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CRITERIA FOR PREDICTING ZEBRA MUSSEL INVASIONS IN THE MID-ATLANTIC REGION

BY

PATRICK BAKER
SHIRLEY BAKER
ROGER MANN

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SCHOOL OF MARINE SCIENCE
VIRGINIA INSTITUTE OF MARINE SCIENCE
COLLEGE OF WILLIAM AND MARY
GLOUCESTER POINT, VIRGINIA 23062

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Authors: Patrick Baker, Shirley Baker, Roger Mann
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VIMS

INTRODUCTION

The following document is from the proceedings of a 1993 zebra mussel workshop, conducted in Baltimore, Maryland. At the workshop forecasts were presented concerning the future of zebra mussels, *Dreissena polymorpha*, in the mid-Atlantic states.

What is the probability that zebra mussels will invade specific bodies of water within a given state? If they do invade, will they become economic and ecological pests as they have in portions of the Great Lakes? These and similar questions are addressed, with the expectation that management strategies can be developed to delay, mitigate, or possibly even prevent zebra mussel invasions, in some areas.

The probability of invasion is related to the frequency with which a specific body of water is inoculated with zebra mussels and their ability to survive in that body of water. The variety of dispersal mechanisms, and the frequency and relative importance of each potential inoculation affect the overall chance that a reproducing population of zebra mussels will become established in a lake or estuary.

Prior experience with zebra mussel invasions in Europe and other parts of North America indicates that, at least initially, population growth is not limited by predators, parasites, or other biological factors. Certain abiotic parameters, however, seem to limit zebra mussel populations in Europe. For these reasons, the criteria for predicting zebra mussel invasion success in the mid-Atlantic region are primarily physical environmental parameters, and especially aspects of water chemistry. The degree to which a particular body of water conforms to the known optimum physiological requirements for zebra mussels is here termed its *susceptibility*. The second part of this document is a review of the physiological requirements used to predict susceptibility. For an example of similar predictions for other regions, see Neary and Leach (1992).

A second species of *Dreissena*, with at present only the common designation "quagga mussel" (its taxonomic identity is uncertain), has been found in parts of the Great Lakes and New York inland waters (May and Marsden, 1992). At present, nothing is known about the dispersal or physiological requirements of the quagga mussel, other than that it lives with *Dreissena polymorpha*, and dominates some deep-water populations (Marsden, 1993). Throughout this chapter, *Dreissena* is used to indicate both the zebra mussel and the quagga mussel.



A zebra mussel is a small, striped mollusk capable of raising havoc. (Although the mollusk can grow up to two inches, it is usually much smaller — fingernail size.) Zebra mussels have cost millions of dollars in the Great Lakes region where they rapidly colonized water-intake pipes, boats, docks, piers, and other structures. *Dreissena polymorpha* was inadvertently delivered to U.S. waters around 1986 through the discharge of European shipping ballast water. —ed.

I. INVASION RISK

DISPERSAL MECHANISMS OF ZEBRA MUSSELS

Invasion risk is here defined as the probability, relative to other bodies of water, that zebra mussels will be inoculated to a specific body of water in sufficient numbers to establish a viable population. As will be explained, risk is related to the numbers of zebra mussels inoculated, and the conditions of inoculation, which are in turn related to the mechanisms of inoculation.

Terminology for biological invasions merits a brief discussion. An *invasion* is the successful (reproducing) establishment of a species in an area in which it had historically been absent. The vector for invasion can be either human-mediated or natural. When an invasion is known to be human-mediated, it can be termed an *introduction*. Thus, *Dreissena* was introduced to Lake St. Clair, in Michigan, and from there they invaded (by natural dispersal) Lake Erie and Lake Ontario. The actual event that leads to an introduction, such as the release of ballast water containing larvae, is termed *inoculation*, and the process by which the new species becomes a self-maintaining population is termed *establishment*. Thus, *inoculation* and *establishment* are events within an *introduction*, which is itself a specific form of *invasion*. These usages come from no single source, and alternate terms are used elsewhere, but the above are generally consistent with modern literature on aquatic biological invasions.

