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Aquatic Nuisance Species Research Program

Environmental Habitat Conditions Associated with Freshwater Dreissenids

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Abstract: The continued spread of two invasive dreissenid bivalve species, zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels, into the southwestern and western United States indicates the need for improving understanding of habitat requirements and constraints for both species. This report summarizes results from published literature and reports that describe physical and environmental characteristics often associated with dreissenids. For example, data from the studies reviewed for this report indicate that at the upper incipient lethal temperature of ~30^{o} C, adult growth may be limited at pH of ~5.5-6.5, calcium concentrations of ~15 mg/L are required for viable populations, and the lethal lower limit of oxygen concentration is ~4 mg/L at 18^{o} C. Developing a better understanding of how dreissenids respond to variable habitats and environments will improve our ability to anticipate potential challenges posed by the continued expanding distribution of these species in the United States.

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Preface

The work reported herein was conducted as part of the Aquatic Nuisance Species Research Program (ANSRP). The ANSRP is sponsored by Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Research and Development Center (ERDC) under the purview of the Environmental Lab (EL). Funding was provided under Department of the Army Appropriation Number 96X3122, Construction General. Dr. Linda S. Nelson, EL, was Program Manager, ANSRP. Program Monitor during this investigation was Joseph Wilson, HQUSACE.

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This investigation was performed under the general supervision of Dr. Tim Lewis, Chief, Aquatic Ecology and Invasive Species Branch, EL; Dr. Edmond Russo, Chief, Ecosystem Evaluation and Engineering Division; and Dr. Elizabeth Fleming, Director, EL.

COL Gary E. Johnston was Commander and Executive Director of ERDC. Dr. Jeffery P. Holland was Director.

1 Introduction

Purpose

This technical report is a review of research describing habitat limitations associated with two invasive dreissenid species, *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel). The ability to predict possible range extensions or to assess potential impacts of invasive species on native ecological systems can be improved by understanding how habitat conditions limit population viability. Dreissenid responses to temperature, pH, calcium concentration and hardness, dissolved oxygen concentration, turbidity, substratum, water velocity, and turbulence are included in this review.

Background

The introduction of the European freshwater zebra mussel (*Dreissena polymorpha*) to North America was first noted in Lake St. Clair during the mid-1980s (Hebert et al. 1989; Griffiths et al. 1991). Within a few years a congener species, quagga mussel (*Dreissena bugensis*), was identified in Lake Ontario (May and Marsden 1992; Dermott 1993). Both species are presumed to have been transported to North America by ships moving from the Black Sea region in Ukraine (Rosenburg and Ludyanskiy 1994) to the Great Lakes. It is most likely that ships carrying light loads and ballast water brought the planktonic larval stages in the ballast (Carlton 1985). Discharge of ballast in the Great Lakes released these larvae. Another possibility is that post-larval mussels attached to anchor chains while ships were stationary in European ports; these mussels were able to survive trans-Atlantic passage in cold, humid air that delays death by aerial exposure (McMahon 1996).

Regardless of the precise method of introduction, zebra mussels rapidly spread throughout the Great Lakes into many major inland rivers and lakes in the northern and central portions of the United States (Ram and McMahon 1996). The connection of Lake Michigan to the Illinois River via the Chicago Ship and Sanitary Canal allowed downstream dispersal of larvae into the Illinois and Mississippi Rivers. Dispersal in a downstream direction from the middle to lower Great Lakes and upper St. Lawrence Seaway also was rapid. Upstream transport was slower and probably enhanced by attachment of mussels to vessel hulls (Keevin et al. 1992). The range of quagga mussels is less extensive, extending throughout the Great Lakes and into the upper St. Lawrence River (Mills et al. 1996).

The ecological and economic effects of these two dreissenids are similar in nature and relate mainly to two aspects of their biology that distinguish this mussel group from other freshwater bivalves: the production of a planktonic veliger larval stage, and the use of byssal threads for attachment to firm substratum (Ackerman et al. 1994). The planktonic veliger stage is common among marine bivalves and allows for dispersal of propagules. However, all freshwater bivalve taxa other than dreissenids have evolved life history strategies that avoid this planktonic stage that is highly susceptible to downstream transport. Unionid mussels brood glochidia larvae in gill marsupia; these are released and attach to fish hosts until they metamorphose and settle as miniature benthic bivalves. *Corbicula* and fingernail clams brood larvae on their gills until they develop into miniature bivalves competent to settle; these are spewed out and initially settle near the adults.

