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An Overview of the Spread, Distribution, and Ecological Impacts of the Quagga Mussel, *Dreissena rostriformis bugensis*, with Possible Implications to the Colorado River System

By Thomas F. Nalepa[1]

Abstract

The quagga mussel (*Dreissena rostriformis bugensis*) was first found in the Great Lakes in 1989 and has since spread to all five lakes. Although its spread through the system was slower than that of the zebra mussel (*Dreissena polymorpha*), once established, it replaced zebra mussels in nearshore regions and is colonizing deep regions where zebra mussels were never found. Outside the Great Lakes Basin, quagga mussels do not appear to be increasing to any extent in the Ohio and Mississippi Rivers, even after being present in these rivers for over a decade. In contrast, numbers in the Colorado River system have continued to increase since the quagga mussel was first reported. It will likely become very abundant in all the reservoirs within the Colorado River system, but attain limited numbers in the mainstem. Ecological impacts associated with the expansion of quagga mussels in the Great Lakes have been profound. Filtering activities of mussel populations have promoted the growth of nuisance benthic algae and blooms of toxic cyanobacteria. In addition, the increase in quagga mussels has led to a major disruption of energy flow though the food web. An understanding of food webs in the Colorado River system, particularly the role of keystone species, will help define future ecological impacts of quagga mussels in this system.

Introduction

Two species of dreissenid mussels, *Dreissena rostriformis bugensis and Dreissena polymorpha* (quagga mussel and zebra mussel), are part of a group of biofouling, filter-feeding bivalves that are spreading around the world (Karatayev and others, 2007). When established in a new water body, these dreissenid species can increase rapidly and attain densities that generate far-reaching changes in physical, chemical, and biological components of the ecosystem. Many studies have documented ecological impacts of these two invading species, and broad patterns have emerged that are consistent across water bodies. Thus, to a certain extent, some ecological impacts can be predicted and prepared for. Yet other impacts have been unexpected and unique to a given taxa or habitat associated with the invaded system.

For several reasons, less is known of the specific life history, environmental tolerances, and impacts of quagga mussels compared to zebra mussels. The zebra mussel colonized North America first and quickly attained high densities, resulting in ecological changes that were widely evident and well documented (Nalepa and Schloesser, 1993). In comparison, the quagga mussel spread less rapidly, and impacts could not, at least at first, be readily discerned from the zebra mussel. Recent evidence, however, suggests that although ecological changes in the Great Lakes resulting from the proliferation of quagga mussels are functionally similar to those of the zebra mussel, the changes are more severe and pervasive in scope. As studies show, the quagga mussel spreads just as rapidly as the zebra mussels once established, is more flexible in colonizing different habitats, and attains higher densities in certain lake areas.

This paper summarizes current knowledge of the spread, life habit characteristics, and broad ecological impacts of the quagga mussel. Given the discovery of quagga mussels in the Colorado River system, such a summary may be useful when assessing ecological risks to this system. Quagga mussel characteristics and ecological impacts are presented in relation to the zebra mussel since both species have been introduced into Western States, and both frequently co-inhabit an invaded system during the early stages of the colonization process. Both dreissenid species attach to hard substrates and create clogging problems for power companies, water plants, and other raw-water users; however, it is beyond the scope of this summary to include a discussion of control options.

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Expansion Patterns and Taxonomic Definition

The quagga mussel was first reported in North America in 1989 in the eastern basin of Lake Erie. Like the zebra mussel, which was discovered several years earlier, the quagga mussel was likely introduced into North America via the discharge of ballast water from transoceanic ships. Based on genetic studies, these first North American individuals appear to have originated from the lower Dnieper River, Ukraine (Spidle and others, 1994; Therriault and others, 2005). Although given a common name, the taxonomic status of the quagga mussel was at first unclear, but was later determined to be *Dreissena bugensis* on the basis of allozyme data and morphological characters (Spidle and others, 1994). In subsequent analysis, this species was also found to be genetically similar to *D. rostriformis*, which is a brackish water species found in the Caspian Sea (Therriault and others, 2004). Given this clear separation in environmental tolerances (freshwater versus brackish water) and following rules of nomenclature, *D. bugensis* is currently considered a freshwater race of *D. rostriformis* and referred to as *Dreissena rostriformis bugensis.*

