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Zebra Mussel Demography and Modeling: Preliminary Analysis of Population Data from Upper Midwest Rivers

*by Resit Akcakaya, Patrick Baker
Applied Biomathematics*



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by **Reşit Akçakaya, Patrick Baker**

**Applied Biomathematics
100 North Country Road
Setauket, NY 11733**

Final report

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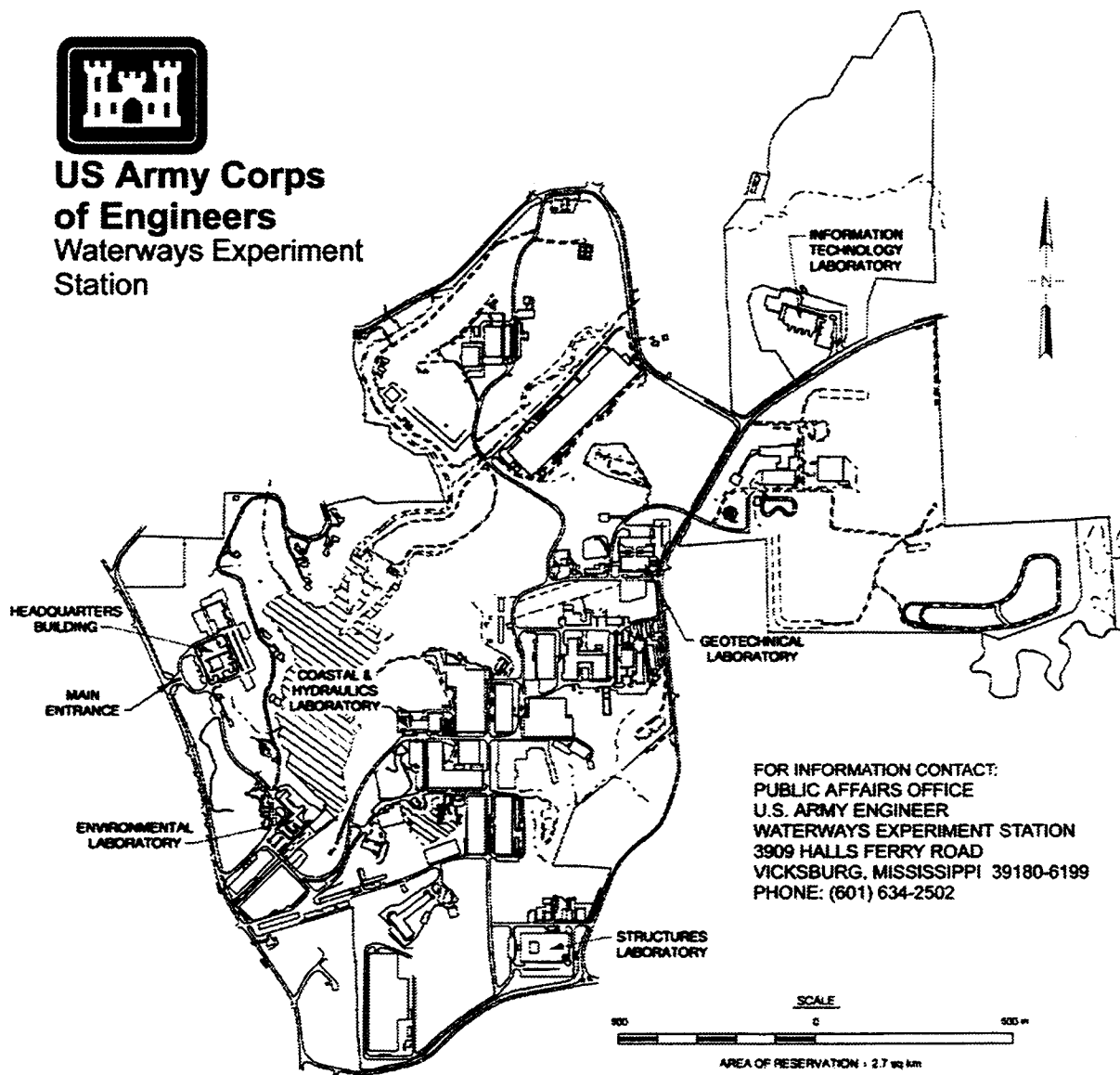
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FOR INFORMATION CONTACT:
PUBLIC AFFAIRS OFFICE
U.S. ARMY ENGINEER
WATERWAYS EXPERIMENT STATION
3909 HALLS FERRY ROAD
VICKSBURG, MISSISSIPPI 39180-6199
PHONE: (601) 634-2502

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Preface

The work described herein was performed under Contract DACW39-97-M-1558 by Applied Biomathematics (AB), Setauket, NY, for the U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, MS. Funding was provided through the Zebra Mussel Research Program (ZMRP). Dr. Edwin A. Theriot, Environmental Laboratory (EL), WES, was Program Manager for the ZMRP.