Dreissenids attach to hard substratum using a true byssus secreted from a ventral gland and comprising many threads that terminate in adhesive discs. Although common among marine mussels (e.g., those that foul pier pilings), all freshwater bivalves other than dreisssenids are infaunal burrowers. Zebra and quaqqa mussels are the only large, calcareous-shelled invertebrates that attach to firm substratum in freshwater. Their ability to occupy a unique niche makes them especially problematic as attached biofoulers and filter and pipe cloggers (Claudi and Mackie 1994).

Negative financial and ecological effects of dreissenids relate to these aspects of biology and to prolific reproduction (Nalepa and Schloesser 1993). Densities can exceed 200,000/m^2 and result in biofouling of industrial and agricultural pipelines, submerged portions of boats and navigational equipment, and possibly increased corrosion potential of steel and iron pipes (Claudi and Mackie 1994). The financial costs associated with these industrial impacts are substantial (O'Neill 1997; Leung et al. 2002; Pimental et al. 2000). Ecologically, zebra mussels have been associated with decreases in plankton abundance, changes in water quality, nutrient concentrations, aquatic plant distribution, and assemblage structure of benthic macroinvertebrates and fishes (MacIsaac et al. 1995; Caraco et al. 1997; Pace et al. 1998; Strayer et al. 1999; 2004;

Hecky et al. 2004; Nalepa et al. 2003). For this reason, much effort has been given to quantifying and identifying suitable habitat parameters associated with dreissenid range expansion.

2 Environmental Factors Affecting Dreissenids

Numerous laboratory and field studies have helped define the environmental conditions most often associated with dreissenids. Efforts to predict or explain dreissenid distributions based on habitat conditions have focused on air temperature, precipitation, pH, calcium concentration, depth, and substrate size (Strayer 1991; Neary and Leach 1992; Ramcharan et al. 1992; Mellina and Rasmussen 1994; Jones and Ricciardi 2005). Although these studies are not discussed individually, pertinent results from each are included in appropriate sections below. Examples of threshold limits and habitat suitability curves used to estimate the potential spread of zebra mussels at regional scales are also included (Figure 1).

