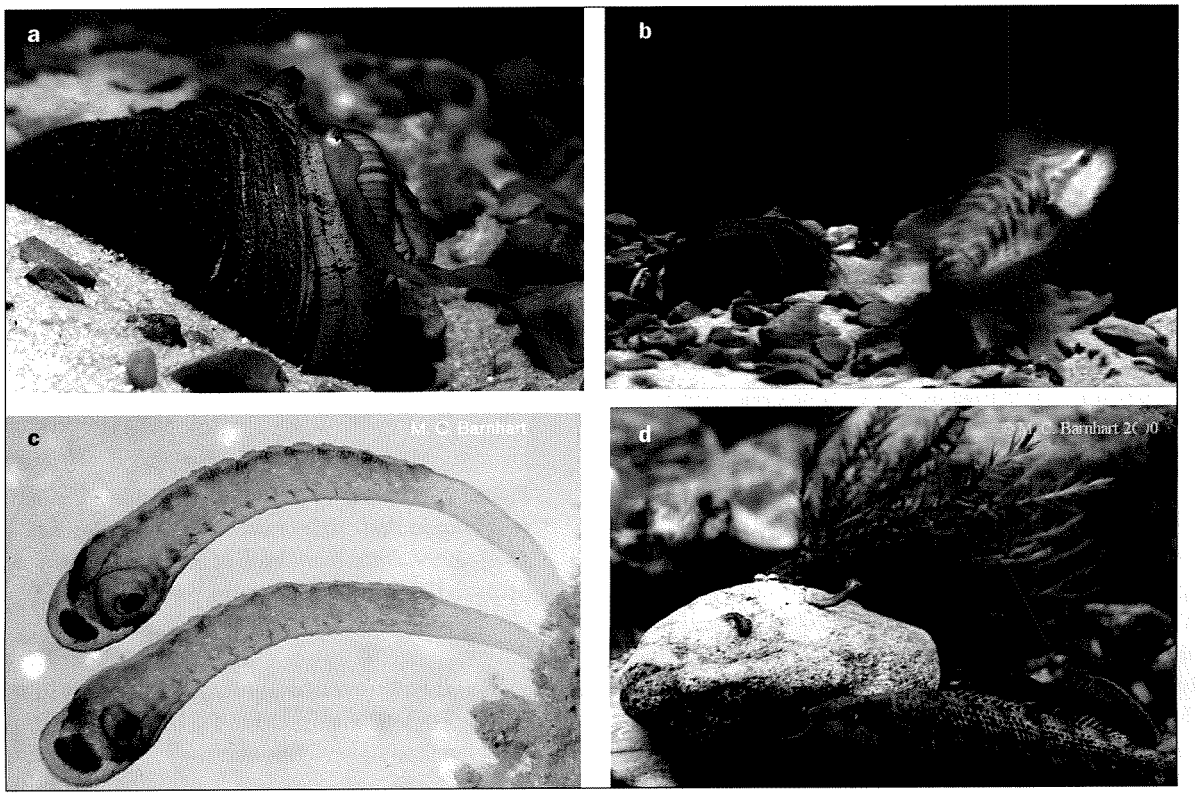


***Figure 3. Some pearly mussel species produce lures or conglutinates that elicit attacks from fish, facilitating the attachment of the glochidium, the mussel larva, to the fish host. (a) Mantle lure of* Lampsilis cardium *(Haag and Warren 1999). (b) Redeye bass (*Micropterus coosae*) attacking mantle lure of* L. cardium *(Haag and Warren 1999). (c) Conglutinates of* Ptychobranchus occidentalis. *(d) Orangethroat darter (*Etheostoma spectabile*) feeding on conglutinates of* P. occidentalis. *Photographs: (c, d) Courtesy of Chris Barnhart, Southwest Missouri State University.***

or turn into hermaphrodites when population density is reduced (Bauer 1987). There may be local adaptation between mussels and hosts, resulting in higher compatibility of glochidia with fish populations from the mussel's native basin than with fish of the same species from distant drainages (Rogers et al. 2001). Some mussels may even be able to skip the glochidial phase and complete their development without a host (Barfield and Watters 1998, Lellis and King 1998). The number of species able to bypass the glochidial stage, and the degree to which direct development versus parasitism may be variably expressed within a species, remains unknown.