This report was prepared by Drs. Reşit Akçakaya and Patrick Baker, AB. The work was performed under the general supervision of Drs. Robert H. Kennedy, Environmental Processes and Effects Division (EPED), and Andrew C. Miller, Ecological Research Division, EL; and Dr. Richard A. Price, Chief, EPED, and Dr. John Harrison, Director, EL. Dr. Miller provided technical consultation during report preparation.

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I. Taxonomy

North American freshwater ecosystems have recently been invaded by two members of the bivalve mollusk family Dreissenidae; the zebra mussel *Dreissena polymorpha*, and the quagga mussel, *D. bugensis* (Griffiths et al., 1991; Spidle et al., 1994). *Dreissena rostriformis*, a third species mistakenly identified as a possible North American invader, appears to be restricted to the Caspian Sea (Rosenberg and Ludyanskiy, 1994). Another member of the family, *Mytilopsis leucophaeata*, is native to oligohaline estuaries of the Atlantic coast of the Americas (Marelli and Gray, 1985), and has invaded similar habitat in Europe (Wolff, 1969). A Caribbean species, *Mytilopsis sallei* has invaded estuaries in Asia (Morton, 1989). All members of Dreissenidae are similar in size (1-3 cm in shell length as adults), and attach epifaunally with a byssus (Eckroat and Steele, 1993), and share a life history that includes planktonic veliger larvae (Siddall, 1980; Morton, 1989; Ackerman et al., 1994). It is thus reasonable to compare life history parameters between species within the family, if *D. polymorpha* data are unavailable or suspect.

Although the quagga mussel, *D. bugensis*, is abundant in the Lake Erie, Lake Ontario, and St. Lawrence River, it has not enjoyed a dispersal comparative to the zebra mussel, *D. polymorpha* (New York Sea Grant, 1997). There is no evidence of *D. bugensis* invasion into the Mississippi basin (Stoekel et al., 1997).

II. *Dreissena* Reproduction and Larval Duration: Literature Survey

McMahon (1991), Ackerman et al. (1994), Mackie and Schloesser (1996), and Nichols (1996) have reviewed the life history of *Dreissena polymorpha*. Zebra mussels can spawn when water temperatures attain 12°C (Borcherding, 1991), but major spawning events in North America tend to occur at higher temperatures (Haag and Garton, 1992). Veliger larval density varies with relatively brief peaks, suggesting typically two synchronous spawning events (Haag and Garton, 1992) per year per population. Table 1 summarizes temporal and thermal data for spawning peaks in some lake systems.

Nichols (1996) suggested that larvae can over-winter in the plankton, and Keppner et al. (1997) reported veligers in water as low as 0.5°C, but recruitment occurs primarily in the summer and is also highly episodic, with episodes of several days accounting for >90% of recruitment (Bij de Vaate, 1991; Mackie, 1993; Martel et al., 1994; Whitney et al., 1994). Over-wintering is thus likely to be ecologically significant only in the absence or failure of more typical summer reproduction events.

Larval duration in the plankton varies highly (Nichols, 1996), and modelers have tended to use a wide range of values (Neumann et al., 1993; Ackerman et al., 1994). Marsden (1992) reported a planktonic duration of 8-15 days, but cites no data to support this. Sprung (1989) made the only attempt to follow cohorts through the plankton in the field, and estimated a larval duration of 18 days at a water temperature (averaged over the duration of the larval period) of 21.7°C, 28 days at 18.6°C, and 33 days at 15.1°C. Fitting these three points to a line produces:

$$y = -2.25 \cdot x + 68 \quad (\text{Equation 1})$$

where y = larval duration in days, and x = mean water temperature during larval development, in Celsius ($R^2 = 0.95$). This predicts larval duration declining with increased temperature. However, this is probably too simplistic, because reproduction does not occur below 12-14°C

(Sprung, 1989; Borchering, 1991; Ackerman et al., 1994). It has been suggested that high water temperatures may be lethal: at 28°C, 95% of larvae in the plankton of the Mississippi River had died (Deitz et al., 1994). Lake Erie briefly attained 30°C in 1989, without an apparent affect on larval abundance within the following week (Haag and Garton, 1991). The above relationship, therefore, if valid, is probably safe to apply only in water of about 15-25°C.

