A Review of Zebra Mussels' Environmental Requirements

a report for the

California Department of Water Resources

Andrew N. Cohen
San Francisco Estuary Institute
Oakland, CA

Many studies have investigated the potential distribution of zebra mussels in different regions based on a variety of environmental factors, including temperature, chemical characteristics, sediment size and turbidity (Table 1). The four sections of this report provide (1) background on the zebra mussel's life cycle; (2) a summary of potential distribution studies, (3) a factor by factor review of the environmental characteristics that are most frequently cited as controlling zebra mussel distribution and abundance, and (4) a more detailed review of the available data regarding calcium requirements.

1. The Zebra Mussel's Life Cycle

Different developmental stages of the zebra mussel have different environmental requirements, and both environmental factors and the presence of different developmental stages vary seasonally. An understanding of the zebra mussel's life cycle and its seasonal pattern of development is therefore useful in considering how environmental factors may affect the mussel's distribution.
Gametogenesis generally begins in the fall or winter, with spawning starting in the spring (Mackie *et al*. 1989; Sprung 1993; Mackie & Schloesser 1996; Nichols 1996; McMahon 1996). The spawning period is often prolonged, continuing in pulses to late summer or early fall. In some regions and circumstances the process be considerably delayed, with the synthesis of gametes peaking in the spring and spawning beginning in late summer (Wang *et al*. 1993, 1994). During spawning large quantities of eggs and sperm are released into the water where fertilization occurs, with a single spawning female potentially releasing tens of thousands to millions of eggs (Mackie *et al*. 1989; Sprung 1993; Mackie & Schloesser 1996; Nichols 1996).

After an initial non-feeding phase, the larvae develop intestines and a swimming organ known as the velum, and begin a feeding phase in 2-9 days after fertilization. The larvae are then called veligers, and they develop progressively through a stage with a D-shaped shell, a veliconcha stage with a more rounded shell, and a pediveliger stage with the initial development of a foot. After a week to a month or more of growth they attain shell lengths of around 200-240 μm and settle to the bottom (Mackie *et al*. 1989; Sprung 1993; Ackerman *et al*. 1994; Mackie &

Table 1. Studies of the Potential Distribution of Zebra Mussels

Region Analyzed	**Environmental Parameters Utilized**	**References**
North America	mean annual air temperature, monthly mean air temperature	Strayer 1991
Ontario	pH, calcium	Neary & Leach 1992
Connecticut	calcium	Murray *et al.* 1993
Virginia	pH, calcium	Baker *et al.* 1993
Hudson River estuary	salinity	Strayer & Smith 1993
Wisconsin	pH, calcium, nitrate, phosphate	Koutnik & Padilla 1994
Mississippi River	monthly mean water temperatures	Armistead 1995
Rhode Island	pH, calcium	Tammi *et al.* 1995a
Rhode Island	calcium	Tammi *et al.* 1995b
North & South Carolina	pH, calcium, turbidity, *Corbicula* abundance	Duke Power 1995
North Carolina	temperature, salinity, pH, calcium, dissolved oxygen	Doll 1997
California	temperature, pH, calcium	Janik 1997
Manitoba	temperature, conductivity, pH, calcium, total hardness, dissolved oxygen, turbidity	Sorba & Williamson 1997
Florida	temperature, salinity, pH, calcium, dissolved oxygen, turbidity, sediment size	Hayward & Estevez 1997
California	temperature, salinity, pH, calcium, dissolved oxygen	Cohen & Weinstein 1998
United States	temperature, pH, alkalinity, dissolved oxygen	Ashby *et al.* 1998

Schloesser 1996). Development times are longer at lower temperatures and with lower food availability. Larvae that are produced in the fall may overwinter by delaying development for several months (Nichols 1996; McMahon 1996).

Settling larvae attach by byssal threads to hard substrates and metamorphose into juveniles. They 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, reaching maximum shell lengths of over 40 mm (Mackie *et al.* 1989; Smirnova & Vinogradov 1990; Mackie & Schloesser 1996).

2. Summary of Potential Distribution Studies

In the earliest attempt at assessing potential distribution of zebra mussels in North American, Strayer (1991) first analyzed the mussels' distribution in Europe relative to climate variables. Based on his results (Table 2 and discussion in Section 3 below), he mapped zebra mussels' potential North American distribution to cover areas with mean annual air temperatures between 0° and 18° C, and areas with monthly mean air temperatures between $^{-}$15° and 27° C. These ranges include most of the United States (including most of California except for the hot southeastern portion of the state) and much of southern Canada. Strayer further argued that zebra mussels' range in Europe was probably not limited by climate factors, and so the potential North American range he estimated should be considered a minimum range rather than a limiting range. He did, however, note that calcium levels might be too low to support zebra mussels in parts of this range.

Table 2. Zebra Mussel Distribution and Temperature in Europe (Strayer 1991)
Data 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)	—

Neary and Leach (1992) mapped the potential occurrence of zebra mussels in Ontario, using criteria based on Sprung's (1987) assessment of the calcium concentrations and pH needed for larval survival (Fig. 1, Table 3); though they noted that the critical values that they derived for calcium (12 and 20 mg/l) were lower than the level that Ramcharan *et al*. (1991) had estimated was limiting zebra mussel distribution in Europe (28 mg/l), and that their analysis might therefore overestimate the area at risk. They started their analysis with data on 6,151 lakes (out of an estimated 262,000 lakes in the province that are over 1 hectare in size) from the Ontario Acid Sensitivity Data Base. Most of these data were based on a single mid-lake grab sample

Figure 1. Larval Production at Different Calcium Levels

Larval production is the number of healthy larvae produced after 3 days, indexed to the number produced at a calciujm concentration of 59 mg/l. Calculated from graphs in Fig. 3 of Sprung (1987).

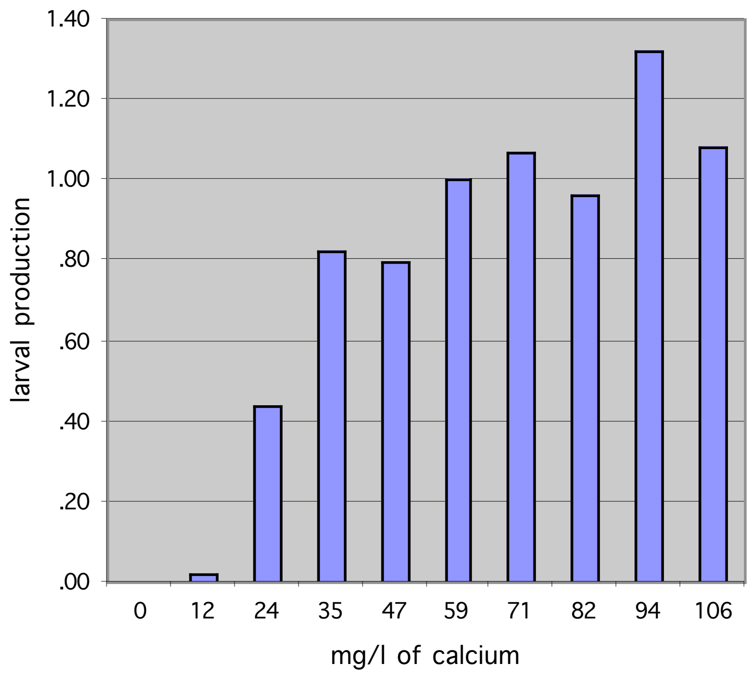

Table 3. Criteria used in Potential Distribution Studies in Ontario (Neary & Leach 1992) and Rhode Island (Tammi *et al.* 1995a)