POPULATION ESTABLISHMENT

One of the most difficult aspects of predicting biological invasions is forecasting when (how soon) an invasion will occur. *Dreissena* invaded the Great Lakes some time shortly prior to 1988 (Hebert *et al.*, 1989), but the mechanism responsible for invasion, ballast water (Carlton, 1993), has existed for decades before *Dreissena* became established. Similarly, the rate and direction of dispersal by both natural and human-mediated means from the Great Lakes has often defied prediction. For example, *Dreissena* has been present in an upper portion of the Susquehanna River, in New York, since at least 1991 (Lange and Cap, 1992), but to date has not appeared in downstream portions. This absence does not mean that zebra mussels will not invade downstream, only that we cannot predict closely when they will.

We do have limited understanding of how some inoculations may be favored over others: *Dreissena* reproduces sexually, releasing male and female gametes into the water. Prior research on other aquatic organisms (Pennington, 1985; Lasker and Stewart, 1992) show that gamete viability decreases dramatically with dilution, so that low-density populations of benthic invertebrates have much lower reproductive success than high-density populations. Not only does this mean that the initial inoculation of *Dreissena* must result in animals in sufficient proximity to spawn successfully, but also that there must be enough offspring produced so that they, too, can reproduce successfully. Larvae disperse in the plankton and face high mortality; those that survive to settlement are widely scattered, and only those that settle near others can reproduce. Thus, the greater the founding population, the greater the chance of subsequent establishment, and the more quickly the population will attain high levels. Dispersal mechanisms which deliver many individuals to the same location are the most likely to spread invasions (Johnson and Carlton, 1993).

There are two practical aspects to the above observation, and its corollary, that not every inoculation will result in invasion. First, it is cost-effective for management agencies to concentrate first on major invasion vectors, rather than trying to prevent every possible mechanism for invasion. Second, when obtaining public cooperation in limiting *Dreissena* invasion, it is important to make individuals believe that their own reasonable efforts can make a difference in *Dreissena* invasion. This latter aspect has been discussed by Johnson and Carlton (1993).

NATURAL DISPERSAL

LARVAL DISPERSAL

Dreissena is unusual among freshwater bivalves in that it has planktonic larvae and postlarvae (Griffiths *et al.*, 1991; McMahon, 1991). Postlarvae drift passively with currents by means of long byssal threads (Martel, 1992). Larvae swim by means of the velum, a ciliated organ, but most bivalve larvae

have swimming rates of less than 1 mm s⁻¹ (Mann and Wolf, 1983; Jonsson *et al.*, 1991; Mann *et al.*, 1991), and therefore cannot swim against most currents. Juveniles and adults can crawl actively but not rapidly, and it is extremely improbable that a juvenile or adult could crawl upstream against a current as far in its lifetime as it would be carried downstream as a larva (planktonic period of about 12 days: Neumann *et al.*, 1993) or postlarva. *Dreissena*, therefore, is ecologically adapted more for lakes (no net currents) or estuaries (bidirectional currents), than for rivers (unidirectional current) (Neumann *et al.*, 1993). Rivers which have attached oxbow lakes, navigational locks, or other calm backwaters, could probably support significant populations of *Dreissena* (e.g. Biryukov *et al.*, 1968). The native range of *Dreissena* is estuaries in southern Russia, Ukraine, and Kazakhstan, and the largest populations outside of the native range, in Europe and North America, have been in lakes, estuaries, and other calm waters (Shtegman, 1968; Wolff, 1969; Sta czykowska, 1977; Griffiths *et al.*, 1991). High densities of *Dreissena* in non-estuarine rivers can be maintained only by a continual input of individuals from upstream lakes or backwaters. Thus, streams without such areas cannot be successfully invaded by *Dreissena*. Unfortunately, most major North American rivers, including those along the eastern coastline of the U.S., have upstream reservoirs that could support *Dreissena* populations, given the correct water quality parameters. High densities of *Dreissena* can be attained in rivers downstream of lakes (e.g. Piesik, 1983; Neumann *et al.*, 1993). There is no data on the effect of reservoir size or flushing rates on downstream *Dreissena* population densities, so for now, all freshwater downstream of a lake capable of supporting *Dreissena* populations must be considered at risk from invasion.