After first discovery in Lake Erie, the quagga mussel proceeded to spread into all the other Great Lakes, first into Lake Ontario, then into Lakes Michigan and Huron in 1997, and finally into Lake Superior in 2005 (Nalepa and others, 2001; Grigorovich, Kelley, and others, 2008). It was found in the Ohio and Mississippi Rivers in the mid-1990s, and in Lake Mead within the Colorado River system in 2007 (U.S. Geological Survey Web site: *http://nas.er.usgs.gov/ taxgroup/mollusks/zebramussel/*). The spread of the quagga mussel within the Colorado River system has been rapid; by the end of 2008, it was reported in over 30 lakes and reservoirs in Arizona, California, Colorado, Utah, and Nevada. The likely vector by which mussels spread from the east to the far west was via the overland transport of recreational boats.

A unique aspect of quagga mussel populations in North America is the presence of two phenotypes. Although genetically similar (Claxton and others, 1998), these two phenotypes prefer vastly different habitats. In the Great Lakes, one phenotype (*D. r. bugensis* "sensu stricto-eplimnetic"; Claxton and others, 1998) is found exclusively in shallow-warm bays and basins, and the other phenotype (*D. r. bugensis* "profunda"; Dermott and Munawar, 1993) is found mostly in deep, cold offshore regions but also in some nearshore areas above the thermocline. The profunda phenotype has not been specifically reported from European waters, but some individuals from the Ukraine resemble North American specimens (A. Protosov, Institute of Hydrobiology, Ukraine, written commun., January 2009). Interestingly, North American specimens of profunda are more genetically similar to North American specimens of the epilimnetic phenotype than to specimens from the lower Dnieper River, Ukraine (Spidle and others, 1994). The dominant phenotype found in various water bodies in the

Western United States, including the Colorado River system, is not clear at this time.

Although the quagga mussel has been found in large river systems in eastern Europe, it tends to reach greatest abundances in lakes and reservoirs (Mills and others, 1996; Orlova and others, 2005). This species was confined to its native range in the lower Dnieper–Bug River systems (northern Black Sea) until the late 1940s/early 1950s when a series of reservoirs were constructed on the Dnieper River system (Orlova and others, 2005). It is believed that these impoundments led to environmental changes (i.e., reduced water velocity, more stable temperatures), which better suited this species. Over the next several decades, the quagga mussel gradually expanded its range into the Volga River and Don–Manych River systems and more recently (2004–2007) into the Rhine, Danube, and Main Rivers in central Europe (Popa and Popa, 2006; Molloy and others, 2007; van der Velde and Platvoet, 2007). Overall, population growth in European rivers has been less rapid than in lakes/reservoirs, and abrupt, unexpected declines have been reported in some river systems (Zhulidov and others, 2006). Similar expansion patterns (i.e., a preference of lakes/reservoirs over rivers) are apparent in North America. For instance, while quagga mussels increased rapidly once established in Lakes Ontario and Michigan (Mills and others, 1999, Nalepa and others, 2009), a recent study in the upper Mississippi and Ohio Rivers found that quagga mussel distributions had not greatly expanded since being reported 10 years earlier, and densities remained uniformly low (Grigorovich, Angradi, and others, 2008). For the Colorado River system, these expansion patterns would indicate that the quagga mussel will increase more rapidly and attain greater abundances in the reservoirs of this system than in the river itself.

Physiological/Environmental Tolerances and Morphological Characteristics

The quagga mussel has several physiological and morphological features that allow it to proliferate in lake habitats where environmental conditions limit zebra mussels. In laboratory studies of both species, quagga mussels had a lower respiration rate under different seasonal temperatures and a higher assimilation efficiency, particularly at low food concentrations (Baldwin and others, 2002; Stoeckmann, 2003). Lower respiration and higher assimilation efficiency allow quagga mussels to better survive and grow under a wider variety of food regimes. In the Great Lakes, quagga mussels are expanding in offshore regions where food resources are naturally low and are also attaining high densities in shallow regions where food can be limiting during certain seasonal periods. These physiological traits are the likely reason why quagga mussels are displacing zebra mussels in many lake areas (Wilson and others, 2006; Nalepa and others, 2009). In addition, quagga mussels can reproduce at lower water

temperatures compared to zebra mussels. Both quagga mussel phenotypes displayed gonadal development and spawned at water temperatures of 4–9 degrees Celsius (°C), whereas zebra mussels showed no reproductive activity at these low temperatures (Claxton and Mackie, 1998). Thus, quagga mussels can not only reproduce and thrive in deep, hypolimnetic regions, but can also spawn earlier in the spring than zebra mussels in shallow, epilimnetic regions.

