Literature Review of the Exotic Mussels *Dreissena polymorpha*, *Dreissena bugensis*, *Limnoperna fortunei* and *Mytilopsis leucophaeata*

A Report for the East Bay Municipal Utility District, the San Francisco Public Utilities Commission, and the Santa Clara Valley Water District

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Introduction

This report on the distribution, biological characteristics, ecological requirements and invasion dynamics of four species of mussels that are exotic to the western United States has been prepared for three water agencies in the San Francisco Bay Area: the East Bay Municipal Utility District, the San Francisco Public Utilities Commision, and the Santa Clara Valley Water District. Both peer-reviewed and gray literature were consulted and are summarized in the narratives below.

The word "mussel" has two distinct meanings in malacology. In saltwater systems, mussel refers to bivalves that have a heteromyarian form (described below), with a typically epibenthic or partially epibenthic habit, and that secrete byssal threads as adults which they use in most cases to attach to objects. In contrast, in some parts of the world mussel is used to refer to all freshwater bivalves, regardless of shape, epibenthic or infaunal habit, and presence or lack of byssal threads. In this report mussel is used in the former sense, to refer to heteromyarian bivalves that secrete byssal threads and have an at least partially epibenthic habit.

Generalized Invasive Mussel Life History and Dispersal Mechanisms

Since all four mussels treated in this review—the zebra mussel *Dreissena polymorpha*, the quagga mussel *D. bugensis*, the golden mussel *Limnoperna fortunei* and the dark false mussel, also called Conrad's false mussel, *Mytilopsis leucophaeata*—share some anatomical and life history characteristics and dispersal mechanisms, it will be useful to summarize these at the outset. References are provided mainly in the more detailed descriptions given under each species.

All four mussels are dioecious (that is, there are separate male and female mussels, though a small percentage of hermaphrodites may also occur) broadcast spawners. Abundant sperm and large numbers of eggs (up to millions of eggs by a single spawning female in some of the species) are released into the water column, where fertilization occurs. There is a brief embryonic stage (typically hours to a few days long), followed by a trochophore larval stage (a stage that is worm-like in form) lasting up to a few days, followed by a veliger larval stage (characterized by a ciliated swimming organ called a velum, and the development of a shell), and at the very end of the larval period, a brief pediveliger stage (characterized by the development of a foot). All of these stages are planktonic, that is they drift in the water column with only weak swimming ability relative to typical water currents. The planktonic larval stage usually lasts between one and four weeks, with the stage typically being briefer in warmer and more productive waters. The veliger is initially lecithotrophic (nourished by its internal yolk), and then planktotrophic (feeding on phytoplankton) (see Morton 1973; Siddall 1980; Sprung 1993; Ackerman *et al.* 1994; Darrigran 2002; and the descriptions below for more details on the larval lives of these mussels).

Following the planktonic larval stage, the pediveliger settles to and attaches to the

bottom (where it is called a postveliger or plantigrade mussel) and metamorphoses into a juvenile mussel, characterized by loss of the velum and growth of the siphons, gills, mouth and foot. Later, with the development of gonads, it becomes a sexually mature, adult mussel. Both juvenile and adult mussels are characterized by their use of tough threads, called byssal threads, to attach themselves to substrates, and by possession of a heteromyarian form, that is with the anterior adductor muscle much smaller than the posterior adductor muscle, and with the anterior portion of the shell narrowed conically, so that the lateral outline of the shell is roughly triangular with the most acute angle at the anterior end (Yonge & Campbell 1968; Morton 1970, 1973, 1979, 1993; Yonge 1976). In contrast most bivalves that live buried in sediment are isomyarian, with the anterior and posterior adductor muscles roughtly equal in size, while oysters and scallops are monomyarian, with the anterior adductor mussel absent and the posterior adductor mussel correspondingly enlarged. In both these cases, the shell is roughly symmetrical relative to a plane perpendicular to the hinge, while mussel shells are not.

All four mussels are epibenthic, that is they are typically not even partially buried in sediments. The juvenile and adult mussels attach to hard surfaces (though sometimes these may be as small as sand grains, or as soft as compacted silt-clay) by a set of a byssal threads. Both juveniles and adults can release these threads, relocate and reattach in a new location, but this is apparently more common in younger mussels (Yonge & Campbell 1968; Koch 1989; Iwasaki 1997. Some seasonal depth migration, migration between substrate types or depths at different ages, or migration in response to changes in current velocities may occur regularly.

In freshwater systems, rapid downstream dispersal can result from currents carrying drifting larvae, carrying juveniles or adults attached to floating vegetation or debris (wood, styrofoam, plastic, detached floats or buoys, etc.), carrying juveniles resuspended by turbulence, or in at least some of the species, carrying juveniles hanging from byssal threads used as drag lines (Martel 1993; Carlton 1993). However, under natural conditions, significant upstream dispersal in fresh waters outside of tidal areas and dispersal overland between freshwater drainages is challenging. Upstream dispersal over very short distances may occur by crawling mussels (up to 7 cm/night; Ackerman *et al.* 1994), by larval or older mussels carried upstream in eddy currents, or by adults or juveniles attached to floating objects blown upstream by the wind against weak downstream currents. Mussels may also be transported upstream if they attach to the hard parts of live mobile aquatic animals (*e.g.* crayfish, or possibly turtles); if they attach to objects that are transported by animals (*e.g.* sticks carried by beavers); if they are consumed and later defecated or regurgitated whole and alive by aquatic animals (e.g. fish, turtles, otter, beaver, muskrat, etc.), birds or terrestrial mammals; or if they adhere to or are entangled in the skin, feathers or fur of birds or terrestrial mammals (Carlton 1993; Johnson & Carlton 1996). Some of these mechanisms could also account for short distance transport between drainages, including attachment to turtles, attachment to sticks carried by beaversor nest-building birds, adherance or entanglement and transport by birds or terrestrial animals, and consumption and live deposition by birds or terrestrial animals (Carlton 1993; Johnson & Carlton 1996). Carlton (1993)) discusses a number of additional, but apparently less likely, scenarios

for moving mussels between water bodies (*e.g.* transport by tornados; the capture, transport and subsequent dropping of a mussel-eating fish by a fish-eating bird; a mussel eating bird attacked and torn apart by bird of prey). Only transport by migratory birds appears to be even theoretically capable of transporting mussels long distances between drainages; evidence that this in fact occurs, however, is lacking (Carlton 1993; Johnson & Carlton 1996).

All four mussels may be transported by a variety of anthropogenic vectors, which have been described in the greatest detail for zebra mussels (*e.g.* Carlton 1993). Most or all of these mussels have been transported across oceans or along sea coasts in ballast water; and for *Mytilopsis leucophaeata*, possibly attached to vessel hulls (Hebert *et al.* 1989; Griffiths *et al.* 1991; Oliver *et al.* 1998; Darrigran & Ezcurra de Drago 2000; Souza *et al.* 2005; Laine *et al.* 2006). Transport of mussels attached to anchors or anchor chains has also been suggested, but seems less likely (Carlton 1993; McMahon 1996). Transport in timber shipments, presumably on logs that had been rafted down or held in rivers, was reportedly an important mechanisms for spreading zebra mussels in Europe (Van der Velde 2002). *Limnoperna fortunei* may have been accidentally transported across seas or oceans attached to live freshwater clams carried for food (Kimura and Tabe 1997; and see below in the section on this mussel's dispersal). Transport in ballast water or hull fouling may also have helped spread zebra and quagga mussels through the Great Lakes. In Europe and eastern North America, commercial barge and other vessel traffic has helped to spread attached zebra and quagga mussels both downstream and upstream, and via canals, between watersheds (Stanczykowska & Lewandowski 1993; Johnson & Padilla 1996; Mills *et al.* 1996; Karatayev *et al.* 1997). Commercial vessel traffic has probably also spread *Limnoperna fortunei* upstream through the Rio Plata watershed in Argentina, Paraguay and Brazil (Darrigran 2002; Karatayev *et al.* 2007b). Recreational vessels also transport mussels through waterways; in addition to the hull, attachment sites include the "inside of outboard and inboard motor systems, outdrive units, trim tabs and plates, hydraulic cylinders, trolling plates, prop guards and transducers; pumping systems (including waste and bilge); anchors and hausepipes; and on rudders, propellors, shafts, and centerboards" (Carlton 1993).

Over the last several decades, the overland transport of recreational and other boats on trailers has become a major mechanism for moving zebra and quagga mussels between watersheds both in North America (Griffiths *et al.* 1991) and Europe (Walz 1989). In the former Soviet Union transport on the boats or equipment of the subsidized inland fishing industry was more important than transport on recreational boats (Karatayev *et al.* 2007b). The mussels travel as adults attached to boat hulls or anchors, on vegetation snagged on anchors or trailers, or as larvae in transported water (Johnson & Carlton 1996). One study in Michigan found zebra or quagga mussel veligers in most of the water samples taken from boating and fishing equipment including live wells, bait buckets, bilge water and engine water, sometimes in concentrations over 25 veligers/liter (Johnson & Carlton 1993); and found that snagged vegetation and live wells were the most frequent mechanisms transporting mussels (Johnson & Carlton 1996). Zebra mussel larvae have been found to survive up to at

least 8 days in live wells (Johnson & Padilla 1996). However, overland introductions between unconnected water bodies are rare compared to the rapid dispersal that often occurs within connected waters (Johnson & Carlton 1996; Johnson & Padilla 1996).

Zebra mussels, quagga mussels and *L. fortunei* have been transported substantial distances in raw water aqueduct systems (Morton 1973, 1975; Lvova 2004). Mussel larvae can also be inadvertently transported in the water used to transport fish or aquatic plants. For example, at least one commercial baitfish dealer transports fish to California from the Oklahoma River, which has zebra mussels (J. Janik pers. comm. 1997), and the three largest dealers of plants for aquariums and ornamental ponds are based in Ohio, where zebra mussels are common (S.J. Nichols pers. comm. 1997). Zebra mussels apparently were accidentally introduced into some water bodies in the former Soviet Union with fish transplants, and in some cases were deliberately planted in new waters to provide food for fish or to improve water quality (Karatayev *et al.* 2007b). In the Netherlands, zebra mussels were introduced into two small ponds as an experiment in the control of eutrophication (Reeders *et al.* 1993), and in the U.S., scuba divers have apparently introduced zebra mussels into a few quarry ponds to improve water clarity. Other potential mechanisms include the transfer of mussels on construction, research, fishing or other equipment moved between water bodies; the accidental transport of mussel larvae on divers' wet suits (Johnson & Padilla 1996); the transport of mussel larvae in the water in bait buckets, of adult mussels attached to crayfish used as bait, and of the mussels themselves used as bait (Carlton 1993); the transport of larvae in water used for fire fighting; the release of adults or larvae from aquariums; and so forth (Carlton 1993).

Background Comments on Some Environmental Parameters

Salinity, Chlorinity, Conductance and Total Dissolved Solids

Salinity was traditionally defined as the sum of all noncarbonate salts in solution, and usually expressed in parts per thousand (ppt) in marine and estuarine waters and in mg/l in fresh waters where concentrations are generally much lower. Sodium and chloride make up about 91% of all salt ions in sea water, but usually constitute a smaller portion of the salt in fresh water, where calcium is often the dominant salt ion. Wetzel (1975) suggested that the salinity of fresh waters is best expressed as the sum of the eight major ions, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, HCO_3^{-}, CO_3^{2-}, SO_4^{2-} and Cl^{-}. The *Practical Salinity Scale of 1978* formally redefined salinity based on the ratio of the specific conductance of a sample to the specific conductance of a standard potassium chloride solution at 15°C and standard atmospheric pressure, with a ratio of 1 yielding a salinity of 35 practical salinity units (psu). For most practical environmental purposes, salinity reported in psu by the new definition is essentially the same as salinity reported in ppt by the older definition.

Since the salt ions in sea water are generally present in constant ratios, salinity can theoretically be calculated from measurements of the concentration of any single ion,

though errors will be minimized by using one of the more abundant ions. This has often been done using chloride, the most abundant anion in sea water. Salinity in seawater (in ppt) is approximately equal to 0.0018 times the chlorinity or chloride concentration (in mg/l) (Sverdrup *et al.* 1942). Chloride generally makes up a much smaller part of the ionic composition of inland fresh waters than of sea water, and across a variety of fresh waters salinity (in ppt) is usually between 0.005 and 0.03 times chlorinity (in mg/l)[1].

Electrical conductance is the ability of a particular body to conduct an electrical current. It is the inverse of resistance. "Specific conductance" is the conductance of a body of unit length and unit cross-section, and for a solution is calculated as the product of the measured conductance and the electrode cell constant d/A, where A = the area of the electrodes and d = the distance between them. The specific conductance of a solution increases with its temperature; most meters with fixed temperature compensation that are used for aquatic measurements assume about a 2% increase in specific conductance with each 1°C increase in temperature.

Conductance is measured in Siemens (S) (equivalent to an older unit, the mho), and for aquatic measurements is usually reported in µS. The corresponding specific conductance is usually calculated as µS/cm normalized to 25°C, though it is sometimes reported in shorthand as µS (thus compounding the common confusion between conductance and specific conductance).[2] Since ions in a solution increase its capacity to conduct electricity, the specific conductance of a water sample is an indirect measure of the concentration of inorganic dissolved solids it contains, including calcium, iron, magnesium, sodium, chloride, nitrate, sulfate and phosphate. As noted above, salinity is now defined in terms of specific conductance, and salinity can be derived from specific conductance values by various formulae (*e.g.* Schemel 2001) or internet calculators (e.g. http://gaea.es.flinders.edu.au/~mattom/Utilities/salcon.html). Table 1 shows the specific conductance values (calculated at two temperatures) for a range of salinity values.

Table 1. Relationship between salinity and specific conductance.

Salinity (ppt)	Specific Conductance (µS/cm) at 15°C	at 25°C
0.5	800	1,000
1.0	1,600	2,000
2.0	3,000	3,800
3.0	4,500	5,600
4.0	5,900	7,300

[1] Calculated from data on the ionic composition of various surface waters given in Sverdrup *et al.* 1942, Cole 1975, Wetzel 1975 and Goldman & Horne 1983.

[2] Although it is often stated that specific conductance is conductance normalized to 25°C, this is incorrect; "specific" refers to the electrode cell geometry rather than the temperature (Schemel 2001). A further source of confusion is that the term conductivity is often used as a synonym for specific conductance (*e.g.* America Society for Testing and Materials 1964), but sometimes is used as a synonym for conductance.

5.0	7,200	9,000
6.0	8,500	10,600
7.0	9,800	12,300
8.0	11,100	13,800
9.0	12,400	15,500
10.0	13,700	17,000

The specific conductance of the water in a water body can be raised by rocks or sediments in the watershed containing calcareous minerals (and is generally lower in drainages containing quartz-rich granite or other igneous rocks), mine drainage (which can contribute iron, sulfate, copper, cadmium or arsenic), agricultural runoff (which can contain high concentrations of phosphate and nitrate) and road runoff (which can contain ions from automobile fluids, break linings, and in some areas, sodium and magnesium salts used for deicing) (Murphy & Waterman 2000).

Total Dissolved Solids (TDS) are defined as the material left after a water sample is passed through a filter (usually a 0.45 micron filter), evaporated and dried, and includes both organic and inorganic ions. It is thus related to, though not the same as salinity. In some waters there is a consistent linear relation between TDS and specific conductance, and TDS (in mg/l) can often be estimated by multiplying specific conductance (in µS/cm) by a factor between 0.55 and 0.75. The factors that increase conductance also increase TDS, which is additionally raised by sources of dissolved organic particles including marsh drainage and forest soil erosion. Water with high TDS is often hard (see hardness, below) (Hem 1996); Murphy & Waterman 2000).

Temperature

During the summer, heat from the sun can produce a warmer and therefore lighter layer of water at the surface of a deep lake or reservoir, which floats on the colder and denser water below. In a typical thermally-stratified water body the upper layer of water, called the epilimnion, is relatively well-mixed and has a relatively uniform warm temperature; below that is a layer called the thermocline where the temperature declines rapidly with depth; and below the thermocline is a cold and often large bottom layer called the hypolimnion where the temperature declines slowly with depth. Then, as the atmosphere cools in the late fall or winter, the surface layer of water is cooled, the thermal stratification breaks up and the water body "overturns." The surface and deep waters mix so that the temperature is uniform throughout the water column (Cole 1975; Wetzel 1975; Goldman & Horne 1983; Hem 1985).

In southern regions where summer surface waters can become too warm for some mussel species, cooler hypolimnetic water in a lake or reservoir may provide a seasonal refuge. However, these hypolimnetic waters may also become depleted in oxygen (see below). Whether a particular water body provides sufficiently cool yet sufficiently oxygenated water at some depth to serve as such a refuge will depend its specific limnological characteristics.

Dissolved Oxygen

Dissolved oxygen is reported either as a concentration (mg/l) or as percent saturation, that is, the percentage of the maximum concentration of oxygen that can be dissolved in water at a specific temperature, in the absence of other factors. Saturation concentrations are higher in colder water. Unpolluted surface waters and fast-running waters are usually saturated with oxygen, because of diffusion of oxygen into the water from the air. Deeper, stagnant or slow moving waters can be lower in dissolved oxygen due to various factors. Photosynthesis releases oxygen into the water and respiration removes oxygen from the water, so if phytoplankton and submerged vegetation are abundant, oxygen levels can reach supersaturation during the day (when sunlight promotes photosynthesis) and decline at night (due to plants' respiration). The decomposition of algae and organic waste uses up oxygen, some inorganic wastes also deplete oxygen, and groundwater entering surface waters through springs may be low low in oxygen.

In deep lakes and reservoirs, the development of a thermocline during the warm part of the year insulates the deeper hypolimnion from direct contact with atmospheric oxygen. This can lead to declining levels of oxygen in the hypolimnion due to biological decomposition or pollution, sometimes approaching or reaching anoxic levels. The epilimnion retains higher levels of oxygen due to replenishment through contact with the atmosphere. With the turnover of water that accompanies cooler weather in the late fall or winter, oxygen is again mixed throughout the water column (Hem 1995; Murphy & Waterman 2000).

In general then, lower levels of oxygen may be found in the deeper waters of eutrophic or polluted lakes or ponds during the warmer months when a thermocline has developed, while surface waters, running waters, and oligotrophic, unpolluted waters will typically have higher oxygen concentrations.

Calcium, Alkalinity and Hardness

Calcium occurs in solution in fresh water as the free ion (Ca^{++}), as calcium carbonate ($CaCO_3$) and in colloidal complex with sediments and organic matter. Standard analytical methods define "dissolved calcium" as the calcium measured in a sample after filtration through a 0.45 µm membrane filter, and "total calcium" as the calcium measured in an unfiltered sample after vigorous digestion (US EPA 1983; Eaton *et al.* 1995). In practice these measurements are likely to be similar unless total calcium levels are quite high, and in some cases the same data have been reported both as dissolved and as total calcium[3] (E. Pederson pers. comm. 1998; J. Kirschner pers. comm. 1998). Calcium concentrations are sometimes expressed as calcium hardness as $CaCO_3$ (with 1 mg/l of calcium = 2.497 mg/l of calcium hardness as $CaCO_3$) (Johnson *et al.* 2000).

[3] For example, we found several examples in the US EPA's STORET database of the same measurements reported as dissolved calcium by one agency and as total calcium by another agency.

Alkalinity is a measure of a solution's acid neutralizing capacity, and is equal to the stoichiometric sum of the bases in solution.[4] In the natural environment carbonate alkalinity usually accounts for most of the alkalinity, and since the dissolution of rocks containing carbonate minerals such as calcite and aragonite (calcium carbonate $CaCO_3$), dolomite (calcium magnesium carbonate $CaMg(CO_3)_2$) and magnesite (magnesium carbonate $MgCO_3$) is the source of much natural carbonate alkalinity, alkalinity is strongly related to the concentrations of calcium and magnesium (Hem 1995); Murphy & Waterman 2000). Alkalinity in fresh water is usually expressed in units of mg/l of $CaCO_3$ (*i.e.* the concentration of $CaCO_3$ that would produce an equivalent alkalinity), or as microequivalents per liter (µeq/l).[5]

Hardness is a characteristic of water caused by the salts of calcium, magnesium, iron or other multivalent cations (ions with a charge greater than +1) that causes curdling of soap and the formation of scale. Total hardness is defined as the sum of the multivalent cations in solution. Calcium and magnesium are the most common multivalent cations, resulting from the dissolution of rocks containing calcium and magnesium carbonate minerals (primarily limestone, chalk and dolomite) or calcium sulfate minerals (*e.g.* gypsum $CaS0_4(2H_2O)$ and anhydrite $CaSO_4$). Calcium and magnesium usually account for most of total hardness, with calcium on average contributing about two-thirds and magnesium contributing about one-third. Iron, manganese and other ions usually contribute only minor amounts (Cole 1975; Murphy & Waterman 2000; Johnson *et al*. 2000). Total hardness in fresh water is usually expressed in units of mg/l of $CaCO_3$, or sometimes as grains per gallon (1 grain/gallon = 17.12 mg/l of $CaCO_3$). Although the concept of hardness is in almost universal use in the analysis of fresh surface waters, the property of hardness is difficult to define and several different systems for categorizing hardness are in common use (Hem 1985). Table 2 shows some of the classification systems found in publications and on websites.

Correlations between calcium, alkalinity and total hardness are to be expected among water bodies with similar types of water chemistry (Cole 1975). Baker *et al.* (1990, cited in Whittier et al. 1995), Whittier *et al.* (1995) and Kozlowski *et al.* (2002) reported linear relationships between calcium and alkalinity in fresh surface waters, and Claudi and Mackie (1994) and Hincks and Mackie (1997) reported correlations between calcium, alkalinity and total hardness (Figure 1, Table 3). However, the regressions reported by them or derived from their data differ (Table 3), so different correlations may apply to different regions. In Alabama and Mississippi, Boyd and Walley (1975) found good nonlinear correlations between calcium, alkalinity and total hardness in most physiographic regions, but the regressions differed between regions and between

[4] Mainly bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}) ions, except in waters with pH>9.5 or with unusual chemical compositions. MInor contributors can include hydroxide ions (OH^-), borates, silicates, phosphates, nitrate, ammonium, sulfides and organic ligands (Hem 1995); Murphy & Waterman 2000; Johnson *et al*. 2000).