Table 1. Occurrence of the two largest *Dreissena* larval abundance peaks in lakes, with respect to time of year (month) and temperatures (initial, maximum) during larval peak event; both sets of values are often estimated from figures (read off original graphs). North American data are given in the top half of the table; European in the lower half. Sources are given below the table.

Lake	Year	1 st Peak		2 nd Peak	
		date	temp.(°C)	date	temp.(°C)
Lake Erie ¹	1989	July 12-25	24, 25	Aug. 5-21	30, 22
Fühlinger See ²	1986	May 26-June 9	16, 20	Aug. 1-13	21, 22
Fühlinger See ²	1987	May 15-29	12, 17	June 5-22	15, 16.5
Heider Bergsee ²	1986	June 11-July 7	16, 25	July 11-Aug. 4	17, 23
Heider Bergsee ²	1987	unclear	unclear	July 3-24	21.5, 22.5

1 Haag & Garton, 1992

2 Sprung, 1989

Postlarval drifting, a second planktonic phase, has been shown to occur for *D. polymorpha* in Lake Erie (Martel, 1993). To date, this phenomenon has not been reported or investigated in other systems, but if it occurs, it clearly represents a challenge when estimating recruitment, for two reasons. First, postlarval drifting greatly increases the planktonic duration, by an unknown factor. Second, it may be possible for a cohort to settle, be recorded, and then emigrate to a new habitat. In those systems for which bivalve postlarval drift is well-studied, it permits an ontogenetic niche shift between juvenile and adult habitat (Baker and Mann, 1997). However, post-larval drifting is unlikely to have a major quantitative effect on population dynamics.

Size at first reproduction of *D. polymorpha* has been reported as low as 6 mm (Nichols, 1996), but 8-9 mm is more widely accepted (Marsden, 1992; Sprung 1992; Mackie and Schloesser, 1996). This is also consistent with size at first reproduction of *Mytilopsis sallei*, a closely related species of similar adult size (Morton, 1989). If, in fact, smaller individuals reproduce, they are unlikely to be important unless that size class completely dominates the adult population. It is not known whether 0-year-class individuals larger than 9 mm are involved in reproduction.

Fecundity values have often been reported (McMahon, 1991; Ackermann et al., 1994), but it is unclear whether these represents measurements or guesses; no quantitative studies are cited in the above manuscripts. Estimates are typically in the tens of thousands, but the only laboratory measurements put egg production per spawning event in the hundreds of thousands (Sprung, 1991). A power model suggests that large individuals can produce millions of eggs. The power

model from Sprung (1991) is:

$$y = 0.606 \cdot x^{4.42} \quad (\text{Equation 2})$$

where y = egg number (in millions) and x = female shell length (in mm) ($R^2 = 0.94$). A linear model, however, that we calculated from data provided in Sprung (1991), also works reasonably well:

$$y = 84 \cdot x - 1200 \quad (\text{Equation 3})$$

where y = egg number (in thousands) and x = female shell length (in mm) ($R^2 = 0.90$). Both models have their limitations. Egg production may be a function of shell volume, which does not increase linearly with length (although a model incorporating volume does not provide a better fit to the data above). The power model, on the other hand, assumes that y intercepts x at a shell length of zero mm. This is clearly unrealistic because minimum size required for reproduction is likely to be substantially larger than zero. A linear model predicts a minimum shell length for reproduction of about 15 mm. This, however, is well above what is reported in the literature.

Even if these models are imprecise, they suggest that mean adult size is critical when estimating potential reproductive output of a population.

