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Biodiversity Loss in Freshwater Mussels: Importance, Threats, and Solutions

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1. Introduction

The loss of biodiversity worldwide has been well documented for decades, and while much of the attention of the media and scientific community has been focused on terrestrial ecosystems, other biomes such as freshwater lakes and streams have received less consideration (Myers et al., 2000). Despite the current decade (2005-2015) being declared an International Decade for Action – 'Water for Life' by the United Nations General Assembly, freshwater ecosystems worldwide are as threatened as ever by the activities of a rapidly growing human population. Surface freshwater ecosystems only constitute 0.8% of the Earth's surface, yet they contain almost 9.5% of the Earth's known species, including as many as one-third all known vertebrate species (Balian et al., 2008; Dudgeon et al., 2006). The impact of human disturbances on this disproportionate amount of biodiversity has made the extinction rate in freshwater ecosystems equal to that of tropical rainforests (Ricciardi and Rasmussen, 1999).

1.1 Freshwater ecosystem services

Because we depend on water both as a biological necessity and for the myriad of resources and services it provides us, over half of the world's population lives within 20 km of a permanent river or lake (Small and Cohen, 1999). Direct benefits and ecosystem functions of freshwater lakes, streams, and wetlands include providing sources of water for municipal and industrial use, irrigation, hydroelectric power generation, transportation corridors, recreation, and producing fish and other resources used for food and medicine. Freshwater ecosystems also provide many indirect ecosystem services such as water filtration, buffering against storms and flooding, cycling of nutrients and organic matter through the environment, and supporting ecosystem resilience against environmental change (Aylward et al., 2005; Jackson et al., 2001). These indirect ecosystem services have very real economic values. One study valued the ecosystem services of freshwater aquatic ecosystems worldwide at $6.5 trillion USD, or 20% of all the world's ecosystem services (Costanza et al., 1997).

As human populations continue to develop aquatic resources to maximize a few of these anthropogenically beneficial services such as water storage, generation of electricity, and fish production, other environmental services that are less directly important to humans are being reduced or lost (Bennett et al. 2009). The reduction of these ecosystem functions can significantly alter an ecosystem's natural character. After more than a century of unprecedented human population growth and global economic development, we have created widespread and long-term ecological disturbances to freshwater ecosystems in almost all parts of the inhabited world (Strayer and Dudgeon, 2010).

Water Supply (Extractive)	Supply of Goods Other Than Water	Non-Extractive/Instream Benefits and Uses
•Drinking, cooking, washing, and other household uses	•Fish	•Flood control
•Manufacturing and other industrial uses	•Waterfowl	•Transportation
•Irrigation of crops, parks, etc.	•Clams and mussels	•Recreation.
•Aquaculture	•Pelts	•Dilution of pollution
	•Plant products	•Water quality protection
		•Hydroelectric generation
		•Bird and wildlife habitat
		•Soil fertilization
		•Enhanced property values
		•Non-user values

Table 1. Ecosystem services provided by freshwater lakes, rivers, and wetlands (after Postel and Carpenter, 1997).

1.2 Human disturbances to freshwater systems

Humans now capture more than 50% of the world's precipitation runoff behind dams for electricity generation and water storage, and through diversion canals for irrigation. 16% of all runoff is consumed, or not returned to the rivers after use, while the remainder of the captured runoff is returned but with altered timing, amount, and quality (Jackson et al., 2001). Water pollution, including siltation, is endemic to almost all inhabited parts of the world and is consistently ranked as one of the major threats to freshwater ecosystems (Richter et al., 1997). Pollution in aquatic ecosystems not only consists of chemical toxicants like heavy metals, industrial waste, and pesticides, but also includes excessive nutrient enrichment and pharmaceuticals and personal care products (PPCPs) (Jobling and Tyler, 2003; Smith et al., 1999). Habitat loss and habitat degradation are also major reasons for worldwide biodiversity loss in aquatic ecosystems, and are caused by a multitude of anthropogenic disturbances (Allan and Flecker, 1993; Richter 1997 et al. 1997). Many freshwater species are also being overharvested for human consumption or the pet trade. This affects mostly vertebrate species, especially fishes, but can impact invertebrate species like mussels and crustaceans as well (Dudgeon et al., 2006). The threat of global climate change is pervasive across all of the Earth's ecosystems, and is also often cited as a major threat to freshwater biodiversity (Sala et al., 2000; Strayer and Dudgeon, 2010).

All of these environmental disturbances alter the "natural" chemical, physical, and biological patterns of a system, and when those conditions are changed, both the absolute and functional biodiversity of that system can be threatened. This loss of biodiversity can in turn create a feedback loop that further alters ecosystem functioning. The theory that ecosystem services depend on the biological diversity of the system is well supported for terrestrial ecosystems (Kinzig et al., 2002; Loreau et al., 2001), and recent studies have shown that maintaining biodiversity in aquatic ecosystems is crucial to the continued functioning of ecosystems and the delivery of ecosystem services as well (Covich et al., 2004).

It is widely accepted that freshwater ecosystems worldwide are suffering from a "biodiversity crisis", with estimates of 10,000-20,000 species currently extinct or threatened

(Abell, 2001; IUCN, 2007; Strayer and Dudgeon, 2010). While almost all taxonomic groups of freshwater organisms are facing unprecedented declines, some groups are especially affected.