[5] More formally called "microequivalent weight." The equivalent weight—also called the combining weight—of a compound is its formula weight divided by the charge of its ionic form. Thus one µeq/l of alkalinity ≈ 100 µg ÷ 2 = 0.05 mg/l of alkalinity as $CaCO_3$ (Hem 1985).

ponds and streams. On the other hand, there is a strong linear relation between the means for calcium and total hardness, and a weaker correlation with alkalinity, across regions, ponds and streams in these states (Figure 2), and a strong linear relation between the means for calcium and total hardness across a selection of rivers in the US (Table 3, Figure 3).

Calcium concentration, alkalinity and hardness all tend to be higher in drainages with calcareous rocks and sediments and lower in drainages with igneous rocks (Murphy & Waterman 2000). Mine drainage and industrial and municipal wastewater effluent can raise calcium and magnesium concentrations and hardness, and municipal wastewater effluent can raise the alkalinity (Murphy & Waterman 2000). Mellina and Rasmussen (1994, citing Wetzel 1975) note that significant seasonal fluctuations in calcium tend to occur in hardwater systems, while fluctuations are minor in softwater systems.

Table 2. Examples of different hardness classification systems reported in publications and on the internet. Hardness ranges are in mg/l of CaO_3.

	Reference						
Hardness Category	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Very soft	–	–	–	–	–	–	0-70
Soft	0-20	0-50	0-17.1	0-60	0-75	0-50	70-140
Moderately soft	20-40	–	–	–	–	50-100	–
Slightly or medium hard	–	–	17.1-60	–	–	100-150	140-210
Moderately or fairly or somewhat hard	40-80	50-100	60-120	60-120	75-150	150-200	210-320
Hard	80-120	100-150	120-180	120-180	150-300	200-300	320-530
Very Hard	>120	>150	>180	>180	>300	>300	–

Ref. 1: Johnson *et al.* 2000.

Ref. 2: http://www.des.state.nh.us/factsheets/ws/ws-3-6.htm (used by the water conditioning industry).

Ref. 3: http://www.water-research.net/hardness.htm (system used by U.S. Department of the Interior and the Water Quality Association); http://www.ext.vt.edu/pubs/housing/356-490/356-490.html; http://www.fcwa.org/water/hardness.htm; http://www.lanfaxlabs.com.au/hardness.htm.

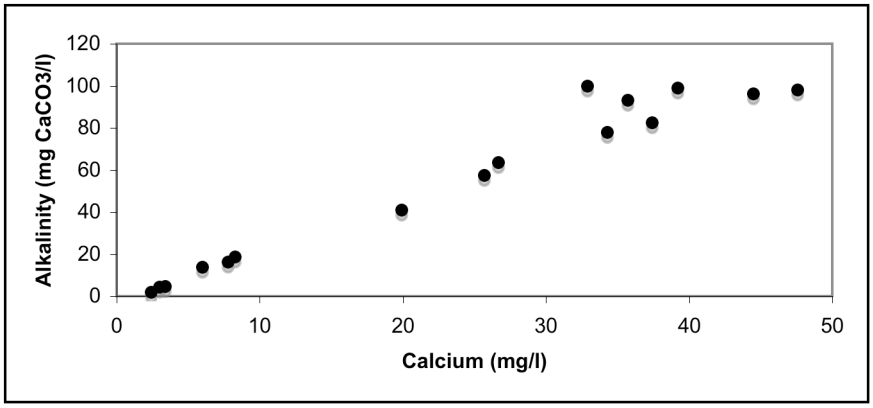
Ref. 4: Dufor & Becker 1964; Briggs & Ficke 1977; Hem 1995; Murphy & Waterman 2000; http://capp.water.usgs.gov/GIP/gw_gip/quality.html.

Ref. 5: http://kywater.org/ww/ramp/rmhard.htm; http://www.ext.colostate.edu/pubs/crops/00513.html; http://www.des.state.nh.us/factsheets/ws/ws-3-6.htm (used by sanitary engineers).

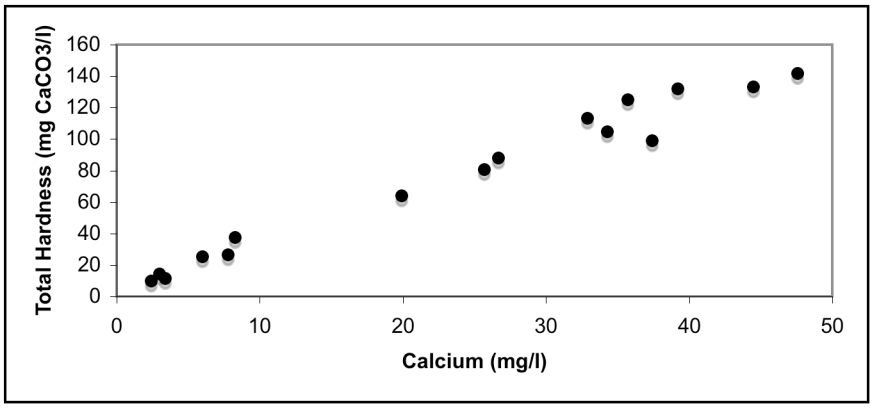
Ref. 6: http://en.wikipedia.org/wiki/Hard_water (converted from mg/l of Ca).

Ref. 7: http://www.thekrib.com/Plants/CO2/khgh.html.

Figure 1. Relationships between mean calcium concentration and mean alkalinity and total hardness for 16 Ontario lakes. Data from Hincks & Mackie 1997, graphed and analyzed here.



r^2=0.956



r^2=0.976

Table 3. Estimated relationships of calcium to alkalinity (in µeq/l) or total hardness (in mg $CaCO_3$/l). The relationships shown between calcium and total hardness may not be valid in very hard water (>200 mg/l of hardness as $CaCO_3$), where the ratio of calcium to magnesium may vary greatly (Claudi & Mackie 1994).

Formula for Calcium (in mg/l)	r^2	Basis	Reference
= -2.75 + 0.0162 x Alkalinity[a]	0.561	8 southeastern US regions	Boyd & Walley 1975
= 0.0002 + 0.0143 x Alkalinity		2,500-3,950 Ontario lakes	Claudi & Mackie 1994
= 0.8 + 0.0176 x Alkalinity[b]	0.95	344 northeastern US lakes	Whittier *et al.* 1995
= 0.587 + 0.0211 x Alkalinity[c]	0.956	16 Ontario lakes	Hincks & Mackie 1997
= -4.54 + 0.0244 x Alkalinity[d]	0.638	18 South Carolina lakes	Kozlowski *et al.* 2002
= -2.38 + 0.346 x Total Hardness[e]	0.894	8 southeastern US regions	Boyd & Walley 1975
= 1.08 + 0.272 x Total Hardness		2,500-3,950 Ontario lakes	Claudi & Mackie 1994
= -2.01 + 0.337 x Total Hardness[c]	0.976	16 Ontario lakes	Hincks & Mackie 1997
= -0.247 + 0.273 x Total Hardness[e]	0.990	10 US rivers	Johnson *et al*. 2000
= 0.267 x Total Hardness[f]			Johnson *et al*. 2000

[a] Linear regressions on data in Boyd & Walley 1975, Table 1.

[b] Derived from line drawn by hand through graphed data points in Whittier *et al.* 1995, Fig. 2a.

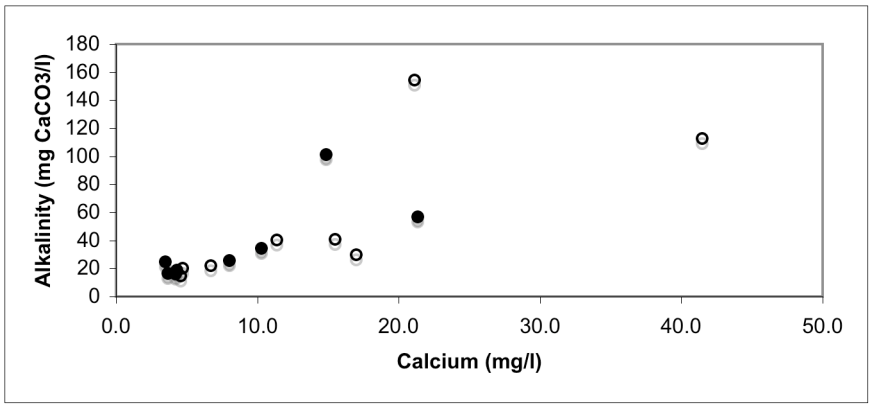
[c] Linear regressions on data in Hincks & Mackie 1997, Table 1.

[d] Derived from regression line in Kozlowski *et al.* 2002, Fig. 6, back-calculated from estimated calcium to measured alkalinity with the equation given on Kozlowski *et al.* 2002, page 4.

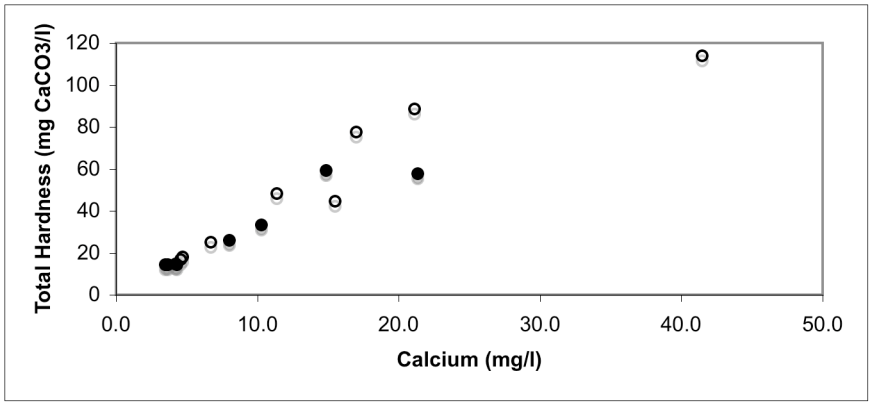
[e] Linear regressions on data in Johnson *et al.* 2000, Table 1, page 13-2.

[f] Derived from assumption that 2/3 of hardness is contributed by calcium and 1/3 by magnesium.

Figure 2. Relationships between mean calcium concentration and mean alkalinity and total hardness for 8 physiographic regions in Alabama and Mississippi. Data from Boyd and Walley 1975, graphed and analyzed here. Filled circles are ponds, open circles are streams.

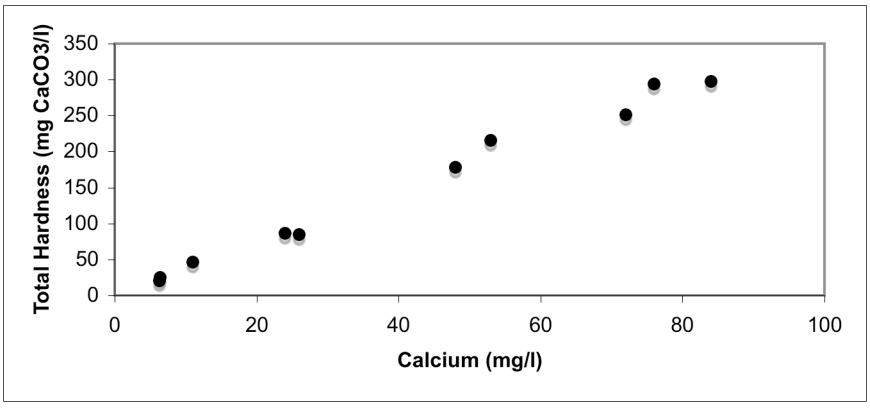


r^2=0.561



r^2=0.894

Figure 3. Relationship between mean calcium concentration and mean total hardness for 10 major rivers in the continental United States. Data from Johnson *et al.* 2000, graphed and analyzed here.



r^2=0.990

pH

The parameter pH expresses the hydrogen ion concentration in water on a negative base-10 logarithm scale (*i.e.* each unit increase in pH represents a 10-fold reduction in hydrogen ion concentration), with 7 being neutral, values less than 7 being acidic, and values greater than 7 being basic. The pH of most natural waters is typically between 6 and 9, but pH may be lowered significantly by acid precipitation or mine drainage. Other influences include unpolluted rain (which can be as acidic as 5.6 due to absorption of CO_2 from the atmosphere, which dissolves to form a weak acid), photosynthesis and respiration by aquatic plants (respectively uptaking and releasing CO_2 in the water, thereby raising and lowering pH), rocks or soil in the watershed that contain carbonate minerals (which raise the pH) or sulfide minerals (which lower the pH), and drainage from marshes or forests (which can contain organic acids from decaying vegetation) (Hem 1995; Murphy & Waterman 2000).

General Patterns of Variation

Spartial and temporal variation in environmental parameters can complicate assessments of the suitability of waters for mussel colonization. However an understanding of recognized patterns of variation can help us to avoid misreadings of the data.

Water temperature varies in a roughly predictable way with season, latitude and elevation. In very shallow waters there may also be signficant diurnal variation. As discussed above, substantial variation with depth may also occur in lakes or reservoirs that stratify during the warmer months. Spring-fed waters and rivers that receive water from the hypolimnion of a stratified water body may be markedly cooler than regional temperature patterns would suggest.

Constituents or characteristics of water that derive in large part from soils or rocks tend to be present at lower concentrations during high flow periods than in low flow periods. Oxygen concentrations, pH and some other chemical characteristics can vary diurnally and seasonally with photosynthetic activity, and with depth in thermally stratified waters. For ions affected by oxidation and reduction, the reduced species are often present at higher concentrations in deeper stratified waters (Hem 1985).

Some of the greatest spatial and temporal variation within water bodies can occur in waters that receive inflows from two chemically distinct sources. Thus the St. Lawrence River receives high calcium water from its headwaters in Lake Ontario, and low calcium water from the Ottawa River which enters the St. Lawrence just upstream of Montreal. For 180 km below the junction, the softer Ottawa River water flows along the north shore of the St. Lawrence, while the harder Lake Ontario water flows along the south shore (Mellina & Rasmussen 1994). Another striking example is the Susquehanna River at Harrisburg, PA. The eastern side of the river receives acidic, high sulfate drainage from a large anthracite-mining region, while the western tributaries carry relatively alkaline, low-sulfate water, and several aspects of the river's chemistry vary accordingly

from bank to bank (Hem 1985). This sort of situation can also produce substantial temporal variation, if the flows from chemically distinct sources vary out of synchrony with each other. Similarly, local variations in chemistry can occur where wastewater effluent, urban runoff or springs enter larger water bodies.

Dreissena polymorpha

Life History

Gametogenesis generally begins in the fall or winter, with spawning (release of eggs) starting in the spring when water temperatures rise above 12°C, although most spawning occurs above 17-18°C (Mackie *et al.* 1989; Sprung 1993; Mackie & Schloesser 1996; Nichols 1996; McMahon 1996). The seasonal timing of gametogenesis and spawning can vary greatly in different locations and years. A histological and biochemical analysis of zebra mussels from an Erie Canal site in 1992 found that gamete synthesis peaked in May, gametes matured in June and July, and spawning began in August (Wang *et al.* 1993). In the following year, when mussels overwintered in better condition, DNA concentrations increased more slowly through the spring and peaked later (Wang *et al.* 1994). The spawning period can be prolonged, continuing in pulses through late summer or early fall.

Eggs and sperm are released into the water column where fertilization occurs, with a single spawning female capable of releasing tens of thousands to millions of eggs (Mackie *et al.* 1989; Sprung 1993; Mackie & Schloesser 1996; Nichols 1996). The embryos develop into swimming trochophore larvae in 6 to 96 hours after fertilization (Mackie *et al.* 1989; Sprung 1993; Ackerman *et al.* 1994). After a lecithotrophic phase which last up to 2-9 days after fertilization, the larvae develop intestines and a feeding and swimming organ known as the velum, beginning the planktotrophic phase (Table 4). By this time they will also have developed D-shaped (straight-hinged) shells about 70-100 µm long (Sprung 1993; Ackerman *et al.* 1994). Once the velum appears the larvae are called veligers, and they develop progressively through the D-shell stage, a veliconcha stage with a more rounded and ornamented shell (also called the umbonal stage), and a pediveliger stage with the initial development of a foot (Mackie *et al.* 1989; Sprung 1993; Ackerman *et al.* 1994; Mackie & Schloesser 1996). Embryonic and larval development times are usually longer in colder water and with poorer food availability. Larvae produced in the fall may sometimes overwinter as larvae, delaying development for several months (Nichols 1996; McMahon 1996). Larval growth rates ranging from 1 to 24 µm per day have been measured in the laboratory or estimated from field data (Mackie *et al.* 1989; Sprung 1993; Neumann *et al.* 1993; Ackerman *et al.* 1994; Mackie & Schloesser 1996; Nichols 1996).

Table 4. Estimated planktonic periods for zebra mussel eggs, embryos and larvae. For some studies, the periods' initial and end points have been inferred from the context.

Phase	Temperature	Duration	Reference
Spawning to fertilization	24°C 12°C	≤ 2.5 hr ≤ 5 hr	Sprung 1993 (delay in fertilization while retaining 50% of initial success)
Fertilization to swimming larva	24°C 12°C	6 hr 20 hr	Sprung 1993; Sprung 1989, cited in Ackerman *et al.* 1994
	20-24°C	48-72 hr	Nichols unpubl., cited in Ackerman *et al.* 1994
	17-24°C	48-96 hr	Leitch & McLeod 1993, cited in Ackerman *et al.* 1994
	17-24°C	6-96 hr	Ackerman *et al.* 1994 (based on review)
Fertilization to D-shell	24°C 21°C 18°C 15°C 12°C	1.3 d 1.5 d 1.9 d 3.2 d 3.8 d	Sprung 1987, 1993; Sprung 1989, cited in Ackerman *et al.* 1994
	20-24°C	3-5 d	Nichols unpubl., cited in Ackerman *et al.* 1994
	17-24°C	7-9 d	Leitch & McLeod 1993, cited in Ackerman *et al.* 1994
	17-24°C	2-9 d	Ackerman *et al.* 1994 (based on review)
Fertilization to veliconcha	?	8-10 d	Stoeckel & Garton 1993
	17-24°C	7-9 d	Leitch & McLeod 1993, cited in Ackerman *et al.* 1994
	20-24°C	8 d	Nichols unpubl., cited in Ackerman *et al.* 1994
	17-24°C	7-9 d	Ackerman *et al.* 1994 (based on review)
Fertilization to pediveliger	20-24°C	10 d	Nichols unpubl., cited in Ackerman *et al.* 1994
	17-24°C	10 d	Ackerman *et al.* 1994 (based on review)
Fertilization to settlement	22°C	21 d	Vanderploeg *et al.* 1994
	20-24°C	35 d	Nichols unpubl., cited in Ackerman *et al.* 1994
	20°C	18-37 d	Sprung 1989, cited in Ackerman *et al.* 1994
	?	90 d	Morton 1969 cited in Ackerman *et al.* 1994
	17-24°C	18-90 d	Ackerman *et al.* 1994 (based on review)
D-shell through veliconcha	≈ 16-24°C	23-27d	De Lafontaine & Cusson 1997 (based on period of occurrence in the Richelieu River)
D-shell to settlement	18-21°C	17 d	Borcherding & van Steveninck 1992 (estimated from growth rates in the Rhine River)
	≈ 21°C	14-21 d	Baldwin 1994
	21°C 14°C	30 d 100 d	Sprung 1993 (estimated from growth rates)
"Planktonic phase"	?	≈ 8 d	Korschelt 1892
	?	8 d	Katchanova 1961, cited in Sprung 1993
	?	usu. 8-10 d	Mackie *et al.* 1989, citing various authors
	?	10 d	Lewandowski 1982, cited in Garton & Haag 1993

?	8-12 d	Hillbricht-Ilkowska & Stanczykowska 1969, cited in Neumann *et al.* 1993
?	≥ 14 d	Neumann *et al.* 1993
?	5-16 d	Griffiths *et al.* 1991, citing Kornobis 1977, Stanczykowska 1977 and Lewandowski 1982
?	12-16 d	Kirpichenko 1964, cited in Mackie *et al.* 1989 and in Nichols 1996
?	21 d	Nichols 1993, cited in Nichols 1996
≈16-24°C	20-25 d	Cusson & De Lafontaine 1997 (in the Richelieu River)
?	5-26 d	Shevtsova 1968, cited in Sprung 1993
16-24°C 15-20°C	18 d 28 d	Neumann *et al.* 1993, based on data from Sprung 1987,1989
20°C ?	18-33 d	Sprung 1989, cited in Sprung 1993
?	≈ 35 d	Walz 1973, 1975, 1978, cited in Sprung 1993, Ackerman *et al.* 1994 and Nichols 1996
?	3-90 d	Nichols 1993, citing Stanczykowska 1977, Sprung 1987 and Mackie *et al.* 1989
over winter	180 d	Nichols & Kovalak 1995, cited in Nichols 1996
over winter	240 d	Kirpichenko 1964, cited in Nichols 1996

Veligers settle to the bottom after 1-4 weeks of growth, or sometimes substantially longer (Table 4), typically at shell lengths of around 200-240 µm (Mackie *et al.* 1989; Sprung 1993; Ackerman *et al.* 1994; Mackie & Schloesser 1996). The settled larvae, called postveliger or plantigrade mussels, attach by byssal threads to rocks, shells or submersed plants, though they sometimes attach directly to sand grains (Mellina & Rasmussen 1994; Nichols 1996; Berkman *et al.* 1998). They then metamorphose into juveniles by losing the velum and forming, enlarging and reorienting the characteristic adult body structures, including siphons, gills, a mouth, a larger foot, and a more rhomboidal shell (Ackerman *et al.* 1994; Nichols 1996). Zebra mussels reach sexual maturity at 1-2 years and shell lengths of 5-12 mm (Mackie *et al.* 1989; Smirnova & Vinogradov 1990; Mackie & Schloesser 1996; Nichols 1996). They live for 2-9 years, attaining maximum shell lengths of over 40 mm (Mackie *et al.* 1989; Smirnova & Vinogradov 1990; Mackie 1993; Mackie & Schloesser 1996).