Scientists have made great progress in identifying hosts for many mussel species. Several important generalizations about host relationships are emerging. First, the degree of host specificity varies greatly among species, ranging from generalists that use dozens of fish species to strict specialists that parasitize only one or a few species. Most mussel species are specialists, and related mussels often use similar fish as hosts, allowing prediction of likely hosts of unstudied mussels (Haag and Warren 2003). Second, host compatibility may depend on temperature: Glochidia that transform successfully on a particular fish species within a certain temperature range may be rejected at temperatures outside this range (Roberts and Barnhart 1999). Finally, parasitized fishes may acquire temporary immunity to further infestations of glochidia from other mussels (Rogers and Dimock 2003), suggesting that competition for hosts may be an important factor in community assembly and evolution of host attraction strategies.

Recently, biologists have made the first attempts to organize the life-history strategies of freshwater mussels into conceptual frameworks (Bauer and Wächtler 2000, Dillon 2000). Development of these frameworks is hampered by a lack of life-history information for most species, particularly for traits such as age at maturity, growth rate, longevity, and fecundity. Solid natural-history studies that establish the ranges of variation in these traits both within and among species will allow refinement of life-history frameworks to encompass the breadth of mussel diversity. These improved frameworks, in turn, will be important in generating testable hypotheses about the evolutionary, ecological, and management consequences of life-history variation. Studies that evaluate the suitability of a broad cross section of the fish community co-occurring with a particular mussel species and those that evaluate intraspecific variability in host compatibility will be especially valuable.

## What is the pace of temporal change in mussel populations?

Pearly mussels are among the most long-lived animals in the world. It has long been thought that most mussel species live for decades (Bauer and Wächtler 2000), with some populations having mean ages of more than 50 years. Most studies of age and growth have been based on the rings laid down in the shell, which have been interpreted as reflecting annual pauses in mussel growth during the winter. This inference is supported by analyses of shell microchemistry (Veinott and Cornett 1996). However, recent studies of growth rates based on direct measurements of marked individuals in the field suggest that growth rings are not annual and that earlier estimates based on growth rings may underestimate longevity by a factor of 3 to 10 (Anthony et al. 2001). If these conclusions are correct, some pearly mussels may be centuries old. These extraordinarily long lives have major consequences for the demography of mussel populations. Until the discrepancy between growth rates estimated from direct measurements and those inferred from shell rings is resolved, studies of mussel growth should verify the accuracy of the aging method by independent means.

Regardless of whether mussels live for decades or for centuries, their long life span suggests several questions about their demography and conservation. Is their distribution and abundance controlled chiefly by day-to-day conditions or by rare events that occur every few generations (i.e., at > 100-year intervals)? Only a few studies have examined the effects of these rare events (Hastie et al. 2001). If pearly mussels are sexually competent for decades, does their recruitment occur during most years or only rarely and under just the right combination of conditions? We have very little information on the demography of mussel populations, but in at least one well-studied population, successful recruitment occurred only once every 5 to 10 years (Payne and Miller 2000). In other populations, at least some recruitment seems to take place during most years. It will be a major challenge to understand events that occur at intervals longer than the human life span.

The long life spans of pearly mussels may have practical consequences as well. Long-lived, slow-growing animals are notoriously sensitive to overharvesting and other sources of mortality, and they may be very slow to recover. Clearly, the 20th-century mussel harvests in the US Midwest were too large to be sustainable (Anthony and Downing 2001). If mussel harvests are to continue in the future, it may be necessary to adopt a very conservative view of what constitutes a sustainable harvest.