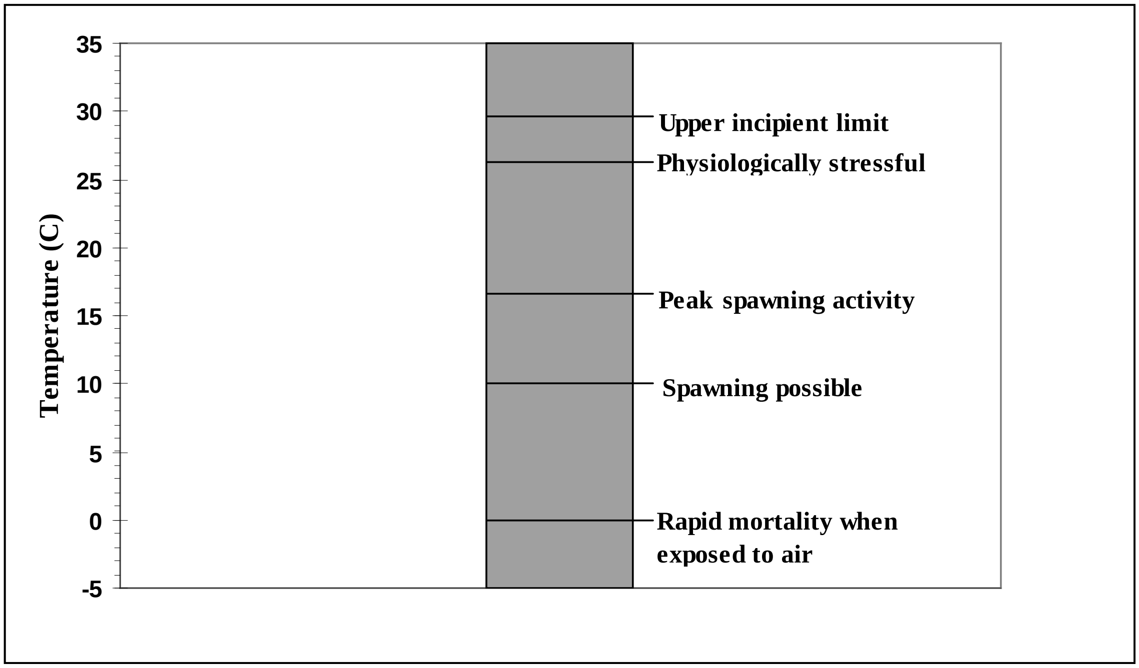

Figure 1. Important biological effects of temperature on dreissenids.

Temperature effects. Ambient temperature regulates metabolic rate in ectothermic organisms (Gillooly et al. 2001). Temperature can therefore be an important factor limiting the viability of dreissenids (Figure 1). The upper incipient lethal temperature of North American zebra mussels in aquatic habitats is ~30° C (Iwanyzki and McCauley 1993; McMahon et al. 1994). However, functional responses of dreissenids can vary based on acclimation effects. During summer months, dreissenids are acclimated to warmer temperatures and are less susceptible to high temperature than during winter months when ambient temperatures are lower. Dreissenids can upwardly adjust their thermal maxima if changes in ambient temperature occur slowly (Thorp et al. 1998). Therefore, gradual increases to temperatures just above average thresholds may be tolerated for a limited time. Nevertheless, it remains the case that dreissenids prefer cool temperate conditions. There is only marginal evidence that dreissenids have accomplished much increased tolerance to warm water in the more southern part of their North American distribution (Allen et al. 1999).

Estimates of the temperature at which zebra mussel spawning begins vary substantially. Spawning activity in European populations begins at water temperatures of 10 to 17° C (Borcherding 1991; Neumann et al. 1993; Sprung 1993), although estimates for some populations have been as high as 17 to 21° C (Sprung 1993). Similar estimates for North American populations range from 18 to 23° C (Garton and Hagg 1993; Fraleigh et al. 1993; Riessen et al. 1993; Nichols 1996). However, many of these estimates represent temperatures at which veligers were first observed rather than the initiation of spawning. Results from most studies indicate that zebra mussel populations probably start spawning at approximately ~10 to 12° C, with peak activity at ~17 to 18° C. These conclusions agree with Sprung's (1993) estimates that larval development can successfully occur at 10 to 24° C, although the rate of development is positively correlated with temperature within this range (higher temperature results in greater developmental rate). Estimates of maximum adult tissue growth rates (~10 to 15° C) and peak spawning activity (~17 to 18° C) also fall within this range. The bioenergetic budgets of mussels indicate stress at temperatures in excess of approximately 26° C (Payne and Aldridge 1993).

Freezing temperatures are not tolerated long by aerially exposed mussels. Mortality of individual zebra mussels occurs within 15 hr when exposed to air temperatures of -1.5° C (Clarke 1993; Clarke et al. 1993). However, adult zebra mussels in small clusters (~10) live twice as long as individual mussels in air temperature treatments up to 10° C. These results indicate that a rapid drop in water level (pool drawdown, dewatering, etc.) during winter months can result in mortality of zebra mussels caused by prolonged exposure to sub-freezing air temperatures.

pH effects. The rate at which enzyme-mediated biochemical reactions occur can be influenced by the pH of an organism's environment. Therefore, the range and variability of pH as well as the buffering capacity of the environment can affect overall habitat suitability for dreissenids (Figure 2). Non-indigenous zebra mussels are less tolerant of low-pH habitats than native bivalve species (McMahon 1991). Lower pH limits for growth among most unionids appears to be ~5.6, whereas similar estimates for adult zebra mussels are ~6.5 (McMahon 1991 and references therein).