Though primarily sedentary, zebra mussels, especially juveniles, may release their byssal threads and move to new attachment sites (Korschelt 1892; Oldham 1930; Martel 1993; Ackerman *et al.* 1994; Mackie & Schloesser 1996). Zebra mussels have been reported to migrate between shallower water in the summer and deeper water in the winter (Korschelt 1892; Mackie *et al.* 1989; Mackie & Schloesser 1996). Juveniles and adults may move short distances by crawling (Korschelt 1892; Oldham 1930; Martel 1993; Ackerman *et al.* 1994), sometimes using byssal threads to assist them (Griffiths *et al.* 1991), and can be carried longer distances when attached to floating vegetation or debris (Mackie *et al.* 1989; Martel 1993; Mackie & Schloesser 1996; Johnson & Carlton 1996). Ackerman *et al.* 1994, note that pediveligers may recruit preferentially to aquatic

plants and later migrate to other substrates by transport on floating plant material. Small juveniles may also travel long distances by drifting in currents, remaining above the bottom with the aid of trailing threads acting as drag lines (Griffiths *et al.* 1991 and Carlton 1993 refer to "bysso-pelagic transport;" Martel 1993 and Ackerman *et al.* 1994 both note that the threads used for drifting are morphologically distinct from byssal threads), with threads in contact with the water surface from which the mussel hangs (Oldham 1930; Ackerman *et al.* 1994; Mackie & Schloesser 1996); by crawling on the underside of the air-water surface (Oldham 1930; Ackerman *et al.* 1994); or by resuspension in turbulent flows (Martel 1993). Large numbers of juveniles have been reported drifting in Lake Erie during periods of strong waves or storms (Martel 1993). If juvenile drift is initiated by the presence of strong currents, it could be an important form of transport in river systems. Occasional transport by crayfish, turtles, birds, muskrats or other organisms may also be possible (Carlton 1993; Mackie & Schloesser 1996; Johnson & Carlton 1996).

Distribution, Dispersal and Invasion History

Zebra mussels are native to the estuaries and lower reaches of rivers draining into the Caspian, Black and Azov seas in eastern Europe, the northern Caspian Sea, and the coastal shallows of the middle and south Caspian Sea (Therriault *et al.* 2004)[6]. Shipping canals constructed in the late 18th and 19th centuries connected these to other watersheds, and zebra mussels quickly spread into the Baltic Sea basin, and from began to spread westward across northern Europe and eastward through the western half of the Soviet Union (Stanczykowska & Lewandowski 1993; Karatayev *et al.* 1997, 2007b; Wolff 2005). They arrived in London by 1824, in Amsterdam by 1826 and in Germany by 1838, having reportedly travelled from port to port and across the English Channel attached to shipments of Baltic timber, though dispersal also occurred on boats and barges through a network of canals that connected the Dneiper, Vistula, Oder, Elbe and Rhine rivers (Van der Velde 2002), and may have occurred in solid ballast. Zebra mussels spread across Great Britain in the 19th century, facilitated by the construction of waterways (Kerney & Morton 1970; Morton 1973,1979; Wolff 2005). By 1840 the mussels had reached Germany, Denmark, the Netherlands, Belgium and France (Karatayev *et al.* 2007b). They continue to spread in Europe, reaching Ireland by 1997 and Spain by 2001 (Karatayev *et al.* 2007b).

Zebra mussels were discovered in North America in Lake St. Clair, between Lake Huron and Lake Erie in the Great Lakes chain, in 1988 (Hebert *et al.* 1989; Griffiths *et al.* 1991). They had probably been introduced earlier in the decade in the ballast water of cargo vessels arriving from freshwater ports in northern Europe—possibly introduced from the Soviet Union as a result of a boom in Canadian and American wheat exports to that country (Karatayev *et al.* 2007b). McMahon (1996) has also suggested that zebra mussels could have been introduced into the Great Lakes as adults attached to anchors

[6] In addition, two reported subspecies, *D. polymorpha aralensis* and *D. polymorpha obtusecarinata*, are reported to be indigenous to the Aral Sea, now extinct there due to increasing use of the sea's freshwater inflows and a dramatic rise in the sea's salinity (Strayer & Smith 1993). It's not clear whether these should be considered subspecies or separate species from *D. polymorpha*.

or anchor chains, though this seems less likely. By 1990 zebra mussels had spread to all five Great Lakes, by 1991 they had spread east along the Erie Canal and into the Hudson River and west into the Illinois River watershed (a tributary of the Mississippi River) via the Chicago Sanitary and Ship Canal[7], and by 1992 had entered the Upper Mississippi River and the Illinois, Tennessee and Arkansas rivers. By the end of 1993, zebra mussels had spread down the Mississippi River to New Orleans, westward up the Arkansas River to Oklahoma, and northeastward to Lake Champlain in Vermont. By 1995 they had invaded waters in 19 states and two Canadian provinces . They entered the northeastern corner of Connecticut in 1998, Virginia in 2002, and Kansas and Nebraska in 2003.[8] In November 2007 zebra mussels were found in Pueblo Reservoir on the Arkansas River, in southeastern Colorado, the westernmost population east of the continental divide[9]; and in January 2008 zebra mussels were found in San Justo Reservoir in San Benito County in California, the first record of an established population west of the continental divide (Ram & McMahon 1996).

Several mechanisms, both natural and anthropogenic, contributed to this dispersal. Dispersal within the Great Lakes was probably accomplished by a combination of advective transport of larvae and drifting juveniles, ballast water transport by cargo vessels (most likely including their introduction to Duluth Harbor at the western end of Lake Superior), and transport on the hulls of commercial and recreational vessels. Within other navigable waterways, transport on the hulls of commercial barges was probably important, particularly for dispersal upstream (Keevin *et al.* 1992; Keevin & Miller 1992; Johnson & Carlton 1996), along with transport on recreation vessels.

Overland transport into unconnected water bodies has been slow compared to the rapid dispersal that often occurs within connected waters (Johnson & Carlton 1996; Johnson & Padilla 1996). The main mechanism for overland introductions has almost certainly been transport with recreational boats hauled on trailers, including adult mussels attached to hulls or other components and equipment, transport of adults on snagged vegetation, and transport of larvae in live wells, bait wells, engine cooling water or other small reservoirs of water (Carlton 1993; Johnson & Carlton 1996). Scuba divers may have intentionally introduced zebra mussels into a few isolated waters, including Millbrook Quarry in Virginia, a quarry near Bethlehem, Pennsylvania, and Base Lake on Offut Airforce Base in Nebraska. Commercial shipments of baitfish and plantings of hatchery-bred gamefish could also contribute to the mussel's dispersal (Kastner *et al.* 1997; Edwards *et al.* 2002).

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[7] The canal connects the Chicago and Calumet Rivers, which drain into Lake Michigan, with the Des Plaines River, which flows into the Kanakee River and thence into the Illinois and Mississippi Rivers.

[8] Maps of zebra mussels' spread in North America can be found at http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/ and http://nationalatlas.gov/dynamic/dyn_zm.html#.

[9] This collection consisted of 2 adults, 1 juvenile and 1 veliger, identified by DNA analysis, according to the USGS' NAS website (http://nas.er.usgs.gov/queries/specimenviewer.asp?SpecimenID=242589), with apparently no further collections of zebra mussel adults or veligers since then despite significant search effort. Thus, it is not yet c lear if there is an established population of zebra mussels in Colorado.

Overland dispersal is facilitated by the zebra mussel's ability to survive out of the water for significant periods of time. In laboratory experiments, these periods are greater at higher humidity and lower temperature, with larger mussels surviving longer than small mussels (Table 5). Based on these data, McMahon *et al.* (1993) concluded that zebra mussels could survive up to 4-5 days out of the water at temperatures of 25°C or above but could survive 10 or more days at temperatures below 15°C, while Ricciardi *et al.* (1995) concluded that they could survive 3-5 days of overland transport.

Table 5. Zebra mussels' maximum survival times (in days) for aerial exposure in laboratory experiments.

Relative Humidity	Temperature 5°C	10°C	15°C	20°C	25°C	30°C	35°C
≤5%	11[a] 13[c]	–	5[a,b] 6[c]	–	2[a] 3[c]	–	1.25[c]
10%	–	3-5[d] 5-10[e]	–	3-5[d] 3-5[e]	–	1[d] 1-3[e]	–
33%	9[c]		5[b] 6[c]		3[c]		1.25[c]
50-53%	17[a] 13[c]	5-10[d] 5-10[e]	7.5[a] 13[b] 8[c]	3-5[d] 5-7[e]	3[a] 3[c]	1[d] 1-3[e]	1[c]
75%	18[c]	–	9[b] 8[c]	–	4[c]	–	1[c]
≥95%	27[a] 48[c]	5-10[d] 10-15[e]	12[a] 22[b] 15[c]	5-6[d] 5-7[e]	5[a] 4[c]	1-3[d] 3-5[e]	0.6[c]

[a] Time to 100% mortality from multiple regression based on laboratory experiments: ln(survival time, in hours) = 5.917 - (0.082 x temperature) + (0.010 x relative humidity) (Payne *et al.* 1992).

[b] Time to 100% sample mortality in 15-27 mm long mussels from Lake Erie (Ussery & McMahon 1994, 1995).

[c] 11-30 mm long mussels (McMahon *et al.* 1993; estimated from graphs).

[d] 10-18 mm long mussels from the St. Lawrence River (Ricciardi *et al.* 1995).

[e] 21-28 mm long mussels from the St. Lawrence River (Ricciardi *et al.* 1995).

Salinity

The upper salinity limit for zebra mussels depends not only on the salt concentration, but also on whether the concentration is relatively stable or rapidly changing, and on the composition of the salt. If salinity is changing rapidly (*e.g.* in an estuary) zebra mussels can tolerate low levels of salinity, but can handle higher levels if the change is slow (*e.g.* in a terminal lake). Laboratory studies reflect this, showing greater tolerance to higher salinity levels when the rate of increase is gradual (Strayer & Smith 1993). For example, Karpevich (1947, cited in Strayer & Smith 1993) found that respiration rates dropped

when salinity was changed abruptly, but that there was no depression in respiration when salinity was changed at a slower rate of 2 ppt every 2 days up to a final salinity of 17 ppt.

Strayer and Smith (1993, citing Mordukhai-Boltovski 1964 and Zhadin 1965) have suggested that zebra mussels may be able to tolerate higher salinity in waters that contain higher proportions of divalent ions (Ca^{++} and Mg^{++}) and sulfates relative to monovalent ions (Na^{+} and Cl^{-}), and that chloride content rather than overall salinity may actually be the critical factor. Temperature could also affect salinity tolerance (with higher tolerance in colder water), and there may be genetic differences in salinity responses in different populations (*e.g.* Baker *et al.* 1993a). For example, in the Volga River the zebra mussels at the most downstream locations can tolerate exposures to high salinities better than the mussels from upstream locations can; and this is mirrored by their response at the cellular level (Smirnova & Vinogradov 1990; Smirnova *et al.* 1993).

In estuaries, zebra mussels have been found in salinities up to a mean of 0.6 ppt in The Netherlands, up to <1 ppt in the eastern Gulf of Riga, and up to <2 ppt in the extreme eastern Gulf of Finland and along the Black Sea (Wolff 1969; Strayer & Smith 1993). Populations of stunted mussels have been observed in the Vistula estuary and lagoon at up to 4.8 ppt, and in the Kiel Canal at 3.8-6.2 ppt (Strayer & Smith 1993). In the Hudson River estuary zebra mussels were found at high densities at sites with maximum salinities up to 3 ppt, and at low densities at maximum salinities up to 5 ppt (Carlton 1992; Walton 1996). Extreme salinity records from estuaries could represent sink populations, that is, populations made up of mussels that spawned in lower salinity water upstream and that cannot reproduce in the higher salinity waters where they have been reported.

Zebra mussels occur in more stable salinities at up to 4 ppt in ponds in the Netherlands delta region (Wolff 1969). They are abundant at salinities of 6-9 ppt in the northern Caspian Sea, but are absent from the main body of the sea at 13 ppt (Strayer & Smith 1993). In the Aral Sea they were abundant at up to 10 ppt; as water diversions raised the salinity, the populations began to decline at around 12 ppt and had virtually disappeared by the time salinities reached 14 ppt (Stayer & Smith 1993).

Laboratory experiments have produced disparate results (Table 6). Barber (1992) reported 100% mortality of adult mussels in 15°C water when salinity was raised from 0 to 2.7 ppt over 52 days. In contrast, Mackie & Kilgour (1992) reported 85% survival of adult mussels in 4°C and 10°C water that were acclimated to 8 ppt salinity over 42 days. Vinogradov *et al.* (1993) referenced one study that reported 100% mortality after 168 days in 5 ppt (Smirnova 1973), another that reported the lethal concentration to be 5-7 ppt (Karpevich 1955), and a third that reported the lethal concentration using stepwise acclimation to be 10-12 ppt (Karpevich 1955). Strayer and Smith (1993, citing Karpevich 1947) noted earlier studies that reported 10 ppt as the limit for long-term survival of gradually acclimated mussels. Studies assessing potential distribution have used limits of 2-15 ppt (Doll 1997; Hayward & Estevez 1997; Cohen & Weinstein 1998; Cohen

2007; Table 6), in part depending on whether salinities are fluctuating or relatively stable, but also reflecting the wide range of limits reported from experiments and field observations.

Table 6. Zebra mussel's upper salinity limit as indicated by different studies.

Limit	Basis	Reference
0.4-2 ppt	Estimated upper limit in tidal estuaries	Strayer & Smith 1993
0.6 ppt	Upper limit of mean salinity where zebra mussels are present in estuaries in the Netherlands delta region	Wolff 1969
0.6 ppt	Upper limit for adult growth, based on literature review	Baker *et al.* 1993a
1 ppt	Upper limit for areas likely to support high densities of zebra mussels, based on literature review	Baker *et al.* 1993a
1-6 ppt	Incipient mortality from 2 week exposure in different Volga River populations	Smirnova *et al.* 1990, based on Antonov & Shkorbatov 1983
0.9-2.0 ppt	Maximum salinity tolerated	Wolff 1969
2 ppt	Upper limit for sustaining large populations, based on literature review	Baker & Baker 1993
2 ppt	Value dividing "low-to-no" from "moderate" potential distribution in waters with fluctuating salinities in analysis in California	Cohen & Weinstein 1998
2.6 ppt	Maximum salinity tolerated	Jansen *et al.* 1967, cited by MacNeill 1991
2.7 ppt	Upper limit for survival of acclimated adults at 15°C in laboratory	Barber 1992, cited by Baker *et al.* 1993a
3 ppt	Maximum salinity tolerance	Morton 1979
3 ppt	Maximum salinity at sites in the Hudson River estuary with high densities (>1,000/m^2) of zebra mussels	Walton 1996
4 ppt	Upper limit where present in ponds in the Netherlands delta region	Wolff 1969
4.7 ppt	Maximum salinity tolerated	Jaeckel 1962, cited by MacNeill 1991
>5 ppt	100% mortality from 18-day exposure	Spidle 1994
5 ppt	Maximum salinity at which zebra mussels have been found in the Hudson River	Walton 1996
6 ppt	Maximum salinity at which zebra mussels have been found in the Kiel Canal	Strayer & Smith 1993
6 ppt	Estimated upper limit in nontidal lagoons or other waters with relatively stable salinities	Strayer & Smith 1993
6 ppt	Upper salinity limit in waters with stable salinities in analysis in California	Cohen 2007
6 ppt	Upper salinity limit of the subspecies that invaded North America, based on literature review	Karatayev *et al.* 2007b

9 ppt	Maximum value where mussels occur in the Caspian Sea	Strayer & Smith 1993
6.5-9 ppt	Mortality above ≈10% from 2 week exposure in different Volga River populations	Smirnova *et al.* 1990, based on Antonov & Shkorbatov 1983
7.6 ppt	LC_{50} for 4 d exposure of unacclimated adults at 19°C in laboratory	Mackie & Kilgour 1992
7.6 ppt	Maximum salinity at which zebra mussels have been found in the Dnieper-Bug estuary	Mills *et al.* 1996
8 ppt	85% survival of acclimated adults at 4° and 10°C in laboratory	Mackie & Kilgour 1992
10 ppt	Upper limit for long-term survival of acclimated mussels	Strayer & Smith 1993 citing Karpevich 1947
10 ppt	Value dividing "unlikely" from "maybe" potential distribution in analysis in North Carolina	Doll 1997
10 ppt	Value dividing "low-to-no" from "moderate" potential distribution in waters with stable salinities in analysis in California	Cohen & Weinstein 1998
10-14 ppt	Estimated upper limit in sulfate-rich brackish lakes	Strayer & Smith 1993
12-14 ppt	Values at which the subspecies *D. p. aralensis* and *D. p. obtusecarinata* disappeared from the Aral Sea as salinities increased (see previous footnote regarding these subspecies)	Strayer & Smith 1993
12 ppt	Maximum salinity tolerated	Van Benthem Jutting 1943, cited by MacNeill 1991
12 ppt	Upper limit for adult survival, based on literature review	Baker *et al.* 1993a
15 ppt	Index of 0 (perfectly unsuitable, or lethal) on the Habitat Suitability Index curve	Hayward & Estevez 1997
18 ppt	Upper limit for the most salinity-tolerant subspecies	Karatayev *et al.* 2007b

Temperature

Freezing kills zebra mussels (Karatayev 1995; McMahon 1996), but even where temperatures are not extreme enough to kill them outright, temperatures that don't support reproduction or adequate growth will prevent the mussels' establishment (Strayer 1991). Strayer (1991) found that zebra mussels were less common in Europe where mean annual air temperatures were below 3-6°C, and where the lowest mean monthly air temperature was below 6°C (Table 7). Several studies in Europe and North America have reported that the lower temperature limits for adult growth are around 10-12°C (Morton 1969; Stanczykowska 1977; Baker *et al.* 1993a), but Bij de Vaate (1989) reported adult growth down to 6°C (Table 8). Most studies report that zebra mussels start to spawn when water temperatures reach 12°C (Borcherding 1991; Neumann *et al.* 1992; McMahon 1996), but limited spawning has been reported at 10°C in the Great Lakes and Europe (Sprung 1993; Nichols 1996; McMahon 1996). In addition, Mills *et al.* (1993) reported the presence of zebra mussels at depths in lake Ontario where

temperatures rarely exceed 5°C, and noted reported observations of spawning at temperatures down to 2.5°C. Spawning peaks at about 12-18°C, which is roughly the optimum temperature for larval development (Sprung 1993). Various studies have used mean summer temperatures in the range of 9-15°C as the lower limiting values for potential distribution (*e.g.* Sorba & Williamson 1997; Doll 1997; Cohen & Weinstein 1998; Cohen 2007, Table 8).

In Europe, Strayer (1991) found that zebra mussels were absent where mean annual air temperatures were above 18°C or where the highest mean monthly air temperatures were above 27°C (based, however, on only a few stations) (Table 7). Baker *et al.* (1993b) commented that the mussel's distribution in Europe may not be indicative of its upper temperature limits, since the Mediterranean Sea serves as a southern barrier. Observations and experiments suggest that water temperatures above 24-30°C are unsuitable for reproduction, spawning or larval growth (Baker *et al.* 1993a), and that temperatures above 26-36°C can be lethal (Table 9). Baker *et al.* (1993a) argue that in temperate regions seasonal temperature fluctuations usually result in some period each year with temperatures that allow successful reproduction, so that adult temperature tolerances are probably more critical in setting range limits. Stanczykowska (1977, cited by Baker *et al.* 1993a) reports that adult growth ceases above 26-33°C. Strayer (1991, citing McMahon & Tsou 1990) noted that temperatures greater than 26-32°C can kill larvae or adults, and further noted (citing Walz 1978) that at high temperatures respiratory costs can exceed assimilation rates resulting in loss of body weight, which could prevent the establishment of zebra mussels without killing them outright. Aldridge *et al.* (1994) found experimentally that between 20° and 32°C an increase in water temperature results in an increase in zebra mussels' energetic costs and a decrease in their feeding rate, and concluded that energy losses start to exceed intake between 24° and 28°C. In southern U.S. waters, zebra mussels have been reported at temperatures up to about 30°C (Spidle 1994), with die-offs occurring at 31°C. Shkorbatov (1986,

Table 7. Zebra mussel's distribution in Europe relative to air temperature. Data are from Strayer 1991 and refer to records of zebra mussels within 100 km of weather stations.

	Zebra Mussel Occurrence		
Parameter	**Common (at >40% of stations)**	**Uncommon (at ≤40% of stations)**	**Absent**
Mean Annual Air Temperature	3°–12°C (n=71)	-1°–3°C (n=9) or 12°–18°C (n=28)	18°–19°C (n=2)
Highest Monthly Mean Air Temperature	15°–26°C (n=101)	13°–15°C (n=5)	27°–28°C (n=4)
Lowest Monthly Mean Air Temperature	-15°–6°C (n=97)	6°–9°C (n=13)	—
Number of Months with Mean Air Temperature ≥10°C	4–7 (n=85)	3 (n=7) or 8–12 (n=14)	—
Mean Annual Air Temperature (lake records)	6°–15°C (n=70)	3°–6°C (n=4)	—

Table 8. Zebra mussel's lower temperature limits as indicated by different studies.