To assess the long-term prospects of the fauna, researchers need good estimates of rates of loss and recovery in pearly mussel populations, and reliable estimates are still lacking (but see Vaughn [2000] for an example). Of course, some events (e.g., severe pollution) kill all mussels instantaneously, but many populations are now threatened by chronic stresses with slower effects. It is particularly difficult to assess the long-term dynamics of long-lived animals like unionaceans, whose populations may persist for a long time under conditions of negative population growth. Many populations today probably have negative growth rates and are destined ultimately to disappear unless environmental conditions change. Such populations represent a large "extinction debt" (Tilman et al. 1994) that will become apparent over the coming decades as these long-lived animals age and die. Clearly, scientists and managers need better projections of the population trajectories of stressed mussel populations, using either demographic or physiological indicators, to warn of impending losses.

Although pearly mussel populations are declining in many places, improvements in water quality following the passage of the Clean Water Act and similar laws have allowed mussels to recolonize some sites that were formerly polluted. This process has not been well studied, but it is of critical importance to the long-term prospects of the fauna. Mussel populations may reestablish within a few decades of habitat improvement, but the community that recolonizes is not always similar to the original community that lived at the site (e.g., Sietman et al. 2001). Researchers and managers working with pearly mussel communities need more information on the extent to which such recolonization is occurring around the world, its pace relative to the concurrent pace of declines at other sites, and the species composition of recolonizers.

## Forces producing spatial patterning in mussel communities

Mussel populations are patchy on scales ranging from centimeters to hundreds of kilometers (figure 4). Large-scale patterning seems to be a result of historical patterns of dispersal, host distribution (Vaughn and Taylor 2000), and climate, but explanations for patchiness at the subkilometer level have been elusive. At this scale, mussels often are aggregated into beds, where many or all of the species found in a stream or river co-occur at densities 10 to 100 times higher than those outside the bed. Historically, explanations for the location of mussel beds focused on simple physical variables such as sediment grain size and current speed, but these explanations have largely failed when tested critically (Strayer and Ralley 1993). More recently, researchers have shown that mussel beds may occur where shear stresses are low and sediments are stable during flooding (Layzer and Madison 1995, Strayer 1999b, Hastie et al. 2001). The restriction of mussel beds to such "flow refuges" occurs because these long-lived animals live in one of the most chronically unstable environments on earth. As opportunities for changing the release schedules of dams increase (Poff et al. 2003), it will become critical to understand how flow regimes affect mussel populations.

However, shear stress and sediment stability provide only a partial explanation for the occurrence and location of mussel beds. Other factors must contribute to the local patterning of mussel populations. Pearly mussels have a complex life history, and the requirements for all life stages must be met