Dreissena are limited in their ability to tolerate salt water, but most major eastern estuaries in North America have large freshwater tidal portions. Even in years of low freshwater input, significant portions of most estuaries remain fresh. *Dreissena* larvae and postlarvae could be retained within the estuary by the same mechanisms used by oyster larvae (Seliger *et al.*, 1982; Mann, 1988). A native species closely related to *Dreissena*, the false mussel *Mytilopsis leucophaeata*, is already present in oligohaline and freshwater portions of estuaries from New York to Texas (Abbott, 1974). Water chemistry of these estuaries, in terms of pH and calcium, is often nearly ideal for *Dreissena*, and many must be considered at risk from *Dreissena* invasion. Furthermore, any freshwater portions of an estuary will eventually be invaded if there are *Dreissena* populations established in upstream lakes or reservoirs. The St. Lawrence River in Quebec and the Hudson River in New York are two North American examples of invaded freshwater estuaries (New York Sea Grant, 1992).

ADULT AND JUVENILE DISPERSAL

Adults and juveniles of *Dreissena* can crawl by alternately attaching and releasing byssal threads. Based on crawling rates of juvenile marine mussels, *Mytilus* spp. (these authors,

unpubl. data), *Dreissena* individuals can probably move several meters per day. A very short stream between a *Dreissena*-infested reservoir and an upstream, non-infested reservoir, would probably not be a barrier against invasion by crawling individuals. Two examples of this situation include a series of ponds in a typical golf course, and the network of ponds, canals, and ditches in many coastal cities in the mid-Atlantic region. *Dreissena* individuals probably cannot circumnavigate a waterfall or spillway, however, nor crawl up a rapidly flowing stream more than several hundred meters in sufficient numbers to establish a new population in an upstream reservoir.

Adult and juvenile *Dreissena* attach to a variety of substrates with sturdy byssal threads. A number of natural mechanisms (amphibious animals) have been proposed that could transfer byssally-attached adults or juveniles between very close but separate bodies of water. These mechanisms have been reviewed by Carlton (1993), and an example includes aggregations attached to the carapaces of turtles, which often migrate between nearby bodies of water. Certain species of turtle may become important in dispersing *Dreissena* within regions with many small lakes, or in coastal regions with many small estuaries isolated from each other by high-salinity barriers, but only low, narrow terrestrial barriers. This last condition is typical of the coastal plain from New Jersey to Texas. In the mid-Atlantic region, the eastern musk turtle (*Stenotherus odoratus*), a common species living in a variety of bodies of water, is noted for having heavy algal fouling (McCauley, 1945; Martoff *et al.*, 1980), and the much larger snapping turtle (*Chelydra serpentina*) can also be heavily fouled (J. Brown, Virginia Inst. Marine Science, pers. comm.).

Waterfowl have been suggested by a variety of authors as potential vectors of transport, and Carlton (1993) reviews evidence both for and against this as a mechanism of invasion. Birds could transport *Dreissena* many kilometers by a variety of means, although the actual numbers transported by any one bird would be small relative to the numbers that could be transported by almost any human-mediated process. The role of large flocks of migratory birds in dispersing *Dreissena* is worth investigating, however.

It should be noted that so far the spread of *Dreissena* in North America across natural barriers can be attributed to human actions alone. Thus while amphibious animals may be mechanisms of invasion, most emphasis should be placed on controlling human-mediated dispersal mechanisms.

HUMAN-MEDIATED DISPERSAL MECHANISMS

OVERLAND TRANSPORT

Overland transport of *Dreissena* associated with recreational vessels, or the trailers that transport them, has received much attention, and is thought to be the primary mechanism whereby inland lakes separated from other

navigable waters will be invaded. Baltimore County, Maryland, has restricted the use of recreational vessels in several municipal reservoirs in response to this threat. McMahon and Payne (1992) have shown that *Dreissena* can survive several days out of water even at high temperatures, and dispersal by overland transport is known to have occurred (Carlton, 1993). Public education has focused on the potential for *Dreissena* attached to vessel hulls to be moved between lakes, but it has recently been noted that under certain circumstances more *Dreissena* will probably be transported on strands of aquatic macrophytes that become entangled in boat trailers (Carlton, unpubl. data).

Known or suspected invasions that have occurred as a result of overland transport have been fewer, so far, than have been expected. The reason may be that, normally, few individuals are introduced by a single inoculation. Several overland invasions have occurred, however, including the invasion of the upper Susquehanna drainage in New York state (Lange and Cap, 1992), and either vessel hulls or their trailers are the most probable vector.