	— — — Distribution Potential — — —		
Parameter	**Unlikely**	**Possible**	**Probable**
Calcium	< 12 mg/l	12-20 mg/l	> 20 mg/l
	or	and	and
pH	< 7.4	≥ 7.4	≥ 7.4

taken in winter. For 3,950 lakes, the data included both pH and calcium measurements; for 2,201 additional lakes that lacked calcium measurements, conductivity values were converted to calcium values using a regression derived from the first set of lakes (calcium (in mg/l) = 0.141 x conductivity (in μS) – 1.175 (r^2=0.88, n=3950)). Using these values and the criteria in Table 3, they then mapped the water quality suitability of areas within 10 km each of the data points; and extended this mapping to additional areas with maps of terrain types based on the potential of soil and bedrock to reduce acidity, using two of the terrain classifications that correlated well with the lake data for calcium and pH. Summary data provided for 6,147 lakes, combined with the strong correlation of high pH with high calcium concentrations, indicate that zebra mussel larval survival would be classified as unlikely in about 78% of the lakes, possible in 10% and probable in 20%. However, since these lakes in the Acid Sensitivity database may have been selected for inclusion based on characteristics that correlate with lower calcium concentrations, these percentages may underestimate the overall susceptibility of Ontario lakes.

Murray *et al*. (1993), using the same calcium criteria as used by Neary and Leach (1992) (Table 4), estimated that a successful invasion is unlikely at 73%, possible at 19% and probable at 8% of the 230 lakes, ponds and river sites that they examined in Connecticut.[1]

Table 4. Criteria used in a Potential Distribution Study in Connecticut (Murray *et al.* 1993)

	— — — Distribution Potential — — —		
Parameter	**Unlikely**	**Possible**	**Probable**
Calcium	< 12 mg/l	12-20 mg/l	> 20 mg/l

Baker *et al*. (1993b), used criteria for pH and calcium which Baker *et al*. (1993a) developed from a literature review (Table 5), with maximum reported monthly mean measurements for May-September, to classify 14 lakes and the tidal freshwater portions of 7 major estuaries in Virginia in terms of their susceptibility to zebra mussels. They classified 24% of lakes and estuaries as having low susceptibility (successful reproduction unlikely), 28% as moderate (successful reproduction and large populations expected in some periods), and 43% as high (expected rapid growth to sustained large populations).[2]

Strayer and Smith (1993) reviewed distributional data relative to salinity in Europe, and based on a salinity tolerance of 2 ppt predicted that zebra mussels could colonize the Hudson River estuary from its head at Troy down to 80 km above the Battery, with an estimated 50-250 billion zebra mussels in this area.

Koutnik and Padilla (1994) estimated the potential distribution and abundance of zebra mussels in Wisconsin lakes, using 3 models developed by Ramcharan *et al*. (1992) from European lake

1 These percentages are based on the calcium data in the appendices in Murray *et al.* (1993), except that Wononpakook Lake is taken from Table 4 (the value in the appendix apparently being an error—Nancy Balcom, Connecticut Sea Grant, pers. comm. 2000). However, the discussion and tables in Murray *et al.* (1993) suggest a lesser degree of susceptibility, with about 12% sites ranked as possible and 5% probable.

2 Although the text in Baker *et al.* (1993b) reports the Mattaponi/Pamunkey river system as having moderate susceptibility, Table 1 and the calcium values reported in that paper indicate a rank of low susceptibility, which was used to calculate these percentages.

Table 5. Zebra Mussel Environmental Requirements (Baker *et al.* 1993a)

Parameter	Adult Survival	Adult Growth (possible)	Adult Growth (optimal)	Larval Growth (possible)	Larval Growth (optimal)
Temperature	0-33° C	6-30(?)° C	?	12-24° C	17-18° C
Salinity	0-12 mg/l	0-0.6 mg/l	?	0-? mg/l	?
pH	7.0-?	7.5-?	?	7.4-9.4	8.4-8.5
Calcium	?	?	34.5-76 mg/l	≥ 12 mg/l	40-? mg/l

data. These models are: (1) an occurrence model derived from a discriminant function analysis using pH and calcium concentration as parameters; (2) a categorical density model derived from a discriminant function analysis using pH, calcium, nitrate and phosphate concentrations; and (3) an abundance or numerical density model derived from a multiple regression using pH, nitrate and phosphate concentrations. The occurrence model showed a potential for zebra mussels to establish in 48% of the lakes examined, while the categorical density and numerical density models indicated a potential for establishment in 84-85% of the lakes.

Armistead (1995) assessed the potential for zebra mussels to colonize down the length of the Mississippi River, comparing 5-year monthly mean water temperatures to laboratory results regarding upper incipient lethal temperatures. He concluded that while southern sites from Louisville, Kentucky to New Orleans, Louisiana exceeded lethal limits at some time during the 5-year period, in some cases exceedances were of short duration and probably would produce little mortality. At New Orleans, however, exceedances were lengthy, and he concluded these water are unsuitable for zebra mussels. He cautioned, however, that the data used were from surface measurements, and that deeper and potentially colder water might provide suitable habitat.

Tammi *et al*. (1995a) used the same calcium and pH criteria as used by Neary and Leach (1992) in Ontario to analyze 52 lakes and ponds and 5 rivers[3] in Rhode Island (Table 3). They estimated that the potential for colonization is unlikely at 93% of these sites, possible at 7% and probable at none. Tammi *et al*. (1995b) used calcium concentrations alone to analyze 78 lakes, ponds reservoirs and rivers in Rhode Island (Table 6), and estimated no chance of survival at 74% of the sites, low survival at 13%, poor-to-moderate growth at 12% and very good growth at 1%.[4]

3 Though the text stated that 52 lakes and ponds and 5 rivers were analyzed, Tammi *et al.* (1995) only reported ratings for 51 lakes & ponds. The percentages here are based on the 51 rated sites.

4 They note, however, that the 1% of water bodies rated as having very good growth potential for zebra mussels consists of a single pond connected to Narragansett Bay, with salinities levels that may make it uninhabitable for zebra mussels.