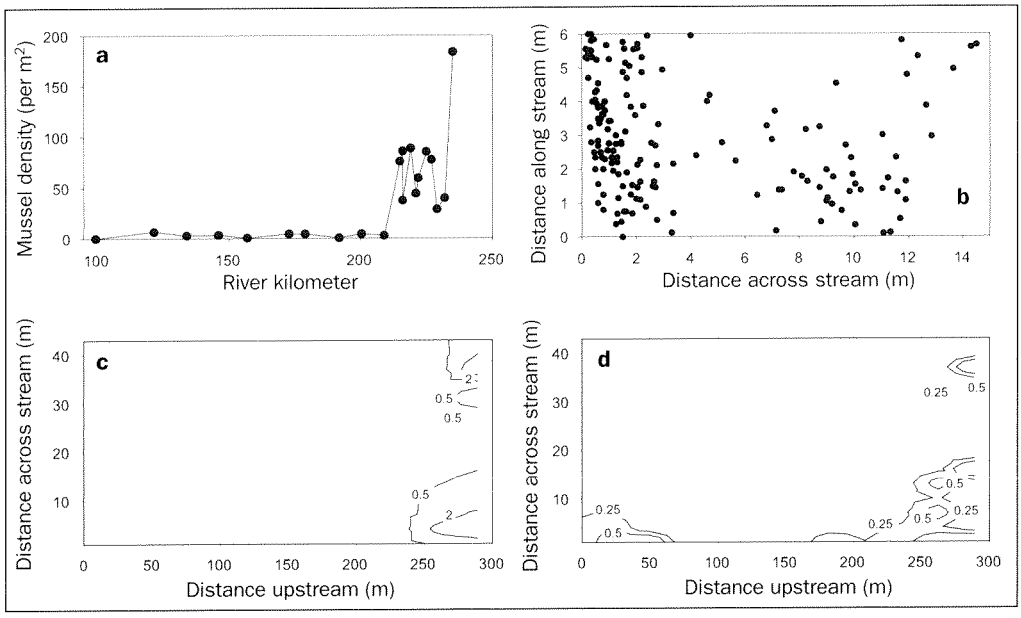


***Figure 4. Patchiness in pearly mussel communities at several spatial scales. (a) Mean density (mussels per square meter) along a 150-kilometer section of the Hudson River, New York. (b) A local patch of a few square meters within a mussel bed in Webatuck Creek, New York. Each dot represents a mussel. (c) Contours showing the mean density (mussels per square meter) along a 300-meter reach of the Neversink River, New York. (d) Locations of flow refuges, identified by the contours of probability that a marked rock stayed in place during a flood. Compare the locations of flow refuges with the locations of mussel beds in the same reach (c). Modified from Strayer and colleagues (1994) and Strayer (1999b).***

by the habitat. Thus, factors such as food quality and quantity, local distribution of fish hosts during the season of glochidial release, well-oxygenated sediments for juvenile survival and growth, and refuge from predators all may determine the local occurrence of mussels. It will be a challenge to understand the importance and interactions of these multiple controlling factors.

Further, the existence of mussel beds raises questions about their origins. Mussel beds could arise from two broad classes of causes. Negative "censoring" mechanisms such as crushing, burial, downstream washout, suffocation, starvation, or predation could remove mussels that colonize areas outside of mussel beds. Day-to-day conditions such as poor-quality food or excessive predation could prevent the development of mussel beds. Because of the long life spans of mussels, censoring events that occur even infrequently may be important. Positive mechanisms such as habitat selection by juveniles or adults or high fecundity in favorable habitats could form mussel beds. Although habitat selection by adults has been investigated, there has been almost no work on habitat selection by settling juveniles, a process that is important for many marine invertebrate larvae (Butman 1987). Mussel beds may even be self-organizing to a degree: Heavy, firmly buried adult mussels could stabilize the sediments in mussel beds. Similarly, sediment mixing by adults may increase pore space and dissolved oxygen (Vaughn and Hakenkamp 2001) and enhance conditions for buried juveniles or host fish. Human actions have stopped recruitment in many mussel beds. For example, low temperatures downstream of hypolimnetic-release reservoirs have prevented mussel reproduction at some sites for decades (Heinricher and Layzer 1999). The beds that exist on these sites today are remnants from the time before the dams were built. Likewise, residual contamination or changes in host fish communities may prevent recruitment in mussel beds. Thus, mussel beds may be relicts of a time when conditions really were suitable for mussels, not indicators of currently favorable conditions. When researching the environmental requirements of populations or assessing populations for conservation status, it is important to distinguish such relict beds from "live" mussel beds that support sustainable recruitment.

## How do mussel populations function spatially?

The patchiness that is characteristic of mussel populations at every spatial scale has important consequences for the functioning of populations and their effects on other parts of ecosystems. As elsewhere in ecology, the consequences of spatial structure are just beginning to be explored.

Mussels are broadcast spawners, releasing large numbers of sperm into a water column that often is well mixed. There have been no studies of sperm dispersal in nature, but recent studies suggest that sperm dispersal may be inadequate, even in fairly dense populations. Two studies (Downing et al. 1993, McLain and Ross 2004) found the proportion of gravid females in a population to be positively correlated with population density. Downing and colleagues (1993) estimated that successful reproduction required population densities as high as 10 mussels per square meter, far greater than local densities in most populations. Further, mussels may move closer together during breeding season (Burla et al. 1974, Amyot and Downing 1998) or even gather into isolated male–female pairs (Shelton 1997). These observations suggest that mussel populations in nature may often be too sparse to provide adequate sperm to breeding females, a result that would have great consequences for the ecology and conservation of these animals. Thus, mussel populations might consist of large areas of low density, which contribute little or nothing to the viability of the population, along with a few high-density

nuclei that drive population growth and the genetic structure of the population. In such populations, the high-density nuclei would be the prime subjects of ecological studies and conservation efforts. However, if sperm density and dispersal are not limiting, then mussel populations might function in a more conventional manner, with all individuals contributing to the breeding population. This problem calls for careful study in various species and habitats.