Limit	Basis	Reference
-2°C	No survival below this value	Claudi & Mackie 1994
0°C	Lower limit for adult survival, based on literature review	Baker *et al.* 1993a
0°C	Lower limit for poor growth	Claudi & Mackie 1994
0°C	Does not survive freezing	McMahon 1996
0°C	Usual lower limit of distribution	Boelman *et al.* 1997
0°C	Index of 0 (perfectly unsuitable, or lethal) on their Habitat Suitability Index curve	Hayward & Estevez 1997
0°C	Lower limit, based on literature review.	Karatayev *et al.* 2007b
2-4°C	Lower limit for gametogenesis	Borcherding 1991
3°C	Lower limit of favorable conditions	Smirnova & Vinogradov 1990
6°C	Lower limit for adult growth, based on literature review	Bij de Vaate 1989
6°C	Lower limit for occurrence in Europe	McMahon 1996
9°C	Value dividing poor from moderate growth	Claudi & Mackie 1994
9°C	Mean summer value dividing "very low" from "low" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
10°C	Minimum needed for growth and reproduction	Karatayev 1995
10°C	Lower limit for limited spawning in Great Lakes	Nichols 1996
10°C	Maximum annual value dividing "low-to-no" from "moderate" potential distribution in analysis in California	Cohen & Weinstein 1998
10°C	Lower limit for mean summer value in analysis in California	Cohen 2007
10-11°C	Lower limit for growth or reproduction, based on literature review (but also cites lower limit of 12-15°C for reproduction)	Karatayev *et al.* 2007b
10-12°C	Lower limit for adult growth in the Great Lakes	Baker *et al.* 1993a
10-12°C	Lower limit for spawning, based on literature review	McMahon 1996
11-12°C	Lower limit for adult growth in European lakes	Stanczykowska 1977
12°C	Lower limit for spawning and larval growth, based on literature review	Baker *et al.* 1993a
12°C	Lower limit for maximum summer value in analysis in California	Cohen 2007
≈12°C	Lower limit for juvenile and adult growth, based on literature review	McMahon 1996
15°C	Lower limit for spawning	Karatayev 1995
15°C	Mean summer value dividing "unlikely" from "definite" potential distribution in analysis in North Carolina	Doll 1997

shown in Smirnova *et al.* 1993) found that zebra mussel populations in Volga River reservoirs began dying at temperatures around 31°C and reached 100% mortality at 33-36°C. In the Zaporozhskoe Reservoir in the Ukraine, zebra mussels survive in water temperatures up to 33°C (Karatayev *et al.* 2007b). Several authors report 30°C to be the upper limit for feeding and growth, and 31-33°C to be the upper limit for short-term

survival (*e.g.* 100% mortality with 1 wk exposure to 31°C, 100 hr exposure to 32°C, or 24 hr exposure to 35°C—Spidle *et al.* 1995; McMahon 1996; Elderkin & Klerks 2005; see also Table 9). Various studies used mean summer temperatures in the range of 30-32°C and maximum temperatures of 31°C as the upper limiting values for potential distribution (Sorba & Williamson 1997; Doll 1997; Cohen & Weinstein 1998; Table 9).

Table 9. Zebra mussel's upper temperature limits as indicated by different studies. Temperatures are water temperatures unless otherwise indicated.

Limit	Basis	Reference
18°C	Absent within 100 km of weather stations with higher mean annual air temperatures (n= 2 of 110)	Strayer 1991
24°C	Zygote mortality in laboratory study	Sprung 1987
24°C	Upper limit for larval growth, based on literature review	Baker *et al.* 1993a
24-28°C	Energy costs exceed intake in experiments	Aldridge *et al.* 1994
25°C	Usual upper limit of distribution	Boelman et al. 1997
26°C	Loss of sperm motility in laboratory study	Sprung 1987
26-30°C	Maximum temperature during spawning in Lake Erie	Haag & Garton 1992
26-32°C	Temperatures that can kill adults or larvae	McMahon & Tsou 1990
26-33°C	Upper limit for adult growth	Stanczykowska 1977
27°C	Absent within 100 km of weather stations with higher highest mean monthly air temperatures (n= 4 of 110)	Strayer 1991
30°C	Upper limit for regular feeding	Smirnova & Vinogradov 1990
30°C	Upper incipient lethal temperature.	Iwanyzki & McCauley 1993
30°C	Upper limit for adult growth, based on literature review	Baker *et al.* 1993a
30°C	Upper limit for poor growth	Claudi & Mackie 1994
≈30°C	Upper limit for juvenile and adult growth, based on literature review	McMahon 1996
30°C	Mean summer value dividing "low" from "very low" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
30-31°C	Abundant in southern US waters where temperatures often reach 30°C, but massive die-offs occur at 31°C	McMahon 1996
30-32°C	Upper limit of tolerance, in several studies	Karatayev 1995
30-35°C	No mortality at 30°C, 100% mortality at 35°C, in 14-day exposure of Lake Erie and Lake Ontario zebra mussels	Spidle 1994
31°C	Upper incipient lethal temperature with mean tolerated exposure of 52-292 hours depending on acclimatization	Armistead 1995
31°C	Upper limit for larvae and adults, based on literature review	McMahon 1996
31°C	Maximum annual value dividing "moderate" from "low-to-no" potential distribution in analysis in California	Cohen & Weinstein 1998; Cohen 2007
<32°C	Upper limit indicated by experiment without acclimation	Domm *et al.* 1993
32°C	Above this temperature, mass deaths occur	Karatayev 1995
32°C	Mean summer value dividing "maybe" from "unlikely" potential distribution in analysis in North Carolina	Doll 1997

32-33°C	Upper temperature limit	Smirnova & Vinogradov 1990
33°C	Upper limit for adult survival, based on literature review	Baker *et al.* 1993a
33°C	Upper limit (100% mortality) for long-term exposure, based on review of northern European data	McMahon & Ussery 1993
33°C	Upper limit, based on literature review	Karatayev *et al.* 2007b
33-36°C	100% mortality in different Volga River populations	Shkorbatov 1986, in Smirnova *et al.* 1993
34°C	Maximum summer temperature with predicted 5-15% survival for Lake Erie and Ohio River zebra mussels	Thorp *et al.* 1998
35-36.5°C	Predicted upper limit (100% mortality) for long-term exposure, based on experimental data on mussels from the Niagara River acclimated to 5-15°C	McMahon & Ussery 1993
37°C	Upper limit indicated by experiment in rapidly rising temperatures	Domm *et al.* 1993
38.8°C	Predicted 100% mortality of North American mussels acclimated to 15°C with temperature rising at 1°C/min	Spidle 1994
39°C	Index of 0 (perfectly unsuitable, or lethal) on their Habitat Suitability Index curve	Hayward & Estevez 1997
40°C	No survival above this value	Claudi & Mackie 1994
40.3°C	Predicted 100% mortality of North American mussels acclimated to 20°C with temperature rising at 1°C/min	Spidle 1994

Shkorbatov (1986, cited by Smirnova *et al.* 1993) and Smirnova and Vinogradov (1990) noted that Volga River populations of zebra mussels varied in their heat tolerance (possibly due to genetic differences), with the southernmost population and a population living in waters heated by power plant discharges showing the greatest tolerance for high temperatures. Thorp *et al.* (1998) came to similar conclusions, finding that zebra mussels from the Ohio River were more tolerant of high temperatures than zebra mussels from Lake Erie, and suggesting that this is an evolved, post-invasion difference that would increase over time.

Dissolved Oxygen

Boelman *et al.* (1997) report that zebra mussels are usually found where dissolved oxygen is over 90% of saturation, which is 5.9-10.2 mg/l at 10-25°C in surface waters between 0-6,000' elevation, and become stressed at levels of 40-50% of saturation (2.6-5.7 mg/l at 10-25°C and 0-6,000'). Smirnova and Vinogradov (1990) reported 80-85% oxygen saturation (5.3-9.6 mg/l at 10-25°C and 0-6,000') as optimal. Oxygen concentrations levels as low as 3.2 ppm have been found in parts of the Illinois River where zebra mussels are abundant (Kraft 1994; Table 10). Sprung (1987) concluded that zebra mussel larvae can survive for a short time at 18°C with oxygen at 20% of saturation (1.5-1.9 mg/l at 0-6,000'), and Karatayev *et al.* (1998) reported adult mussels need 25% saturation (1.7-2.8 mg/l at 10°-25°C and 0-6,000'). Under anoxic conditions, all zebra mussels die within 6 days at 17-18°C and within 3 days at 23-24°C (Baker *et*

Table 10. Zebra mussel's minimum dissolved oxygen requirement, as indicated by different studies.

Limit	Basis	Reference
1.5 mg/l	Index of 0 (perfectly unsuitable, or lethal) on the Habitat Suitability Index curve	Hayward & Estevez 1997
1.5-1.9 mg/l	Only short survival of larvae	Sprung 1987
1.7-2.8 mg/l	Minimum for adults (=25% saturation for 10-25°C and 0-6,000 feet elevation)	Karatayev 1995; Karatayev *et al.* 1998
1.8-2.4 mg/l	Lower limit at 20°C, based on literature review.	Karatayev *et al.* 2007b
3.2 mg/l	Lowest concentration where mussels were abundant	Kraft 1994
4 mg/l	Lethal lower limit for adults at 18° C	Sprung 1987; McMahon 1996
4 mg/l	Value dividing "unlikely" from "maybe" potential distribution in analysis in North Carolina	Doll 1997
4 mg/l	Value dividing "very low" from "low" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
4 mg/l	Maximum annual value dividing "low-to-no" from "moderate" potential distribution in analysis in California	Cohen & Weinstein 1998; Cohen 2007

al. 1993a, citing Mikheev 1968). Most studies have used a limit of around 4 mg/l to assess zebra mussels' potential distribution (Doll 1997; Sorba & Williamson 1997; Cohen & Weinstein 1998; Cohen 2007).

Low oxygen requirements in cold water may allow mussels to survive winters under ice. However, severe pollution accompanied by low oxygen levels reportedly eradicated zebra mussels from much of the Rhine River during the 1970s (Neumann *et al.* 1993), and low oxygen may in part account for their poor success in eutrophic lakes (Stanczykowska & Lewandowski 1993; McMahon 1996).

Calcium, Alkalinity and/or Total Hardness

Of the three related parameters of calcium, alkalinity and hardness, most experimental and field studies focused on calcium concentrations (see below), and most studies of potential zebra mussel colonization in North America included calcium concentration as a key factor (Table 11; and reviewed by Cohen & Weinstein 2001 and Cohen 2005). However, studies relying on European versus North American data have general reported different calcium thresholds needed for establishing zebra mussel populations. Studies of European lakes concluded that zebra mussel needed 25-28 mg/l of calcium to become established (Ramcharan *et al.* 1992; Karatayev 1995; Padilla 1997). In contrast, zebra mussels have been reported from several sites in North America with calcium concentrations between 4 and 28 mg/l (Mellina & Rasmussen 1994; Strayer *et al.* 1996; Balcer 1996a; De Lafontaine & Cusson 1997; Eliopoulos & Stangel 1999; M. Hauser pers. comm. 1997; S. Nierzwicki-Bauer pers. comm. 2001; Cohen & Weinstein 2001; Drake & Bossenbroek 2004; Jones & Ricciardi 2005; see discussion below), where they have often been assumed to represent established, reproducing

Table 11. Studies of the potential distribution of zebra mussels in North America

Region Analyzed	Environmental Parameters Utilized	Reference
North America	air temperature	Strayer 1991
Ontario	calcium, pH	Neary & Leach 1992
Connecticut	calcium	Murray *et al.* 1993
Virginia	calcium, pH	Baker *et al.* 1993b
Hudson River estuary	salinity	Strayer & Smith 1993
Wisconsin	calcium, pH, nitrate, phosphate	Koutnik & Padilla 1994
southern Green Bay	temperature, depth, substrate	Ignacio & Miller 1994
Maryland	calcium, pH, salinity, temperature	Chaillou & Christmas 1994
Mississippi River	temperature	Armistead 1995
Northeastern US	calcium, alkalinity	Whittier *et al.* 1995
Rhode Island	calcium, pH	Tammi *et al.* 1995a, b
Mid-Atlantic region	calcium, pH, conductivity, oxygen	Bochenek 1995
North & South Carolina	calcium, pH, turbidity, *Corbicula* abundance	Duke Power 1995
North Carolina	calcium, pH, temperature, salinity, oxygen	Doll 1997
California	calcium, pH, temperature	Janik 1997
Manitoba	calcium, total hardness, pH, temperature, conductivity, oxygen, turbidity	Sorba & Williamson 1997
Florida	calcium, pH, temperature, salinity, oxygen, turbidity, sediment size	Hayward & Estevez 1997
California	calcium, pH, temperature, salinity, oxygen	Cohen & Weinstein 1998; Cohen 2007
United States	alkalinity, pH, temperature, oxygen	Ashby *et al.* 1998
South Carolina	calcium, pH, temperature, salinity, oxygen	Kozlowski *et al.* 2002
United States	air temperature, frost frequency, precipitation, solar radiation, elevation, slope, catchment area, geology	Drake & Bossenbroek 2004
United States	calcium	Whittier *et al.* 2007

populations. Models based on North American data have estimated calcium thresholds as low as 8.5 mg/l (Hincks & Mackie 1997), and assessments of potential distribution in North America have used thresholds as low as 9 mg/l (Kozlowski 2002).

Cohen and Weinstein (2001) noted that three hypotheses could explain the discrepancies between the North American and European data:

1. European and North American zebra mussels may be genetically distinct (due, for example, to founder effect in the establishment of the North American population), with the North American mussels having a lower calcium threshold.

2. In the regions examined by the European studies, zebra mussels may be limited to waters with greater than 25-28 mg/l of calcium by some undetermined, co-varying environmental factor, rather than by calcium.

3. Zebra mussels found at sites in North America with less than 25-28 mg/l of calcium may be non-reproducing "sink" populations resulting either from larvae drifting in from reproducing populations established at upstream sites with higher calcium levels, or from mussels repeatedly introduced by anthropogenic transport. The apparent North American calcium threshold would thus represent the concentration needed for settlement and growth, with the apparent European threshold representing the concentration needed for successful gonad development, gametogenesis, fertilization, or embryonic or early larval development.

Cohen and Weinstein (2001) concluded that the third hypothesis was most likely correct, that sink populations had been assumed to be reproducing populations, probably combined with some noise in the data resulting from the paucity of calcium measurements, spatial and temporal variation in calcium variation within water bodies at some sites, and possibly some mis-identification of mussels at some inland sites with few records (especially where the records were of veligers).

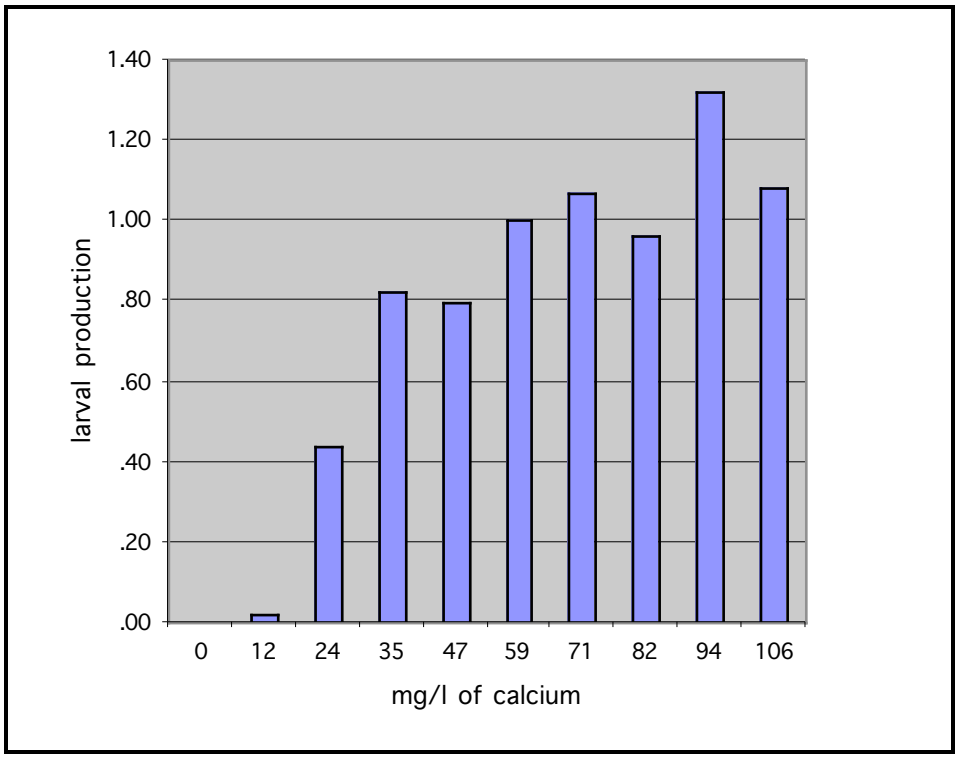
Numerous laboratory and field studies have directly or indirectly examined aspects of zebra mussels' calcium needs. Sprung (1987) induced zebra mussels to spawn and exposed the earliest developmental phase (eggs to 3-day-old larvae) to water with calcium carbonate added to produce various estimated calcium concentrations ranging from 12 to 106 mg/l along with a standard mix of other salts.[10] After three days, Sprung found that solutions with no calcium produced no larvae, while solutions with at least 40-60 mg/l of calcium had roughly similiar rearing success. Below 40 mg/l, rearing success declined and the proportion of crippled larvae increased (Figure 4). At 12 mg/l virtually no larvae were produced, and about 90% of the few that were produced were crippled.

Vinogradov *et al.* (1987) examined the calcium flux between the tissues of three species of freshwater bivalves and ambient water at calcium concentrations ranging from near zero to about 22 mg/l; zebra mussels were the most sensitive of the three species to low calcium levels, losing calcium when ambient concentrations were below 13-14 mg/l. In a second study, Vinogradov *et al.* (1993) tested the effect on calcium metabolism of acclimatizing mussels in very low salt waters (with calcium levels of 0.8-1.5 mg/l), and found that unacclimatized zebra mussels lost calcium when calcium levels dropped below 14 mg/l, while acclimatized mussels lost calcium when ambient calcium dropped below 22 mg/l, and lost it at a faster rate.

Ram and Walker (1993) found that 70% of adult zebra mussels died within 14 days in deionized water, with small mussels dying quicker than large ones. However, since all mussels survived when NaCl or $MgSO_4$ was added to the deionized water, they concluded that the lethal effect was due to osmotic stress rather than a lack of calcium.

[10] Nichols (1996) noted that since calcium was not measured directly in these experiments, the reported calcium concentrations may not be accurate.

Figure 4. Zebra mussel larval production at different calcium levels. Larval production is the number of healthy larvae produced after 3 days, indexed to the number produced at calcium concentrations of 59 mg/l. Calculated from graphs in Fig. 3 of Sprung (1987).



Based on reported increases in blood calcium in a freshwater bivalve exposed to deionized water, they suggested that zebra mussels and other freshwater bivalves may be able to draw on calcium reserves in shell or tissue to maintain osmolality when stressed, and that larger animals, having larger reserves, may fare better. Dietz *et al.* (1994) similarly found that zebra mussels died within five days in deionized water, but could survive over 51 days in water that had minimal concentrations of NaCl, potassium and magnesium but no calcium. Like Ram and Walker (1993), they concluded that the mussels survived by mobilizing calcium from their shells in order to maintain necessary levels of calcium in their blood.

McCauley and Kott (1993) placed the gills of adult zebra mussels collected from Lake Erie in solutions with a range of calcium concentrations, at a pH of 7.4. Ciliary activity ceased after 24-hour exposures to calcium concentrations below 8 mg/l.

Hincks and Mackie (1993, 1994) placed adult and juvenile zebra mussels from Lake Erie in flow-through aquariums with 15 levels of calcium (0-35 mg/l), 15 levels of alkalinity (2.5-80 mg/l as $CaCO_3$), and 15 combinations, and found that survival and growth rates (measured by shell length) increased with increasing calcium and alkalinity. Gonads matured normally at all alkalinity levels, but males released sperm only if calcium levels were above 15 mg/l. They also placed juvenile mussels in flow-through bio-boxes in three Ontario lakes. In the two lakes with the highest calcium

concentrations (25 and 44 mg/l), growth rates were similar to rates observed in the Great Lakes, but in a lake with 7 mg/l of calcium growth rates were only 9-14% of the Great Lakes' rate and mortality was higher. Hincks and Mackie (1997) later reared adult and newly-settled juvenile zebra mussels from Lake St. Clair in water from 16 Ontario Lakes (Table 12). Six of these lakes had mean calcium levels of 2.4-8.3 mg/l and mean pH values of 6.4-8.4. In these low calcium and lower pH waters all adults died within 35 days, juvenile growth rates were near zero or negative, and no veligers were produced. The other lakes all had mean calcium levels of 20-48 mg/l and mean pH values of 8.2-9.3. In these waters adult survival was 52-100%, juvenile growth rates ranged from 3 to 29 µm/day (low compared to field measurements of up to 125 µm/day in Lake St. Clair), and almost no veligers were produced (0 to 7 veligers from an initial population of 21 adults in each treatment).They found that the best fit model of adult mortality was a logistic regression on calcium and pH, with mortality decreasing with increasing calcium for pH between 6.0 and 8.5, and mortality increasing with increasing calcium at higher pH values. They found significant curvilinear relationships between juvenile growth rates and each of the variables calcium, alkalinity and total hardness, which were themselves correlated (see Figure 1). The best fit regression for calcium showed negative growth below 8.5 mg/l, maximum growth at 32 mg/l, and declining growth rate at higher calcium levels. They found no significant relationship between the number of veligers produced and any of the environmental variables.

Table 12. Zebra mussel survival, growth and reproduction in water from 16 Ontario lakes. From Hincks & Mackie 1997.

Water Source	Mean Calcium (mg/l)	Mean pH	% Adult Survival at 35 days	Mean Juvenile Growth Rate (µm/day)	Production of Veligers over 70 days
Dickie Lake	2.4	6.4	0	0	0
Lake of Bays	3.0	7.4	0	-12	0
St. Nora Lake	3.4	7.1	0	-7	0
Lake Muskoka	6.0	8.4	0	0	0
Beech Lake	7.8	8.0	0	-5	0
Big Clear Lake	8.3	8.1	0	-12	0
Balsam Lake	19.9	8.7	90	5	1
Buckhorn Lake	25.7	9.3	95	22	3
Devil Lake	26.7	8.6	81	24	1
Lake St. Clair	32.9	8.7	81	3	0
Big Rideau Lake	34.3	8.2	67	29	1
Upper Rideau Lake	35.4	8.7	81	13	2
Lake Erie	35.7	8.5	71	24	0
Lake Ontario	39.2	8.2	76	20	0
Lake Scugog	44.5	8.5	100	6	7
Lake Simcoe	47.6	8.4	52	9	2

Balcer (1996a) collected zebra mussels ≤20 mm long from Lake Erie and the Mississippi River and mussels 25-30 mm long from Duluth-Superior Harbor, and placed them in cages in Duluth-Superior Harbor where reported calcium concentrations range from 13-23 mg/l. All sizes survived well and grew during summers but there was high mortality during winters, especially for smaller mussels (80-95% mortality for 7-12 mm mussels, 54-97% mortality for 15-20 mm mussels, and 12-46% mortality for 25-30 mm mussels). The shells of many of the surviving and most of the dead mussels were thin and eroded, with holes in many of the smaller mussels. Balcer (1996b) collected zebra mussels from Lake Erie, the Mississippi River and Duluth-Superior Harbor and reared them in the laboratory in water with 15, 30, 35, 45 and 60 mg/l of calcium, and in two treatments with calcium concentrations that varied in the 15-35 mg/l range. Water temperatures were increased from 10 to 20°C over 11 weeks, and then varied between 20 and 23°C for 7 weeks. Survival was good in all treatments until temperatures reached 20°C; thereafter mortality rose and reached 80% by week 17. Mussels in all treatments released sperm and eggs after temperatures reached 21°C.