Table 6. Criteria used in a Potential Distribution Study in Rhode island (Tammi *et al.* 1995b)

	— — — — — Distribution Potential — — — — —				
Parameter	**No Survival**	**Low Survival**	**Poor to Moderate Growth**	**Moderate to Good Growth**	**Very Good Growth**
Calcium	≤ 6 mg/l	7-9 mg/l	10-24 mg/l	25-35 mg/l	> 35 mg/l

Duke Power (1995) used calcium concentration, pH, turbidity and the abundance of another exotic clam, *Corbicula fluminea*, to assess the potential for zebra mussel infestations at 16 water bodies in its service area in North and South Carolina. It concluded that infestation is unlikely at 19% of sites, possible at 44% of sites and probable at 37% of sites.

Doll (1997) ranked habitat suitability at 338 sites in North Carolina based on calcium, pH, mean summer temperature (June-September), dissolved oxygen and salinity (Table 7). The calcium data used were the averages of all recorded measurements in 1953-1995 from the U.S. geological Survey, while temperature data (average of 1988-1994 data) and data for pH, oxygen and salinity (average of monthly measurements in 1989-1994) were from the North Carolina Division of Water Quality. Doll did not combine the individual rankings for these five parameters into an overall ranking for each site; however, the individual parameter rankings indicate that most inland waters are too calcium-poor, and most coastal waters too salty, to support zebra mussels.

Table 7. Criteria used in a Potential Distribution Study in North Carolina (Doll 1997)
Study did not combine invidual factor rankings into an overall ranking.

	— — — Distribution Potential — — —		
Parameter	**Unlikely**	**Maybe**	**Definite**
Calcium	< 9 mg/l	9-15 mg/l	> 15 mg/l
pH	<6.8 or >9.5	6.8-7.4 or 8.7-9.5	7.4-8.7
Mean Summer Temperature	<15° or >32° C	31-32° C	15-31° C
Dissolved Oxygen	<4 mg/l	4-8 mg/l	>8 mg/l
Salinity	>10 mg/l	5-10 mg/l	<5 mg/l

Janik (1997), using data from the California Department of Water Resources, found calcium, pH and temperature to be suitable for zebra mussels at three sites along the California Aqueduct.

Sorba and Williamson (1997) used calcium, total hardness (as $CaCO_3$), pH, mean summer (June-September) temperature, dissolved oxygen, conductivity and turbidity (Secchi disk depth) to assess Manitoba's waters (Table 8). They estimated overall rankings based on the lowest potential for any single parameter, finding very low colonization potential at 34% of sites, low potential at 19%, moderate potential at 22% and high potential at 25%.

Table 8. Criteria used in a Potential Distribution Study in Manitoba (Sorba & Williamson 1997)

	— — — Distribution Potential — — —			
Parameter	**Very Low**	**Low**	**Moderate**	**High**
Calcium	<9 mg/l	9-20 mg/l	20-25 mg/l	≥25 mg/l
Total Hardness	<25 mg/l	25-45 mg/l	45-90 mg/l	≥90 mg/l
pH	<6.5	6.5-7.2	7.2-7.5 or 8.7-9.0	7.5-8.7
Mean Summer Temperature	<8° or >30° C	9-15° or 28-30° C	16-18° or 25-28° C	18-25° C
Dissolved Oxygen	<4 mg/l	4-6 mg/l	6-8 mg/l	≥8 mg/l
Conductivity	<22 μS/cm	22-36 μS/cm	37-82 μS/cm	≥83 μS/cm
Secchi Disk Depth	<10 cm or >250 cm	10-20 cm or 200-250 cm	20-40 cm	40-200 cm

Based on a review of the scientific literature, Hayward and Estevez (1997) constructed habitat suitability index (HSI) curves for zebra mussels ranging from 0.0 (perfectly unsuitable or lethal) to 1.0 (perfectly suitable or optimal) for each of seven parameters: temperature, salinity, calcium, pH, dissolved oxygen, turbidity (Secchi disc depth) and sediment size (phi). They accumulated tidal, diurnal, lunar and seasonal variation, and information on larval and adult stages, into single, annualized, life-cycle HSI curves for each parameter. They then used these curves to calculate HSI values for 281,780 data records from 9,028 Florida sites in the US EPA's STORET database. They calculated composite HSI values for each sample at each site, and took the median of sample HSI values to represent that site. These were above 0.5 for 21% of the sites, and above 0.8 for 3% of the sites. Most waters appeared to be too turbid and too low in calcium and pH to support zebra mussels. They also calculated and mapped HSI values aggregated by U.S. Geologic Survey Hydrologic Units.

Cohen & Weinstein (1998) used April-September data on calcium, pH, mean and maximum temperature, dissolved oxygen and salinity to assess colonization potential at 160 sites in California, including rivers, lakes, reservoirs, aqueducts and canals (Table 9). They used STORET data supplemented by water quality data from other agencies and researchers. They combined the rankings for individual factors to produce overall rankings of low-or-no colonization potential at 54% of sites, moderate potential at 2% of sites and high potential at 44% of sites (Table 10). They concluded that most coastal watersheds, the west side of the Sacramento Valley, the San Joaquin River and the southern part of the Delta provide suitable habitat for zebra mussels, including many critical water supply facilities such as the California Aqueduct (as Janik (1997) had concluded earlier), the South Bay Aqueduct, the Delta-Mendota Canal, the Los Angeles Aqueduct, the Colorado River Aqueduct, the All American Canal, and the reservoirs associated with these systems. They found that colonization would be prevented throughout most of the Sierra Nevada and the upper Sacramento River watershed by low calcium, sometimes in combination with low pH; at many southern California sites by warm summer water temperatures; in some inland brackish waters by high salinity; and in some northeastern California lakes by periodic desiccation, possibly combined with high or fluctuating salinities.

Ashby *et al*. (1998) evaluated the potential for zebra mussel infestation at 453 U.S. Army Corps of Engineers projects across the U.S., based on alkalinity, pH, temperature and dissolved oxygen, and concluded that more than half the sites have suitable water quality for zebra mussels.

Table 9. Criteria used in a Potential Distribution Study in California (Cohen & Weinstein 1998)

	— — — Distribution Potential — — —		
Parameter	**Low-to-no**	**Moderate**	**High**
Calcium	<15 mg/l	15-25 mg/l	>25 mg/l
pH	<7.3 or >9.0	7.3-7.5 or 8.7-9.0	7.5-8.7
Mean Summer Temperature	–	0-15° C	16-31° C
Maximum Temperature	<10° or >31° C	10-31° C	10-31° C
Dissolved Oxygen	<4 mg/l	4-8 mg/l	>8 mg/l
Salinity	>10 mg/l	5-10 mg/l	<5 mg/l

Table 10. Criteria for Combining Individual Factor Rankings Used in a Potential Distribution Study in California (Cohen & Weinstein 1998)

Overall Ranking	Calcium	pH	Temperature	Dissolved Oxygen	Salinity
High	at least one factor ranked High and neither ranked Low-to-no		each factor ranked High or Moderate		
Moderate	both factors ranked Moderate		each factor ranked High or Moderate		
Low-to-no	at least one factor ranked Low-to-no				