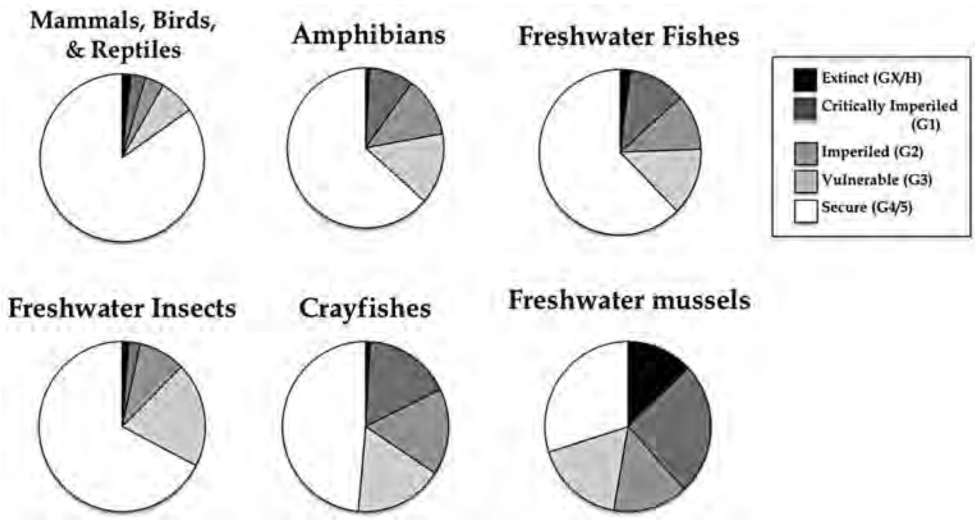

Fig. 1. Conservation status of selected groups of terrestrial and freshwater organisms using NatureServe conservation status designations (after Master et al., 2000).

2. Freshwater mussels: North America's most threatened animals

Of all groups of threatened aquatic animals, freshwater mussels (also known as unionid or pearly mussels) are the most imperiled, with 67% of North American species considered threatened (Williams et al., 1993). 35 North American freshwater mussel species have gone extinct since 1900 (Williams et al., 1993), and some scientists have estimated a 1.2% per decade extinction rate for this group, with others predicting that unless effective conservation action is taken 127 more species will become extinct over the next 100 years (Ricciardi and Rasmussen, 1999).

2.1 Classification of freshwater mussels

Freshwater mussels (order Unioniformes) belong to the subclass Paleoheterodonta, class Bivalvia, and phylum Mollusca. A total of 18 bivalve families have at least one species found in freshwater, although only about 9 have radiated to any degree there (Bogan, 1993). The order Unioniformes contains the largest number and diversity of groups with 180 out of 206 genera and 797 out of 1026 species. Within the Unioniformes, the family Unionidae is the largest, comprising nearly 80% of both the genera and species within the order (Bogan and Roe, 2008). Other important families include Hyriidae (17 genera, 83 species), Mycetopodidae (12 genera, 39 species), Sphaeriidae (8 genera, 196 species) (Bogan and Roe, 2008). As the order Unionidae is the most diverse, and has had the most research dedicated to it, we shall from here on out refer to freshwater mussels simply as Unionids, or unionid mussels.

2.2 Freshwater mussel distribution

Freshwater mussels are found on every continent with the exception of Antarctica, but reach their highest level of diversity in the Nearctic geographic region, with one-third of all species (297 recognized taxa) being found there (Bogan, 2008). The Neotropical region has 179 described species, the Oriental has 121, the Palaearctic 92, the Afrotropical 74, and the Australasian region has 29 (Bogan, 2008). Data on the conservation status of freshwater mussels globally is incomplete, with relatively strong data from only a few areas (North America, Europe, and Australia). In other areas (Africa and South America), detailed taxonomic information including the total number of species currently or historically present is lacking, which makes determining changes in species abundance and richness difficult (Bogan, 2008). There has been increased interest in the biodiversity of freshwater mussels worldwide over the last few decades, though, as scientists have realized just how rapidly this group is declining (Graf and Cummings, 2007). Hopefully this increased awareness will lead to more surveys in these understudied areas to fill in the gaps in basic knowledge that currently exist.

	Family	Genera	Species
Order Arcoida	Arcidae	1	4
Order Mytiloida	Mytilidae	3	5
Order Unioniformes	Etheriidae	1	1
	Hyriidae	17	83
	Iridinidae	6	41
	Margaritiferidae	3	12
	Mycetopodidae	12	39
	Unionidae	142	620
Order Veneroida	Cardiidae	2	5
	Corbiculidae	3	6
	Sphaeriidae	8	196
	Dreissenidae	3	5
	Solenidae	1	1
	Donacidae	2	2
	Navaculidae	1	2
Order Myoida	Corbulidae	1	1
	Erodonidae	2	2
	Teridinidae	1	1
Order Anomalodesmata	Lyonsiidae	1	1
	Total	209	1026

Table 2. Classification of freshwater mussels (6 orders and 19 families), including number of genera and species for each family (after Bogan, 2008).

2.3 Endemism and conservation

One of the major reasons for the high proportion of extinct and endangered freshwater mussels is the high degree of endemism found in this group, which is characteristic of many freshwater organisms. Endemic species have a limited geographical range, often limited to a single drainage basin or lake, and often have unique characteristics suited to that particular locale (Strayer and Dudgeon, 2010). Local rarity also puts a species at a much higher risk of extinction due to the fact that limited distribution puts most or all of a population at risk to environmental stresses simultaneously (Gaston, 1998) and also limits the ability of a population to recover through recruitment from other populations, especially in species with low dispersal ability, such as unionid mussels (Burlakova et al., 2010). One recent study showed that endemic species were critical determinants of the uniqueness of unionid communities, and as such, should be made a conservation priority (Burlakova et al., 2010).

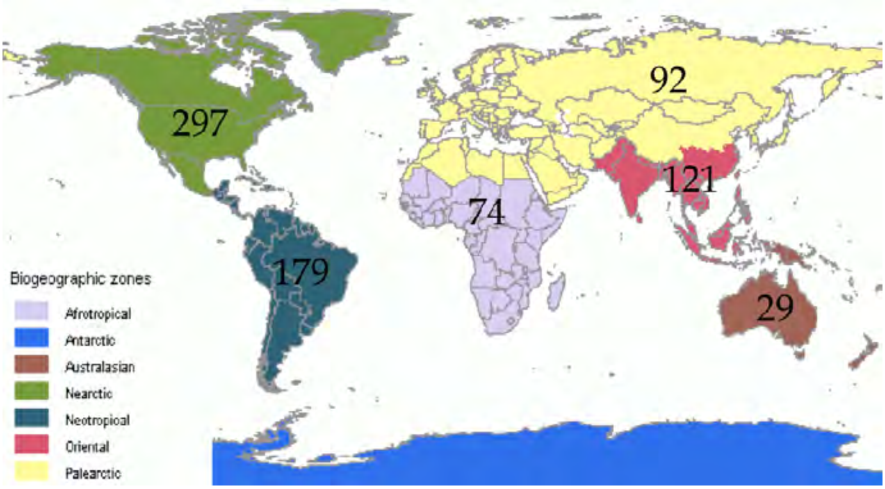

Fig. 2. Map showing the distribution of freshwater mussel species by biogeographic region.