As noted, population growth of quagga mussels in large river systems such as the Ohio and Mississippi has been slow (Grigorovich, Angradi, and others, 2008). Large rivers usually have elevated levels of suspended inorganic sediments (silt and clay), which negatively affect dreissenids in various ways. Inorganic particles foul gills and interfere with respiratory function. Also, these particles, although filtered, have no nutritional value. Mussels expend energy in expelling these particles that is better spent for growth and reproduction. Since quagga mussels are less widely distributed than zebra mussels in the Ohio and Mississippi Rivers (Grigorovich, Angradi, and others, 2008), it seems logical to assume that quagga mussels are less suited physiologically to handle suspended particulates. Yet laboratory experiments have shown that the two species respond similarly to elevated levels of suspended material; to a degree, both species were able to adapt to increased levels of turbidity (Summers and others, 1996). Regardless of some ability to adapt, both species are negatively affected by high concentrations of suspended sediments. The potential for zebra mussel growth was zero/negative at suspended sediment concentrations greater than 100 milligrams per liter (mg/L) (Madon and others, 1998). Concentrations typically found in the Ohio and Mississippi Rivers are below this level, whereas levels in the Missouri River are far above it (Summers and others, 1996). This may explain why few zebra mussels and no quagga mussels were found in the Missouri River system in a recent study (Grigorovich, Angradi, and others, 2008).

While quagga mussels thrive in deep, continuously cold environments, of relevance to their expansion in the Southwest United States is their tolerance to high summer temperatures. In several laboratory studies, quagga mussels were found to be less tolerant of elevated water temperatures compared to zebra mussels. The upper thermal tolerance limit for quagga mussels was about 30 °C, but could be as low as 25 °C because mussels could not be maintained in the laboratory at the latter temperature (Domm and others, 1993; Spidle and others, 1995). Given this, it is unlikely temperature will limit populations in the mainstem of the Colorado River system where temperatures range between 5 and 20 °C (Kennedy, 2007). In Lake Mead, mean monthly temperatures in the summer are 26–29 °C in shallow regions (<4.5 meters (m) water depth), and thus temperature-induced stress may eventually limit populations in this region. However, mean temperatures do not exceed 22 °C in deeper regions (>18 m water depth) (*http://www.missionscuba.com/lake-mead/lake-mead_average-water-temp.htm*). When considering temperature limits, other environmental factors must also be considered such that laboratory studies of upper lethal temperatures are often not good predictors of success in the natural environment. Quagga mussels exposed to unfiltered Ohio River water survived high, sublethal temperatures (>30 °C) better than zebra mussels (Thorp and others, 2002). This was attributed to the differential ability of quagga mussels to obtain and assimilate food at higher temperatures. Relevant to this issue, it is noted that quagga mussels are presently very abundant even in the shallow, warmer regions of Lake Mead (B. Moore, University of Las Vegas, oral commun., November 2008).

Besides temperature, another important environmental variable that affects quagga and zebra mussel distributions, and eventual population densities, is calcium concentration. Mussels require calcium for basic metabolic function and for shell growth. Based on field distributions, quagga mussels apparently have a slightly higher calcium requirement than zebra mussels. In the St. Lawrence River, quagga mussels were not found in waters with calcium concentrations lower than 12 mg/L, while zebra mussels were present (but not abundant) at concentrations as low as 8 mg/L (Jones and Ricciardi, 2005). Calcium concentrations in the Colorado River system are far greater than the values above, so calcium limitation is not an issue (Whittier and others, 2008). Indeed, high concentrations in this system (>80 mg/L) may favor quagga mussels over zebra mussels (Zhulidov and others, 2004). A summary of mussel tolerance limits for other environmental variables, such as dissolved oxygen, pH, and salinity, is provided in Cohen (2007).