Juveniles or adults, not larvae, will be transported overland by the above mechanisms. To be introduced to the new location, the *Dreissena* must detach from the vessel or trailer. Juveniles are more likely to move than adults (Eckroat *et al.*, 1993). If the *Dreissena* are attached to macrophytes associated with the boat trailer, it is simply necessary for the plant to detach in the new body of water. Furthermore, a piece of drifting plant with attached *Dreissena* could drift rapidly down a river until it reached a lake, where a population could be established, whereas adult *Dreissena* sinking individually into a river would be less likely to reach a downstream lake or successfully establish a population.

BALLAST WATER, BILGES, BAIT WELLS

It is believed that the introduction of *Dreissena* into the North American Great Lakes was accomplished by the release of ballast water, containing larvae or postlarvae, from the holds of ore carriers from Europe. Evidence for this route has been well documented (see Carlton, 1993, for review). Guidelines to prevent further introductions of exotic species by ballast water into the Great Lakes have been set up, but compliance is not thought to be 100% (J. Carlton, pers. comm.), and probably a single inoculation under optimal conditions is sufficient to permit invasion. Furthermore, ballast into other North American freshwater ports remains undocumented. For example, Richmond, Virginia, a freshwater estuarine port, is regularly visited by container ships from Antwerp, Belgium, and other European ports (Meehan Overseas Terminal, Inc., 1991). Alexandria, Virginia, another freshwater port, is visited six to seven times annually by ships from Quebec City, Quebec, in the St. Lawrence River, where *Dreissena* is established (Robinson Terminal Warehouse Corp., Alexandria, VA, pers. comm.). The amount of ballast water exchanged, and the nature of the exchange, is undocumented and unregu-

lated, but represents a potential vector for the introduction of *Dreissena* into Virginia. Port logs, sometimes available upon request, will no doubt reveal many further points of potential introduction, and it may be chance that the Great Lakes were invaded by *Dreissena* before another North American body of water.

Bait wells, bilge water, shipments of live fish or bait, and many other means of transporting water between bodies of water may harbor larvae or postlarvae for several days, although to date no specific examples of this occurring in North America are known. This means of transport is reviewed at length by Carlton (1993).

VESSEL TRANSPORT BETWEEN ESTUARIES

Once established in Lake St. Clair and Lake Erie in 1989, *Dreissena* was subsequently identified at many isolated points elsewhere in the Great Lakes and in the Erie Canal, New York. The vector of dispersal in these cases was thought to be vessel hulls with byssally-attached adults or juveniles (Griffiths *et al.*, 1991). Since vessels can move upstream or across salinity barriers relatively rapidly, they are a major mechanism for expanding the range of *Dreissena*. Postlarvae and juveniles attached to the hull of a recently moved vessel can detach at a new moorage, and accumulate on nearby stationary substrate. Alternately, adults attached to the hull can spawn at a new location. The relative importance of these two phenomena depends on the number of postlarvae or juveniles transferred in the first case, or the number of adults and the amount of time spent at the new moorage in the second case. The resettlement of postlarvae and juveniles from vessel hulls as a means of dispersal is likely to be favored during the reproductive season, by vessels with relatively clean hulls that do not spend extended periods at any particular mooring. Even a high density of microscopic *Dreissena* postlarva and juveniles would be unnoticed by persons visually inspecting vessel hulls in an attempt to prevent the spread of *Dreissena*. On the other hand, some vessels, especially barges, spend weeks or months at any particular moorage, giving fouling organisms attached to their hulls multiple opportunities to spawn. In such cases, vessels with large fouling populations of adult *Dreissena* would be favored as a method for introducing this species.

Barges in particular represent a major vector for *Dreissena* dispersal. They have large hull areas for colonization from the source population, they are infrequently cleaned, and they often have long residence periods at any particular moorage. Once moved, barges may be moored for months or even years, giving any fouling organisms many opportunities to reproduce. In addition, freshwater regions are attractive to many vessel owners for long-term moorage, because of the relative lack (prior to *Dreissena*) of fouling organisms. The hulls of other vessels that travel between

estuaries are generally smaller and cleaner than barge hulls, but the possibility of introduction via these cannot be ruled out. Even a small, possibly unnoticed portion of a hull could harbor tens of thousands of adult, juvenile, and postlarval *Dreissena*.