3. Ecology and life history of freshwater mussels

Freshwater mussels are long-lived organisms, often living for decades, and some species can survive over 100 years (Bauer 1992). Typically, unionids live buried in fine substrate in unpolluted streams and rivers with benthic, sedentary, suspension-feeding lifestyles. The mussels use their exposed siphons to inhale water and use their gills to filter out fine food particles, such as bacteria, algae, and other small organic particles. Their benthic, sessile lifestyle, their obligatory dependence on fish hosts for reproduction, and their patchy distribution as a result of specific habitat requirements all contribute to their decline in the face of human disturbances. Freshwater mussels have complex life cycles with extraordinary variation in life history traits (Table 3).

3.1 Reproduction

Freshwater mussels are broadcast spawners, with males releasing sperm into the water to fertilize the eggs that are retained internally in the females' body (Wachtler et al., 2001). The defining characteristic of Unionids is their specialized larval stage known as glochidia that are released from a gravid female's modified "marsupial" gills where they developed from embryos following fertilization (McMahan and Bogan, 2001). One female mussel can produce up to 4 million or more glochidia and eject them in a sudden and synchronized action (Bauer 1987). If the glochidia are released in the proximity of a suitable host fish, they clamp onto the gills of the host, which then carries the glochidia for weeks or months until they are mature and ready to live freely on the bottom of the stream or lake. Because glochidia are heavy, short-lived, non-motile, and poorly carried in currents, facultative dispersal by fish species is necessary for the spread and maintenance of most Unionid populations (Strayer et al., 2004).

Trait	*Unionoidea*	*Sphaeriidae*
Life span range	< 6 to > 100 years	< 1 to > 5 years
Age at maturity	6 to 12 years	>0.17 to <1 year
Reproductive mode	gonochoristic	hermaphroditic
Fecundity (young/female/season)	0.2 – 17 million/female per breeding season	2 – 136/female/season
Juvenile size at release	50 – 450 μm	600 – 4150 μm
Juvenile survivorship	extremely low	high
Adult survivorship	high	intermediate
Semelparous or iteroparous	iteroparous	semelparous or iteroparous
Reproductive efforts per year	1	1-3
Non-respired energy allocated to:		
(i) growth (%)	85-98	65-96
(ii) reproduction (%)	3-15	4-35

Table 3. Comparison of life history traits of freshwater mussels (Unionoidea and Sphaeriidae) in North America (after McMahon and Bogan, 2001).

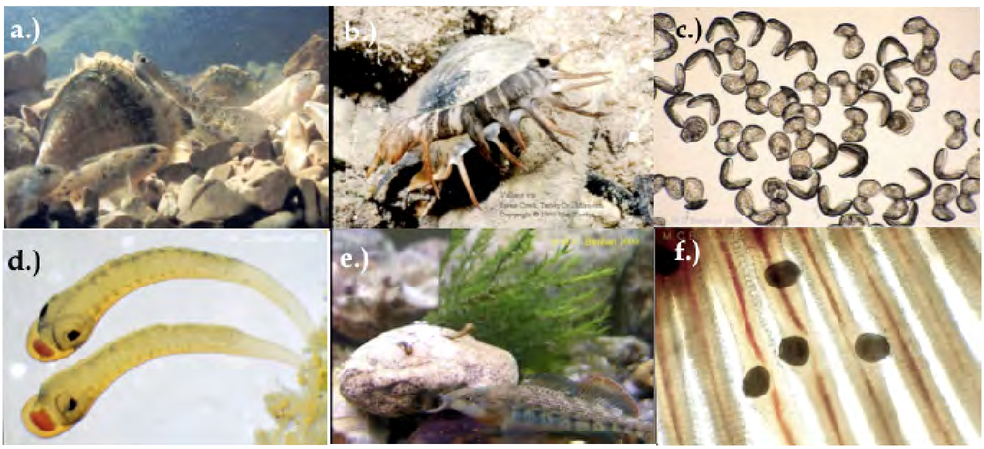

Fig. 3. a.) Fish-imitating lure of a gravid female broken-ray mussel, *Lampsilis reeveiana*; b.) Crawfish-imitating lure of the rainbow-shell mussel, *Villosa iris*; c.) Glochidia of the fluted kidneyshell, *Ptychobranchus subtentum.* Each glochidia is approximately 220 micrometers long; d.) Fish-imitating conglutinate of the Ouchita kidneyshell, Ptychobranchus occidentalis; e.) Rainbow darter, *Etheostoma caeruleum, attacking a conglutinate of* Ptychobranchus occidentalis; f.) Glochidia attached to the gills of a host fish. After attachment, the host fish's gill tissue forms a cyst around the glochidia. All photos are courtesy of Chris Barnhart (http://unionid.missouristate.edu).

In many mussel species, the gill, mantle margin, or other tissue has evolved into a lure that very realistically mimics a small minnow or invertebrate prey item used to attract a host fish. When a host fish nips at the lure, the glochidia are released into the vicinity of the fish's mouth, thus greatly increasing the odds of the glochidia attaching onto the fish's gills (Haag and Warren, 1999). Other species release large packages of glochidia called conglutinates, which often mimic prey items themselves, that rupture and release glochidia upon being bitten by potential hosts (Grabarkiewicz and Davis, 2008). These unique reproductive strategies have important implications for unionid conservation that will be discussed later in this chapter.