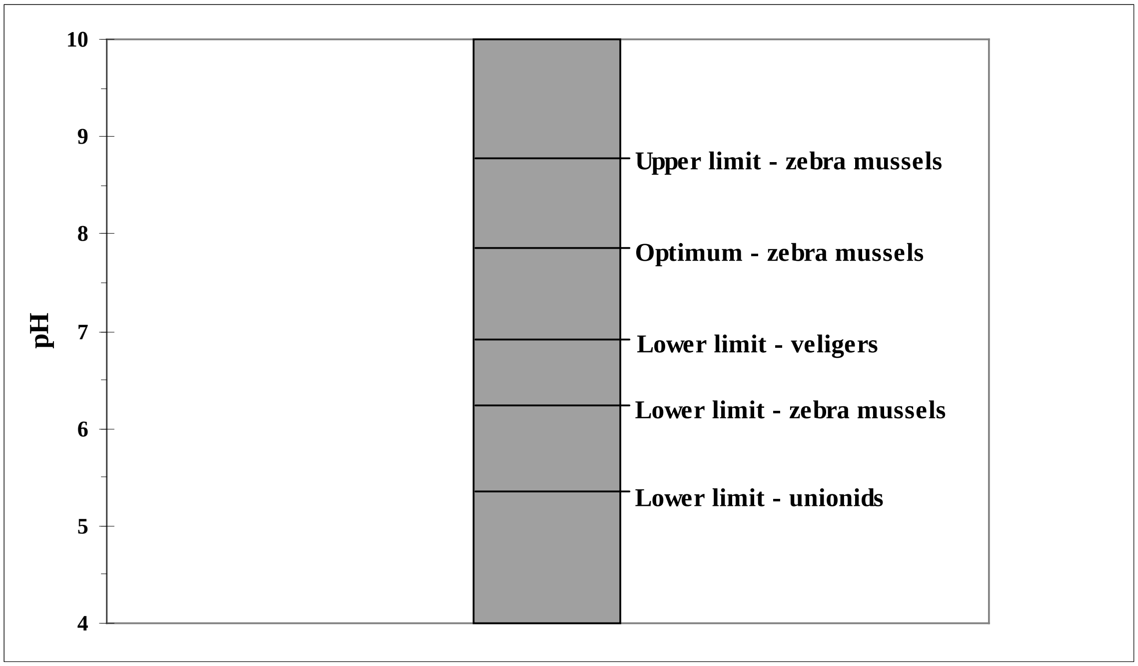

Figure 2. Important limitations of pH on the viability of dreissenids.

Zebra mussel veligers are especially intolerant of "low" pH. Indeed, the lower pH limit for development is 7.4. At the high end of the range, pH above 9.4 is not tolerated (Sprung 1987; Hincks and Mackie 1997). The optimum pH for zebra mussels is approximately 8.4. The specific mechanism behind this low pH threshold for zebra mussels relative to other freshwater mollusks is not clear, although there is evidence that the ability of adults to regulate hemolymph Ca^{++} (balance of sodium and calcium levels) declines at $pH<6.8$ (Vinogradov et al. 1993).

Overall, these physiological studies agree with distribution records that indicate an absence of zebra mussels in European lakes with $pH<7.3$ (Ramcharan et al. 1992). In addition, high pH (> approximately 9.3 to 9.6) cannot be tolerated by zebra mussels (Bowman and Bailey 1998).

Calcium Concentration and Hardness. Hardness represents the total concentration of divalent salts (calcium, magnesium, iron, etc.) present in water. Calcium and magnesium are both important factors affecting ecophysiological processes. However, calcium concentration (Ca^{++} mg/L) is often reported separately because of its effect on osmoregulation and shell formation in zebra mussels (Vinogradov et al. 1993; McMahon 1996). Although calcium concentration may limit distribution and viability of zebra mussels (Figure 3), it is not necessarily indicative of density (Ramcharan et al. 1992; Mellina and Rasmussen 1994). As with pH, zebra mussels demonstrate less effective osmoregulation at moderate or low pH levels than native unionids (McMahon 1991; Vinogradov et al. 1993).