Given the ability of *Dreissena* to tolerate moderately saline waters for at least a short period, vessel traffic represents a major intracoastal vector for the spread of *Dreissena* between estuaries. *Dreissena* is present in both the Hudson and Susquehanna Rivers (New York Sea Grant, 1992), and could potentially spread from those sites to most other estuaries with barge traffic between New York and Florida. At present no records on commercial or recreational traffic between freshwater estuarine ports in North America have been compiled. The length of time that *Dreissena* can tolerate full seawater, perhaps by completely closing their valves, is unknown, but they have been shown to be able to survive several days out of water, attached to pleasure craft hulls, under certain circumstances (McMahon and Payne, 1992), and can survive several days without oxygen (Mikheev, 1968).

Introduction of *Dreissena* to a body of water via the hull of a vessel does not automatically ensure establishment. Establishment is favored by high survival of *Dreissena* during the passage overland or through high salinity, by large numbers (e.g. millions) of individuals, by favorable water conditions for growth and reproduction in the host estuary, and by long moorage of the fouled vessel.

INTENTIONAL INTRODUCTION

The possibility of deliberate, misguided introductions of *Dreissena* must be seriously considered. *Dreissena* populations are believed to be responsible for a dramatic increase in water clarity in Lake Erie (Wright and Mackie, 1990; Greenberg *et al.*, 1992; MacIsaac and Sprules, 1992; Leach, 1993), and would probably do the same for any small lake to which they were successfully introduced. Water clarity, while of uncertain ecological advantage, is enormously attractive aesthetically, and the impact of *Dreissena* on water clarity in Lake Erie has been well-publicized (e.g. Di Vincenzo, Newport News *Daily Press*, Dec. 5, 1991; Walker, 1991; Cohen, 1992; Sisson, 1993). Other reasons to intentionally introduce *Dreissena* could be a desire to increase biodiversity, provide food for other organisms, or to provide a new bait source. If *Dreissena* are used as bait, there is also a risk of recreational fishermen dumping left-over bait into a pond or lake. Many previous introductions of freshwater mollusks are believed to have been carried out by private landowners, intentionally or through carelessness (Carlton, 1993), and *Dreissena* are exceptionally easy to collect and transport. Because *Dreissena* larvae disperse, a small lake that retains and concentrates successive generations may be as much at risk from a single introduction as a large lake.

II. SUSCEPTIBILITY TO INVASION

PHYSIOLOGICAL REQUIREMENTS OF ZEBRA MUSSELS

This section reviews published data on the physiological requirements of *Dreissena* with respect to water quality and chemistry. Four common aspects appear critical to the persistence and reproduction of *Dreissena* populations; temperature, salinity, alkalinity (pH), and calcium content. Table 1 summarizes this information for adults and larvae.

TEMPERATURE

Stanczykowska (1977) stated that adult *Dreissena* began growth at 11-12° C in European lakes, similar to a value of 10-12° C reported by Mackie (1991) for *Dreissena* in the Great Lakes. Bij de Vaate (1989), however, reported that growth of *Dreissena* in the Netherlands occurred at temperatures as low as 6° C, and in a review of European lakes with *Dreissena*, Strayer (1991) reported that the largest populations were in lakes with a mean annual temperature of only 6-9° C, inferring that temperatures exceeded 6-9° C only half of the year. Borcharding (1991), who reported gametic growth at temperatures as low as 2-4° C, suggested that reported differences could be due in part to food quality and quantity for different populations. Differences may also reflect methods of measuring or defining growth. Schneider (1992) predicted that growth rate is strongly affected by temperature, with slower growth rates at low temperatures. The minimum temperature tolerance for survival appears to be just above freezing (Strayer, 1991). Nowhere in the mid-Atlantic region are there temperature regimes cold enough to limit *Dreissena* populations. The maximum temperature that permits growth by adult *Dreissena* has been reported variously as 26-33°C (Stanczykowska, 1977).