3.2 Feeding behavior and habitat preferences

As adults, freshwater mussels live on the surface or in the top layers of sediment; filter feeding suspended phytoplankton, bacteria, detritus, and other organic matter out of the water (Strayer et al., 2004). Juveniles often bury themselves in sediment below the surface, filtering interstitial water (Grabarkiewicz and Davis, 2008) or feeding pedally by scooping food into their mouths with their foot (Yeager et al., 1994). Unionids are highly sedentary, moving only short vertical and horizontal distances to reproduce or in response to seasonal or environmental cues (Amyot and Downing, 1998; Balfour and Smock, 1995). They are found in a wide range of habitats, from soft sediment bottoms in lakes and ponds to cobble and rock substrates in fast-moving rivers, although the majority of species are found in clear, highly oxygenated streams and rivers with sand, gravel, or cobble bottoms (Grabarkiewicz and Davis, 2008).

3.3 Small-scale spatial distribution

Freshwater mussels are often found in large multispecies aggregations known as mussel beds that can have densities of 10-100 individuals per square meter (Strayer et al., 2004). The biomass of freshwater mussels can higher than all other benthic macroinvertebrates by an order of magnitude (Layzer et al., 1993), and as a result of their large size and sheer numbers they can significantly influence both the biotic and abiotic conditions around them. Although the critical factors determining the location of mussel beds are still unclear, most researchers agree that water velocity and substrate, most notably where water velocity is low enough to limit shear stress and allow for substrate stability but high enough to prevent siltation, are strongly influential. Land use, geology, water quality, and availability of food and suitable host fish species are also strongly correlated with mussel presence/absence in other studies (Arbuckle and Downing, 2002; Newton et al., 2008; Strayer, 1983, 1999; Strayer et al., 2004). These habitat requirements result in a "patchy" distribution of mussels in riverine systems in non-continuous beds that may or may not be reproductively connected by host fish (Strayer et al., 2004).

4. The role of freshwater mussels on ecosystem functioning

As ecosystem engineers that modify their environment, freshwater mussels play many ecological roles where they are found in large numbers. These roles are a function of their life histories and behaviors, and can strongly affect both the biotic and abiotic components of the ecosystems in which they live. Loss of unionid biodiversity can result in loss of these functions and changes to the ecological regimes in those areas where mussels are in decline (Vaughn and Hakencamp, 2001).

4.1 Removing suspended particles

As suspension feeders, Unionids can remove large amounts of phytoplankton, bacteria, and inorganic nutrients from the water column, enhancing water clarity and quality (Strayer et al., 1999). When present in large numbers, they can filter an amount of water equal to or greater than that of daily stream discharge. In a study conducted in the River Spree in Germany, Welker and Walz (1998) found that freshwater mussels created a zone of "biological oligitrophication" by decreasing phytoplankton and phosphorus in the water column. Unionids can also play other important roles in nutrient cycling, such as removing pelagic nutrient resources and depositing them into nearby sediments as faeces or psuedofaeces (Roditi et al., 1997; Spooner and Vaughn, 2006). Mussels also influence nutrient cycling by serving as nutrient sinks in growing populations, or as nutrient sources in declining ones (Vaughn and Hakencamp, 2001).

4.2 Benthic influences

The presence of live mussels can increase in sediment organic matter, which has been shown to positively influence abundance and diversity of other benthic invertebrates and phytoplankton (Spooner and Vaughn, 2006). Benthic invertebrate diversity can also be increased by the presence of mussel shells (Allen and Vaughn, 2011). Other benthic organisms use the shell as habitat and flow refuges, and in large numbers, the presence of mussel shells can increase landscape-level species diversity and abundance (Gutierrez et al., 2003). The influence of Unionids on benthic communities is so great that Aldridge et al., (2006) found that the abundance of freshwater mussels successfully predicted invertebrate abundance and richness in seven lowland rivers in the UK. Mussels also act as environmental engineers, bioturbating the sediment as they move both vertically and horizontally (Allen and Vaughn, 2011). This activity can increase the depth of oxygen penetration in the sediment, homogenize sediment particle size (McCall et al., 1995), and affect the flux rates of solutes between the sediment and water column (Matisoff et al., 1985).

4.3 Ecological impacts of declining Unionid populations

Freshwater mussels are declining in both species richness and abundance, which can reduce their influence on ecosystem functioning and have multiple negative impacts on the ecosystem as a whole. If unioniddiversity declines but total abundance remains the same, these ecological functions should continue being performed if all mussel species perform these functions at equivalent rates (i.e. are functionally redundant). However, both common and rare species are in decline (Vaughn, 1997; Vaughn & Taylor, 1999), and it has been shown that some mussel species are more effective in carrying out the ecosystem functions described above (McCall et al., 1995; Vaughn et al., 2007). It is likely, therefore, that the ecological functions performed by freshwater mussels will continue to decline along with mussel populations, which can significantly impact the overall ecological functioning of freshwater systems (Vaughn, 2010).

5. Causes for the decline in freshwater mussel abundance and diversity

There are many causes for the decline in freshwater mussel biodiversity (Strayer et al., 2004; Downing et al., 2010). Dudgeon et al. (2006) describe five major contributors to the loss of freshwater biodiversity in general: over-exploitation, pollution, flow modification, exotic species invasion, and habitat degradation. These five factors are also driving the decline in freshwater mussel biodiversity and, along with the threat of global climate change, can create smaller and more isolated populations susceptible to genetic bottlenecks and burdened with extinction debts.