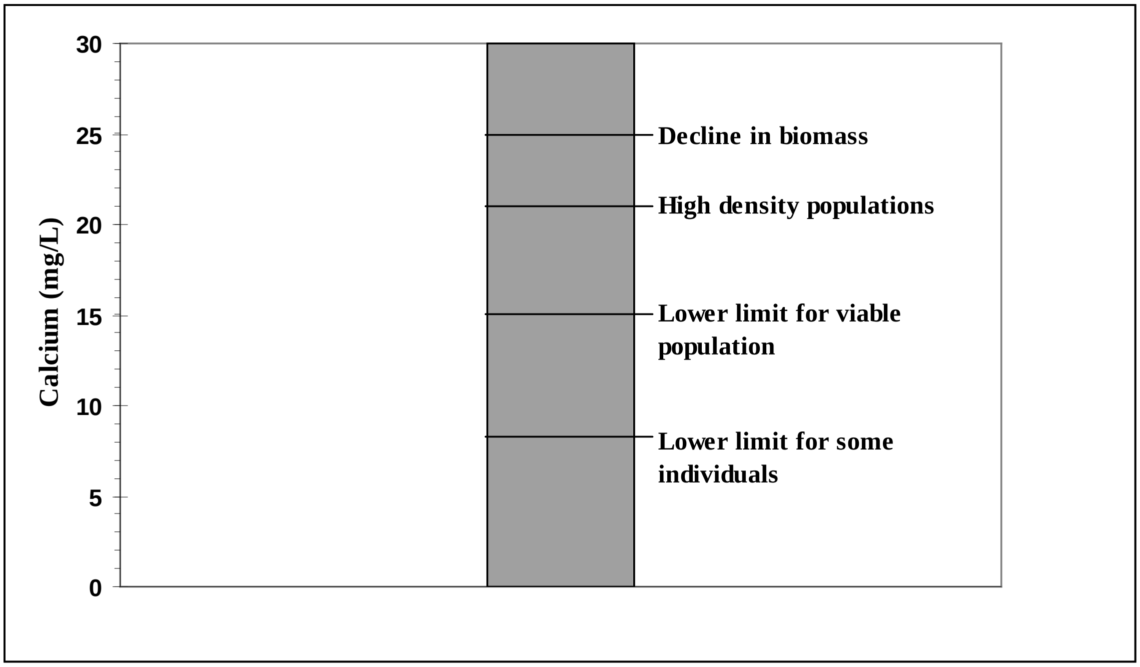

Figure 3. Important biological associations of calcium concentration and dreissenids.

European populations of zebra mussels seem to have greater low-level Ca^{++} thresholds for survival and growth than North American populations. Strayer (1991) reviewed data from 70 European lakes and found no evidence of zebra mussels in lakes with calcium concentrations <20 mg/L. Other data from European lakes indicate a greater low-end calcium concentration limit of 28.3 mg/L (Ramcharan et al. 1992). North American populations of zebra mussels require calcium concentrations of ~15 mg/L to remain viable (Mellina and Rasmussen 1994; Strayer et al. 1996; Allen and Ramcharan 2001), although individuals can persist in habitats with calcium concentrations as low as 8.5 mg/L (Hincks and

Mackie 1997; Jones and Ricciardi 2005). Moderate to high densities are often associated with calcium concentrations greater than 21 mg/L (Mellina and Rasmussen 1994; Hincks and Mackie 1997), although some field data indicate a decline in zebra mussel biomass at concentrations greater than ~25 mg/L (Jones and Ricciardi 2005).

Dissolved Oxygen (DO). Invasive species are too often viewed as "physiologically tough" simply because of their invasive nature. However, zebra mussels are generally less tolerant of low DO than other North American bivalves (McMahon 1991; Matthews and McMahon 1994; McMahon 1996). This would be expected from their byssal attachments habit (adapted to life in wave-washed and highly oxygenated littoral zones of large lakes). However, developing simple threshold limits is complicated by the fact that respiratory tolerance probably varies with condition, study design, and other factors (Aldridge et al. 1995). Sprung (1987) determined that the lethal lower limit of oxygen concentration for adult zebra mussels in laboratory experiments was ~4 mg/L at 18^{o} C. However, at the same temperature, zebra mussels in cage experiments within a North American lake survived oxygen concentrations of 1.0 to 1.7 mg/L (Yu and Culver 1999).