The spatial scale at which glochidia and their fish hosts are dispersed is also important in understanding the ecology and genetics of mussel populations. Glochidia are heavy, short-lived, nonmotile, and presumably poorly dispersed by water unless they are contained in a structure such as a mucous net that reduces sinking rates. Dispersal by fish hosts must vary greatly across fish species. Nevertheless, many mussels use small benthic fishes such as darters and sculpins as hosts (Watters 1994), so dispersal distances of encysted glochidia may be much less than 100 meters (McLain and Ross 2004), less than the distance between neighboring mussel beds. Thus, for many mussel species, dispersal between neighboring mussel beds may be small, colonization of newly created habitats or defaunated streams may be slow, and genetic differentiation may occur even at small spatial scales. Mussel species that use wide-ranging hosts may exhibit very different population dynamics and genetic structure (Berg et al. 1998). Of course, barriers to dispersal, whether natural or anthropogenic, may have profound effects on mussel distribution and genetic structure (King et al. 1999). Researchers and managers need to pay much more attention to the dispersal of glochidia and infested fish in order to manage mussel populations that have been dismembered through human actions, and to understand their population dynamics and genetic function.

If imperfect dispersal of sperm, glochidia, and infested fish limits the spatial range of demographic interactions to near neighbors, then metapopulation models may be well suited to unionacean populations. These models have been applied in ecology to address a wide range of ecological and conservation issues (Hanski 1999). Despite their promise, metapopulation models have received only limited application to unionaceans (e.g., Vaughn 1997, 2000) and warrant further investigation. Modern genetic techniques such as microsatellite DNA markers (Eackles and King 2002) may soon allow researchers to understand the fine-scale population structure of unionacean populations, providing information about gene flow between mussel beds and recolonization rates of newly available habitats that is needed to assess the utility of metapopulation models.

The activities of unionacean mussels—consuming phytoplankton and other particles, releasing nutrients, depositing feces and pseudofeces (biodeposits), and mixing sediments (Vaughn and Hakenkamp 2001)—may be important in ecosystems, paralleling the central roles played by other bivalves (Dame 1996). These activities have characteristic spatial dimensions and are affected by the spatial dispersion of the mussel population. Thus, the zone of depletion of phytoplankton by an individual mussel is likely to be small (< 0.1 cubic meter), especially in a well-mixed stream or lake. If mussels are dense enough that these zones of depletion overlap, shadows of phytoplankton-depleted and nutrient-enriched water may extend for long distances (even kilometers) downstream of mussel beds (Caraco et al. 1997, Wildish and Kristmanson 1997). In contrast to the large-scale, diffuse effects of phytoplankton removal and nutrient release, biodeposition and sediment mixing may cause intense effects at local scales (from centimeters to the size of mussel beds). As research proceeds on the effects of unionaceans on ecosystems, it will be important to specify the spatial scales over which these effects occur and to relate the effects to the spatial structure of the mussel population.

The factors that control mussel populations arise at various distances from the mussels. Early attempts to explain distribution and abundance, as in other areas of ecology, concentrated on local conditions around the mussels. However, while local conditions undoubtedly are important for mussels, more distant factors, such as geology and land use in the watershed, may have strong effects as well. Mussel ecologists are working with models based on GIS (geographic information system) software to identify the attributes of riparian zones and watersheds that matter most to mussels, the mechanisms by which these attributes affect mussels, and the spatial scales over which these factors operate (Arbuckle and Downing 2002).

Thus, reciprocal interactions between mussel populations and their environments occur over a range of spatial scales. Some of these neighborhoods of interaction are less than 1 meter in size (biodeposition), whereas others probably extend for tens of kilometers (effects of land use, dispersal of species with wide-ranging hosts). Specifying the sizes of these different neighborhoods of interaction and understanding the functional consequences of unionacean patchiness are important challenges for ecologists in the coming years.