Baldwin *et al.* (1997; B.S. Baldwin pers. comm. 1998) placed zebra mussels from the St. Lawrence River in water from the St. Lawrence with 30 mg/l of calcium and in water from four uncolonized sites in northern with 3-22 mg/l of calcium (Table 13). Juvenile (5 mm shell length) and adult (15 mm shell length) mussels had comparable survivorship over 5 weeks with ≥4 mg/l of calcium, although mussels in 4 mg/l of calcium rapidly lost weight. Embryonic development and veliger survival over 14 days was comparably successful in 22 and 30 mg/l of calcium, but unsuccessful in 3-4 mg/l.

Table 13. Zebra mussel survival and early development in waters from northern New York. From Baldwin *et al.* 1997; B.S. Baldwin pers. comm. 1998.

Water Source	Calcium (mg/l)	Juvenile and Adult Survival after 35 d	Juvenile and Adult Growth over 35 d	Development of Embryo to Shelled Veliger Stage	Veliger Survival after 14 d
Raquette River	3	low	negative	failed	0 %
Upper St. Regis Lake	4	high	negative	failed	0 %
Upper Saranac Lake	4	high	negative	failed	0 %
Black Lake	22	high	positive	successful	≈60 %
St. Lawrence River	30	high	positive	successful	≈60 %

Hansen *et al.* (1998) placed newly-settled and adult zebra mussels from the Hudson River in water from the Hudson River (with 17 mg/l of calcium) and Lake George (with calcium declining from 12-14 mg/l to 10-11 mg/l over the course of the study). Mussels survived in both waters for 19 weeks, but mussels in Hudson River water were 11% longer and had 25%-40% more dry tissue mass than those in Lake George water; the latter also showed some dissolution of the shell (Hansen *et al.* 1998; A. Hansen pers. comm. 1998; S. Nierzwicki-Bauer pers. comm. 2001). In another experiment, veligers

from Lake Champlain placed in Lake George water (with 11 mg/l of calcium and pH of 7.5) did not survive, but survived longer when either calcium or pH was raised to Lake Champlain levels (16.5 mg/l of calcium and pH of 7.8), and survived best (nearly as well as controls reared in Lake Champlain water) when both calcium *and* pH were raised to Lake Champlain levels (S. Nierzwicki-Bauer pers. comm. 2001).

Lynn (J. Lynn pers. comm. 1998) placed adult zebra mussels from hard waters in water with 12-15 mg/l of calcium and artificially spawned them. He reported that the eggs had over 50% success in completing first cleavage at 4-8 mg/l of calcium, with dramatically declining success below 4 mg/l. However, there was a high degree of variability, with success rates ranging from 10 to 90% in tests using the same conditions.

In general, we might expect that larger adult mussels would be less sensitive to environmental extremes, including low ambient calcium concentrations, than smaller adult and juvenile mussels, that these would be less sensitive than larvae, and that the earliest developmental stages (gametes, embryos or small veligers) or perhaps the processes of gonads and gametes development and fertilization, would be the most sensitive at all. Among the experimental work on this issue in juveniles and adults (Table 14), Vinogradov *et al.* (1987, 1993) found that adults experienced a net loss of calcium when held in ambient calcium concentrations of 13-22 mg/l, depending on the specific treatment; while in contrast, Hincks and Mackie (1997) calculated that 8.5 mg/l of calcium is the limiting value for juvenile growth, and Baldwin *et al.* (1998) found normal survival of juveniles and adults for up to 35 days in 4 mg/l of calcium (Table 13). At the veliger stage, various researchers found that later stage veligers did very poorly at calcium levels between 4 and 11 mg/l, but did better or had normal success at levels between 16.5 and 22 mg/l (Table 14). Sprung (1987) tested very early development stages (eggs to early stage veligers) and found that their rate of sucessful development declined below 40 mg/l and approach zero at around 12 mg/l (Figure 4). Hincks and Mackie (1993) reported that males did not release sperm unless calcium concentrations were above 15 mg/l.

Information regarding zebra mussels' calcium needs also comes from observations and analyses of their distribution in Europe and North America. European data suggest a threshold in the vicinity of 25-28 mg/l of calcium. In 76 lakes in parts of Europe that had been occupied by zebra mussels for more than 50 years, zebra mussels were found only in waters with at least 28.3 mg/l of calcium (Ramcharan *et al.* 1992; Padilla 1997). In 527 lakes in Belarus, zebra mussels were found only in lakes with more than 25.4 mg/l of calcium (Karatayev 1995).

As noted earlier, however, several studies have described zebra mussel populations in North American waters with reported calcium concentrations below 28 mg/l. Mellina and Rasmussen (1994) collected zebra mussels in the Hudson River estuary from Catskill to New Hamburg where they measured calcium concentrations at 24-26.4 mg/l. Strayer (1996) reported on the collection of zebra mussels throughout the freshwater portion of the Hudson River estuary since 1991, noting that calcium concentrations in this reach ranged from 22-30 mg/l.Strayer (1996) and Cohen and Weinstein (2001) examined the

Table 14. Summary of experimental studies relative to zebra mussel's possible calcium thresholds. The indicated calcium level is the minimum concentration needed to satisy the endpoint, as indicated by data or analyses in the cited sources.

Endpoint	Indicated Calcium Threshold (mg/l)	Reference
Fertilization/Embryonic Development		
Release of sperm	15	Hincks & Mackie 1994
Normal success in egg fertilization	between 4 and 22	Baldwin *et al.* 1998
≥50% mean success in completing first cleavage	4	J. Lynn pers. comm. 1998
Larval Development		
Development of some larvae, 0-3 days	between 0 and 12	Sprung 1987
Significant numbers of healthy larvae, 0-3 days	between 12 and 24	Sprung 1987
Some veliger production	between 8 and 20	Hincks & Mackie 1997
Normal success in development from fertilization to D-shell veliger	between 4 and 22	Baldwin *et al.* 1998
Normal success in development from D-shell veliger to juvenile	between 4 and 22	Baldwin *et al.* 1998
Veliger survival	between 11 and 16.5	S. Nierzwicki-Bauer, pers. comm. 2001
Juvenile Stage		
Normal juvenile (5 mm shell) survival for 35 days	between 3 and 4	Baldwin *et al.* 1998
Normal juvenile growth rate	between 7 and 24	Hincks & Mackie 1993
Juvenile growth (based directly on data)	between 8 and 20	Hincks & Mackie 1997
Juvenile growth (based on regression)	8.5	Hincks & Mackie 1997
Adult Stage		
Normal adult (15 mm length) survival for 35 days	between 3 and 4	Baldwin *et al.* 1998
Maintenance of tissue weight for 35 days	between 4 and 22	Baldwin *et al.* 1998
Activity of gill cilia	8	McCauley & Kott 1993
Some adult (10-15 mm shell) survival for 35 days (based directly on data)	between 8 and 20	Hincks & Mackie 1997
Nonnegative calcium flux in unacclimatized adults	13-14	Vinogradov *et al.* 1987
Nonnegative calcium flux in unacclimatized adults	14	Vinogradov *et al.* 1993
Nonnegative calcium flux in acclimatized adults[1]	22	Vinogradov *et al.* 1993
Some adult (10-15 mm shell) survival for 35 days (based on regression)[2]	0-25 at pH of 7.5-8.3, ≈30 at pH≤7.4	Hincks & Mackie 1997

[1] Acclimatized for 28 days in diluted artesian water with 0.8-1.5 mg/l of calcium.

[2] Threshold calculated from multiple logistic regression model, for adult survival of ≤5%. By the same model, calcium levels must be *below* 50 mg/l for adult survival at pH≥9.1.

data on the spread and growth of this population and concluded that zebra mussels had probably reproduced within this reach, at least in some years. Additional data revealed a calcium range in this reach of 12-38 mg/l (US EPA's STORET database). This wide a range is not surprising, since this reach receives water from two or possibly three sources with distinct calcium concentrations: from the upper Hudson River with calcium levels of 4-25 mg/l and from the Mohawk River with calcium levels of 12-60 mg/l, and possibly also some slight mixing with seawater, which has a typical calcium concentration of 410 mg/l (Hem 1985; the data in STORET, which shows a gradual rise in the calcium range downstream from 12-30 mg/l at Green Island to 16-38 mg/l at Poughkeepsie, supports this).

Just upstream from Montreal the Ottawa River, with low calcium water and no zebra or quagga mussels, enters the higher calcium water of the St. Lawrence River, derived from the zebra-and-quagga-mussel-infested Lake Ontario. In 1991-92, Mellina and Rasmussen (1994) collected zebra mussels downstream of Montreal as far as Ile d'Orléans near Quebec. They found mussels at all sampled sites on the south bank of the river, where calcium levels ranged from 16 to 38 mg/l, and no zebra mussels at 11 north bank sites, where calcium levels ranged from 8 to 14 mg/l. They concluded that 15 mg/l is the calcium threshold for zebra mussels. In 2003, Jones and Ricciardi (2005) sampled for zebra mussels in the St. Lawrence River down to around Montreal, including several sites at and just below the confluence with the Ottawa River. Zebra mussels were found at 19 sites where calcium concentrations on that day measured 8-30 mg/L, but absent from one site where the calcium concentration measured 8-30 mg/L. Cohen and Weinstein (2001) and Cohen (2007) concluded that the zebra mussels in the river below the confluence with the Ottawa River are almost certainly recruited from upstream sites and not the result of local reproduction, so their distribution in this reach cannot be used as an indicator of appropriate conditions for reproduction. Their presence on the south bank and absence from the north bank in 1991-92 could be due to differences in veliger supply (the veliger-rich water derived from Lake Ontario and the upper St. Lawrence dominating the flows along the south bank, while water from the zebra-mussel-free Ottawa River dominated the north bank) rather than differences in calcium or other environmental parameters at the sampling sites. The sites sampled by Jones and Ricciardi would also represent recruitment from upstream sites and are probably sink populations,[11] and the sites at and below the confluence with the Ottawa River may be subject to substantial fluctuations in calcium levels with changes in the relative flows from the two tributaries, so any correlations between calcium measurements taken on a single day and the presence or absence of mussels at these sites on that day are further suspect.

Calcium concentrations range from 12-15 mg/l throughout most of Lake Superior (Beeton & Chandler 1963; Goldman & Horne 1983; Balcer, 1996a; STORET database), where there are at least ten reports of zebra mussels, all of which appear to be one-time occurrences rather than established populations (Table 15). However, zebra mussels have been collected in Duluth-Superior Harbor at the western tip of the lake since 1989 (Balcer 1994), and became markedly more abundant starting in 1998 (D. Jensen pers.

[11] Anthony Ricciardi agrees with that assessment, pers. comm. 2008.

comm. 2001). Reported calcium concentrations range from 13-23 mg/l in the harbor (based on relatively few measurements), where the St. Louis River provides an inflow of higher calcium water (Balcer 1996a; D. Jensen pers. comm. 2001). The large numbers present since 1998 suggest local reproduction, though this may be substantially augmented by the continuous release of very large numbers of larvae in ballast water arriving from the lower Great Lakes[12], as well as adults attached to ships' hulls or in seachests[13]. In Duluth-Superior Harbor, where the water is a mix of higher calcium St. Louis River water and lower calcium Lake Superior water, there could be substantial spatial and temporal variaiton in calcium concentrations with changes in flows. Studies that relate the reproductive success of the zebra mussels at locations in the harbor to the calcium levels at those locations have not been conducted.

Table 15. Zebra mussel records in Lake Superior outside of Duluth-Superior Harbor. Records from Cohen & Weinstein 2001 and USGS NAS website (http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/zebramusseldistribution.asp).

Site	Date	Notes (NAS record number)
Thunder Bay, ON	1990	one 13 mm adult, on a boat or barge hull (NAS116121)
Batchawana Bay, ON	1991	
Cape Gargantua, ON	1991	
Marquette, MI	Oct 1992	one 1-mm juvenile on sampler at power plant (NAS116680)
Two Harbors, MN	Apr 1993	small cluster in shipping channel near ore dock (NAS 117074)
Ontonagan River, MI	Oct 1997	1 or 6 (?) adults; discarded (NAS117925)
Chequamegon Bay, WI	Aug 1998	near ore dock (NAS118237)
Whitefish Bay, MI	Nov 1999	3-4 (?) adults, 1 cm long (NAS118433)
EPA Sampling Station	Aug 2002	veliger, in central part of lake (NAS252642)
Marquette, MI	May 2004	one 12 mm adult in upper harbor, may have fallen off a barge (NAS159150)

Lake Champlain is a long narrow lake oriented north-south along the border between New York and Vermont. Water flows north through the lake, which drains from its north end through the Richelieu River into the St. Lawrence River at Quebec. Calcium concentrations generally decline northwards, from average values of 25-31 mg/l (with a range of 13-60 mg/l) at the south end of the lake, to 14-20 mg/l (range of 8-47 mg/l) in the central and northern parts, and a range of 16-18 mg/l in the Richelieu River (Vermont DEC 1996-1998; De Lafontaine & Cusson 1997). Zebra mussels were first found in the lake in 1993 at its extreme southern end (Eliopoulos & Stangel 1997),

[12] For example, in 1995 Lake Superior received 62% of the total amount of ballast water discharged into the Great Lakes, with 81% coming from the lower lakes (Aquatic Sciences 1996).

[13] In 1990, zebra mussels 2-3 cm long were found on the rudder gearbox and in the seachest of a ship arriving in Duluth-Superior Harbor, and on a boat or barge hull in Thunder Bay on Lake Superior (Cohen & Weinstein 2001). The seachest is the compartment on a ship where ballast water first enters from outside the hull, whence it is pumped to the ballast tanks.

possibly introduced by boats from the Great Lakes, the Erie Canal or the lower Hudson River reaching the lake via the Champlain Canal, or by boats trailered overland. The mussels spread northward and by the summer of 1996 veligers or adults were found throughout most of the lake. They are generally most abundant in the southern end of the lake, are common in many parts of the lake where calcium concentrations are at least 18 mg/l, and have been found at two sites with median calcium concentrations of 13-14 mg/l in the northeast arm of the lake (M. Hauser pers. comm. 1997; Vermont DEC 1998; Eliopoulos & Stangel 1997, 1998, 1999, 2000). Veligers were observed in the Richelieu River starting in 1996 (De Lafontaine & Cusson 1997), and juveniles and adults starting in 1997, primarily in the upper (southern) part of the river (Cusson & De Lafontaine 1998). Flow velocities and retention times in the lake are not well understood (M. Hauser pers. comm. 2001). Larval production in the southern part of the lake is high (Eliopoulos & Stangel 1997-2000; M. Hauser pers. comm. 2001), and some observations suggest that larvae are carried northward in pulses from the southern end. A high proportion of the larvae collected at upstream sites in the Richelieu River were late-stage veligers, suggesting that they were not spawned locally (De Lafontaine & Cusson 1997). An order of magnitude decline in veliger densities from the southern to the northern part of the lake, and a futher order of magnitude decline to the northern part of the Richelieu River, also suggests that reproduction occurs only in the southern, higher calcium portions of the system. However, Eliopoulos & Stangel (1998) argue that peak veliger densities at a northern lake site that are higher than densities at central lake sites may indicate local reproduction in the northern lake. Recruitment in northern sites could also be augmented by drifting juveniles or adults attached to boat hulls.

Lake George has a mean calcium concentration of 11 mg/l (Hansen *et al.* 1998), and in laboratory experiments veligers reared in Lake George water died (S. Nierzwicki-Bauer pers. comm. 2001). However, since 1999 over 20,000 adult mussels have been collected in a 1,500 m^2 area at the south end of the lake. Since no veligers or newly settled juveniles have been collected, and since the number of mussels collected in an ongoing effort has progressively declined and the mean size of the mussels has progressively increased, the population is apparently not reproducing and is dying out (S. Nierzwicki-Bauer pers. comm. 2007). A concrete boardwalk was constructed along the shore of this area in 1998, and a culvert emptying into the area carries groundwater and stormwater runoff with calcium levels that are reportedly four times ambient lake levels (*i.e.* 40-50 mg/l of calcium). The presence of a substantial population of apparently non-reproducing adult mussels in this small area could have resulted from (1) large numbers of adult mussels in spawning condition brought into the lake attached to the equipment used to construct the boardwalk, and/or (2) a temporary, local increase in calcium levels caused by calcium inputs from the boardwalk construction or discharge from the culvert, augmented by the impoundment of water behind a silt curtain deployed during construction (S. Nierzwicki-Bauer pers. comm. 2001).

Zebra mussels have been reported from twelve other inland water lakes with mean reported calcium concentrations below 28 mg/l (Cohen & Weinstein 2001; Table 15). The calcium concentrations in four of these are between 25 and 27 mg/l, in three are between 20 and 25 mg/l, in two are 18 mg/l, and in three are between 4 and 11 mg/l.

Three lakes in Ontario (Buckhorn, Opinicon and Balsam lakes) with calcium levels between 20 and 26 mg/l are on the Rideau or the Trent-Severn waterways. Both of these are popular boating routes that connect with waters with established zebra mussel populations, and thus may serve as pathways for frequent reintroductions of mussels. In Connecticut, West Twin Lake receives the downstream flow from East Twin Lake, which has higher calcium levels and an established zebra mussel population, and thus may be the spawning site for the veligers and settled adults observed in West Twin Lake. The zebra mussel records include observations of adults in six of the lakes, are based on veligers only in five of the lakes, and in one is unstated. Records based only on visual identification of veligers, especially if based on few specimens, can easily involve misidentification (L. Johnson pers. comm. 2001). The records in the three lakes with reported calcium levels below 18 mg/l are of veligers only. Subsequent annual sampling in one of these lakes, Lake Dunmore, which yielded no further observations of zebra mussels suggests that they are not established there (Eliopoulos & Stangel 2001-2003; Stangel 2004; Stangel & Shambaugh 2005). The mean calcium values for four of the lakes are based on a total of 15 samples, while the values for the other eight lakes are based on 4 or fewer samples, or on an unknown number of samples. With so few samples, it's unclear whether the range of calcium concentrations in these lakes might substantially exceed the reported values. When these three issues are considered together (Table 16), none of these lakes represents a compelling case for an established zebra mussel population reproducing in low calcium waters. While Lake Bomoseen apparently does have a well-established population of zebra mussels (Eliopoulos & Stangel 2000-2003; Stangel 2004; Stangel & Shambaugh 2005), its reported mean calcium concentration of 18 mg/l is based on only two measurements, leaving significant uncertainty regarding what range of concentrations the mussels may be exposed to during critical life history stages.

The Tennessee River may be another site where zebra mussels occur in low calcium water. Zebra mussels were first reported in both the lower Ohio River and the lower Tennessee River (a tributary of the Ohio) in the fall of 1991. Over the next few years, large numbers of adults and veligers were observed in the Ohio River but only a few adults and no veligers were seen in the Tennessee River. Sickel and Leek (1994) suggested that zebra mussels failed to establish in the Tennessee River due to low calcium concentrations, which they said averaged around 20 mg/l in the Tennessee River compared to about 40 mg/l in the lower Ohio River. However, zebra mussels were soon present throughout the length of the Tennessee River, with veligers detected at nearly all power plants on the river (Kerley 1998, 1999), though presence and abundance are highly variable from year to year (Whittier *et al.* 2008). Whittier *et al.* (2008) noted that the river drains areas with very different calcium concentrations, which they mapped as highly variable or high in calcium in the upper watershed and high or low in calcium in the lower watershed. In Tennessee River reservoirs and tributaries, calcium ranges from around 1 mg/l to around 37 mg/l, with a median value below 20 mg/l at its mouth (Whittier *et al.* 2008). It's possible that any zebra mussels that settled in low calcium portions of the river resulted from spawning in upstream, higher calcium reaches, but the data needed to assess this are not yet available.

Table 16. Zebra mussel records in inland waters with calcium concentrations <28 mg/l. Asterisked lakes are connected by channels or waterways to higher calcium waters with established zebra mussel populations.

Water Body	Records and life stages collected	Mean calcium mg/l	n	Reference
Devil Lake, ON	1994: one veliger	27	15	Kraft 1995; Hincks & Mackie 1997; A. Dextrase pers. comm. 1998
Buckhorn Lake, ON*	1996	26	15	Hincks & Mackie 1997; A. Dextrase pers. comm. 1998
Dogwood Lake, IN	1998: veligers	26	4	Indiana DNR 1998; Indiana CLP 1998
Lake Opinicon, ON*	1991-94: veligers &/or adults	25	?	A. Dextrase pers. comm. 1998; http://www.rideau-info.com/local/zebra.html
West Twin Lake, CT*	1999-2007: adults &/or veligers	21	1	Murray *et al.* 1993; N. Balcom pers. comm. 2001
Houghton Lake, MI	1993: veligers	20	1	Benson 1998; STORET data
Balsam Lake, ON*	1991: veligers & adults	20 25	15 ?	Hincks & Mackie 1993, 1997; A. Dextrase pers. comm. 1998
Lake St. Helen, MI	1994: adults	18	1	Benson 1998; STORET data
Lake Bomoseen, VT	1999-2004: adults &/or veligers	18	2	Eliopoulos & Stangel 2000-2003; Stangel 2004; Stangel & Shambaugh 2005; M. Hauser pers. comm. 2001
Crotch Lake, ON	1995: veligers	11	?	A. Dextrase pers. comm. 1998
Lake Muskoka, ON	1991: one veliger	5 6 7	? 15 ?	Hincks & Mackie 1993, 1997; Kraft 1994; A. Dextrase pers. comm. 1998
Lake Dunmore, VT	1999: veligers	4	4	Eliopoulos & Stangel 2000-2003; Stangel 2004; Stangel & Shambaugh 2005; M. Hauser pers. comm. 2001

As described earlier, the various assessments conducted of zebra mussels' calcium requirements have come to a range of different conclusions (Table 17). A few studies have also stated limits in terms of alkalinity or hardness. Claudi and Mackie (1994), for example, give the limiting value for alkalinity that divides poor growth from no survival as 18 mg/l as $CaCO_3$, (=360 µeq/l) and the limiting vaue for total hardness as 23 mg/l as $CaCO_3$. Whittier *et al.* (1995) used a limit of 400 µeq/l of alkalinity.