DO limits for organisms are also reported in terms of oxygen saturation. Boelman et al. (1997) indicated that zebra mussels are often associated with habitats where oxygen saturation exceeds 90%, although Smirnova et al. (1993) suggest that the optimal oxygen saturation level for zebra mussels is 80 to 85%. In a review of Russian literature, Karatayev et al. (1998) noted research indicating a lower critical oxygen saturation threshold of 25% for zebra mussels (Mikheev 1961; Spiridonov 1972; Shkorbatov et al. 1994). Individuals survived less than a week when exposed to anaerobic conditions at 18 to 20^{o} C (Karpevich 1952; Mikheev 1964; Spiridonov 1972). Sensitivity to oxygen deprivation is inversely related to zebra mussel size (Mikheev 1964). The overall sensitivity of zebra mussels to low DO probably limits their ability to thrive in eutrophic, hypolymnetic, or highly polluted environments (Stanczykowska 1977; Mackie et al. 1989; Neumann et al. 1993).

Turbidity. Turbidity is an indirect estimate of the concentration of particles suspended in the water column. These particles are often referred to as seston, which includes both inorganic soil particles as well as organic particulate matter including organisms and detritus.

The dynamic nature of seston is fundamentally different in lentic and lotic systems because of a persistent current as well as potentially rapid changes in river discharge rates. These flow-related factors affect the magnitude, temporal variability, and inorganic/organic ratio (I/O) of seston content in riverine habitats. In lentic habitats, zebra mussels demonstrate the ability to clear seston from the water column resulting in direct temporal changes in turbidity estimates and energy flow (Hebert et al. 1991; Leach 1993; Kryger and Riisgard 1988). Zebra mussels also have the ability to alter the size of their labial palps relative to their gills during development (e.g., mussels in more turbid environments have larger palps than those in less turbid environments - Payne et al. 1995; see also Theisen 1982). The palps are important in particle sorting and optimize efficient ingestion of organic particles captured on the filtering gill lamellae (Russell-Hunter and Buckley 1983). Although turbidity may influence habitat suitability for dreissenids, the fundamental differences of seston dynamics among aquatic environments probably explains why no definitive critical thresholds have been suggested in the literature.

Strayer (1991) examined data from 30 European lakes and found that zebra mussels were often absent from habitats where Secchi disk depths were less than 1 m. However, Secchi disk estimates in less turbid environments might reflect seston clearing by zebra mussels rather than a limiting habitat factor. Seston quality in rivers can influence growth and assimilation efficiency of zebra mussels (Alexander et al. 1994). Inorganic to organic ratios (I/O) of 1.71-2.0 have been reported sufficient to cause declines in feeding and assimilation efficiency, which could limit the abundance of zebra mussels in large, turbid rivers (Madon et al. 1998; Schneider et al. 1998).

Substratum. Dreissenids are most often associated with hard, stable substrata (Griffiths et al. 1991; Dermott and Munawar 1993; Leach 1993; Karatayev et al. 1998), to which they attach to using a proteinaceous byssal thread (Morton 1993). Dreissenid density (Mellina and Rasmussen 1994) and biomass (Jones and Ricciardi 2005) are both correlated with substratum particle size in the St. Lawrence River. Although zebra mussel colonies can expand outwards and cover softer substrata as densities increase (Hunter and Bailey 1992: Berkman et al. 2000; Haltuch et al. 2000), firm substratum is usually required for initial establishment. Populations in waterbodies with uniformly soft sediment are less likely to approach the density or ubiquity of those in habitats dominated by coarse-grained substratum.

Submerged macrophytes often contain large numbers of zebra mussels and can serve as an important vector for dispersal after becoming uprooted or fragmented (Horvath and Lamberti 1997). Unionids also represent an ideal hard-surfaced, stable substratum upon which zebra mussels can become attached. Some studies indicate that zebra mussels preferentially attach to unionids resulting in increased unionid stress and mortality (Mackie 1993; Ricciardi et al. 1995; 1996). However, there are alternative explanations for these observations, including mobility of zebra mussels away from less stable substratum to the more stable substratum provided by unionids (Toczylowski et al. 1999).

Mobility has been reported as a mechanism for zebra mussels, particularly smaller individuals, to avoid less suitable changes in environmental conditions. Mackie et al. (1989) reported smaller individuals emigrated from shallow lake depths in summer to deeper habitat in the winter. Vertical migration of smaller individuals toward the surface of high-density colonies can be an important behavioral response to avoid unfavorable water chemistry conditions (elevated nitrate/ammonium and low dissolved oxygen concentrations) (Burks et al. 2002). Although zebra mussels may remain attached to a suitable substratum indefinitely, it is important to acknowledge their ability to detach and migrate if environmental conditions deteriorate.