## Diagnosing and reversing declines in mussel populations

Mussel populations have declined severely in many parts of the world (figure 5), leading to the extinction or endangerment of many species (figure 1d). The causes of these declines and the remedies for reversing them are not entirely clear. Accounts of mussel populations dying out from human activities appeared as early as the mid-19th century. Many of the early (pre-1950) losses of mussel populations had obvious causes, such as gross pollution or habitat destruction from dam building or channelization. In some cases, these acute impacts have been corrected, leading to limited recovery of mussel populations. It is thought that diffuse and chronic impacts, rather than acute impacts, now present the greatest threats to mussel populations. It has been difficult to identify and remediate these threats. Much of the modern literature on pearly mussel declines is anecdotal, providing a laundry list of possibilities instead of critical analyses of causes. Professional judgment in the field, represented by a sample of 45 articles on

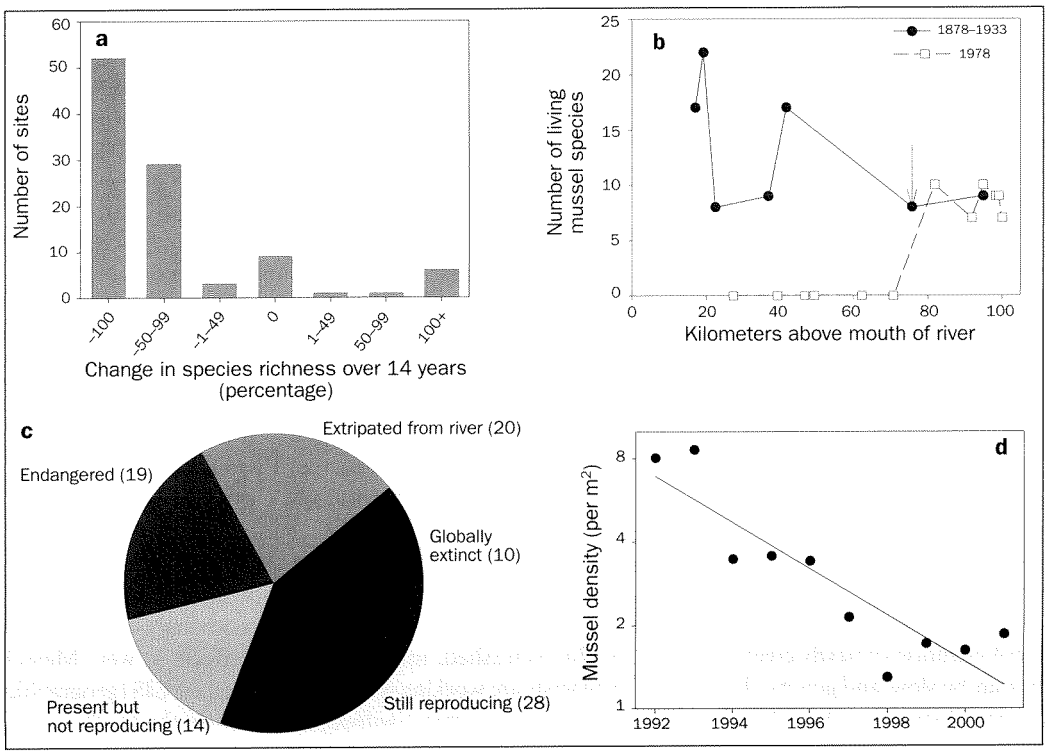


***Figure 5. Local and regional declines in mussel populations from various causes. (a) Changes in species richness in Iowa streams running through intensively agricultural landscapes (1984–1985 to 1998). Data are from Poole and Downing (2004). (b) Losses of mussel populations from Clinton River, Michigan, as a result of industrial and urban development in the mid-20th century. Data are from Strayer (1980). (c) Status of the 91 species of freshwater mussel species that formerly occurred in the Tennessee River, which now consists largely of a series of reservoirs. Modified from Neves and colleagues (1997). (d) Declining populations of pearly mussels in the freshwater tidal Hudson River, New York, as a result of the invasion of the exotic zebra mussel (*Dreissena polymorpha*) in 1992. Updated from Strayer (1999a).***