5.1 Commercial harvesting

Humans have gathered freshwater mussels for meat, pearls, and mother-of-pearl shells for thousands of years, although commercial harvesting on a large scale did not begin in North America until the early 19th century (Strayer et al., 2004). During this period, commercial musselers harvested untold numbers of unionids for their pearls, which were sold in domestic and international markets. Local populations of mussels were decimated following exhaustive harvesting, after which time the musselers moved on to other, previously untapped, streams (Anthony and Downing, 2001). Overharvest made marketable pearls rarer, and the pearl fishery declined near the end of the century. Around the same time, however, new manufacturing processes allowed for the production of clothing buttons from North American mussel shells, and another round of unregulated exploitation occurred that devastated many populations that had been missed by the pearl frenzy in the previous decades (Neves, 1999). As plastic buttons began to replace those made from mussel shells in the 1930s and 40s, the rising market of the Japanese cultured pearl industry sparked a new demand for mussel shells. It was found that beads of freshwater mussel shells, when placed inside saltwater pearl oysters, made superior nuclei for the formation of cultured pearls (Anthony and Downing, 2001). This most recent boom has lasted until the mid 1990's, when a combination of declining mussel stocks, increased regulation, foreign competition, and disease outbreaks in Japanese pearl oysters has significantly reduced freshwater mussel harvest in North America (Neves, 1999).

5.2 Pollution

Because mussels are such long-lived organisms, chronic exposure to pollutants can cause direct mortality or reduced fitness. This pollution can come from many different sources, such as municipal wastewater effluent, industrial waste, and agricultural and mining runoff (Bogan, 1993), and because unionids live in the sediment, the legacy effects of accumulated toxins can have long-term effects on populations (Strayer et al., 2004). Freshwater mussels can suffer direct mortality from acute or long-term exposure to high levels of organic and inorganic pollutants, and experience sublethal effects on growth, enzyme production, abnormal shell growth, reduced metabolism, and reduced fitness in general (Keller et al., 2007). Because of their complex life cycles, there are several critical life stages where unionids can be exposed to these pollutants, and each stage can have different sensitivities to them (Cope et al., 2008).

In addition to chemical toxicants, excessive sediment can also be a pollutant. Poor agricultural and forestry practices, benthic disturbance by dredging operations, runoff from construction sites, road building, urbanization, loss of riparian vegetation, erosion of stream banks, and changes in hydrologic patterns all contribute to unnaturally high amounts of fine particle sedimentation that affects mussels directly by clogging gills and feeding siphons, and indirectly by blocking light necessary for algal production (Brim Box and Mossa, 1999) and reducing visibility needed for fish hosts to find the lures of breeding female mussels (Haag et al., 1995). Siltation can also create a hardpan layer in the substrate, making it unsuitable for burrowing in (Gordon et al., 1992).

5.3 Flow alteration

Restriction or alteration of flow patterns is another major cause of mussel biodiversity loss. The construction of dams restricts the timing, frequency, and magnitude of natural flow regimes, and affects mussels by altering the stability of the substrate, the type and amount of particulate organic matter (an important food source for mussels), the temperature of the water, and water quality (Poff et al., 2007). Studies have shown decreased mussel populations below large dams, with populations increasing with increased distance downstream from dams and with increasing flow stability (Strayer, 1993; Vaughn and Taylor, 1999). Altered flow regimes after dam construction have been implicated in the extinction of several mussel species, and have resulted in the local extirpation of many more (Layzer et al., 1993). Dams also impair recruitment of juveniles by restricting access to host fish and dispersal of glochidia (Watters, 1999). Urbanization of catchment basins can also alter flow regimes by increasing the amount of impervious cover and channelizing storm runoff, causing higher, faster, and more frequent erosive storm flow events (Walsh et al., 2005). Direct withdrawals of surface and ground water for human consumption can also reduce available habitat, increase water temperatures, and impair mussels' ability to feed, respire, and reproduce (Golladay et al., 2004; Hastie et al., 2003).

5.4 Non-native organisms

Invasion of exotic species is a global phenomenon that threatens terrestrial and aquatic ecosystems alike. The zebra mussel (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) are the two non-native species of greatest concern in North America (although there is some debate over the impact of *C. fluminea*) (Strayer et al., 1999). *D. polymorpha* is highly invasive and fecund, and will attach to any solid substance including the shells of living Unionid mussels. They can occur in densities greater than 750,000 individuals/m^2, with veliger (their pelagic larvae) densities reaching 400/liter of water (Leach, 1993). Zebra mussels spread rapidly, and one group of researchers has noted a 4-8 year delay from time of introduction of *D. polymorpha* and extirpation of Unionid mussels in many ecosystems (Ricciardi et al., 2003). They compete for food and habitat with native mussels, although it is believed that epizoic colonization (infestation) of the surface of Unionid mussel shells is the most direct and ecologically destructive characteristic of *D. polymorpha* (Hunter and Bailey, 1992; Mackie, 1993). Infestation densities of zebra mussels have been found to exceed 10,000/Freshwater mussel (Nalepa et al., 1993).

Fig. 4. Invasive zebra mussels, *Dreissena polymorpha,* infesting a native fatmucket, *Lampsilis siliquoidea*. Photo courtesy of Chris Barnhart (http://unionid.missouristate.edu).

5.5 Habitat destruction and alteration

Many researchers believe that habitat destruction and alteration are one of the greatest threats to freshwater ecosystems and mussel populations worldwide (Ricciardi and Rasmussen, 1999; Richter et al., 1997; Sala et al., 2000; Osterling et al. 2010). Habitat modification is a general term that encompasses many of the threats described earlier, such as sedimentation, flow alteration, substrate modification, and others, but also include activities such as gravel and sand mining, channelization for boat transportation, clearing of riparian vegetation, and bridge construction (Watters, 1999). Increasing amounts of sediments, either from land surface runoff or instream erosion, is one of the largest contributors to mussel habitat loss, as it makes existing habitat unsuitable for many mussel species (Brim Box and Mossa, 1999). Altered stream behavior caused by modified flows, poor riparian zone management, and runoff from impervious cover can also result in habitat loss through bed scouring, channel morphology changes, and altered sediment regimes in the system (Brierley and Fryirs, 2005).