III. *Dreissena* Growth: Literature Survey

Reported *D. polymorpha* growth rates (as measured by shell length) vary widely, but actual attempts to quantify shell length increase have indicated rapid growth during the first year of life, and slower growth thereafter. Various authors have reported negative exponential relationships between initial size and growth (Bij de Vaate, 1991; Smit et al., 1992; Morteaux and Khalanski, 1994), although these relationships are either weak or very close to linear. Immediate post-settlement juveniles grow 65-75 μ per day, up to the size of about 1.2 mm, in Lake Erie (calculated from Martel et al., 1995). Later juveniles, 4-16 mm, grew at about 95 μ per day in a European lake system (calculated from Bitterman et al., 1994). A review of European literature showed growth rates in lakes, after the first year of life, of 5-7 mm per year, regardless of initial growth rate (calculated from Bij de Vaate, 1991). Maximum size appears to be near 4-5 cm, and maximum age appears to be 6-7 years (Bij de Vaate, 1991; McMahon, 1991; Marsden 1992).

Growth rates of 0-year-class individuals in rivers are at least equal to those in lakes, and may be elevated. Juveniles about 1-15 mm in a power plant water intake canal grew at 171 μ per day throughout the summer (calculated from Morteaux and Khalanski, 1994). At these rates, newly settled juveniles easily achieved 15-16 mm growth by early autumn. Martel (1995) reported daily growth rates of 0-year-class individuals of 89-139 μ (mean 92 μ) per day in an Ontario river. Zero-year-class individuals in October (about 4 months old) had a modal shell length of 16-17 mm. At the other end of the scale, Jantz and Neumann (1992, 1998) reported a growth interval of only 8.2 mm (individuals 5 mm at start of the trial) in river-water flumes. This is a much slower growth rate than for a comparable period in Ontario (Martel, 1995), although growth rates in flumes may not be representative of that in rivers.

Schneider (1992), in a review of other studies, reported that maximum tissue growth of *D. polymorpha* occurred from about April to June, with actual declines in mass following spawning episodes. Although tissue growth may be a reasonable index of *D. polymorpha* size, these findings are at variance with trends for shell length, the most commonly measured index of size.

In Europe, shell length increase follows a sigmoidal rate across the growth season, which generally starts in spring when water temperatures reach 6-7°C, and continues until sometime between August and October in most studies. Water temperature appears to be correlated with the start of rapid growth, but is unrelated to the cessation of growth (Table 2). Typically, growth rate is depressed during the summer during periods of warmer temperatures. The transitions from zero growth to maximum and back again are relatively brief. Effectively, shell length increase is nearly linear throughout the majority of the growing season (Bij de Vaate, 1991; Smit et al., 1992; Sprung, 1992; Morteaux and Khalanski, 1994; Jantz and Neumann, 1998). If this is true for North America as well, the June-October sampling period of Martel (1995) represents less than the total annual growth period. After omitting the extremes in season duration estimates, the mean shell growth season in Europe is 151 days in lakes and 184 days in rivers (Table 2). Although it is tempting to infer from this that the growing season in rivers is longer than in lakes, the sample size is small ($n = 4$ & 5 , respectively), and drawn from different sites and studies.

Estimates of growth rates are important for population analysis and predictions. They are needed when creating static life tables, in order to correctly separate age classes. The abundances in these age classes can then be used to estimate survival rates. The variability in the above reported growth rates, however, suggests that it is important to estimate growth rates and the duration of the growth season, separately for each system being studied.

Table 2. Seasons of rapid shell length increase for *Dreissena polymorpha*, with temperatures (°C), from the literature.

Locality	growth start	start temp.	max. temp.	growth end	end. temp.	total days
Ijsselmeer, Netherlands, 1983 ¹	Apr. 20	6	23	Aug. 21	21	122
Ijsselmeer (lake), Netherlands, 1984 ¹	Apr. 31	7.5	21.5	Aug. 25	21.5	118
Markemeer (lake), Netherlands, 1984 ¹	Apr. 10	6	21	Sept. 22	14.5	165
Heider Bergsee (lake) Germany, 1987 ²	Mar. 31	7	24.5	Aug. 31	19.5	152
Volkerameer (lake), Netherlands, 1988 ³	Mar. 31	NA	19.8	Sept. 12	NA	165
Volkerameer (lake), Netherlands, 1988 ³	Apr. 5	NA	20.2	Oct. 17	NA	195
lower Rhine (river) Netherlands, 1988 ³	Mar. 1	NA	19.6	Aug. 18	NA	174
lower Rhine (river) Netherlands, 1988 ³	Apr. 5	NA	23.1	Oct. 22	NA	197
lower Rhine (river) Netherlands, 1988 ³	Mar. 31	NA	22.2	Oct. 22	NA	204
upper Rhine (river) Germany, 1992 ⁴	Feb. 25	6	24	Aug. 21	21	174
upper Rhine (river) Germany, 1993 ⁴	Feb. 25	7	24	June 21	22	84
Moselle River, France, 1992 ⁵	Apr. 15	NA	25	Oct. 7	NA	176
Moselle River, France, 1993 ⁵	Mar. 21	NA	22.3	Oct. 7	NA	197