3. Review of Factors

Temperature

Zebra mussels do not survive freezing (McMahon 1996), but Strayer (1991) noted that even if temperatures are not low enough to kill zebra mussels outright, their establishment may be prevented by a growing season that is too short to allow growth and reproduction. In Europe, zebra mussels have become abundant where average winter temperatures are as low as 6° C, but are less common in colder environments (Stanczykowska and Lewandowski 1993). Strayer (1991) reported zebra mussels to be less common in Europe at sites within 100 km of weather stations with mean annual air temperatures below 3-6° C (Table 2). Various studies in Europe and North America have reported lower temperature limits for adult growth that are in the range of 10-12° C (Morton 1969; Stanczykowska 1977; Mackie 1991), but Bij de Vaate (1989) report growth at temperatures down to 6° C in the Netherlands (Table 11). In North America, zebra mussels normally begin to spawn at 12° C and above, and spawning thresholds of 12° have also been reported in Germany (Borcherding 1991; Neumann *et al*. 1992), but limited spawning has been reported at 10° C in the Great Lakes and Europe (Sprung 1993; Nichols 1996; McMahon 1996). Spawning peaks at about 12-18° C, which is also roughly the optimum temperature for larval development (Sprung 1993).

Strayer (1991) reported that zebra mussels are absent from European sites within 100 km of weather stations with mean annual air temperatures above 18° C or highest mean monthly air temperatures above 27° C (Table 2) (based, however, on very few stations). Baker *et al*. (1993b) noted that it may not be possible to determine the zebra mussel's upper temperature limit from its Old World distribution, since the Mediterranean Sea acts as a southern barrier. Laboratory experiments and field observations suggest that water temperatures above 22-26° C are unsuitable for reproduction or spawning (Table 12), however, Baker *et al*. (1993a) argue that in temperate regions seasonal temperature fluctuations will 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. 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 respiratory costs can exceed assimilation rates at high temperatures, resulting in

Table 11. Lower Water Temperature Limits for Zebra Mussels as Indicated by Different Studies

Limit	Basis	Reference
-2° C	No survival below this value	Claudi & Mackie 1994
0° C	Does not survive freezing	McMahon 1996
0° C	Lower limit for adult survival, based on literature review	Baker *et al*. 1993a
0° C	Usual lower limit of distribution	Boelman et al. 1997
0° C	Lower limit for poor growth	Claudi & Mackie 1994
0° C	Index of 0 (perfectly unsuitable, or lethal) on the Habitat Suitability Index curve	Hayward & Estevez 1997
2-4° C	Lower limit for gametogenesis	Borcherding 1991
3° C	Lower limit of favorable conditions	Smirnova & Vinogradov 1990
6° C	Lower limit for occurrence in Europe	McMahon 1996
6° C	Lower limit for adult growth, based on literature review	Bij de Vaate 1989
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	Maximum annual value dividing "low-to-no" from "moderate" potential distribution in analysis in California	Cohen & Weinstein 1998
10° C	Lower limit for limited spawning in Great Lakes	Nichols 1996
10-12° C	Lower limit for spawning, based on literature review	McMahon 1996
10-12° C	Lower limit for adult growth in the Great Lakes	Baker *et al*. 1993a
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 juvenile and adult growth, based on literature review	McMahon 1996
15° C	Mean summer value dividing "unlikely" from "definite" potential distribution in analysis in North Carolina	Doll 1997
16° C	Mean summer value dividing "low" from "moderate" potential distribution in analysis in Manitoba	Sorba & Williamson 1997

Table 12. Upper Temperature Limits for Zebra Mussels 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
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
28° C	Mean summer value dividing "low" from "moderate" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
≈30° C	Upper limit for juvenile and adult growth, based on literature review	McMahon 1996
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 regular feeding	Smirnova & Vinogradov 1990
30° C	Mean summer value dividing "very low" from "low" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
30-31° C	Mortality above ≈10% in different Volga River populations	Smirnova *et al*. 1990, based on Shkorbatov 1986
30-31° C	Abundant in southern US waters where temperatures often reach 30° C, but massive die-offs occur at 31° C	McMahon 1996
31° C	Upper limit for larvae and adults, based on literature review	McMahon 1996
31° C	Upper incipient lethal temperature with mean tolerated exposure of 52-292 hr depending on acclimatization	Armistead 1995
31° C	Maximum annual value dividing "low-to-no" from "moderate" potential distribution in analysis in California	Cohen & Weinstein 1998

Table 12. Continued

Limit	Basis	Reference
31-33° C	Mortality above ≈50% in different Volga River populations	Smirnova *et al*. 1990, based on Shkorbatov 1986
32° C	Mean summer value dividing "unlikely" from "maybe" 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
33-36° C	100% mortality in different Volga River populations	Smirnova *et al*. 1990, based on Shkorbatov 1986
39° C	Index of 0 (perfectly unsuitable, or lethal) on the Habitat Suitability Index curve	Hayward & Estevez 1997
40° C	No survival above this value	Claudi & Mackie 1994

loss of body mass, which could prevent the establishment zebra mussels without necessarily killing them outright.

Stanczykowska (1977, cited by Baker *et al*. 1993a) reports 26-33° C as the upper temperature range for adult growth. Several authors have reported 30° C as the upper limit for efficient feeding and adult growth, and 31-33°C as the upper limit for short-term survival (Table 12). In southern U.S. waters, juveniles and adults have been reported growing at temperatures up to about 30° C, with massive die-offs occurring at 31° C.

Smirnova and Vinogradov (1990) and Smirnova *et al*. (1993) note that Volga River populations of zebra mussels vary in their heat tolerance, with the southernmost population (at Astrahan) and a population living in waters heated by power plant discharges (at Kostromo) being the most tolerant of high temperatures.

Salinity

Zebra mussels' salinity limits depend not only on salinity levels, but also on the rate of change of salinity and on the composition of the salt. Zebra mussels can only tolerate low levels of salinity in waters with short-term salinity fluctuations (such as estuaries), but can handle higher levels of stable salinity. Laboratory studies reflect this, showing greater tolerance to higher salinity levels when the increase in salinity is gradual rather than abrupt (Strayer & Smith 1993). Some researchers have argued that zebra mussels can tolerate higher salinity in waters that contain higher proportions of divalent ions (Ca^{++} and Mg^{++}) and sulfates relative to monovalent ions (Na^{+} and Cl^{-}), or that chloride content rather than total salinity is the critical factor (Strayer & Smith 1993). Others have suggested that temperature may affect salinity tolerance (with higher tolerance in colder water), and that different populations may have different genetic capacities to tolerate salinity (*e.g*. Baker *et al*. 1993a). For example, Volga River populations of zebra mussels vary in their salt tolerance, with the population nearest the sea (at Astrahan) tolerating the highest salinities, and the population furthest from the sea (at Rybinsk) being the least tolerant; and this is mirrored by their cellular response to high salinities (Smirnova & Vinogradov 1990; Smirnova *et al*. 1993).