The shell morphology of the quagga mussel differs from the zebra mussel in that it has a rounded ventral margin compared to one that is sharply defined. The lack of a flattened ventral surface does not allow the quagga mussel to attach as tightly to hard surfaces as the zebra mussel, and may prohibit it from easily colonizing habitats with strong water velocities such as found in some rivers. Unlike zebra mussels, however, quagga mussels do not necessarily need to attach to hard substrates. They can lie unattached on their longer, wider lateral side, which is an advantage in soft substrates because it prevents sinking. The profunda phenotype has an incurrent siphon that is far longer than the incurrent siphon of both the epilimnetic phenotype and the zebra mussel (fig. 1). This elongated siphon, which can be three-fourths the length of the shell, is a characteristic of bivalves adapted to inhabiting soft sediments. It allows filtration above the layer of fine inorganic particles generally found suspended at the sediment-water interface.

General Ecological Impacts

Ecological impacts of dreissenids, both quagga mussel and zebra mussel, are a function of achieved densities and characteristics of the invaded system. Where conditions are favorable and dreissenids become abundant, fundamental changes in energy and nutrient cycling occur, and all

Figure 1.   Comparison of the incurrent siphon of the zebra mussel (top), quagga mussel-epilimnetic phenotype (middle), and quagga mussel-profunda phenotype (bottom). Note the longer siphon of the profunda phenotype.

components of the food web are affected. Several articles have provided excellent, detailed summaries of ecological impacts of dreissenids (Strayer and others, 1999; Vanderploeg and others, 2002), so only far-reaching changes that have strong implications to resource managers will be presented here. Dreissenids are filter feeders and hence remove phytoplankton and other particulates from the water. These filtered particles are ingested and assimilated or deposited on the bottom as feces or pseudofeces. Feces is material that is ingested but not assimilated, and pseudofeces is material that is filtered but not ingested (rejected). As a result of these filter-feeding activities, dreissenids divert food resources from other food web components, such as invertebrates inhabiting both the water (zooplankton) and bottom sediments (benthos). On average, dreissenid colonization in a given lake or river has been accompanied by a greater than 30 percent increase in water clarity, a greater than 35 percent decline in

phytoplankton biomass, and a greater than 40 percent decline in zooplankton (Higgins and Vander Zanden, 2010). Impacts on benthic invertebrate communities have varied depending on feeding mode and habitat of the particular species (Ward and Ricciardi, 2007). Species able to feed on dreissenid biodeposits (i.e., feces and pseudofeces) or positively influenced by greater habitat complexity offered by mussel beds (predation refuge) have increased in abundance. On the other hand, species that filter feed or depend on fresh sedimentary inputs of phytoplankton have declined. Changes in the abundance and composition of pelagic and benthic invertebrate communities ultimately affect the fish community because fish rely on these invertebrate groups as a source of food. Fish impacts depend on habitat, diets, and population state of the particular species (Vanderploeg and others, 2002; Strayer and others, 2004; Mohr and Nalepa, 2005), but dreissenid impacts on the fish community are now becoming more apparent as quagga mussels increase and expand into new habitats.

The re-direction of energy and nutrient flow by dreissenids has been broadly termed the "nearshore shunt" (Hecky and others, 2004). In brief, dreissenids have shifted nutrient resources from pelagic to benthic zones and have focused them in nearshore relative to offshore regions. As an example, phosphorus concentrations in nearshore waters of the Great Lakes are increasing despite stable or decreased external loads (Higgins, Malkin, and others, 2008). The likely reason is that phosphorus associated with particles is being sequestered, mineralized, and excreted in soluble form by dreissenids found at high densities in nearshore areas. In addition, phosphorus associated with dreissenid feces and pseudofeces is being deposited on the bottom, enriching bottom sediments and near-bottom waters. The combination of greater light penetration resulting from increased water clarity and the greater availability of phosphorus has led to increased growth of benthic algae and macrophytes (Lowe and Pillsbury, 1995; Skubinna and others, 1995). In particular, there has been resurgence in the nuisance benthic algae *Cladophora* in the Great Lakes since dreissenids became established (Higgins, Malkin, and others, 2008). Overall, nearshore regions have become more nutrient enriched and benthic productivity has increased, whereas offshore regions have become more nutrient starved and pelagic productivity has declined.