Gametogenesis in *Dreissena* has been reported at temperatures as low as 2-4° C in the presence of good food quality (Borcharding, 1991), and spawning is known to occur at 12° C (Sprung, 1987; Bij de Vaate, 1989; Borcharding, 1991) and at 22-23° C (Haag and Garton, 1992). Sprung (1987) reported a loss of sperm motility in *Dreissena* at 26° C, and zygote failure above 24° C. This last evidence indirectly supports predictions by Strayer (1991) that populations of *Dreissena* will be heat-limited in the southernmost regions of North America. Haag and Garton (1992), however, reported that *Dreissena* in Lake Erie spawned during a period of water temperatures above 26°C; the maximum temperature at this time was 30°C. Temperatures as high as 30°C, therefore, may not inhibit reproduction. Strayer (1991), in a review of climatological conditions in Europe, reported that the highest mean monthly temperature tolerated by *Dreissena* was 26.4°C. Optimum larval rearing temperatures in the laboratory were reported to be about 17-18° C by Sprung (1987).

In temperate regions, with seasonal temperature fluctuations, the maximum temperature that permits *Dreissena* reproduction is less important than the temperature tolerance of adults, since there will always be optimal temperature windows at some point of the year for spawning. *Dreissena* tolerates extended periods of temperatures in excess of 25° C, so the majority of the United States and southern Canada are within the temperature tolerance of this species.

SALINITY

Mackie and Kilgour (1992) reported an LC₅₀ of 7.6 salinity at 96 hours for unacclimated adult *Dreissena*, at 19° C. Over a period of 42 days, *Dreissena* which had been slowly acclimated had only 15% mortality at 8.0 salinity at 4° or 10° C. Barber (1992), however, reported 100% mortality within 52 days of adult *Dreissena* in water slowly raised from 0 to 2.7, at 15° C. Wolff (1969) cites an unpublished source stating that *Dreissena* could survive salinities as high as 12.2, although the circumstances of exposure were not given. In the Delta region of the Netherlands, adult *Dreissena* tolerate continual salinity of 4 in ponds, but were not found in estuaries with mean salinities above 0.6, in which salinity fluctuated with tides (Wolff, 1969). Wolff (1969) concluded that the higher mean salinities could be tolerated only if there were not tidally-driven fluctuations.

The apparent difference in reported salinity tolerance in *Dreissena*, between Mackie and Kilgour (1992) and Barber (1992) (above), may reflect a strong interaction of salinity and temperature (with higher tolerance at lower temperatures), or it may reflect physiological differences in the experimental animals. Hebert *et al.* (1989), and Garton and Haag (1991), reported high genetic variability, for an introduced species, among *Dreissena* in the Great Lakes and this may be reflected in variation in physiological tolerances.

Table 1. Physiological Requirements of Zebra Mussels: Summary

Values expressed as ranges; optimums are enclosed in parentheses. References are given in text of Section II.

Adult Survival	0.33°C	0-12ppt	7.0-?	unknown
Adult Growth	6-3°C	0.6ppt (0-0.6ppt)	7.5-?	(34.5-76)
Larval Growth	12-24°C (17-18°C)	Oppt-?	7.4-9.4 (8.4-8.5)	12-106+ (40-?)

When plotting potential spread of *Dreissena* in North America, it is safest to assume that they can tolerate salinities of at least 12.2 for a few days. This would be significant for *Dreissena* fouling slow-moving vessels, such as barges, that are periodically moved between freshwater portions of estuaries. For example, a barge fouled by *Dreissena* in the Susquehanna River, in Pennsylvania or Maryland, could probably be towed to a new anchorage (and a new watershed) in Philadelphia, Pennsylvania, or Alexandria, Virginia, without submitting the *Dreissena* to lethal osmotic stress. On the other hand, only areas with salinity below 1 are likely to maintain high *Dreissena* densities. Walton (1993) found *Dreissena* in salinities as high as 6 in the Hudson river, but high densities ($>1000\text{ m}^{-2}$) were maintained only at a site that never exceeded 3 salinity, and was often fresh.

The salinity tolerances of *Dreissena* spawning adults, eggs, veliger larvae, or planktonic postlarvae, have not been reported. Mann *et al.* (1991), however, in a review of physiological tolerances of oysters of the genus *Crassostrea*, reported that the ranges of salinity tolerances for spawning adults or for larvae were equal to or less than those for adult survival.

pH, CALCIUM, OTHER IONS

pH in North American fresh waters varies depending on rainfall acidity and bedrock composition. Adult *Dreissena* have a heavy periostracum covering all but the oldest, thickest portion of the shell (pers. obs.). The periostracum in freshwater mollusks is thought to aid in prevention of shell dissolution (McMahon, 1991), and *Dreissena* may thus be able to survive periods of relative acidity. The minimum pH tolerance of adult *Dreissena* appears to be 7.0, the point at which shell dissolution exceeds calcium uptake (Vinogradov *et al.*, 1993), but Ramcharan *et al.* (1992), in a literature survey of European lakes, reported that significant populations of *Dreissena* persisted only above a mean pH of 7.5.