Zebra mussels occur up to a mean salinity of 0.6 ppt in Netherlands estuaries, up to <1 ppt in the eastern Gulf of Riga, and up to <2 ppt in the extreme eastern Gulf of Finland and in estuaries bordering the Black Sea (Wolfe 1969; Strayer & Smith 1993). It has been collected in stunted populations in the saltiest portions of the Vistula estuary and lagoon at up to 4.8 ppt, and in the Kiel Canal at 3.8 and 6.2 ppt (Strayer & Smith 1993). In the Hudson River estuary it was found at high densities at sites with maximum salinities up to 3 ppt, and at lower densities at sites with maximum salinities up to 6 ppt (Baker *et al*. 1993a).

Zebra mussels are present in ponds in the Netherlands delta region with stable salinities up to 4 ppt (Wolff 1969). They are abundant in the northern Caspian Sea at salinities of 6-9 ppt, but are not present in the main body of the sea at 13 ppt (Strayer & Smith 1993). They were abundant throughout the Aral Sea at salinities of 10 ppt; as water diversions raised the salinity of the sea, mussel populations began to decline at around 12 ppt and had virtually disappeared when salinities reached 14 ppt (Stayer & Smith 1993). Stable salinity levels, or proportionally higher concentrations of calcium and magnesium, may be among the factors enabling zebra mussels to live in these relatively salty waters (Stayer & Smith 1993).

Laboratory studies, conducted at a range of temperatures and with different acclimation procedures, have produced disparate results. Barber (1992) reported that adult mussels and exposed to salinity levels rising slowly from 0 to 2.7 ppt in 15° C water had all died after 52 days. In contrast, Mackie & Kilgour (1992) reported 85% survival of adult mussels that were slowly acclimated to 8 ppt salinity over 42 days in 4° C and 10° C water (Table 13). Vinogradov *et al*. (1993) noted one study that reported 100% mortality after 168 days in 5 ppt, another that reported the lethal concentration to be 5-7 ppt, and a third that reported the lethal concentration using stepwise acclimation to be 10-12 ppt, while Strayer and Smith (1993) noted earlier studies that reported 10 ppt as the limit for long-term survival of gradually acclimated mussels

Table 13. Upper Salinity Limit for Zebra Mussels as Indicated by Different Studies

Limit	Basis	Reference
0.4-2 ppt	Estimated upper limit in tidal estuaries	Strayer and 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
2 ppt	Maximum value where reproduction has been observed in tidal reaches of the Rhine River	Strayer and Smith 1993
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
2.7 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 at sites in the Hudson River estuary with high densities (>1,000/m^2) of zebra mussels	Walton 1993, cited by Baker *et al*. 1993a
4 ppt	Upper limit where present in ponds in the Netherlands delta region	Wolff 1969
6 ppt	Maximum salinity at which zebra mussels have been reported in estuaries (Kiel Canal and Hudson River)	Strayer & Smith 1993; Baker *et al*. 1993a
6 ppt	Estimated upper limit in nontidal lagoons or other waters with relatively stable salinities	Strayer & Smith 1993
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
8 ppt	85% survival of acclimated adults at 4° and 10° C in laboratory	Mackie & Kilgour 1992

Table 13. Continued

Limit	Basis	Reference
10 ppt	Upper limit for long-term survival of acclimated mussels	Strayer & Smith 1993
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 where mussels dissappeared as salinities increased in the Aral Sea	Strayer & Smith 1993
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

pH

Ramcharan *et al*. (1992) analyzed 76 European lakes and found that zebra mussels are absent from those with pH below 7.3. Vinogradov *et al*. (1993) found that loss of sodium and calcium exceeded uptake at pH levels below 6.8-6.9, and that zebra mussels were generally more vulnerable than other freshwater bivalves to disruption of ion metabolism from reductions in pH level. Sprung (1993) reported that in laboratory experiments a pH of 7.4 to 9.4 is needed for veliger development, with peak success at around pH 8.4 in 18-20° C. Baker and Baker (1993) reported that the "preponderance of evidence" suggests that pH levels below about 7.0 will not sustain large zebra mussel populations. Different authors reviewing the literature have selected minimum pH requirements ranging from 6.5 to 7.5 (Table 14) and maximum pH requirements ranging from 9.0 to 9.5 (Table 15).

Table 14. Lower pH Limit for Zebra Mussels as Indicated by Different Studies

Limit	Basis	Reference
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
7.2	Value dividing "low" from "moderate" potential distribution in analysis in Manitoba	Sorba & Williamson 1997
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
7.3-7.4	Lower limit for larvae based on literature review	McMahon 1996
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	Value dividing "unlikely" from "possible" potential distribution in analyses in Ontario and Rhode Island	Neary & Leach 1991, Tammi *et al.* 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

Table 15. 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 & Weinsten 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
9.5	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

Calcium and Hardness[5]

Strayer (1991) noted that most European surface waters are hard with > 20 mg/l of calcium, while many North American waters are soft, and suggested that water hardness could limit zebra mussel distribution in North America. Reviewing data for 70 European lakes, he found zebra mussels mainly reported in lakes with calcium levels above 20-40 mg/l, and absent from lakes with < 20 mg/l . In a discriminant analysis of 30 lakes with and without zebra mussels, he found

5 Standard analytical methods define "dissolved calcium" as calcium measured in a sample after filtration through a 0.45 μm membrane filter, and "total calcium" as calcium measured in an unfiltered sample after vigorous digestion (US EPA 1983; Eaton *et al.* 1995). In practice these measures are likely to be close unless total calcium levels are quite high, and in some cases the same data is reported both as dissolved and as total calcium (Pederson pers. comm. 1998; J. Kirschner pers. comm. 1998; also observed by the author in STORET data). In this report, I treat concentrations reported as dissolved calcium or total calcium as equivalent measures and report them simply as calcium concentrations.

"Calcium hardness" is sometimes reported, in milliequivalents per liter (meq/l) of calcium ion (Ca^{++}). This can be converted to calcium concentration as 1 meq= 20.05 mg of calcium (Masters 1991). Many sample measures also include "total hardness," which is the concentration of all multivalent metallic cations in solution, primarily consisting of calcium and magnesium (Mg^{++}) in natural waters, with much smaller quantities of other cations such as iron (Fe^{++}), manganese (Mn^{++}), strontium (Sr^{++}) and aluminum (Al^{+++}) sometimes present (Masters 1991). Because of the varying proportions of these ions, total hardness cannot be simply converted to calcium hardness or calcium concentration. However, in the majority of fresh waters where ionic concentrations are not too high (*i.e.* carbonate-dominated waters), the proportions do not vary too much (*e.g.* Ca:Mg ratios of ≈3-6 by weight in the mean composition of river waters for the world and individual continents exclusive of Australia—Wetzel 1983), such that 1 meq of total hardness translates to about 13-16 mg/l of calcium.

that hardness and lake depth (primarily), and lake area and transparency (to a lesser extent) accounted for 52% of the variation ($F=14.67$, $p<0.01$). Strayer noted that many species of freshwater mollusks are restricted to relatively hard waters, and that Sprung's (1987) studies suggested that zebra mussel larvae needed hard water with a minimum of about 20 mg/l of calcium (Fig. 1). Smirnova and Vinogradov (1990), noting the inability of zebra mussels to live in soft waters, suggested that this is related to the species origin in the Caspian Sea in water with high concentrations of calcium and magnesium sulfates.