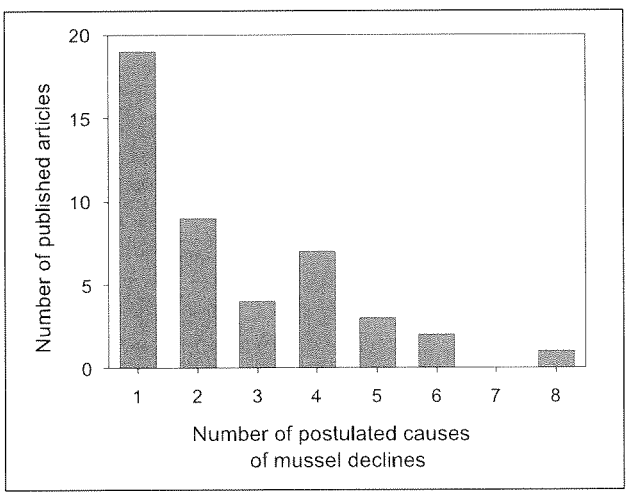


***Figure 6. Number of causes of mussel declines postulated by the authors of 45 published articles in an informal review of the literature.***

unionacean declines, suggests that pollution, water quality degradation, and habitat destruction and alteration are the most likely candidates for causes of declines (table 1). Fewer than half the articles we canvased attributed population declines to a single cause (figure 6), and up to eight causes were suggested by one author.

The difficulty of dealing with multiple, chronic threats begs the question of how researchers might proceed to accurately diagnose the causes of declines. Faced with a similar problem, epidemiologists developed criteria to associate environmental factors with disease (box 1; Hunter 1997). These criteria may also be useful in mussel ecology. In mussel ecology, as in medicine, it will be especially difficult to deal with the long-term and cumulative effects of chronic impacts, with the interactions between multiple factors, and with the time lags between the action of a stressor and the appearance of its effects. For example, populations that have survived extensive loss of suitable habitat often face continued losses over a long period because of a time lag between habitat loss and eventual population collapse (Cowlishaw 1999).

There are a number of possible remedies for these declines. It may be possible to reduce inputs of sediments, nutrients, and other pollutants from poor land-use practices or to stop destructive practices such as in-stream gravel mining. Stream restoration can improve habitat. Dams might be removed or modified by adding fish passages or changing release schedules to lessen their impacts on mussels. While it may be difficult to control the impacts of established exotic species such as the zebra mussel, managers can work to prevent the establishment of additional harmful exotics. Large-scale, collaborative conservation efforts will be needed to deal effectively with these problems.

However, these remedies may not produce rapid recovery of mussel populations, for three reasons. First, residual contamination from past episodes of pollution may have left a toxic legacy in streams and rivers. Some juvenile mussels live

*Table 1. Frequency of explanations for unionacean declines offered by authors of 45 published articles.*

| Postulated cause | Frequency (percentage) |
|---|---|
| Pollution, water quality degradation | 47 |
| Habitat destruction and alteration | 47 |
| Damming and impoundment | 33 |
| Introduction of exotic species | 29 |
| Hydrologic change | 20 |
| Exploitation and harvesting | 18 |
| Recruitment failure, lack of fish hosts | 13 |
| Watershed alterations | 13 |
| Riparian alterations | 7 |
| Predation | 7 |

*Note:* Some articles focused on unionacean declines at specific localities while others covered broad regions. Explanations offered by less than 5% of the articles include the small-population phenomenon, climatic change, reduced ranges, competition with native species, and genetic change.

buried in sediments and feed on sediment particles and their associated pore water (Yeager et al. 1994), which are often badly contaminated. Ironically, the bulk of the toxicity literature is based on water-only exposures, even though studies have shown that sediment-associated contaminants probably contributed to the decline of mollusks in many large rivers, such as the upper Mississippi (Frazier et al. 1996). Future research on contaminants that affect pearly mussels should identify the primary exposure routes (surface water, sediments, pore water, food) for contaminants of concern (Naimo 1995).