Headcutting, channelization, and other modifications in river geomorphology are also major causes of habitat alteration in mussel species. Headcutting occurs when an alteration on the bottom of a stream causes a localized washout that progressively moves up the river channel, deepening and widening the channel and releasing large amounts of sediment into the water column. Not only does this process physically destroy mussel habitat, the release of sediment smothers previously suitable downstream habitat as well (Harfield, 1993). Many rivers and streams have been channelized to allow easier boat and barge traffic and for transport of felled logs downstream. Dredging stream channels deposits huge amounts of sediment on the stream bottom, smothering mussels already present and preventing recolonization of future generations. Dredging also drastically alters the natural flow regime and homogenizes habitat, the natural flow regime, and results in habitat homogenization (Watters, 1999). Instream gravel mining operations have been shown to modify the spacing and structure of pools and riffles, change species diversity and abundance of fishes and invertebrates, and alter ecosystem functioning in streams (Brown et al., 1998). These changes can strongly impact freshwater mussels, as most unionids have evolved to thrive in shallow riffle areas with stable, moderately coarse substrate, and are extremely intolerant to disturbance, especially in their larval stages (Brim Box and Mossa, 1999).

5.6 Climate change

There is now strong evidence that both global and regional climate change is occurring and will cause an increase in mean air temperature, more erratic precipitation patterns, and more severe floods and droughts. (Bates et al., 2008) These changing patterns pose serious threats to both terrestrial (Thomas et al., 2004) and freshwater (Sala et al., 2000) ecosystems. One group of researchers predicted that up to 75% of fish species could become extinct in rivers suffering from declining flows as a result of both climate change and human withdrawals (Xenopoulos et al., 2005). Most of the research done on the effects of climate change in freshwater systems has focused on fish and other vertebrates, with very little direct study of the effect on unionids. However, it is well known that temperature affects several aspects of mussel physiology and life history, including reproduction, growth, and recruitment of juveniles (Bauer, 1998; Kendall et al., 2010; Roberts and Barnhart, 1999). It is possible that some mussel species will be able to acclimate to a gradual increase in water temperature, but it is the predicted spikes in maximum temperature and prolonged duration of high temperatures that are likely to impact many mussel populations, especially in small streams where water temperature is more closely linked to air temperature (Hastie et al., 2003).

The change in precipitation patterns could also impact mussel populations through increased flooding and prolonged droughts. Although periodic, low-intensity flooding can have beneficial effects on mussel populations such as flushing fine sediments and pollutants out of substrates (Gordon et al., 1992), extreme storm events can dislodge mussels from the sediment and alter mussel bed habitat (Hastie et al., 2001). In a record multi-year drought in Georgia, Golladay et al. (2004) observed a greater than 50% loss in total mussel abundance in some reaches in the study area. As mussels are limited in their ability to move horizontally, they are unlikely to reach refuges in response to complete dewatering of their habitat. Even reduced flows can have negative effects on respiration, feeding, growth, and glochidial recruitment; and can increase predation by terrestrial consumers like raccoons (Golladay et al., 2004; Hastie et al., 2003).

The response by unionid mussels to climate change will vary depending on several factors. Geographic location will play an important role as climate change is expected to affect different parts of the world differently (Parry et al., 2007). Climate change, as with most types of ecological changes, will produce winners as well as losers (McKinney and Lockwood, 1999; Somero, 2010). Endemic species with restricted geographical ranges are expected to be especially hard hit (Malcolm et al., 2006), as are species that are already close to their upper thermal tolerance ranges (Spooner and Vaughn, 2008). The threat of climate change does not exist in isolation. It also interacts with other disturbances such as land use, direct human-caused flow alterations, and biotic exchange of non-native species; and the severity of these other threats along with geographic location will influence the effects caused by a changing climate (Sala et al., 2000).

5.7 The extinction debt

As serious as the current conservation status of many freshwater mussels are, there most likely exists a substantial extinction debt in many mussel populations (Haag, 2010). Freshwater mussels naturally exist in spatially “patchy” populations separated by areas occupied by no or only a few individuals. These patches remained connected, however, by glochidia transported by host fishes travelling throughout the matrix of mussel beds and unoccupied areas (Strayer, 2008a). Thus, population declines caused by stochastic events such as major floods or droughts could be restored through recruitment from neighboring populations. Many of the threats unionids are facing today, though, such as the building of dams, decline or extinction of host species, increased difficulty of host fish finding female mussels’ “lures” or conglutinates due to decreased visibility, and lack of suitable habitat for juvenile mussels, limit reproductive success and gene flow between patches.

As pelagic spawners that release sperm into the water column, it has also been shown that reproductive success declines dramatically with decreasing mussel density, with almost no fertilization occurring at densities below 10 individuals/m^2 (Downing et al., 1993). This lack of reproductive connectivity creates a genetic bottleneck in the remaining populations. These life history characteristics, along with the well-documented decline in mussel diversity and abundance, point to significant future losses in even seemingly stable mussel populations unless action is taken to reduce the perturbations causing the initial decline and increase connectivity between populations (Haag, 2010).

6. Solutions to the decline of freshwater mussels

Because of the growing awareness of the importance of freshwater mussel diversity and freshwater ecosystems in general, there have been increasing efforts to restore and rehabilitate mussel populations and their habitats. Most strategies focus on reversing the root causes of the decline in unionid abundance and diversity listed in the preceding section, along with restoring and protecting existing mussel populations.

6.1 Reduction in commercial harvesting

Although the commercial harvest of freshwater mussels has greatly contributed to the historic decline of Unionids, it is not generally considered to be a major threat to them at present. There are several reasons for the reduction in commercial harvesting of freshwater mussels. The replacement of mussel shell with plastics in the 1940s and 50s in the button industry reduced demand for shells, and more recently the collapse of the Japanese oyster pearl fishery has reduced the demand for pearl nuclei in that industry (Neves, 1999). Enforced regulation on commercial harvesting, as well as low prices for mussel shell, have also provided a respite for mussel populations (Strayer et al., 2004).