Ramcharan *et al*. (1992) analyzed 76 European lakes and found that zebra mussels are present only where calcium concentrations are at least 28.3 mg/l. Padilla (1997) found similar results for over 500 lakes in the former Soviet Union. In North America, however, zebra mussels have been reported as present and sometimes abundant at calcium levels ranging from 12 to 25 mg/l (Mellina & Rasmussen 1994; Cusson & Lafontaine 1997; Vermont Department of Environmental Conservation 1998; S. Nichols, pers. comm. 1998) (Table 16).

In laboratory studies, zebra mussels did not survive calcium levels below 15 mg/l, where metabolic equilibrium was lost (Vinogradov *et al*. 1993). In tests of rearing success, the lowest number of deformed larvae occurred at over 35 mg/l of calcium (Figure 1; Sprung 1987). In general, laboratory studies have shown that zebra mussels are less able than other freshwater bivalves to regulate hemolymph ion levels and acid/base levels in waters with moderate acidity and calcium concentrations. Thus we might expect them to be restricted to waters with higher pH and calcium levels compared to most other freshwater bivalves.

Most studies of potential zebra mussel distribution have used values of 12 or 15 mg/l as the minimum calcium threshold below which the establishment of a population is unlikely, though threshold values of 2, 7 and 9 mg/l have also been used (Table 16).

Potassium

Vinogradov *et al*. (1993) reported that zebra mussels are well adapted to waters with extremely low potassium levels, with equilibrium concentrations (where uptake = loss) determined in laboratory assays ranging from about 10-100 μM/l.

Doll (1997) noted that zebra mussels are generally not found in waters with potassium concentrations greater than 39 mg/l. Fisher and Stromberg (1992, cited by Baker *et al*. 1993a) report that the 24-hr LC_{50} for potassium (as KCl) is about 100 mg/l.

Table 16. Lower Calcium Limit for Zebra Mussels, as Reported 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
5-6 mg/l	"No survival" range	Claudi & Mackie 1994
7 mg/l	Value dividing "no survival" from "low survival" in analysis in Rhode Island	Tammi *et al*. 1995b
8.5 mg/l		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	Lower limit of distribution	Boelman *et al*. 1997
10 mg/l	Value dividing "low survival" from "poor to moderate growth" in analysis in Rhode Island	Tammi *et al*. 1995b
10-11 mg/l	"Poor growth" range	Claudi & Mackie 1994
10-12 mg/l	Minimum value for maintaining metabolic equilibrium in laboratory trials	Vinogradov *et al*. 1993
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 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
12-15 mg/l	Lower limit for adults based on literature review	McMahon 1996
12-19 mg/l	Reported at these values in Lake Champlain, Richelieu River, St. Lawrence River and Duluth Harbor	Mellina and Rasmussen 1993; Cusson and Lafontaine 1997; Vermont Department of Environmental Conservation 1998; S. Nichols pers. comm. 1998
12-24 mg/l	Range between values producing <5% to >40% of the "normal" number of healthy larvae in 3-day exposure trials	Sprung 1987

Table 16. Continued

Limit	Basis	Reference
13-14 mg/l	Minimum value for maintaining metabolic equilibrium in laboratory trials	Vinogradov *et al*. 1987, cited in Vinogradov *et al*. 1993
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
20-25 mg/l	Reported to be abundant at these values in Lake Champlain, St. Lawrence River, Oneida Lake and the Hudson River	Mellina and Rasmussen 1993; Vermont Department of Environmental Conservation 1998
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

Dissolved Oxygen

The lethal lower limit for adult zebra mussels is apparently about 4 mg/l of oxygen at 18° C (Sprung 1987; Table 17). In anoxic conditions, zebra mussels survived a maximum of 6 days at 17-18°C and a maximum of 3 days at 23-24° C (Baker *et al*. 1993a). Boelman *et al*. (1997) report that zebra mussels are usually found where dissolved oxygen is over 90% of saturation and become stressed at levels of 40-50% of saturation. Smirnova and Vinogradov (1990) report 80-85% oxygen saturation as optimal. Lower oxygen requirements in colder water may allow overwintering mussels to survive under ice. However, low oxygen levels in severely polluted waters 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 (McMahon 1996).

Turbidity

In a discriminant function analysis of 30 lakes with and without zebra mussels, Strayer (1991) determined that hardness and lake depth (primarily), and lake area and transparency (to a lesser extent) accounted for 52% of the variation ($F=14.67$, $p<0.01$). He found that zebra mussels were uncommon in lakes with Secchi disk depths under 1 meter, and at least one researcher has suggested that high turbidity may control zebra mussel distributions by interfering with feeding (Strayer & Smith 1993). However, Doll (1997) noted that zebra mussels don't appear to be inhibited by high turbidity, having been found in parts of the Mississippi River with > 80 NTU of total suspended solids.

Table 17. Minimum Dissolved Oxygen Concentrations Required for Zebra Mussels, 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
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
6 mg/l	Value dividing "low" from "moderate" potential distribution in analysis in Manitoba	Sorba & Williamson 1997

Substrate

Zebra mussel larvae need hard substrates to settle on. Mellina and Rasmussen (1994) found that substrate availability explained between 38% to 91% of the variability in density of zebra mussels in the Hudson and St. Lawrence rivers and Oneida Lake and explained 75% of the variability in 72 other lake sites described in the literature, with mussels being more abundant in coarser substrate. 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 mats (Ramcharan *et al*. 1992, Mellina & Rasmussen 1994; Nichols 1996; Berkman *et al*. 1998).

Water Velocity

Water velocities affect larval settlement and fertilization. Zebra mussel larvae are unable to settle from water that is flowing faster than about 1.5-2.0 m/sec, which limits their distribution in many rivers (Boelman *et al*. 1997). Flowing river waters also lower fertilization success by washing gametes downstream, and associated turbulence can damage or kill fragile larvae (Sprung 1993; Horvath *et al*. 1996). Smirnova and Vinogradov (1990) report velocities of 0.1-1.0 m/sec as favorable, and that feeding declines above 1.0-1.5 m/sec as fast flowing water deforms the zebra mussel's siphon. These factors probably account for zebra mussel densities being lower in rivers than in lakes (Strayer 1991; Horvath *et al*. 1996). In Europe, zebra mussels are rarely found in rivers less than 30 m wide (Table 18), perhaps due to the higher velocities found in smaller rivers (Strayer 1991).