Dreissenids have also been implicated in the resurgence of cyanobacteria blooms in some bays and basins of the Great Lakes and in some inland lakes (Vanderploeg and others, 2001; Knoll and others, 2008). Blooms were common in the Great Lakes before the mid-1970s as a result of excessive nutrient input (phosphorus), primarily from point-source loads. After nutrient abatement programs were initiated in the mid-1970s, cyanobacteria blooms were rarely observed. Blooms began to reappear just after dreissenid colonization in the early 1990s, and now extensive blooms occur almost every summer (Vanderploeg and others, 2002). Cyanobacteria are a group of phytoplankton associated with taste and odor problems in drinking water, and some species/strains produce toxins that

are detrimental to human, animal, and ecosystem health. The most frequent bloomer in the Great Lakes is *Microcystis*, a taxa that produces microcystin, a hepatotoxin. During bloom events, microcystin concentrations often exceed the World Health Organization limit for drinking water of $1 \cdot \mu g \, L^{-1}$ (Dyble and others, 2008). Dreissenids promote cyanobacteria through the process of selective rejection (Vanderploeg and others, 2001). As dreissenids indiscriminately filter phytoplankton from the water, they reject toxic strains of cyanobacteria as pseudofeces because of unpalatable taste or size. The rejected cells are still viable, and when the pseudofeces is resuspended in the water during turbulent mixing events, these cells grow rapidly because of diminished nutrient competition from phytoplankton that are filtered and assimilated by the mussels. An increase in cyanobacteria has not occurred in all water bodies invaded by dreissenids (i.e., Hudson River, some Dutch lakes). Some factors influencing whether or not a bloom occurs include the fraction of water column filtered by dreissenids, relative taste/size of the particular strain of cyanobacteria, and nutrient and light regimes (Vanderploeg and others, 2001).

A Case History: Quagga Mussels in Lake Michigan

The quagga mussel was first found in northern Lake Michigan in 1997 and within 5 years had spread throughout the lake (fig. 2) (Nalepa and others, 2001, 2009). Regular monitoring of populations at 40 sites of various water depths in the south indicated that abundances at sites shallower than 50 m increased rapidly after 2002 and began to peak by 2007 (Nalepa and others, 2009). Abundances at sites deeper than 50 m did not begin to increase until 2005 and were still

increasing as of 2007. The quagga population in the main basin of the lake consists entirely of the profunda phenotype. While zebra mussels were present in the lake since 1989 and ecological impacts were long evident, several important aspects of the quagga mussel expansion were relevant in effecting additional ecological changes. First, in shallow regions (<50 m) the quagga mussel population attained mean densities that were seven times greater than mean densities ever achieved by zebra mussels. Second, the quagga population is presently increasing in the deeper, offshore regions where zebra mussels were never found. The net result is that overall dreissenid biomass (wet weight; tissue and shell) in the lake has increased dramatically since the expansion of quagga mussels. Based on lakewide sampling, dreissenid biomass increased from $2.6 \cdot g \, m^{-2}$ in 1994/1995 when only zebra mussels were present to $188 \cdot g \, m^{-2}$ in 2005 when quagga mussels became dominant (Nalepa and others, 2009). Estimated lakewide biomass increased to $529 \cdot g \, m^{-2}$ in 2007, which is a 203-fold increase in just 12 years.

The proliferation of quagga mussels in Lake Michigan has led to many ecological changes that were not evident when only zebra mussels were present in the lake. Spring chlorophyll concentrations have declined fourfold, recently falling to below 1 microgram per liter ($\mu g/L$) (G. Fahnenstiel, National Oceanic and Atmospheric Administration, unpub. data, 2009). Chlorophyll is an indicator of phytoplankton biomass, and levels usually peak in the spring because of an increase in diatoms. Diatoms are a phytoplankton group rich in essential nutrients and thus are an important food source for many pelagic and benthic invertebrates. The decline in the spring diatom bloom can be linked to the filtering activities of quagga mussels. During unstratified conditions in the spring, the water column is well mixed, and bottom-dwelling mussels in deep areas (below the thermocline) have access to phytoplankton found throughout the water column. Further, because mussels occur at the sediment surface, they can filter out diatoms before this rich food settles to the bottom and is available to sediment-dwelling organisms.