One difficulty in both estimating zebra mussels' calcium requirements and in using the resulting estimates for predictions is that the mussels' calcium needs probably vary to some degree with changes in other environmental factors. Several studies have concluded that zebra mussels' calcium threshold varies with pH, usually declining with increasing pH (Ramcharan *et al.* 1992; Hincks & Mackie 1997; S. Nierzwicki-Bauer pers. comm. 2001). Vinogradov *et al.* (1993) found that lowering the pH below about 7 increased the rate of calcium loss in waters with low calcium levels. Zebra mussels' better survival in natural waters with higher calcium concentrations could in part be due

Table 17. Zebra mussel's minimum ambient calcium concentration, as indicated by different studies.

Limit	Basis	Reference
2 mg/l	Value apparently dividing "unlikely" from "possible" potential distribution in analysis in North & South Carolina	Duke Power 1995
7 mg/l	Value dividing "no survival" from "low survival" in analysis in Rhode Island	Tammi *et al.* 1995b
8 mg/l	Minimum to maintain ciliary activity in excised gills	McCauley & Kott 1993
8.5 mg/l	Lower limit for growth, from regression model	Hincks & Mackie 1997
9 mg/l	Value dividing "unlikely" from "maybe" potential distribution in analysis in North Carolina	Doll 1997
9 mg/l	Value dividing "very low" from "low" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
10 mg/l	Value dividing "no survival" from "poor growth".	Claudi & Mackie 1994
10 mg/l	Value dividing "low survival" from "poor to moderate growth" in analysis in Rhode Island	Tammi *et al.* 1995b
10 mg/l	Lower limit of distribution	Boelman *et al.* 1997; Miller *et al.* 1992
10-14 mg/l	Minimum value for maintaining metabolic equilibrium in laboratory trials	Vinogradov *et al.* 1987, 1993
12 mg/l	Value producing <5% of the normal healthy larvae after exposing egg to 3-day-old veligers	Sprung 1987
12 mg/l	Value dividing "unlikely" from "possible" potential distribution in analyses in Ontario, Connecticut and Rhode Island	Neary & Leach 1991; Murray *et al.* 1993; Tammi *et al.* 1995a
12 mg/l	Lower limit for larval growth, based on literature review	Baker *et al.* 1993a
12 mg/l	Lower limit for sustaining large populations, based on literature review	Baker & Baker 1993
12-15 mg/l	Lower limit for adults based on literature review	McMahon 1996
12-28 mg/l	Range of lower limiting values used to prioritize risk in analysis in California	Cohen 2007
15 mg/l	Minimum concentration needed for sperm release	Hincks & Mackie 1993
15 mg/l	Lower limit for establishment	Mellina & Rasmusen 1994
15 mg/l	Lower limit for larvae based on literature review	McMahon 1996
15 mg/l	Value dividing "low-to-no" from "moderate" potential distribution in analysis in California	Cohen & Weinstein 1998
20 mg/l	Value dividing "low" from "moderate" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
25-28 mg/l	Lower limit, based on literature review.	Karatayev *et al.* 2007b
25.4 mg/l	Lower limit for occurrence in 527 lakes in Belarus	Karatayev 1995
28.3 mg/l	Lower limit for occurrence in 76 lakes in Europe	Ramcharan *et al.* 1992
34.5 mg/l	Lower limit for large populations in 76 lakes in Europe	Ramcharan *et al.* 1992

to the presence of magnesium in those waters (S.J. Nichols pers. comm. 2001). Zebra mussels may also obtain some calcium from their diet: mollusks typically meet 70-80% of their calcium needs by absorbing calcium ions from the water column, and the rest through food (Vinogradov *et al.* 1993). Zebra mussels may also be able to resorb some calcium from their shells in order to meet metabolic requirements. One additional complexity is that calcium uptake by rapidly growing zebra or quagga mussel populations can reduce calcium concentrations and alkalinity (*e.g.* 4-5 mg/l reductions in calcium in offshore waters of Lake Ontario; Barbiero *et al.* 2006).

pH

Ramcharan *et al.* (1992) analyzed 76 European lakes and found that zebra mussels were absent from those with pH below 7.3. In laboratory experiments, Vinogradov *et al.* (1993) found that zebra mussels suffer a net loss of sodium and calcium at pH levels below 6.8-6.9, and that zebra mussels are generally more vulnerable than other

Table 18. Lower pH Limit for Zebra Mussels as Indicated by Different Studies

Limit	Basis	Reference
6.3-6.8	Minimum to maintain ciliary activity in excised gills	McCauley & Kott 1993
6.5	Lower limit for adults based on literature review	McMahon 1996
6.5	Value dividing "very low" from "low" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
6.5	Index of 0 (perfectly unsuitable, or lethal) on the Habitat Suitability Index curve	Hayward & Estevez 1997
6.8	No survival below this value	Claudi & Mackie 1994
6.8	Value dividing "unlikely" from "maybe" potential distribution in analysis in North Carolina	Doll 1997
6.8-6.9	Lower limit below which there is net loss of calcium and sodium	Vinogradov *et al.* 1993
7.0	Lower limit for adult survival, based on literature review	Baker *et al.* 1993a
7.0	Lower limit for sustaining large populations, based on literature review	Baker & Baker 1993
7.3	Lower limit of occurrence in 76 lakes in Europe	Ramcharan *et al.* 1992
7.3	Value dividing "low-to-no" from "moderate" potential distribution in analysis in California	Cohen & Weinstein 1998; Cohen 2007
7.3-7.4	Lower limit for larvae based on literature review	McMahon 1996
7.3-7.5	Lower limit, based on literature review.	Karatayev *et al.* 2007b
7.4	Value dividing "unlikely" from "possible" potential distribution in analyses in Ontario and Rhode Island	Neary & Leach 1991; Tammi *et al.* 1995
7.4	Lower limit for veliger development in laboratory trials	Sprung 1993
7.4	Lower limit for larval growth, based on literature review	Baker *et al.* 1993a
7.4	Lower limit for establishment	Karatayev 1995
7.5	Value dividing poor from moderate growth	Claudi & Mackie 1994
7.5	Lower limit for adult growth, based on literature review	Baker *et al.* 1993a

freshwater bivalves to disruption of their ion metabolism from low pH. Sprung (1993) reported that veligers develop properly in the laboratory only at a pH between 7.4 and 9.4, with peak success at around pH 8.4 in 18-20°C. McCauley and Kott (1993) found that ciliary activity ceased in gills excised from adult Lake Erie zebra mussels and placed them in solutions with a pH at or below 6.3-6.8. Baker and Baker (1993a) found that pH levels below about 7.0 will not sustain large zebra mussel populations based on the "preponderance of evidence." Overall, researchers have generally concluded that zebra mussels' pH range is between 6.5-7.5 (Table 18) and 9.0-9.5 (Table 19).

Table 19. Upper pH Limit for Zebra Mussels as Indicated by Different Studies

Limit	Basis	Reference
9.0	Value dividing "low" from "moderate" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
9.0	Value dividing "low-to-no" from "moderate" potential distribution in analysis in California	Cohen & Weinstein 1998
9.4	Upper limit for veliger development in laboratory trials	Sprung 1993
9.4	Upper limit for larval growth, based on literature review	Baker *et al.* 1993a
9.4	Upper limit for vulnerable waters in analysis in California	Cohen 2007
9.5	Value dividing "unlikely" from "maybe" potential distribution in analysis in North Carolina	Doll 1997
9.5	Index of 0 (perfectly unsuitable, or lethal) on the Habitat Suitability Index curve	Hayward & Estevez 1997

Substrate

Zebra mussel larvae generally need hard substrates (rocks, artificial structures, vegetation, debris, etc.) to settle on. Mean weighted particle size explained 38-91% of the variation in the density of zebra mussels in the Hudson and St. Lawrence rivers and Oneida Lake, and explained 75% of the variation in zebra mussel density in 72 other lake sites described in the literature, with the mussels being more abundant in coarser substrate (Mellina & Rasmussen 1994). However, in lakes with little hard substrate, zebra mussels may initially settle on sticks, logs, shells or plants, or sometimes attach directly to sand grains, and later settle onto each other, eventually forming large aggregations (Ramcharan *et al.* 1992; Mellina & Rasmussen 1994; Nichols 1996; Berkman *et al.* 1998; (Jones & Ricciardi 2005). The value of substrate size as a predictor of mussel density may thus decline over time; in a study in the St. Lawrence River in 2003, substrate size was found to account for only 20% of the variation in zebra mussel biomass, and up to 900 g/m^2 of zebra mussel biomass was found on sands and silts (Jones & Ricciardi 2005). In waters where quagga mussels have become more abundant than zebra mussels, zebra mussels remain the dominant species attached to aquatic vegetation (Karatayev *et al.* 2007b).

Zebra mussels prefer to settle initially on filamentous substrates such as some aquatic plants, or on the underside of artficial substrates (Ackerman *et al.* 1994), and later move to other substrates. Post-settlment relocation occurs all year, but peaks in the spring (Ackerman *et al.* 1994).

Dreissena bugensis

Life History

Quagga mussels' life cycle appears to be similar to that of zebra mussels as described above. They are dioecious broadcast spawners, fertilization occurs in the water column, and the larvae develop through a planktonic larval stage before settling to the bottom. We found no data indicating any significant differences in fecundity or larval development times. Quagga mussels appear to be more capable of settling and growing on soft sediments and on fine sediments than zebra mussels; factors that contribute to this include shell shape, with the zebra mussel's flat ventral surface being an adaptation for attaching tightly to a hard surface, and the quagga mussel's rounded shell being more adapted to a life in sediment (Mills *et al.* 1993; Morton 1993; Dermott & Munawar 1993). Quagga mussels living in deep water have very fragile shells (Roe & MacIsaac 1997), suggesting that they allocate a greater part of their energy to soft tissue and less to shell growth than do quagga or zebra mussels that are closer to the surface. This may be an adaptation to waters where both food availability and predation pressure are less.

The quagga mussels found in North America have been reported to occur in two morphologically distinct forms, one that occurs in some deep sections of Lakes Erie and Ontario ("profunda") and one that is more common in shallow water (Dermott & Munawar 1993; Spidle 1994; Claxton & Mackie 1998). Some small differences in the timing of gametogenesis and spawning have been observed (Claxton & Mackie 1998). Genetic studies suggest that the two forms are phenotypic variants rather than genetically distinct taxa (Spidle 1994; Spidle *et al.* 2005), but further analysis using faster evolving genes may yet show genetic differences (Claxton & Mackie 1998).

Quagga mussels have a much wider depth distribution than zebra mussels, abundantly colonizing deep waters as well as shallow waters (Roe & MacIsaac 1997). Physiological and ecological characteristics that may account for this include quagga mussels' ability to spawn in colder waters (Roe & MacIsaac 1997), their greater ability to colonize soft sediments, and possibly a greater ability to grow where in waters with poor food resources (Baldwin *et al.* 2002).

Distribution, Dispersal and Invasion History

Quagga mussels are native to the Dnieper-Bug Liman, a large coastal lake connected to the northern Black Sea, and the lower Bug and Inguletz rivers, which drain into the liman (Therriault *et al.* 2004; Karatayev 2007b). Quagga mussels spread to the nearby

Dneiper and Dneister rivers starting in the 1940s, the Don and Volga rivers in the early 1980s, the Moscow River in 2002, the Danube River in 2004 and the Rhine River in 2006 (Mills *et al.* 1996; Lvova 2004; Orlova *et al.* 204; Zhulidov *et al.* 2005; Popa & Popa 2006; Karatayev 2007b; Nalepa 2008). This spread was facilitated by ship transport through canals and by the construction of reservoirs that provided suitable habitat (Mills *et al.* 1996).

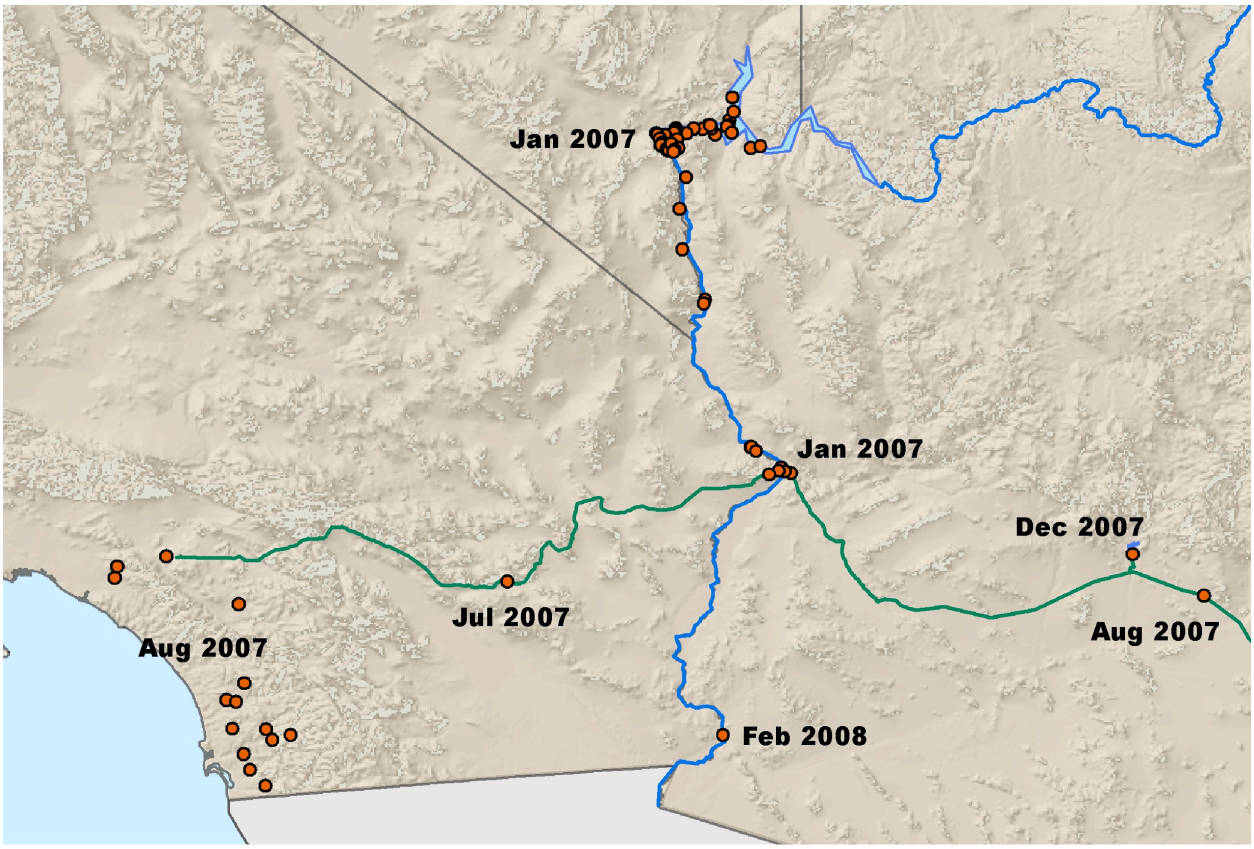
Quagga mussels were first collected in North America in eastern Lake Erie in 1989 (Mills *et al.* 1993, 1996, 1999), though they were not recognized as a distinct species from zebra mussels until one was detected in 1991 in a genetic screening for a study of zebra mussel genetic diversity, and later identified as *Dreissena bugensis* (May & Marsden 1992; Spidle 1994; Spidle *et al.* 1994).[14] By 1992 they were about as abundant as zebra mussels in Lake Ontario (in collections quagga mussels were 37-52% of dreissenids), though rare in neighboring waters (in the Erie Canal, Niagara River and the outlet to Onondaga Lake quagga mussels were <1-2% of dreissenids) (May & Marsden 1992). By 1993 they ranged from Lake St. Clair (between lakes Huron and Erie) to the St. Lawrence River at Quebec (Mills *et al.* 1999). In 1994 they were found in Lakes Cayuga and Seneca, in the Great Lakes Basin (Mills *et al.* 1996). In 1997 they were collected in the Straits of Mackinac, between lakes Huron and Michigan, and in western Lake Huron (Nalepa *et al.* 2001; USGS NAS website). They were collected in Lake Michigan starting in 2000, and by 2005 reached densities >1,000/m^2 over much of the lake and replaced zebra mussels as the dominant benthic species (Nalepa *et al.* 2001; Nalepa 2008; see Table 21). Quagga mussels were collected in Duluth-Superior Harbor at the western end of Lake Superior in 2005, where they appear to be established (Grigorovich *et al.* 2008).

Outside of the Great Lakes Basin they were reported in the Mississippi River near St. Louis in 1995 (Mills *et al.* 1996), and the USGS NAS website[15] reports a few additional specimens collected in the upper Mississipi River in 2004-2006 and in the Ohio River in 2004-2005. In 2000 they were collected in Dutch Springs Reservoir, and in 2007 in Clover Creek Quarry, both of them in Pennsylvania, and both possibly the result of introductions by scuba divers (USGS NAS website). In 2005 they were collected in the Mohawk River at Crescent, New York (USGS NAS website). It's unclear which of these may represent established populations.

In January 2007, quagga mussels were discovered in the western basin of Lake Mead, in Lake Mojave, in Lake Havasu, at a few intermediate points on the Colorado River, and in Gene Wash Reservoir on the Colorado River Aqueduct (CRA), which takes water from Lake Havasu. By August of 2007 they had been discovered in 16 additional reservoirs on the CRA system, in Riverside, Orange and San Diego Counties, and in the central and eastern basins of Lake Mead, a little further upstream in the Colorado River system (Figure 5). A single adult was found in August 2007 near Phoeniz, Arizona

[14] Debate continues in the taxonomic community as to whether the quagga mussel is a separate species, *D. bugensis*, or a subspecies, *D. rostriformis bugensis*. Without taking a position on this question, for simplicity we use the name *D. bugensis* in the present work.
[15] At http://nas.er.usgs.gov/.

Figure 5. The spread of quagga mussels in the southwestern U.S. Cohen/SFEI map.



in the Central Arizona Project (CAP), which also takes water from Lake Havasu, and in December 2007 quagga mussels were discovered, apparently established, in a marina in Lake Pleasant, a reservoir northwest of Phoenix that receives water from the CAP. All of these records on both aqueduct systems could have resulted from veligers carried from Lake Havasu or further upstream in the Colorado River system. The Lake Pleasant marina population could clearly also have resulted from overland transoprt on a trailered boat: in February 2007, a 55-foot houseboat arriving from Lake Mead with abundant live quagga mussels on its hull was intercepted and quarantined at the same marina. In February 2008, quagga mussels were collected in shallow ponds near Imperial Dam that received water from the Colorado River. However, during the summer the water in these ponds apparently gets too hot for quagga mussels, and no further observatins were reported at this site (Cohen unpublished data).

There have been a few less certain and perhaps less reliable reports of quagga mussels in the West. In July 2007, federal agencies reported the detection of three quagga mussel veligers in Lake Powell, upstream of Lake Mead on the Colorado River. These were detected by microscopic examination of plankton samples and confirmed by genetic testing. However, no further observations of dreissenid veligers or adults have been made in the lake. In July 2008, Quagga mussel larvae were reported in Lake Granby in Colorado, just west of the continental divide. Initial detection was again by

microscopic examination of plankton samples, and coirmed by genetic analysis by two independent laboratories. However, the calcium levels in Lake Granby and surrounding waters appear to be too low to support dreissenid mussels, and several researchers (including myself) have expressed skepticism about their establishment, and perhaps even their presence, in the lake. No further specimens of veligers or adults have been observed. Just recently, in September 2008, there was a report of dreissenid mussels detected in two water bodies in Utah (Pelican Lake and Red Fleet Reservoir); genetic analysis of these samples has not yet been completed.

As with zebra mussels, quagga mussels' introduction to North America may have been facilitated by a boom in Canadian and American wheat exports to the Soviet Union in the early 1980s, with the mussels arriving in the U.S. in the ballast tanks of returning ships (Karatayev *et al.* 2007b). Dispersal in the eastern U.S. was probably accomplished by a combination of larval drift, possibly some transport in ballast water within the Great Lakes, and transport attached to boats moving through the water or trailered over land.Scuba divers may have intentionally or perhaps accidentaly introduced quagga mussels into Clover Creek Quarry (also known as Blue Hole Quarry) and Dutch Springs Reservoir in Pennsylvania. Overland transport on a trailered boat is the likeliest method for quagga mussels to have reached Lake Mead. Subsequent spread in the southwestern U.S. was accomplished by veligers drifting downstream and transported through water supply aqueducts, though a few sites (such as Lake Pleasant in Arizona) may be the result of overland transport on boats. There have been several incidents of boats from lakes Mead, Mojave or Havasu intercepted with quagga mussels on their hulls at California border check stations.

Overland dispersal is facilitated by the quagga mussel's ability to survive out of the water for significant periods of time. In laboratory experiments, these periods are greater at higher humidity and lower temperature, with larger mussels surviving longer than small mussels (Table 20). Based on these data, Ricciardi *et al.* (1995) concluded

Table 20. Quagga mussels' maximum survival times (in days) for aerial exposure in laboratory experiments.

Relative Humidity	Temperature 10°C	15°C	20°C
<5%	–	5[a]	–
10%	–	–	1-3[b]
33%	–	5[a]	–
50-53%	–	6[a]	1-3[b]
75%	–	7[a]	–
≥95%	<10[b]; 10-15[c]	13[a]	3-5[b]

[a] Time to 100% sample mortality in 14-30 mm long mussels from Lake Erie (Ussery & McMahon 1994, 1995).

[b] 12-18 mm long mussels from the St. Lawrence River (Ricciardi *et al.* 1995).

[c] 21-24 mm long mussels from the St. Lawrence River (Ricciardi *et al.* 1995).

that quagga mussels could survive 3-5 days of overland transport, the same as for zebra mussels although their survival in the laboratory experiments was slightly less.

In many reservoirs and canals in the Ukraine and Volga River basin, in the lower Great Lakes, and in some other water bodies where zebra mussels arrived first, quagga mussels have replaced zebra mussels as the dominant bivalve in 5-10 years, especially but not exclusively in deep waters (Mills *et al.* 1996, 1999; Ricciardi & Whoriskey 2004; Zhulidov *et al.* 2004; Orlova *et al.* 2004; Wilson *et al.* 2006; Karatayev *et al.* 2007b; Nalepa 2008; Table 21). In the Don River, quagga mussels initially replaced zebra mussels in dominance, but subsequently declined relative to zebra mussels (Zhulidov *et al.* 2006). Where quagga mussels have largely replaced zebra mussels, one cause may

Table 21. Displacement of zebra mussels by quagga mussels.