6.2 Best management practices to reduce pollution

Although water pollution has significantly declined in many industrial countries thanks to national-level legislation such as the Clean Water Act in the United States and the Water Resources Act in the UK, it is still a major threat to freshwater ecosystems and unionid mussels in most parts of the world. Acute toxicity studies in freshwater mussels have been performed on only a small number of known organic and inorganic contaminants present in the surface water of North America, and sublethal toxicity studies are even more rare (Keller et al., 2007). More studies are needed on a broader array of substances to provide regulators with better information for setting acceptable pollution standards in surface waters where freshwater mussels are found.

Non-point source nutrient and sediment pollution from agriculture, timber extraction, and urban runoff is regularly cited as one of the most serious threats to freshwater ecosystems (Richter, 1997). Best management practices that control runoff into surface water have been shown in numerous studies to improve the physical and chemical quality of streams (Caruso, 2000; D'Arcy & Frost, 2001; Lowrance et al., 1997). One of the most effective ways controlling sediment and nutrient inputs into streams is an intact, functional riparian zone. Well-vegetated riparian zones slow and reduce surface run-off into streams, capture large amounts of sediment in the runoff, store excess nutrients for uptake into riparian vegetation, and stabilize stream banks which further reduces instream sedimentation (Allan, 2004).

6.3 Restoring natural and adequate stream flows

Reversing the trend of increasing human control of the flow of rivers and streams worldwide is not likely in the near future. As the human population grows over the foreseeable future, the global demand for domestic and irrigation water is projected to increase correspondingly (Robarts and Wetzel, 2000). Although the world’s rivers have been fragmented and controlled by more than 1 million dams (Jackson et al., 2001), there are methods of operating these dams to minimize the negative effects they have on downstream ecosystems. In several case studies in the United States, water managers, conservation organizations, and scientists have attempted to regulate releases from dams to mimic the timing, duration, and magnitude of natural flood events, and to minimize the number of low flow days in the rivers downstream (Poff et al. 1997; Richter et al., 2003). In one study in Tennessee, recolonization of mussel populations occurred after hydroelectric dam managers altered their release schedule to ensure minimum flows (Layzer and Scott, 2006). There is also a growing movement for the complete removal of dams. As their ecological implications are being realized by scientists and the public, and as dam managers are facing higher operating costs in maintaining aging structures and complying with federal endangered species laws, dam removal is being seen as a viable option for river restoration in many circumstances (Hart et al., 2002; Pejchar and Warner, 2001).

When water levels drop, either through natural wet and dry cycles or through human withdrawals or regulation, the amount of physical habitat available to mussels and other benthic organisms is reduced. Many states and countries have passed legislation that requires minimum ecological flows in streams and rivers. There are over 200 methods for determining exactly how much water is needed for a particular stretch of river, all of which take into consideration the specific ecological function or species water managers are trying to preserve (Arthington et al., 2006). Most of these methods focus on fish or other vertebrate species, and often flows suitable for the preservation of these target species is not sufficient for freshwater mussels or other invertebrates (Gore et al., 2001, Layzer and Madison, 1995). Obviously, more study into the flow requirements of freshwater mussels along with a greater emphasis on this group by regulators is necessary if the hurdle of inadequate flows is to be overcome.

6.4 Control of non-native species

Controlling invasive, non-native organisms in freshwater ecosystems has met with limited success for most species, despite passage of laws such as the Non-indigenous Aquatic Nuisance Prevention and Control Act of 1990 in the United States. The zebra mussel is still expanding its range, although the rate of spread has slowed in recent years as the most easily colonized waterways have already been occupied (Johnson et al., 2006). The early spread of *D. polymorpha* was due to physical connectivity of waterways to infected areas, whereas current range expansion is due to overland human-facilitated transport by recreational boaters (Johnson et al., 2001). Thus, it seems, the future distribution of *D. polymorpha* will depend on human behavior, although their ultimate range will be limited to ecosystems with suitable pH, calcium concentrations, and temperature (Strayer, 2008b). Although various chemical, thermal, mechanical, and thermal treatment options have been somewhat successful in controlling *D. polymorpha* near shoreline structures and water intake valves, and consumption by natural predators can be high (Hamilton et al., 1994, Perry et al., 1997), the overall fecundity of the species makes eradication or control in most open-water areas unlikely (Strayer, 2008b).

6.5 Restoring habitat

Many of the solutions to physical habitat loss have already been addressed in the previous sections, such as restoration of riparian vegetation; the use and enforcement of best management practices in construction, agriculture, and forestry; dam removal; and restoration of natural flow regimes. These practices will reduce terrestrial inputs of substrate-smothering sediment, ensure that adequate amounts of water are present, and restore natural stream channel morphology more suitable for freshwater mussels. It is also possible to directly restore benthic habitat through riparian and instream construction projects designed to stabilize banks and stream channels and increase the habitat heterogeneity that supports high levels of benthic diversity. Several studies in Finland (Muotka et al., 2002), Japan (Nakano & Nakamura, 2006), and the United States (Miller et al., 2009) have found increased macroinvertebrate abundance and richness in streams following stream channel restoration projects, and while these studies did not look at freshwater mussels specifically, they provide a basis of reference for mussel-specific restoration techniques. Osterling et al. (2010) indicated that restoration activities to improve environmental conditions of mussels' habitats should focus on reducing fine material transport into streams, because sedimentation of inorganic and organic materials and high turbidity can impact mussel recruitment.

6.6 Minimizing the effects of global climate change

The ability of freshwater organisms to adapt to climate change is dependent on a particular species' ability to disperse and migrate to cooler environments in higher latitudes or elevations (Poff et al., 2002). As unionid mussels have limited dispersal and reproductive potentials under the best of circumstances, this puts this group at a higher risk than many other groups (Hastie et al., 2003). There are two main approaches to dealing with the threat posed by climate change: (1) to reduce further changes in climate and (2) to manage the consequences of current and predicted changes. To review the numerous methods being debated and currently attempted to control climate change is beyond the scope of this chapter; however it is important to note that a few of these methods (construction of dams for "clean" hydroelectric power, intensification of agriculture for biofuels) have the potential to further degrade freshwater ecosystems beyond their current state if not planned and managed correctly (Bates et al., 2008).