Since dreissenids became established in Lake Michigan, water clarity in nearshore areas has increased twofold (Bootsma and others, 2007), and similar increases have been noted in offshore areas since quagga mussels became abundant (G. Fahnenstiel, National Oceanic and Atmospheric Administration, oral commun., 2009). Dissolved phosphorus in nearshore waters has also increased (Bootsma and others, 2007). The combination of increased light and available phosphorus has led to a proliferation of *Cladophora.* Biomass of this nuisance algae has increased nearly threefold along the rocky western shoreline between the pre-mussel period and 2006, with most of the increase occurring since quagga mussels became abundant (Bootsma and others, 2007). In late
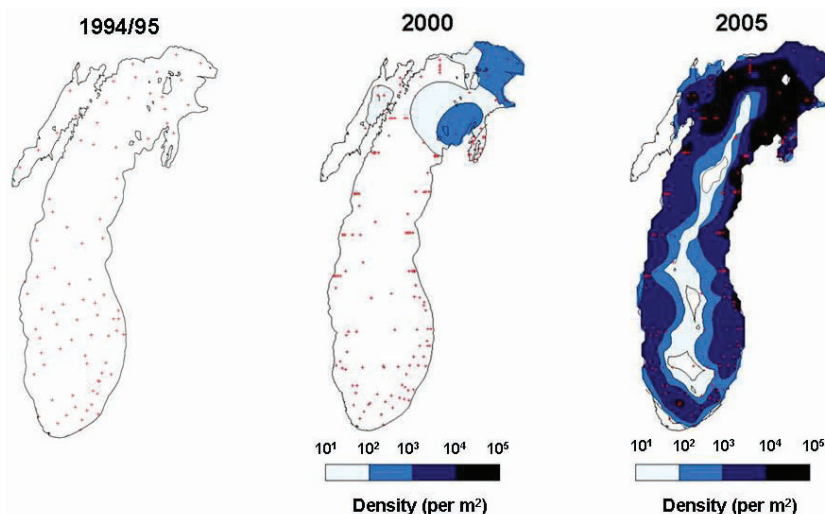

Figure 2.   Mean density (number per square meter) of quagga mussels in Lake Michigan in 1994/1995, 2000, and 2005. The small red crosses are the locations of sampling sites.

summer when temperatures increase, the *Cladophora* dies, floats to the surface, and gets washed up on shoreline beaches. The decaying algae harbors bacteria, creates a foul smell, and severely limits beach use (*http://dnr.wi.gov/org/water/greatlakes/cladophora/*).