Larval development in *Dreissena* appears to be tightly regulated by pH. Sprung (1987) reported *Dreissena* egg survival between only pH 7.4 and 9.4, and optimal survival between pH 8.4 to 8.5, at temperatures of 18-20°C. Even if these values vary among *Dreissena* populations, or with rearing conditions, it appears that at least during the reproductive season, *Dreissena* requires slightly alkaline water.

Calcium, a major component of mollusk shells, appears to be limiting in some cases. Ca^{2+} (from CaCO_3) is expressed either as "hardness" (milliequivalents, or meq), or as mg per liter. European lakes with large populations of *Dreissena* have hardness levels of about 1.73 to 3.16 meq (Strayer, 1991), or a minimum of about $34.5\text{ mg Ca}^{2+}\text{ l}^{-1}$, a

mean of about $45\text{-}52\text{ mg Ca}^{2+}\text{ l}^{-1}$, and a maximum of $76\text{ mg Ca}^{2+}\text{ l}^{-1}$ (Ramcharan *et al.*, 1992). These values should not be considered limits, but only the range for which large populations of *Dreissena* have been recorded in Europe. Actual requirements for adult *Dreissena* have not been determined in the laboratory. Sprung (1987) reported minimum embryo survival at $12\text{ mg Ca}^{2+}\text{ l}^{-1}$, and optimum survival at levels of $40\text{ mg Ca}^{2+}\text{ l}^{-1}$ (2.0 meq) and above. Larvae grew relatively well at calcium levels of 106 mg l^{-1} , the maximum level tested.

Other salts, including MgSO_4 , NaCl , KHCO_3 , NaHCO_3 , and MgCl_2 , do not appear limiting to *Dreissena* embryos (Sprung, 1987). Potassium (KCl) is lethal at levels of about 100 ppm (LC50 for 24 hours) (Fisher and Stromberg, 1992), but concentrations rarely approach this level in natural waters. Ramcharan *et al.* (1992), in a review of European lakes, reported that the mean phosphate (PO_4) level of lakes with stable populations of *Dreissena* is about 0.12 mg l^{-1} , with a maximum level of 0.18 mg l^{-1} and a minimum of 0.05 mg l^{-1} , although *Dreissena* have been reported in lakes with no measurable free phosphate. Phosphorus and nitrogen may have indirect roles on *Dreissena* population growth rates, since they are critical nutrients for freshwater phytoplankton, and thus affect abundance of phytoplankton, the primary food source for *Dreissena*. Ammonia (NH_3) is lethal at a level of about 2 mg l^{-1} (Nichols, 1993), but this level is lethal to many other aquatic organisms as well.

OXYGEN

Sprung (1987), with limited data, concluded that *Dreissena* larvae survived for short periods at oxygen levels as low as 20% of saturation, at 18°C. This oxygen level in natural systems is considered to be a hypoxic condition, and aquatic systems with oxygen levels of 20% for significant periods have problems far worse than zebra mussel infestations. During periods of highest pollution in the 1970s, hypoxia eradicated *Dreissena* from much of the Rhine River in Germany (Neumann *et al.*, 1993). Survival of adults in hypoxia is unknown, but juvenile oysters have been shown to be significantly more tolerant of hypoxia than larvae (Widdows *et al.*, 1989), so adult and juvenile *Dreissena* are probably more tolerant of hypoxia than are larvae. Under anoxic conditions, 100% mortality of *Dreissena* occurs in about 6 days at 17-18°C, and 3 days at 23-24°C (Mikheev, 1968). McMahon and Alexander (1991) concluded that *Dreissena* are poorly adapted for survival at low oxygen levels in warm water (25°C), which indirectly supports Strayer's (1991) predictions of a warm-water limitation to *Dreissena* invasion. In general, however, only severely stressed aquatic systems would have oxygen levels low enough to inhibit *Dreissena* invasions.

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