As far as managing the effects of climate change on freshwater ecosystems, there are two major aspects to this as well: (1) to reduce pollution, habitat loss, and other anthropogenic disturbances that are already placing stress on freshwater systems, and (2) to establish a network of protected areas based on species' current and projected ranges, and to manage the connecting matrix between them (Hannah et al., 2002; Heino et al., 2009; Poff et al., 2002). Ways of reducing anthropogenic stress on freshwater ecosystems include riparian zone management, reducing nutrient loading, habitat restoration, and minimizing human-driven water withdrawal (Poff et al., 2002), and have already been discussed in previous sections. The concept of freshwater protected areas and dispersal corridors between populations will be covered in the following section.

6.7 Protecting and restoring freshwater mussel populations

Protected areas have been a mainstay of terrestrial and marine conservation efforts for decades, yet have only recently been part of the discussion about conserving freshwater species and habitat (Abell et al., 2007). Freshwater protected areas (FPAs) have been used in the past mostly to protect fish species from overharvesting by providing areas closed to fishing for at least part of the time. FPAs have the potential to do more than just limit fish harvests, though. Effectively planned and executed protected areas can protect specific habitat types against degradation, ensure minimum surface and groundwater flows, protect riparian zones, and protect rare and endangered species (Saunders et al., 2002; Suski and Cooke, 2007).

One of the key aspects that have limited the effectiveness of FPAs against ecosystem degradation, especially in rivers and streams, is that many of the stressors affecting these systems come from diverse, non-point sources upstream from critical habitat and threatened populations. The success of localized protected areas or catchment management strategies can be limited due to the large scale connection of aquatic ecosystems with terrestrial activities, especially where streams with their longitudinal connectivity are concerned (Saunders et al., 2000). Therefore, many researchers have pointed out the need for catchment-scale protection for threatened freshwater ecosystems that truly limit the impacts to sensitive areas (Abell et al., 2007; Dudgeon et al., 2006; Heino et al., 2009). Although there has been little published data on freshwater mussels and protected areas, some researchers have noted the possibility of refuges for some species (Ricciardi et al., 1998; Saunders et al., 2002), and preservation and protection of critical mussel habitat has the potential to significantly aid in the recovery of unionids.

Naturally reproducing unionid populations can take decades to recover after severe and prolonged disturbances. As mentioned earlier, mussels are dependent on critical densities to facilitate successful reproduction (Downing et al., 1993), and many areas where unionids have been extirpated lack access to restocking populations (Strayer et al., 2004). In these situations, artificially stocking mussels can help restore populations and eventually enable them to become self-sustaining (Strayer et al., 2004). Mussel relocation and reintroduction have been met with varying levels of success, mostly due to lack of knowledge of specific habitat requirements and handling techniques (Cope and Waller, 1995). Many successful propagation techniques have also been developed over the last few years (Barnhart, 2006; Henley et al., 2001), and although field trials of lab-reared mussels are limited, artificial propagation techniques hold much promise to enhance unionid populations in the future, provided the degraded environmental conditions that caused the decline in the first place are corrected.

7. Conclusions

The loss of biodiversity across biomes and habitats has direct and profound implications for human populations around the world (Sala et al., 2000). The functioning of both terrestrial and aquatic ecosystems is dependent on the diversity of their constituent organisms (Covich et al., 2004; Kinzig et al., 2002; Loreau et al., 2001), and the dependence of humans on these ecosystem services makes protecting and restoring biodiversity a priority for both the present and future generations. Freshwater ecosystems have received less consideration from the public and researchers, despite the critical linkages between freshwater systems and human well-being (Aylward et al., 2005; Costanza et al., 1997; Jackson et al., 2001). It is clear that through our actions we are degrading and damaging our freshwater ecosystems beyond their abilities to recover (Allan and Flecker, 1993; Dudgeon et al., 2006; Richter et al., 1997; Strayer and Dudgeon, 2010), and continuing these unsustainable activities puts all the world's inhabitants at risk.

Freshwater unionid mussels are an often-overlooked part of freshwater biodiversity, and one that is the most threatened (Ricciardi and Rasmussen, 1999; Williams et al., 1993). Unionids are key components to their ecosystems, carrying out many important ecological functions (McCall et al., 1995; Strayer et al., 1999; Vaughn and Hakencamp, 2001) and influencing the diversity of benthic communities (Aldridge et al., 2006; Gutierrez et al., 2003; Spooner and Vaughn, 2006). Their unique reproduction strategy, feeding behaviors, specific habitat requirements, and valuable shell and pearls have put them at risk to human-driven disturbances, and have contributed to their worldwide decline in both abundance and richness (Bogan, 1993; Vaughn, 1997). The drivers of the decline in unionid biodiversity are the same as those of freshwater diversity in general: pollution, habitat destruction, overharvest, altered flows, invasion by non-native species, and climate change, but because of their lifestyles and high degree of endemism, they are being especially hard hit (Strayer et al., 2004).

The solutions to the decline in unionid biodiversity are simple, but not easy. Reducing pollution (Caruso, 2000; Lowrance et al., 1997), restricting harvesting (Strayer et al., 2004), ensuring ecologically sustainable flows (Arthington et al., 2006; Layzer and Scott, 2006), habitat protection and restoration (Miller et al., 2010; Muotka et al., 2002; Wilson et al., 2011), combating non-native invaders (Strayer, 2008b), mitigating and planning for the effects of climate change (Heino et al., 2009; Poff et al., 2002), creating connected freshwater protected areas (Heino et al., 2009; Saunders et al., 2002) and artificially enhancing wild populations (Cope and Waller, 1995; Strayer et al., 2004) are all necessary to restore freshwater ecosystems and the mussels that occupy them.

It is clear that any successful freshwater conservation plans must be large in scale and long-term in scope, and take into consideration the multiple chronic stressors that are causing the alarming decline in freshwater pearly mussels. It is equally clear that failure to take concrete steps to halt and reverse the trend of biodiversity loss in unionid mussels could result in the permanent loss of this unique and important group of animals.

8. References

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