Table 18. Zebra Mussel Occurrence and River Width in Europe (Strayer 1991)

Stream width	Frequency of Occurrence	n
<3 m	0%	102
3–10 m	0%	59
10–30 m	10%	10
30–100 m	33%	6
> 100 m	83%	23

Size or Depth of Waterbody

In a discriminant function analysis of 30 European lakes with and without zebra mussels, Strayer (1991) found that hardness and lake depth (primarily), and lake area and transparency (to a lesser extent) accounted for 52% of the variation ($F=14.67$, $p<0.01$). Reviewing data for 73 European lakes, Strayer (1991) found that zebra mussels were less common in lakes smaller than 0.3 km^2, and suggested that zebra mussels' absence from shallow, productive lakes could be due either to periods of anoxia, or to intense predation by water birds. Stanczykowska and Lewandowski (1993) similarly found that relatively large and deep European lakes that have low to moderate levels of algae and nutrients have higher densities of mussels than relatively small and shallow lakes that are higher in algae and nutrients.

In a review of 16 European studies, Strayer (1991) found that zebra mussels occurred more commonly in wider streams, and were rarely found in streams less than 30 m wide (Table 18).

Precipitation

Strayer (1991) analyzed the distribution records of zebra mussels relative to weather data at 110 weather station across Europe. He found that zebra mussels were less frequently recorded within 100 km of weather stations that reported strong seasonal patterns of precipitation (*i.e.* those stations with the lowest mean monthly precipitation being < 0.3 of the highest mean monthly precipitation).

Nutrients

In general, zebra mussels seem to do best in waters with moderate levels of nutrients, with mussels being absent, or present only at low densities, in eutrophic and oligotrophic waters.

Strayer (1991, citing Walz 1978) suggested that lakes with low productivity might not provide enough food for zebra mussels. Ramcharan *et al.* (1992), in a study of 76 European lakes, found that waters that are exceptionally low in algal nutrients tend to lack or have very low densities of zebra mussels. Doll (1997) noted that zebra mussels are generally not found in waters with nitrate concentrations below 0.009 mg/l. Ramcharan *et al.* (1992) reported that zebra mussels were absent from European lakes with phosphate concentrations below 0.05 mg/l, but Baker *et al.* (1993a) stated that zebra mussels have been reported in lakes with no measurable free phosphate, and Doll (1997) noted that they have been found at phosphate levels as low as 0.001 mg/l.

Stanczykowska *et al.* (1983) found zebra mussels to be absent from most hypereutrophic lakes in Poland, and Stanczykowska and Lewandowski (1993) found that Polish lakes with high or very high levels of nutrients and algae had no or low densities of zebra mussels, while lakes with medium to low levels of nutrients and algae tended to have medium to high densities of zebra mussels. Also, zebra mussels declined or disappeared as lakes became more eutrophic. Strayer (1991) suggested that zebra mussels' absence from shallow, productive lakes in Europe could be due to periods of anoxia, or to intense predation by water birds. Ramcharan *et al.* (1992) found that zebra mussel density was negatively correlated with phosphate and nitrate in European lakes, and that they were absent where phosphate levels exceeded 18 mg/l, which also suggests that eutrophic lakes are less suitable habitats. Ramcharan *et al.* (1992) speculate that this may be due to lower oxygen levels, or to dense algae clogging the mussels' gills. Doll (1997), however, noted that zebra mussels are fairly tolerant of polluted waters and survive organic enrichment except when oxygen levels are depleted.

4. Further Assessment of Calcium Requirements

Complicating Factors

Calcium levels can vary substantially in some water bodies, changing with location, depth or time (Table 19). Calcium generally varies more in hardwater than in softwater lakes, in part because when calcium is near saturation levels increased photosynthetic activity can substantially increase the precipitation of calcium carbonate from the epilimnion (Wetzel 1975). This variation must be kept in mind when assessing calcium data relative to zebra mussel distributions.

A further complexity is that zebra mussels' calcium requirements vary with changes in other environmental factors. Several studies conclude that zebra mussels' calcium threshold varies with pH, mainly declining with increasing pH (Ramcharan *et al.* 1994; Hincks & Mackie 1997; Nierzwicki-Bauer, pers. comm. 2001). Zebra mussels' higher survival in waters with naturally high calcium concentrations may possibly be due to higher magnesium levels, rather than higher calcium levels *per se* (Nichols, pers. comm. 2001). Zebra mussels may also obtain some calcium from their diet: mollusks typically meet between 70-80% of their calcium needs by absorption through their gills and mantle, and the rest from their food (Vinogradov *et al.* 1993). Finally, zebra mussels may be able to resorb some calcium from their shells in order to meet metabolic requirements.

Table 19. Examples of Variation in Calcium Concentrations Within a Water Body

Water Body	Factor	Calcium Levels	Reference
Glen Lake, ON	Season	22-24 mg/l in winter 19-21 mg/l in spring/summer	Neary & Leach 1992
Wintergreen Lake, MI	Season	>50 mg/l at surface in winter ≈20 mg/l at surface in June near 0 mg/l at surface in Aug.	Wetzel 1975
Lawrence Lake, MI	Depth & Season	40 mg/l at surface in Mar. (just before ice melt) >70 mg/l at surface, and >85 mg/l at 12 m depth in Oct. & Dec.	Wetzel 1983
Blue Lake, WA	Depth	9 mg/l at surface 16 mg/l at 36 m depth	Edmondson 1963
Lower Goose Lake, WA	Depth	16 mg/l at surface 64 mg/l at 27 m depth	Edmondson 1963
Soap Lake, Grant Co., OR	Depth	16 mg/l at surface 16 mg/l at 17 m depth 8 mg/l at 18 m depth	Edmondson 1963
Soap Lake, Okanogan Co., OR	Depth	40 mg/l at surface 20 mg/l at 16 m depth	Edmondson 1963

Reported Distributions and Calcium Limits

The calcium requirements for zebra mussels estimated by various studies or determined from reviews of the scientific literature vary widely (Table 16). In general , studies based on European distributions have indicated that relatively high calcium concentrations are needed for establishment (above ≈25 mg/l), while studies based on North American distributions have generally concluded that the mussels can establish at lower concentrations (ca. 7-15 mg/l). For example, as noted above, Ramcharan *et al*. (1992) found that zebra mussels were found only in lakes with calcium concentrations greater than 28 mg/l in Europe, and Padilla (1997) reached similar conclusions for lakes in the former Soviet Union. However, zebra mussels have been reported as abundant in North America at calcium levels of 20-25 mg/l (Mellina and Rasmussen 1994; Vermont Department of Environmental Conservation 1998), and present at calcium levels of 4-19 mg/l (Mellina and Rasmussen 1994; Cusson and Lafontaine 1997; Vermont Department of Environmental Conservation 1998; S. Nichols, pers. comm. 1998) (Tables 20, 22).