Water Velocity and Turbulence. Many studies investigating habitat requirements of dreissenids have focused on lentic populations because colonization in North America first occurred in the Great Lakes. Although zebra mussels have now expanded their range throughout many major river systems, there has been relatively little research focused specifically on how threshold responses may differ in lotic and lentic ecosystems. The most obvious difference between these two types of ecosystems is the presence/absence of a prevalent, primarily unidirectional current. The presence of current in a riverine system can potentially affect variability in water quality parameters as well as direct responses of dreissenids to the physical environment.

Zebra mussel densities are generally lower in rivers than in lakes (Strayer 1991; Horvath et al. 1996), although riverine population densities can reach high levels in backwater, side-channels, and reservoirs upstream of impoundments. Densities may be lower in rivers due to several factors directly or indirectly associated with water velocity. A water velocity exceeding 1.5 m/sec may directly affect the ability of dreissenid larvae to settle (Boelman et al. 1997) or limit a larva's mobility in searching for suitable substratum after settling.

The settling stage of larvae is very sensitive to physical and environmental stress and appears to have very high mortality rates (90 to 99% - Mackie et al. 1989; Sprung 1989; Nalepa and Schloesser 1993). Turbulence associated with river currents may contribute to increased larval mortality due to stress-related increases in physical injury, energy expenditure, and ingestion rates as well as decreased growth rates (Horvath and Lamberti 1999; Peters and Marrase 2000; Rehmann et al. 2003). River currents may also displace gametes resulting in decreased fertilization rates (Sprung 1993).

Temporal variability in precipitation and run-off can affect seston composition and feeding efficiency of zebra mussels (see **Turbidity** above). Smirnova and Vinogradov (1990) reported declines in adult feeding efficiency at a current velocity of 1.0-1.5 m/sec due to deformation in the siphon of zebra mussels. However, current velocities as low as ~20 cm/sec can inhibit clearance rates of both adults and juveniles (Ackerman 1999). The direct and indirect effects of current velocity may explain why zebra mussels tend to be limited to larger river systems (<30 m wide) in Europe (Strayer 1991) and North America.

3 Differences in Habitat Associated with Quagga and Zebra Mussels

Initial research indicated that coexisting quagga and zebra mussel populations were segregated based on depth and temperature. In Europe, zebra mussels occupied relatively shallow habitats (2 to 8 m) whereas quagga mussels were found at depths up to 28 m (Stanczykowska 1977; Mills et al. 1996). North American dreissenids of both species were found at much greater depths in the Great Lakes (zebra mussels ≤110 m; quagga mussels ≤130 m) (Mills et al. 1993; Dermott and Munawar 1993), although habitat segregation between the two species in shallow and deep water was similar to that observed in Europe. Colder water temperatures (<10° C) in deeper habitats where quagga mussels were found seemed to suggest that zebra mussels were more sensitive to lower temperatures than quagga mussels (Mills et al. 1993). These observations were supported by experiments examining differences in critical temperature thresholds for both species. Claxton and Mackie (1998) found that quagga mussels in the hypolimnion of Lake Erie spawned at a lower temperature (9° C) than the critical thermal minima reported for zebra mussels (~12° C). Other experiments indicated that zebra mussels have a greater upper thermal limit (30 to 31° C) for survival than quagga mussels (25° C) (Iwanyzki and McCauley 1993; McMahon et al. 1994; Spidle et al. 1995). These results supported the assumption that zebra mussels were often associated with shallow habitats with warmer temperatures, whereas quagga mussels were often located in deeper habitats with relatively cooler temperatures.

Despite early evidence suggesting that quagga and zebra mussels may coexist by partitioning habitat, other studies have indicated that quagga mussels are spreading into more shallow lake and riverine habitats and may eventually displace zebra mussels in some regions (Pligin 1984; Mills et al. 1993, 1996; Adrian et al. 1994; Mitchell et al. 1996). Mitchell et al. (1996) found that quagga mussels in a thermally enriched area of Lake Erie were more abundant than zebra mussels in shallow habitats. The authors suggested that quagga mussels may survive in deeper habitats because of warmer winter temperatures (inverse stratification) rather than an innate ability to survive relatively colder summer temperatures. Claxton and Mackie (1998) found that quagga mussels transplanted to the epilimnion initiated spawning two weeks before zebra mussels, although zebra mussels transplanted to the hypolimnion did not even demonstrate significant gametogenic development. These results indicate that quagga mussels are capable of occupying and reproducing in both deep and shallow habitats, whereas successful reproduction in zebra mussels is limited to warmer, shallow zones.