Water Body	Date	Quagga Mussel Abundance	Zebra Mussel Abundance	Reference
Dneiper River: Kiev Reservoir	1953-70	not present	1st record	Mills *et al.* 1996
	1971	1st record	—	
	1975	4,952 g/m^2	2,797 g/m^2	
	1976-77	9,330 g/m^2	59 g/m^2	
	1978	10,900 g/m^2	18 g/m^2	
Dneiper River: hydropower intake structures	1964	7%	93%	Mills *et al.* 1996
	1966	15%	85%	
	1973	98%	2%	
Volga River: Kuybyshev Reservoir	1992-93	10-54%	46-90%	Orlova *et al.* 2004
	2001	83-100%	0-17%	
Volga River: Saratov Reservoir	1992	<1-4	96-99%	Orlova *et al.* 2004
	1998	55-100	0-45%	
Volga delta	1993	0%	100%	Orlova *et al.* 2004
	1994	4%	96%	
	1995	24%	76%	
	1996	32%	68%	
	2000	96%	4%	
Lake Ontario: Canadian shore	1993	≤100/m^2	50-17,000/m^2	Wilson *et al.* 2006
	2003	93-100%	0-7%	
Soulanges Canal, on the St. Lawrence River	1991	0%	100%	Ricciardi & Whoriskey 2004
	1992-95	<4%	>96%	
	2002	79%	21%	
Southern Lake Michigan: 0-30 m	1999	0/m^2	2,100/m^2	Nalepa 2008
	2006	≈11,500/m^2	≈0/m^2	
Southern Lake Michigan: 30-50 m	1999	0/m^2	≈1,500/m^2	Nalepa 2008
	2006	≈12,500/m^2	≈0/m^2	

be declines in phytoplankton stocks resulting from zebra and quagga mussel feeding, with quagga mussels being better adapted to waters with low food resources (Baldwin *et al.* 2002). Quagga mussels have also become abundant in deep waters in the Great Lakes where zebra mussels were rare or absent, and have been found down to 55 m in eastern Lake Erie (Roe & MacIsaac 1997) and down to 130 m in Lake Ontario (Mills *et al.* 1993, 1996, 1999). As noted above, causes may include a greater ability to spawn in cold waters, to colonize soft sediments, or to grow where food levels are low.

Salinity

In the Dnieper-Bug estuary, quagga mussels have been found at a maximum salinity of 4.0 ppt, compared to 7.6 ppt for zebra mussels (Mills *et al.* 1996). In 40-day laboratory trials of Ukrainian mussels, quagga mussels also showed lower salinity tolerance, with high survival rates at up to 4 ppt at 18-21°C (compared to 6 ppt for zebra mussels), and high survival at up to 5 ppt at 7-15°C (compared to 8 ppt for zebra mussels) (Mills *et al.* 1996). Quagga mussel embryos and larvae were also found to be less salinity tolerant than zebra mussels (Wright *et al.* 1996). In another experiment, however, adult quagga and zebra mussels from the Great Lakes showed no differences in their response to salinity, with neither species surviving 18-day exposures to 5 ppt (Spidle *et al.* 1995), and Mills *et al.* (1996) concluded that in North America, there is no evidence that the salinity tolerance of the quagga mussel is any greater than that of the zebra mussel." For both species, survival time at elevated salinities is shorter at higher temperatures (Spidle 1994; Mills *et al.* 1996). Therriault *et al.* (2004) report quagga mussels' salinity range as up to 3 ppt in its native geographic range and up to 2 ppt in its introduced range. Karatayev *et al.* (2007b) concluded, based on a literature review, that quagga

Table 22. Quagga mussel's upper salinity limit as indicated by different studies.

Limit	Basis	Reference
2 ppt	Range limit in introduced areas	Therriault *et al.* 2004
3 ppt	Range limit in native area	Therriault *et al.* 2004
3.5 ppt	Upper limit, based on literature review	Karatayev *et al.* 2007b
4 ppt	Maximum salinity at which quagga mussels have been found in the Dnieper-Bug estuary	Mills *et al.* 1996
4 ppt	Upper salinity limit in waters with stable salinities in analysis in California	Cohen 2007
4-5 ppt	Upper salinity limit for Ukrainian quagga mussels at 18-21°C after acclimation over 40 days	Mills *et al.* 1996
>5 ppt	100% mortality from 18-day exposure	Spidle 1994
5 ppt	Upper limit, based on literature review	Karatayev 1995
5 ppt	68% survival of Ukrainian quagga mussels at 7-15°C after acclimation over 40 days	Mills *et al.* 1996

mussels' upper salinity limit is 3.5 ppt. For an analysis of potential distribution in California, Cohen (2007) used an upper limit of 4 ppt in waters with relatively stable salinities. The published estimates and information on quagga mussels' salinity limit are summarized in Table 22.

Temperature

Karatayev *et al.* (2007b) reported that quagga mussels' lower temperature limit for adult survival is 0°C, though they are also found in the upper Volga River which freezes in the winter. In Lake Erie, quagga mussels spawned at 9°C at a depth of 23 m in 1994 and at 9-11°C in 1995, based on a histologic examination of their tissues (Claxton & Mackie 1998). Quagga mussels collected from the lake at 55 m depth in 1996 also showed evidence of spawning: 80% of the females had at least some mature eggs and 20% had spent gonads. The temperature at the time of collection was 4.8°C (Roe & MacIsaac 1997). Quagga mussels are also reported to begin spawning in the deep waters of Lake Michigan when water temperatures there reach 6°C. Karatayev *et al.* (2007b) reported that quagga mussels need water temperatures of 5-7°C to spawn. For an analysis of potential distribution in California, Cohen (2007) used lower limits of 5°C for mean summer temperature and 6°C for maximum summer temperature, based on a literature review of spawning requirements. All of these figures are lower than the reported minimum spawning temperatures for zebra mussels, which are usually reported as 10° or 12°C. The fact that quagga mussels are typically more abundant than zebra mussels at greater depths (Mills *et al.* 1993, 1996; Roe & MacIsaac 1997; Ricciardi & Whoriskey 2004) does suggest that quagga mussels are a more cold tolerant species than zebra mussels, although other factors may be at work (*i.e.* finer substrates, lower oxygen concentrations and less food availability at depths).

Several studies have compared quagga and zebra mussels' upper temperature limits. A study that exposed these mussels to various combinations of temperature and turbidity concluded that zebra mussels survived high temperatures better than quagga mussels (Thorp *et al.* 1998), but that result is clouded by the use of mussels collected at different latitudes. Quagga mussels acclimated to 20°C and then exposed to water temperatures rising at the rate of 0.3°C/min gaped open and did not respond to prodding at 36.4°C while zebra mussels only did so at 37.0°C (Domm *et al.* 1993). When moved directly from 20°C to 32°C water, quagga mussels lasted an average of 75 minutes before gaping and not responding, while zebra mussels lasted 275 minutes (Domm *et al.* 1993). Quagga mussels acclimated to 5°, 15° and 20°C and transferred to 30°C water suffered high mortality rates within 11-14 days, while all zebra mussels subjected to the same conditions survived these exposures (Spidle 1994; Spidle *et al.* 1995). Most quagga mussels died and all zebra mussels survived in two attempts to acclimate them to 25°C (Spidle *et al.* 1995). These data have led most researchers to conclude that the upper temperature limit is lower for quagga than for zebra mussels (*e.g.* Mills *et al.* 1996, Thorp *et al.* 1998; Karatayev *et al.* 2007b), perhaps as low as 25°C for quagga mussels compared to over 30°C for zebra mussels (Spidle *et al.* 1995).
However, there are some confounding data. In the Dneiper River, quagga mussels tolerate about one degree higher temperatures than do zebra mussels (Table 23). And

in 12 trials of exposures to temperatures that rose from three acclimation temperatures (5°, 15° and 20°C) at 4 rates (1°C rise each 5, 15, 30 or 60 minutes), the temperature which caused 50% mortality (LT_{50}) for quagga mussels was estimated in a logit model to be significantly lower than the LT_{50} for zebra mussels in all but one trial, while the LT_{100} (the temperature producing 100% mortality) was significantly lower *only* in one trial (Spidle 1994; Spidle *et al.* 1995).[16] These latter results suggest that while zebra mussel *populations* may have a greater average tolerance to high temperatures than quagga mussel populations, the tolerance of the most high-temperature tolerant *individuals* within populations may not differ between the species. If so, then a quagga mussel population introduced to waters that experience periodic high temperatures could suffer initially high mortalities of the more high-temperature-sensitive individuals, leaving a population that is as tolerant of high temperatures as are zebra mussels. For an analysis of potential distribution in California, Cohen (2007) used the same upper temperature limit for both quagga and zebra mussels.

Table 23. Effects of high temperatures on Dreissenid populations in the Dneiper River, Ukraine. From Mills *et al.* 1996, citing Antonov & Skorbatov 1990.

	Zebra mussels	Quagga mussels
Onset of mortality	27-27.3°C	28.1°C
50% mortality	28.2-28.4°C	29.3°C
First fully open shells	28.6°C	29.7°C

Field observations suggest an upper limit for some populations of quagga mussels of at least 30°C. In January 2007, quagga mussels that appeared to be at least 1-2 years old were found in surface waters around the shallow margins of Lake Mead, where summer temperatures routinely reach 30°C (J. LaBounty & T. Burke pers. comm. 2007). In the Zaporozhskoe Resevoir in the Ukraine, quagga mussels survive in water temperatures up to 30.5°C (Karatayev *et al.* 2007b). Karatayev *et al.* 2007b) concluded that quagga mussels' upper limit is 31°C, and Cohen (2007) used that value for an analysis of potential distribution in California. The published estimates and information on quagga mussels' upper temperature limit are summarized in Table 24.

[16] These results are consistent with those of Thorp *et al.* 1998, who found that while zebra mussels were significantly more tolerant of higher summer temperatures, there was high survival (>50%) of quagga mussels at 30°C in many of their experiments even though the predicted survival curve peaked near 25°C. They concluded that the temperature response of a quagga mussel population is more variable than the response of a zebra mussel population, implying a greater genetic variability. The data of Spidle (1994) and Spidle *et al.* (1995) and the data and conclusions of Thorp et al. (1998) are inconsistent with those of Domm *et al.* (1993) who found that the range of responses to high temperatures was much wider for a sample of zebra mussels than for a sample of quagga mussels, and thus if the LT_{100}s were the same the LT_{50}s should be lower for zebra mussels than for quagga mussels. *Domm et al.*'s results (from experiments on Lake Erie mussels) do seem more consistent with findings that in North America the genetic diversity of quagga mussels is lower than that of zebra mussels (*e.g.* May & Marsden 1992; Spidle 1994).

Table 24. Quagga mussel's upper temperature limit as indicated by different studies.

Limit	Basis	Reference
25°C	Upper limit indicated by experiment on Lake Erie and Lake Ontario zebra mussels, with acclimation	Spidle 1994; Spidle *et al.* 1995
29.7°C	Upper limit for Dnieper River quaaga mussels	Mills *et al.* 1996, citing Antonov & Skorbatov 1990
30°C	Estimated limit for more than a few days' exposure	Spidle 1994
30°C	Apparent temperature where distributed in Lake Mead	LaBounty & Burks pers. comm. 2007
30.5°C	Temperature where distrbuted in Ukraine	Karatayev *et al.* 2007b
31°C	Upper limit, based on literature review	Karatayev *et al.* 2007b
31°C	Upper limit in analysis in California	Cohen 2007
<32°C	Upper limit indicated by experiment, without acclimation	Domm *et al.* 1993
34.3°C	Predicted 100% mortality of North American mussels acclimated to 15°C with temperature rising at 1°C/min	Spidle 1994
34°C	Maximum summer temperature with predicted survival of <10% for Lake Erie quagga mussels	Thorp *et al.* 1998
35.3°C	Predicted 100% mortality of North American mussels acclimated to 20°C with temperature rising at 1°C/min	Spidle 1994
36.4°C	Upper limit indicated by experiment in rapidly rising temperatures	Domm *et al.* 1993

Dissolved Oxygen

Karatayev *et al.* (2007b) reported that quagga mussels' require 1.5 mg/l of oxygen at 20°C. McMahon (1996) speculated that quagga mussels might be more tolerant of hypoxic conditions than zebra mussels, based on their more effective colonization of hypolimnetic waters, but their ability to spawn at lower temperatures and their greater ability to colonize soft sediments could also explain this. For an analysis of potential distribution in California, Cohen (2007) used the same lower limit of 4 mg/l for quagga and zebra mussels, based on a literature review of zebra mussels' requirements.

Calcium, Alkalinity and/or Total Hardness

I found no experimental studies that addressed quagga mussels' calcium limit, and probably because their spread in Europe and North America has been relatively limited, only two papers that suggested that their distribution shed light on this question. In 2003, Jones and Ricciardi (2005) sampled for quagga and zebra mussels in the St. Lawrence River down to around Montreal, including several sites at and just below the confluence with the Ottawa River. They found quagga mussels at 16 sites where calcium concentrations measured 12.4-30.0 mg/L on the day of sampling, but absent from four sites below the Ottawa River confluence where the calcium concentrations

measured 7.6-10.0 mg/L. In contrast, they found zebra mussels at sites with calcium measurements down to 8.0 mg/l, which these authors suggest indicates that quagga mussels have a higher calcium threshold than zebra mussels, at least for settlement and growth. The populations below the Ottawa River confluence are almost certainly sink populations, that is, populations made up of mussels that spawned in higher calcium water upstream in the upper St. Lawrence River or in Lake Ontario and that drifted downstream and settled in lower calcium sites where they cannot reproduce (Cohen 2007; Ricciardi pers. comm. 2008). In addition, the sites below the confluence with the Ottawa River may be subject to substantial fluctuations in calcium levels with changes in the relative flows from the two rivers, so conclusions based on correlations between calcium measurements taken on a single day and the presence or absence of mussels at these sites on that day should be suspect.

In the other study, Zhulidov *et al.* (2004) reported that in the Don River system in Russia quagga mussels dominated at sites with higher calcium concentrations (apparently over 100 mg/L), while zebra mussels dominated at sites with lower calcium concentrations (45-78 mg/L), suggesting a higher calcium requirement for quagga mussels. Since the sites of quagga mussel dominance are geographically separated from the sites of zebra mussel dominance (in the Manych River, a tributary of the Don River, versus the mainstem of the Don), other factors could be at work. In any event, for both species he reported calcium concentrations are too high to indicate a threshold for establishing a population, and both species were present at all sampled sites.

For an analysis of potential distribution in California, Cohen (2007) used the same range of values for the lower calcium threshold (12-28 mg/l) to prioritize colonization risk for both quagga and zebra mussels, these values being derived from an analysis of the available data on zebra mussels' calcium requirements.

pH

I found no studies or information on quagga mussels' pH limits, and no distributional data suggesting any difference from zebra mussels. For an analysis of potential distribution in California, Cohen (2007) used the same pH range of 7.3-9.4 for both quagga and zebra mussels, based on a literature review of zebra mussels' requirements.

Substrate

Quagga mussels colonize soft substrates more readily than zebra mussels do, and it has been suggested that they in fact prefer soft substrates (Jones & Ricciardi 2005). In the Dneiper-Bug estuary and in Ukrainian reservoirs, zebra mussels are more abundant on larger sediments (sands and silty sands) and quagga mussels are more abundant on finer sediments (silty-sands and silts) (Mills *et al.* 1996). However in a study in the St. Lawrence River in 2003, quagga mussel biomass was greater on larger substrate sizes (cobbles or boulders rather than sand, silt or mud), and substrate size explained 11% of the variation in quagga mussel biomass (Jones & Ricciardi 2005). In the Great Lakes,

quagga mussels colonize sand and sandy silt between 10 and 30 m depth, and silty substrated below 40 m depth (Mills et al. 1996). In many locations, quagga mussels have displaced zebra mussels on hard substrates (Ricciardi & Whoriskey 2004; Jones & Ricciardi 2005), but not on aquatic vegetation (Karatayev *et al.* 2007b).

Limnoperna fortunei

Life History

Generally less is known about the life history characteristics and environmental requirements of *Limnoperna fortunei* (hereafter just *Limnoperna*) than is know for the two dreissenid species, largely because of its restriction until relatively recently to waters in China and Southeast Asia. Morton noted in 1973, when there was already a substantial and rapidly growing European zebra mussel literature, that *Limnoperna* had "roused little interest. There is a dearth of information on this animal, most records being found in obscure and ancient journals." Like zebra and quagga mussels, *Limnoperna* is dioecious, with males and females releasing sperm and eggs into the water to fertilize, and the embryos develop into free-swimming larvae. *Limnoperna* is, however, smaller (Tyicallength 20-30 mm, maximum lengths normally 30-40 mm), and has a thinner shell and probably a briefer lifespan (2-3 years, but see below for longer records) (Morton 1975, 1979; Iwasaki 1997; Iwasaki & Uryu 1998; Karatayev *et al.* 2007a). Ricciardi (1998) suggested that the planktonic larval stage is likely to fall within the range of other mytilids, that is, 30-70 days (citing Ackerman *et al.* 1994). However, the larval stage was estimated to last 15-20 days in both Korea and Argentina (Darrigran 2002).

In the Uji River in Japan, gonads began to develop in May and matured in June, spawning occurred in July-September and the gonads degenerated in both sexes in October. Young mussels, 2-8 mm long, appeared during the spawning period, grew to an average length of 20 mm by the following summer and reproduced. Mussels up to 35 mm in length were seen during spring and summer, but no mussels over 26 mm were found after September (Iwasaki & Uryu 1998). Morton (1975) reported nearly the same annual growth pattern in Hong Kong, but with different spawning periods. Morton (1975, 1977) initially reported a single long annual breeding season from January-March to September, with spawning occurring in 2 or 3 sessions, but later (Morton 1982) reported two distinct spawning seasons, with gametogenesis starting in March and September, ripe gonads in May-June and November-December, and spawning in June-July and December-February. He noted that spawning takes place during high temperatures and low dissolved oxygen in the summer, and low temperatures and high dissolved oxgen in the winter. In Río de la Plata, generally two main spawning periods per year were observed, a stronger one in the austral fall (sometime between February and July), and a weaker one in the spring or summer (between September and January), though this was not consistent in the earlier years of the invasion; there was also one weak winter spawning reported (July-August) (Darrigran *et al.* 1999, 2003).

Limnoperna fortunei reach maturity in 3-4 months (Karatayev *et al.* 2007a), at about 6 mm length in Argentina (Darrigran *et al.* 1999). Maximum reported sizes are 32 mm in Hong Kong, 35 mm in the Uji River in Japan, and 60 mm in Korea (Morton 1975; Iwasaki & Uryu 1998), and Karatayev *et al.* (2007a) report the maximum length to be 42 mm. *L. fortunei*'s life span is reported to be 2 years in the Uji River in Japan, 2 or occasionally 3 years in Plover Cove Reservoir in Hong Kong, 2-3 years in South America, 4-5 years in Korea, and over 10 years in central China (Morton 1975, 1977, 1982; Iwasaki & Uryu 1998; Darrigran 2002). Karatayev *et al.* (2007a) report the typical life span to be 3 years.

Distribution, Dispersal and Invasion History

Limnoperna fortunei is native to China and probably Korea, and possibly Thailand (where it has been reported in the Kwai River, and possibly at Sopa Falls in Pisanuloke), the Mekong River in Laos and Cambodia; Vietnam; and Indonesia) (Morton 1975, 1982; Darrigran 1997; Iwasaki 1997; Ricciardi 1998; Kimura *et al*. 1999; De Oliveira *et al.* 2006). On the other hand, the Southeast Asia records may represent one or more separate, tropical species. Morton (1982) reported *L. fortunei*'s distribution in China as the Pearl River and, under a probably synonymous name (*Limnoperna lacustris*), the Changjiang (Yangtze) River and lakes Huama and Dongting to the north and south. *Limnoperna fortunei*'s initial appearance in the Hong Kong water supply system in 1966 and subsequent spread through the system's reservoirs, tunnels, culverts and pipelines suggests that it was probably introduced in raw water imports from the East River in China, which began in 1965 (Morton 1973, 1975)[17]. It was first found in Japan in the Kiso River drainage (in the Ibi, Nagara and Kiso rivers) in 1990, and spread to Lake Biwa by 1992 and to the Uji and Yodo rivers downstream from the lake by 1995 (Kimura & Tabe 1997; Iwasaki 1997; Kimura *et al.* 1999. According to Kimura and Tabe (1997), it was accidentally introduced into Japan with live imports of the edible clam *Corbicula* sp. from China. Various authors report that it invaded Taiwan in the 1990s (Ricciardi 1998; Darrigran (2002); Orensanz *et al.* 2002; De Oliveira *et al.* 2006), but Iwasaki (1997) described it as native to Taiwan, Korea and China. It has been regarded as a pest in China, Taiwan, Hong Kong and Korea because it clogs water systems and affects water quality (Kimura & Tabe 1997; Iwasaki 1997; Goto 2002; though Morton (1975, 1982) reported that it was not a serious pest in Hong Kong where its impacts consisted of minor reductions in flow), and as a pest in the Pearl River in China because it fouls boats and jetties (Morton 1975).

Literature in the 1980s and 1990s reported the subspecies *L. fortunei kikuchii* as being present in bays and estuarine/brackish waters through much of southern Japan, either as an introduction or an endemic species. *L. fortunei kikuchii* was distinguished from *L. fortunei fortunei* in Japan's fresh waters by shell shape and color, muscle scars and salinity tolerance. In the late 1990s, a series of studies documented significant chromosomal and DNA differences between these two taxa even where they nearly co-

[17] Morton (1973) reports raw water imports from the East River starting in 1967 and the first record in Hong Kong in 1968, while Orensanz *et al.* (2002) report the first record in Hong Kong as 1965. We rely here on the more detailed treatment of Morton (1975).

occurred in the same river, and *L. fortunei kikuchii* was ultimately identified as *Xenostrobus securis*, a species introduced from Australia or New Zealand (Abdel-Razek *et al.* 1993; Ieyama 1996; Kimura & Sekiguchi 1996; Kimura & Tabe 1997; Kimura *et al.* 1999).