Table 20. Reports of Zebra Mussel Populations in North American Waters with Low Calcium Concentrations

Location	Calcium Level	Reference
Abundant		
St. Lawrence River	16-38 mg/l	Mellina and Rasmussen 1994
Hudson River, NY	12-38 mg/l	Mellina and Rasmussen 1994; Strayer *et al.* 1996
Lake Champlain, VT	>18 mg/l	Vermont Department of Environmental Conservation 1998
Present		
Duluth Harbor, Lake Superior	13-23 mg/l	Balcer 1996; S. Nichols, pers. comm. 1998
Richelieu River	16-18 mg/l	Cusson & De Lafontaine 1997; De Lafontaine & Cusson 1997
Lake Champlain, VT	13-14 mg/l	Vermont Department of Environmental Conservation 1998

Cohen and Weinstein (2001) investigated whether the main low calcium populations reported in North America (Table 20) might consist of "sink" populations of mussels that are able to grow but not reproduce at those sites, and which had arrived as larvae or drifting juveniles from higher calcium, up-river sites where reproduction is possible. They found that the populations in the St. Lawrence River, Lake Champlain and Richelieu River in waters with less than 28 mg/l of calcium all have possible sources of larvae and juveniles in higher calcium waters upstream (Table 21). In Duluth Harbor at the western end of Lake Superior, zebra mussels were reported in low numbers since 1989, with calcium concentrations of 13-23 mg/l reported in 1994-95. The mussels could have arrived as larvae in the approximately 800,000 metric tons of ballast water from the lower Great Lakes that is discharged into Duluth Harbor each year. Larger numbers of mussels reported in Duluth Harbor since 1998 probably indicate establishment, but calcium levels during that period are unknown. Cohen and Weinstein (2001) concluded that the few records of zebra mussels at other sites in Lake Superior, whose open waters have calcium concentrations of 12-15 mg/l, do not represent established populations. However, they found that there was good evidence that substantial reproduction occurred in parts of the lower Hudson in at least some years, where mean reported calcium concentrations were 23-24 mg/l, with a range of 12-38 mg/l .

Table 21. Possible Sources of Reported Populations of Zebra Mussels in Low-calcium Waters in North America

Site of Population	Possible Source(s)	Comment
left bank of St. Lawrence River below Montrea	eastern Lake Ontario; St. Lawrence River above Montreal	Not present on the right bank of the St. Lawrence below Montreal, where calcium is 8-14 mg/l.
Hudson River below Troy	Mohawk River	Pattern of colonization suggests some reproduction in the lower Hudson, augmented by larvae from the Mohawk.
northern Lake Champlain & Richelieu River	southern Lake Champlain	The general flow of water from south to north through Lake Champlain and into the Richelieu River could carry larvae or drifitng juveniles; adults could travel attached to boat hulls.
Duluth Harbor in Lake Superior	lower Great Lakes	Zebra mussels could be regularly released in ballast water from the lower Great Lakes. Not present elsewher in Lake Superior, where calcium levels are lower.

Cohen and Weinstein (2001) also located unpublished records of zebra mussels in 13 inland lakes with less than 28 mg/l of calcium. Seven of the lakes are not connected to canals or to other, higher calcium waters that could serve as sources of veligers, and had reported mean calcium levels of 4-26 mg/l (Table 22). There were few calcium measurements (<4) in most of these lakes, so the reported means may not be representative. In lakes with few records of zebra mussels, establishment is uncertain, and where the records are of veligers only, misidentification or cross-contamination from other sampling sites is possible (Johnson, pers. comm. 2001).

Table 22. Zebra Mussels Reported in Inland, Isolated, Low-calcium Waters

Site	Mean Calcium Level	n
Dogwood Lake, IN	26 mg/l	4
Houghton Lake, MI	20 mg/l	1
Lake St. Helen, MI	18 mg/l	1
Lake Bomoseen, VT	18 mg/l	2
Crotch Lake, ON	11 mg/l	?
Lake Muskoka, ON	6 mg/l	15
Lake Dunmore, VT	4 mg/l	4

Table 23 summarizes the evidence regarding zebra mussels' calcium requirements. It is clear they can reproduce and become established at concentrations above 28 mg/l, and there are a few reliable records indicating that populations have reproduced in waters with mean calcium concentrations in the 20-28 mg/l range, but there is little to suggest that they can do so at lower concentrations. A more precise assessment could be achieved with:

- experimental studies of zebra mussels' responses to low ambient calcium concentrations during reproductive and early larval development stages;
- further examination of zebra mussel records, particularly those based on collection of veligers at low-calcium sites;
- more extensive population sampling and physiological/histological examinations to determine whether zebra mussels reported from low calcium waters are in fact established and reproducing; and
- better data on the temporal/spatial range and variation in calcium concentrations in the apparently low calcium waters where zebra mussels have been reported.

Table 23. Summary of Evidence of Zebra Mussels' Calcium Threshold

Calcium Level	Evidence
>28 mg/l	Many abundant, reproducing populations are established at these calcium levels. In two studies of large numbers of European lakes, zebra mussels were only found in lakes with more than 25 or 28 mg/l of calcium.
20-28 mg/l	Experiments indicate good adult survival; and embryonic, larval and juvenile development and growth rates comparable to those in higher calcium waters. Zebra mussel adults have apparently been established in Duluth-Superior Harbor since 1998, where calcium was measured at 13-23 mg/l in 1994-95, and mussels kept in cages in the harbor since 1968 had normal gonad development. The population in the harbor may be in part supported by regular inputs of veligers or adults via ships from the lower Great Lakes. Large populations are present and reproduction has apparently occurred in the lower Hudson River where mean calcium concentrations are 23-25 mg/l, although calcium concentrations from 12-38 have been recorded and the concentrations at the sites and times where reproduction occurred are not known; and the large populations could be due in part to recruitment of larvae or juveniles from upstream. Zebra mussel veligers or adults have been reported from seven inland lakes with mean calcium levels of 20-27 mg/l; for at least a few of these the records are probably due to veligers drifting in from upstream or individuals introduced via boats.
15-20 mg/l	There is little experimental evidence or field data regarding threshold limits to zebra mussel reproduction or establishment within this calcium range. Zebra mussels were reported from two inland lakes with mean reported calcium of 18 mg/l based, respectively, on one and two measurements.
<15 mg/l	Some experiments found good adult survival down to 0 or 4 mg/l, while another reported no survival at 8 mg/l. Two studies reported loss of calcium or shell at ≤14 mg/l; and survival at low calcium levels may in part be at the cost of mobilizing calcium from shell or tissues. Weight loss in juveniles or adults was reported in waters up to 8 mg/l, and depressed growth rates in waters of 12-14 mg/l. One experiment found 50% success in fertilization and first cleavage at 4-8 mg/l, but other experiments found no release of sperm and poor or no larval production at concentrations up to 15 mg/l. Zebra mussels have been reported in the northeast arm of Lake Champlain at sites with 13-14 mg/l, and in three isolated, inland lakes with mean reported calcium of 4-11 mg/l, but it is not clear if these are established populations or if the reported calcium measurements reflect typical concentrations at these sites.

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