Whereas zooplankton biomass in the lake has declined since quagga mussels became abundant (S. Pothoven and H. Vanderploeg, National Oceanic and Atmospheric Administration, unpub. data, 2009), perhaps the most dramatic change in the invertebrate component of the lower food web has been the loss of the native amphipod *Diporeia* spp. (Nalepa and others, 2009). This organism once dominated benthic biomass in Lake Michigan (>70 percent) and was a keystone species in the cycling of energy between lower and upper trophic levels. *Diporeia* lives in the top few centimeters of sediment and feeds on organic material settled from the water column, being particularly dependent upon the spring settling of diatoms as a food source. Declines in *Diporeia* were first observed in the early 1990s, just a few years after zebra mussels became established in the lake in 1989. As zebra mussels spread, declines in *Diporeia* became more extensive and by 2000 *Diporeia* had disappeared from large areas of the lake shallower than 50 m in water depth. The decline of *Diporeia* extended to lake areas greater than 50 m once quagga mussels expanded to these depths. This amphipod is high in lipids and a rich food source for fish, and studies have shown that its decline is having a negative impact on the fish community. For one, growth and condition of lake whitefish (*Coregonus clupeaformis*), an important commercial species that feeds heavily on *Diporeia*, have decreased 27 percent since the mid-1990s (Pothoven and others, 2001). Also, the abundance and energy density of many prey fish have declined where *Diporeia* was no longer present (Hondorp and others, 2005). Prey fish (alewife, *Alosa pseudoharengus*; sculpin, *Cottus* spp.; bloater, *Coregonus hoyi*; etc.) serve as prey for the larger piscivores (salmon, trout; *Oncorhynchus* spp.) within the lake. Lakewide biomass (wet weight) of prey fish declined from 91 kilotonnes in 2005 to 31 kilotonnes in 2007, which is down from 450 kilotonnes in 1989 (C. Madenjian, U.S. Geological Survey, oral commun., 2009). Most of the recent decline can be attributed to the collapse of the alewife population, which is a pelagic planktivore, but at times feeds on *Diporeia*. In contrast, lakewide biomass (wet weight) of quagga mussels was 36 kilotonnes in 2005 and estimated at 113 kilotonnes in 2007 (Nalepa and others, 2009). Thus, total biomass of the quagga mussel population in the lake is now estimated to be about 3.8 times greater than total prey fish biomass. Mussel mass represents a major energy sink and a disruption of energy flow through the food web. Some fish species are feeding on quagga mussels, but the problem with fish switching from food sources like *Diporeia* to mussels lies in the ingestion of the mussel shell, which comprises more than 80 percent of the total dry mass in quaggas. The shell offers little nutrition to the fish and represents an energetic cost to the fish in terms of handling, ingestion, retention time, and egestion. Further, there

is an energetic cost to the mussel to produce the shell. Thus, energy is lost to the food web when the shell is ingested and also lost when the shell is produced.

Implications to the Colorado River System

It is difficult to predict all the relevant ecological changes that will result from the quagga mussel invasion of the Colorado River system. In the Great Lakes, some changes, such as increased water clarity, decreased phytoplankton biomass, and an increase in benthic productivity, could have been predicted from the European experience. Yet other important impacts, such as the return of cyanobacteria blooms and the loss of the native amphipod *Diporeia,* were unexpected. Ecological impacts are a function of mussel densities, and since mussels are proliferating in large reservoirs of the Colorado River system (i.e., Lake Mead; Moore and others, 2009), some changes in these reservoirs might be expected. In contrast, high levels of suspended sediment and high inorganic:organic particle ratios will limit, if not prevent, mussel expansion in the mainstem portions of the river (Kennedy, 2007). Yet even if mussels do not proliferate in the mainstem, some ecosystem changes may occur. The mainstem river is coupled to upstream reservoirs, and mussel-mediated changes in the water quality (i.e., dissolved nutrients, phytoplankton, zooplankton) of such reservoirs as Lake Powell and Lake Mead will likely impact food web structure or trophic linkages in the downstream riverine ecosystem. Concerns over increased algal blooms in the reservoirs are real, since blooms of some species have already occurred before the quagga mussel invasion (*Pyramichlamys dissecta* and *Cylindrospermopsis* r*aciborski*), and *Microcystis,* which now regularly blooms in some shallow, warm regions of the Great Lakes, is a component of phytoplankton communities in these reservoirs (St. Amand and others, 2009). Most certainly, productivity will shift from the pelagic to the benthic region, and an increase in biomass of many benthic invertebrates will likely result. Because bottom habitat drives the food web in some Colorado River reservoirs (Umek and others, 2009), this shift may benefit many bottom-feeding fish species, including some of the natives (i.e., razorback sucker, *Xyrauchen texanus*). On the other hand, the threadfin shad (*Dorosoma petenense*), a pelagic planktivore and a forage base for some sport fish, may be adversely affected much like the alewife was affected in the Great Lakes.

Currently, the quagga mussel population is expanding in the Colorado River system, but eventually the population will stabilize as abundances reach equilibrium with the surrounding environment. During this process, both acute and chronic ecological impacts will be realized as ecosystem components respond at different rates, leading to outcomes that can be both interactive and cumulative over time (Strayer and others, 2006). It may take many years, but eventually the

ecosystem will reach a new, different steady state. Monitoring of key ecosystem parameters during this process is essential in understanding interactions that form the basis for a new paradigm of resource management.

Acknowledgments

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