In 1991, *L. fortunei* was discovered at Bagliardi Beach in Argentina in the upper part of the Río de la Plata estuary (Pastorino *et al.* 1993; Darrigran & Pastorino 1993, 1995). It increased from initial densities of 4-5/m^2 to around 30,000/m^2 in 1992, 80,000/m^2 in 1993 and 150,000/m^2 in 1998, then declined and apparently stabilized at around 40,000/m^2 (Darrigran & Pastorino 1995; Darrigran 1997; Darrigran *et al.* 1999, 2003; Darrigran & Ezcurra de Drago 2000). It spread upstream to the Río Paraná by 1995, the Río Uruguay by 1997, the Río Paraguay by 2000 and the Río Pilcomayo by 2002 (covering an average distance of 240 km/year); to Lago Guaíba by 1998 and Lagoa de Patos by 2000, in the Brazil coast region; and to the Río Tercero Reservoir by 2000 (Darrigran 1997, 2002; Darrigran & Ezcurra de Drago 2000; Orensanz *et al*. 2002; Mansur *et al.* 2003; Karatayev *et al.* 2007b). Its rapid advance upstream in the Plata, Paraná and Paraguay rivers was apparently the result of transport on commercial and recreational vessels (Darrigran 2002; De Oliveira *et al*. 2006; Karatayev *et al.* 2007b), its introduction to Lago Guaíba and Lagoa de Patos may have been by ballast water (De Oliveira *et al.* 2006), and its introduction to the Río Tercero was probably accomplished on trailered boats (Karatayev *et al.* 2007b). Fouling problems have been reported in water treatment plants, power-generating plants and industrial facilities in Argentina (Darrigran & Ezcurra de Drago 2000; Darrigran 2002) and in boat engines in Brazil (De Oliveira *et al.* 2006); environmental effects include the displacement or smothering of native mollusks and other species and enhancement of habitat for some benthic organisms, especially oligochetes and leeches (Darrigran & Ezcurra de Drago 2000; Darrigran 2002).

Darrigran and Pastorino (1995) and Darrigran (1997) concluded that because *L. fortunei* had not been collected previously it arrived in the Río de la Plata estuary in the year 1991.[18] Three major commercial harbors—Buenos Aires, Montevideo and La Plata—are located in the estuary. Noting a dramatic increase in imports in 1989-91 (on the order of a 50x increase in the value of the imports) from Hong Kong and to a lesser degree from Korea, Darrigran and Pastorino (1993, 1995) and Darrigran (1997) further concluded that the mussel was probably introduced in "tanks containing untreated fresh water" that were emptied into Argentine port waters and that Hong Kong was the source. Later these authors clarified that they were referring to transport in ballast water tanks (Darrigran & Ezcurra de Drago 2000; Darrigran 2002).[19]

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[18] This is not compelling; data on other invasions suggest that introduction could easily have occurred earlier—and thus via some mechanism unrelated to the 1989-91 rise in imports and hence from a source other than Hong Kong—and gone undetected for some years.

[19] However, Morton (1987) reported that *L. fortunei* had not yet spread into natural watercourses in Hong Kong, and it's unclear whether Hong Kong has a freshwater or low salinity port where *L. fortunei* could have been loaded into a ballast tank. Alternately, introduction via ballast water could have occurred from another site, such as a freshwater port on one of China's large rivers. Also, Kimura and Table (1997) stated that *L. fortunei* was introduced from China to Japan attached to *Corbicula* sp. imported for consumption, and Darrigran (1997) noted that the Asian clam *Corbicula fluminea* arrived in the Río de la

Overland dispersal is facilitated by *L. fortunei*'s ability to survive out of the water for periods of time. Iwasaki (1997) found that small *L. fortunei* (5-10 mm) exposed to air at 26-30°C and 72-81% humidity lived up to 4 days, 10-15 mm mussels lived up to 8 days, and mussels over 15 mm long lived up to 9 days in the laboratory.

Salinity

In the Río de la Plata estuary, *L. fortunei* has been collected in salinities up to 14 ppt at the time of collecting (Karatayev *et al.* 2007a, b), but is normally found at up to 3 ppt (Darrigran 2002; Orensanz *et al.* 2002). It has been collected upstream in the Río de la Plata watershed in the Correntoso River where salinity ranges from 0.06-0.35 ppt and in the Salado del Norte River where salinity ranges from 0.5-4.0 ppt (Darrigran & Ezcurra de Drago 2000). Japanese populations reportedly tolerate up to 3 ppt (Darrigran 2002, citing Kimura *et al.* 1995). In Hong Kong, *L. fortunei* was first observed in Plover Cove Reservoir in the late spring of 1969, a few years after the reservoir was constructed from a tidal cove and shortly after its salinity had dropped from initial levels of 1.4-2.3 ppt to 0.5-0.6 ppt[20] (Morton 1977). Ricciardi (1998) reports *L. fortunei*'s salinity range as 0-12 ppt, and Karatayev *et al*. (2007a) reports its upper salinity limit to be 15 ppt.

Temperature

Limnoperna fortunei occurs in Hong Kong waters at a temperature range of 14-31°C (Morton 1975, 1977), in Lake Huama in northern China at a range of 8-30°C (Morton 1982), in a water intake that draws from the Yodo River in Japan at a range of 5-31°C, and in the Uji River in Japan where winter water temperatures reach 7-9°C (Iwasaki & Uryu 1998; Goto 2002). In South America it has invaded temperate areas where the range of water temperatures is 14-24°C and subtropical areas where the range is 15-33°C, according to Darrigran (2002); while Karatayev *et al.* (2007b) gives the temperature range for the temperate areas as 10-29°C and for the subtropical areas up to 32-33°C. Karatayev *et al.* (2007a, b) reported *L. fortunei* in waters in Japan with winter temperatures of 5-6°C, and in Paldang Reservoir in Korea with winter surface temperatures down to 0°C. Ricciardi (1998) states that adults occur in temperatures of 8-35°C, and that larvae develop between 11° and 33°C. Karatayev *et al.* (2007a, b) report that *L. fortunei*'s overall temperature limits are 0-35°C.

Limnoperna fortunei reproduces in the Uji River in Japan when water temperature reaches 21-27°C, in central China at 16-21°C, and in Korea at 23-28°C (Morton 1982; Iwasaki & Uryu 1998; Ricciardi 1998). In the Plover Cove Reservoir in Hong Kong, there are two spawning peaks, one in summer during the annual temperature maximum of 27-28°C, and one in winter at or just after the annual temperature minimum of 16-17°C, a distinct and unusual spawning pattern (Morton 1982). Karatayev *et al.* (2007a, b)

Plata between 1965 and 1975, possibly introduced by ships' crews who brought it with them for consumption; so another possibility is that *L. fortunei* entered the Río de la Plata when empty *Corbicula* shells were discarded into the estuary by ships' crews from Asia.

[20] Converted from chorinity values by multiplying by 0.0018 (Sverdrup *et al.* 1942).

report that *L. fortunei* needs a minimum water temperature of 17°C in order to spawn. At the Yacyretá Hydroelectric Plant on the Paraná River, veligers were present only when water temperatures were at least 18-19°C (Darrigran *et al.* 2007).

Dissolved Oxygen

Limnoperna fortunei has been collected at Punta Lara in Argentina, where dissolved oxygen has been measured at 1.7 mg/l (Darrigran & Pastorino 1995). In the Paraná River in Brazil, *L. fortunei* died in large numbers when dissolved oxygen concentrations dropped from 7.0 to around 0.3 mg/l for two months at the start of the flood season (De Oliveira *et al.* 2006). Karatayev *et al.* (2007a, b) state that *L. fortunei* needs a minimum of 0.5 mg/l of oxygen at 20°C.

Calcium, Alkalinity and/or Total Hardness

In Hong Kong, *L. fortunei* is found in a calcium range of 2.4-4.8 mg/l, an alkalinity range of 10-16 mg/l as $CaCO_3$, and a total hardness range of 8-17 mg/l as $CaCO_3$ (Morton 1975). In the Paraguay River in Argentina it has been collected in a calcium range of 4-25 mg/l and at 0-11 °dH of hardness, and is abundant at 10 mg/l of calcium and 0-4 °dH of hardness (Ezcurra de Drago *et al.* 2004). Ricciardi (1998) and Karatayev *et al.* (2007a, b) state that *L. fortunei*'s lower calcium limit is 3 mg/l of calcium, and report it at high densities in the middle Paraná River where calcium levels are 3-4 mg/l.

pH

Limnoperna fortunei has been collected in Hong Kong at a pH range of 6.4-7.0 (Morton 1975), and in Argentina in rivers where pH ranges from 7.2 to as high as 8.7 (Darrigran & Ezcurra de Drago 2000). In the Paraguay River it is found at 7.0-8.2, and is abundant at 7.6-7.7 (Ezcurra de Drago *et al.* 2004). Darrigran (2002) gave its pH range as 6.2-7.4, and Karatayev *et al.* (2007a)creported that its lower pH limit is 5.5.

Substrate

Limnoperna fortunei attaches to hard substrates, both natural (rocks, roots, trunks and stems of aquatic plants, driftwood, other bivalves including other *L. fortune*i, gastropods and crabs; compacted silt-sand (caliche) and silt-clay bottoms) and artificial (docks, pipes, concrete walls, *etc.*) (Darrigran & Pastorino 1995; Darrigran & Ezcurra de Drago 2000; Darrigran 2002; Orensanz *et al.* 2002; Karatayev *et al.* 2007a). It is occasionally found on silt or mud (Karatayev *et al.* 2007a). In the Uji River in Japan, Iwasaki & Uryu (1998) found *L. fortune*i mainly on the undersides of boulders. In Plover Cover reservoir in Hong Kong, Morton (1975, 1977) found that *L. fortunei* preferrentially settled at depths of 20-30 feet, settling mainly in crevices, on shaded horizontal surfaces if in shallow water, and on illuminated vertical surfaces if in deeper water. When juveniles or adults move or are disturbed, they prefer to resettle in crevices and on dark substrates. Juveniles in particular tend to move upward along vertical walls and resettle just below the air-water interface (Iwasaki 1997).

Mytilopsis leucophaeata

Life History

Marelli and Gray (1983) stated that "the biology and natural history of *M. leucophaeata* are largely unknown," and Rajagopal *et al.* (2005b) noted that "*M. leucophaeata*...is a poorly studied animal." As with the other three mussels in this report, it is a dioecious broadcast spawner, with fertilization occurring in the water, a planktonic larval stage, and a byssally-attached, epibenthic adult stage. Jenner and Janssen-Mommem (1993) report that "it is currently thought" that *M. leucophaeata* reaches sexual maturity at a size of about 11 mm, but Bamber and Taylor (2002) state that it is potentially mature at 2.4 mm, and the mean size at maturity is >7 mm at about 2 months of age. In the Netherlands *M. leucophaeata* grows to 13-14 mm in the first year, and reaches 24-27 mm in three years (Bamber & Taylor 2002), and in Finland it grows to a maximum length of 17 mm in its first growing season (Laine *et al.* 2006). In Antwerp Harbor in Belgium, however, it only grows 3-6 mm/yr, and based on the size of the largest individuals its maximum lifespan is estimated to be at least 5 years (Verween *et al.* 2006). Its maximum reported length is 22 mm in North America and 27 mm in Europe (Verween *et al.* 2006).

Temperatures above 13°C are reportedly needed for gamete maturation (Laine *et al.* 2006). In the Netherlands, spawning starts when temperatures rise above 15°C (Jenner & Janssen-Mommem 1993). In a Florida bay, spawning occurred when late spring rains caused a sudden drop in salinity, with water temperatures at around 26°C (Siddall 1980). In the Noordzeekanal in the Netherlands, spawning occurred in June-September when water temperatures were at least 20°C (Bamber & Taylor 2002). Verween *et al.* (2007a) mention both 15°C and 20°C as the temperatures at which different studies found spawning starts. In the laboratory, larvae held at 26°C develop into a D-shell veliger about 2 days after fertilization, into a veliconcha by around 6 days after fertilization, and settle and metamorphose by 6-8 days after fertilization, at a mean shell length of 210 µm (Siddall 1980; Ackerman *et al.* 1994).

Distribution, Dispersal and Invasion History

Mytilopsis leucophaeata is native to the Gulf of Mexico from Tampico, Mexico to Florida, and the Atlantic Seaboard from Florida probably as far north as Chesapeake Bay. It was reported from the Hudson River in 1937 (Rehder 1937) and in 1952 (Jacobson 1953), where it is now well established in the estuary up to around Beacon (at river mile 63) (MacNeill 1991), and reported in southern New England by the 1980s (Marelli & Gray 1983, 1985; Carlton 1992; Therriault *et al.* 2004). Records north of Chesapeake Bay probably represent introductions by ballast water or ship fouling (Jacobson 1953, arguing that the 1952 collection was a separate introduction from the 1937 record, with the mussel absent in the interim; MacNeill 1991; Carlton 1992), though some authors have reported the Hudson River as part of its native range (Bamber & Taylor 2002). In 1988, two live *M. leucophaeata* were collected in the Mississippi River two miles above the confluence with the Missouri River. The location is used as a barge fleeting area,

primarily by oil companies, and it's likely that the mussels arrived from the Gulf Coast attached to a barge (Koch 1989). In 1992 it was collected in Kentucky Lock on the inland waterway system and has been regularly collected in Kentucky Lake (Miller *et al.* 1993). In the U.S., Felder (1994) reported that *M. leucophaeata* "is not a biofouler and will not cause problems in freshwater systems."

Mytilopsis leucophaeata was collected in Belgium in 1835, presumably introduced via shipping, possibly in solid ballast (Marelli & Gray 1983). It was found in the Netherlands in 1895, in France in 1898 and in Germany in 1932 (Bamber & Taylor 2002; Rajagopal *et al.* 2005a, b; Verween *et al.* 2006). Ship movements presumably accounted for some or perhaps much of this spread, though construction equipment moved from the Netherlands to the Kiel Canal in the early decades of the 20th century may have been responsible for *M. leucophaeata*'s arrival in Germany (Gollasch & Rosenthal 2006). Sometime prior to 1962 *M. leucophaeata* was also reported near Kaliningrad in the southern Baltic Sea, but it is apparently not established there (Laine *et al*. 2006).

Mytilopsis leucophaeata's spread in Europe accelerated in the past decade, and is probably due to transport as hull fouling or in ballast water (Bamber & Taylor 2002; Verween *et al.* 2006; Laine *et al.* 2006). It was collected in Britain in 1998 at Cardiff Docks and in the Cliffe Fort Lagoon at the mouth of the Thames (Bamber & Taylor 2002), and was discovered, by genetic analysis, as a cryptic invader collected in the Dneister Liman on the Black Sea in 2002 (Therriault *et al.* 2004). It appeared in Spain and Finland in 2003 (Escot *et al.* 2003; Laine *et al.* 2006; Verween *et al.* 2006). It has caused significant fouling problems at power stations in the Netherlands, Belgium and Finland (Bamber & Taylor 2002; Verween *et al.* 2006).

In 2004 *M. leucophaeata* was reported from a third continent, in estuarine waters near the Port of Recife in Brazil, at maximum densities of 177,000/m^2 (Souza *et al.* 2005). It may have arrived in ballast water (Souza *et al.* 2005) or as hull fouling. In 2004-2006, Farrapeira *et al.* (2007) found *M. leucophaeata* to be common in fouling on the hulls of several cargo ships, fishing boats and other vessels operating out of the Port of Recife.

Salinity

Mytilopsis leucophaeata has been collected in the Chesapeake Bay area in salinities up to 12 ppt (Castagna & Chanley 1973), in a Florida embayment at 8-22 ppt (Siddall 1980), in Cliffe Fort Lagoon in England at 6-15 ppt (Bamber & Taylor 2002), in the Noordzeecanal in the Netherlands at 1-15 ppt (Rajogopal *et al.* 2005a), in Belgium near Antwerp at 0.1-12 ppt (Verween *et al.* 2007b), and on the German Baltic Sea coast at 0.3-8 ppt (Laine *et al.* 2006). It commonly occurs in the Netherlands between 2.0 and 2.5-3.0 ppt salinity, and is uncommon below 0.4 ppt (MacNeil 1991, citing Wolff 1969). It is found in the Rhine River at ≈0.2-0.6 ppt[21] (Rajagopal *et al.* 2005b), and in the Hudson River is common upstream to where the salinity range is 2-6 ppt, and occasionally found up to where salinity is 0-3 ppt (Deaton *et al.* 1989; MacNeill 1991; Walton 1996 MacNeil (1991) cites various sources that report a maximum tolerated salinity for *M.*

[21] Converted from chorinity values by multiplying by 0.0018 (Sverdrup *et al.* 1942).

leucophaeata of 26 ppt, and normal ranges with minimum salinities of 0.1-1.9 ppt and maximum salinities of 3-18 ppt. Verween *et al.* (2006) report it as tolerating 1-18 ppt, and Laine *et al.* (2006) give its salinity range as fresh water to well over 20 ppt. Deaton *et al.* (1989) reported 100% mortality after 80 days in 0 ppt (deionized water), and 50% mortality after 80 days in fresh water (5-10 mOsm). Miller *et al.* (1993) stated that *M. leucophaeata* cannot reproduce in freshwater and is carried from brackish to inland waters on the hulls of commercial and recreational vessels. Verween *et al.* (2007a) reported that adult *M. leucophaeata* can survive in salinities from 0.1-31 ppt and says that both fresh and sea water "are outside the range for survival of *M. leucophaeata*."

In experiments, *M. leucophaeata* demonstrated a remarkable ability to survive sudden large changes in salinity (of up to 30 ppt in either direction), and to survive for many weeks at salinities from 0 to 30 ppt (Castagna and Chanley 1973; Table 25).

Table 25. Response of *Mytilopsis leucophaeata* to sudden experimental salinity changes and exposures to salinity extremes. From Castagna & Chanley 1973; the mussels, 5.5-16.5 mm long, were collected from a salt pond near Chesapeake Bay.

Salinity at Collection Site	1st transfer to:	Number (%) Surviving after 2 weeks	2nd transfer to:	Number (%) Surviving after 2 weeks	3rd transfer to:	Number (%) Surviving after 2 weeks
7 ppt	17.5 ppt	20 (100%)	0 ppt	17 (85%)	30.0 ppt	11 (65%)
7 ppt	17.5 ppt	20 (100%)	2.5 ppt	19 (95%)	27.5 ppt	19 (100%)
7 ppt	17.5 ppt	20 (100%)	27.5 ppt	16 (80%)	2.5 ppt	16 (100%)
7 ppt	17.5 ppt	20 (100%)	30.0 ppt	19 (95%)	0 ppt	2 (11%)

In another experiment, *M. leucophaeata* larvae reared at 10, 24 and 32 ppt all developed and metamorphosed normally, with all treatments growing at the same rate and to the same size (Siddall 1980). Verween *et al.* (2007a) conducted a series of salinity and temperature tolerance tests on 4-hour-old embryos and 2-day-old larvae, using 48 hour exposures. The larvae survived well over the entire salinity test range of 5-25 ppt and over the temperature range of 5-25°C, with only 14% mortality in the most stressful combination of temperature and salinity. For the embryos, survival was generally good over a temperature range of 15-24°C and a salinity range of 3-22 ppt. Only at the extremes of the tested values (10 and 30°C, and 0 and 25 ppt) were the mortality rates high. Embryos were more tolerant of low salinities at high temperatures than at low temperatures, thus the mussels may be more likely to become established in low salinity or fresh water in tropical regions than in temperate ones.

Marelli and Gray (1983) suggested that *M. leucophaeata*'s upstream limits could be controlled by the physiological tolerances of the larvae, or by a lack of salinity pulses that may be needed to trigger spawning (*i.e*. Siddall 1980 reported that spawning in a Florida bay followed a sudden drop in salinity in the spring).

Temperature

Mytilopsis leucophaeata has been collected in Florida in an embayment where temperatures ranged from 13-30°C (Siddall 1980), in the Noordzeecanal in the Netherlands where temperatures ranged from 5-20°C (Rajogopal *et al.* 2005a), and near Antwerp in the Westerscheldt River where temperatures ranged from 7-26°C (Verween *et al.* 2007b). In Finland it is most abundant in a bay that is warmed by cooling waters from a power plant, where temperatures range annually from around 5°C to over 25°C; it also occurs in areas outside of this bay where the water is ice-covered in the winter and near 0°C, but it is not clear if it reproduces in these waters (Laine *et al.* 2006). With temperatures of 13-15°C apparently needed for gamete maturation and spawning (Jenner & Janssen-Mommem 1993; Verween *et al.* 2005), it may be that heating of the water by a power plant is what's allowing this warmwater species to establish in these northern waters (Laine *et al.* 2006).

In laboratory experiments, *M. leucophaeta* was more tolerant of exposure to high temperatures (36-41°C) than were zebra mussels (Rajogopal *et al.* 2005a, b). As noted above, Verween *et al.* (2007a) found good survival of embryos exposed to temperatures from 15°C to 24°C for 48 hours at a range of salinities, and observed high ates of mortality only at the extreme test temperatures of 10°C and 30°C. Two-day-old larvae survived well over the entire test range from 5-25°C, at a range of salinities.

Dissolved Oxygen

Mytilopsis leucophaeata was collected in the Westerscheldt River near Antwerp where oxygen levels were 0.8-12 mg/l (Verween *et al.* 2007b). I found no other information bearing on *Mytilopsis leucophaeata*'s minimum oxygen requirement.

Calcium, Alkalinity and/or Total Hardness

Mytilopsis leucophaeata was collected in 12-56 mg/l of calcium (Deaton *et al.* 1989). I found no other information bearing on *Mytilopsis leucophaeata*'s calcium threshold.

pH

I found no information on *Mytilopsis leucophaeata*'s pH limit.

Substrate

Like the other mussels, *M. leucophaeata* settles preferentially on natural or artificial hard surfaces. Up to 100% coverage of stones and boulders was reported in Finnish waters, where it also attached to a fucoid seaweed (Laine *et al.* 2006). Koch (1989) reported *M. leucophaeta* attached to a freshwater clam in the Mississippi River, and the original species description was based on a specimen attached to an oyster shell (Marelli & Gray 1983).

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