Quagga mussels and zebra mussels are both similar in their preference for hard, stable substrata. Jones and Ricciardi (2005) found a direct relationship between substratum particle size and biomass of both quagga and zebra mussels. However, quagga mussels are more capable of colonizing soft substrates than are zebra mussels (Dermott and Munawar 1993; Dermott and Kerec 1997). The presence of quagga mussels in deeper lake habitats, where soft substratum is more prevalent, probably explains the early assumptions of habitat segregation between dreissenids in shallow and deep habitats. However, quagga mussels may be more competitive over a wider range of habitat conditions than zebra mussels as long as summer temperatures do not exceed critical maximum limits for an extended length of time.

4 Summary

The introduction and rapid spread of freshwater dreissenids in North America has resulted in major negative economic and ecological impacts (Pimentel et al. 2005; Connelly et al. 2007). Operational costs for industries faced with potential problems associated with dreissenids have increased greatly. Ecological changes in affected aquatic ecosystems have included altered assemblage structures, food web dynamics, and energy flow. By examining habitat requirements and limitations of quagga and zebra mussels, it is possible to gain a better understanding of how to prevent or minimize the spread of dreissenids to new areas and to predict what habitats are most vulnerable to future invasions.

The most important factors in determining the suitability of habitat for dreissenids are temperature, pH, and calcium concentration. Habitats that do not exceed and rarely attain 30° C, a pH of ~7.0, and calcium concentrations less than ~20 mg/L seem to be suitable for establishment of persistent dreissenid populations. Oxygen saturation levels of 80 to 85% are considered optimal, although oxygen requirements can change seasonally with temperature. The interacting effects of turbidity, food quality, and water velocity can affect growth and assimilation rates in zebra mussels and may explain why abundance is generally lower in riverine habitats compared to lakes. Although dreissenids are often associated with hard, stable substratum, quagga mussels seem to be capable of colonizing habitats with soft substratum, and zebra mussels have demonstrated an ability to emigrate from less suitable habitats when environmental conditions warrant. Both species are capable of attaching to other individuals within a population. Therefore, the importance of stable substratum may decrease over time as populations grow and spread outward along the bottom.

There have been relatively few studies specifically designed to distinguish between habitat requirements of quagga and zebra mussels. Furthermore, the majority of these studies have been limited to examining species differences in temperature effects on survival, growth, and reproduction. Initial observations seemed to indicate that quagga and zebra mussels responded differently to these factors in a way that would result in habitat partitioning between deeper, colder (quagga mussels more prevalent) and shallower, warmer (zebra mussels more prevalent) habitats. However, more recent research and observations indicate that quagga mussels may eventually displace zebra mussels in habitats where summer temperatures do not exceed 25 to 30° C for extended periods or when increases in temperature beyond this level occur gradually. Further research efforts should focus on habitat requirements and critical limits of pH and calcium concentration for quagga mussels. Results from these studies would allow a more comprehensive assessment of dreissenid impacts, abundance, and distribution throughout North American waterways.

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14. ABSTRACT

The continued spread of two invasive dreissenid bivalve species, zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels, into the southwestern and western United States indicates the need for improving understanding of habitat requirements and constraints for both species. This report summarizes results from published literature and reports that describe physical and environmental characteristics often associated with dreissenids. For example, data from the studies reviewed for this report indicate that at the upper incipient lethal temperature of ~30^{o} C, adult growth may be limited at pH of ~5.5-6.5, calcium concentrations of ~15 mg/L are required for viable populations, and the lethal lower limit of oxygen concentration is ~4 mg/L at 18^{o} C. Developing a better understanding of how dreissenids respond to variable habitats and environments will improve our ability to anticipate potential challenges posed by the continued expanding distribution of these species in the United States.

15. SUBJECT TERMS

Dreissenids	Habitat threshold	Quagga mussel
Freshwater dreissenids	Invasive species	Zebra mussel

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