Second, negative density dependence can cause sparse populations to continue to decline even after the original cause of decline is removed. The most likely cause of negative density dependence in mussels is low reproductive success in sparse populations. It may be necessary to artificially increase population density to counteract negative density dependence, although research verifying the need and determining the best practices for such intervention is in its infancy.

Finally, mussel populations will not recover if they have been extirpated from a region and if there is no source of propagules to reestablish the population. This is especially a concern in modern streams and rivers, in which dams and poor-quality habitat often block dispersal. Again, if populations are to be reestablished, human intervention will be necessary. Fortunately, research on life history and on rearing techniques (Henley et al. 2001) is beginning to make it possible to rear large numbers of juvenile pearly mussels in the laboratory, a process that has proved difficult in the past because of the exacting food requirements of juveniles. There have even been limited trials to stock these laboratory-reared juveniles into extirpated or depleted populations. Laboratory propagation for restocking has potential as a conservation tool, provided that restorationists understand and correct the reasons that mussels disappeared in the first place and take care to avoid genetic problems.

**Box 1. Nine criteria used by epidemiologists to associate environmental factors with disease**

1. Determine the strength of the association between population decline and the putative causative agents.
2. Determine the consistency of the association between these factors and decline.
3. Define the specificity of the association.
4. Distinguish the temporal sequence of cause before decline.
5. Detect a biological gradient of increasing intensity of causative agents with increased rates of decline.
6. Determine the plausibility of a cause, given knowledge about biology and ecology.
7. Determine the coherence of the link between cause and decline, with knowledge of the causal agent's mode of action.
8. Produce experimental evidence that changes in impact can be induced by reduced exposure to the causative agent.
9. Establish an analogy with other well-known causes of decline.

*Source:* Hunter 1997, modified to determine causative factors for population decline.

Clearly, researchers and managers need better information on the impacts of human activities on pearly mussels, particularly at large spatial scales. Nevertheless, given the high rates of decline in many pearly mussel populations (figure 5), conservation actions cannot be postponed until those declines are fully understood. Adaptive management (Walters 1986) may be a useful tool in situations like this, when managers must take action on the basis of imperfect information. Using adaptive management may be especially difficult with long-lived organisms, however, because the full effects of a management regime may not be apparent for decades or even centuries. It would therefore be valuable to develop leading indicators of the response of a mussel population before that response is fully expressed. Such indicators, whether physiological (e.g., scope for growth; Bayne et al. 1985) or demographic, will need careful evaluation before they are adopted.

## Conclusions

We draw several conclusions from this brief overview of recent pearly mussel research. First, conservation concerns have caused a rapid increase in research on mussels, especially since about 1990 (figure 2). This research has produced findings of fundamental importance. Widespread surveys have confirmed that pearly mussels are indeed in trouble in

developed parts of the world, with many species extinct or on the edge of extinction (figure 1d, figure 5). Along with parallel data on other freshwater plants and animals, these findings emphasize the enormous pressure that humans are placing on freshwater ecosystems. Nevertheless, it is proving to be difficult to identify and manage all of these human impacts, especially those with diffuse and chronic effects. It will be important to confront hypotheses developed from expert judgment (table 1) with an aggressive program of rigorous scientific research, and not to assume that scientists and managers have all the information necessary for managing mussel populations. Yet conservation actions to protect mussels must be pursued equally aggressively, without waiting for research to provide final answers. Adaptive management may be a useful tool, particularly if researchers can find good leading indicators of the long-lived pearly mussels, whose full response may take decades or centuries to unfold.

Second, although pearly mussels are among the largest and most familiar of freshwater animals and have been studied by scientists for decades, recent research has uncovered major surprises. In some cases, this research has shown that accepted knowledge was wrong, but more often it has revealed important variations around familiar themes or has found phenomena that simply were not suspected to occur. It is likely that researchers will continue to make discoveries with major implications for the ecology, evolution, and conservation of pearly mussels. When we read authoritative textbooks or look at the enormous volume of paper held in science libraries, it is sometimes easy to forget how much is still unknown. As research since 1980 has shown, pearly mussels still hold secrets that await discovery.

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