1. Bij de Vaate, 1991

2. Sprung, 1992

3. Smit et al., 1992

4. Jantz & Neumann, 1998

5. Morteaux and Khalanski, 1994

IV. *Dreissena* in Rivers: Literature Survey

Planktonic larvae, although important for dispersal of marine invertebrates, are uncommon among freshwater invertebrates. Most freshwater ecosystems that persist through evolutionary time are rivers, with unidirectional currents, and weakly swimming larvae would be swept downstream, with no way to return to the parent population. Most freshwater bivalves either lack planktonic larvae, or attach larvae to fish hosts for dispersal (McMahon, 1991). Large estuaries, however, often have extensive, stable freshwater/oligohaline tidal regions (Baker et al., 1993a, 1993b), and such habitats are probably the site of *Dreissena* evolution in eastern Europe and central Asia (Rosenberg and Ludyanskiy, 1994). Most large lakes in North America and Europe are geologically recent (following the last ice age), and lack native organisms with planktonic larvae; *D. polymorpha* have done extremely well in these systems (Stanczykowska and Lewandowski, 1993; New York Sea Grant, 1997).

In Europe and in North America, *D. polymorpha* has invaded river systems. Studies on these systems reveal that, as one might expect, recruits in the river come from a considerable distance upstream, and larvae from those populations are carried downstream (Borcherding and de Ruyter van Steveninck, 1992; Neumann et al., 1993; Kern et al., 1994; Horvath et al., 1996; Stoekel et al., 1997). Recruitment from lakes to rivers can permit densities in rivers to become quite high (Martel, 1995; Miller and Payne, 1997; Stoekel et al., 1997). In these systems, there is always an upstream source population: e.g. the Badensee for the Rhine River, Lake Michigan for the Illinois River, Lake Ontario for the St. Lawrence River, and Lake Pepin and other natural and artificial impoundments on the upper Mississippi River. Backwaters and canals, although small and geologically young, may also host *D. polymorpha* populations that can contribute larvae to the river (Biryukov et al., 1968). In the Ohio River, most impounded areas upriver of dams are small, and not very lake-like. Zebra mussel populations at the Olmsted bed in the study area (see below) likely came from veligers that originated in the Illinois River. These could have settled during high water in 1993 when high water in the Mississippi River backed up the Ohio River and over the Olmsted mussel bed.

Two metapopulation models are proposed for *D. polymorpha* in rivers. The first is a source-sink model (Horvath et al., 1996). This model assumes that the vast majority of recruits will come from a still-water source population in which reproduction and larval recruitment can occur, but from which there is downstream "leakage" (dispersal) of planktonic larvae or postlarvae. Further, it assumes that river populations are "sinks" that do not contribute to recruitment. Horvath et al. (1996) base this model on a study of *D. polymorpha* in small and large rivers on the lower Michigan peninsula. Contrary to prior reports (Strayer, 1991), *D. polymorpha* presence in streams appears to depend mainly upon whether or not there is an upstream source population, not stream size (Horvath et al., 1996). (This does not rule out the susceptibility of small streams to freezing or overheating as limits to *D. polymorpha* populations, however.) The primary evidence in support for the source-sink model seems to come from observed *D. polymorpha* distribution in rivers. In small streams, *D. polymorpha* became successively rarer downstream of a source population, to about 10-12 km away (Horvath et al., 1997). In the Mississippi River, *D. polymorpha* abundance appears to be reduced below the region of in-stream impoundments, compared to above it, except in localities near upstream source populations in tributaries (New York Sea Grant, 1997). In the Rhine, Borcherding and de Ruyter van Steveninck (1992) were unable to unequivocally demonstrate that larvae were produced

within the river itself, as opposed to upstream lake sources or in-stream reservoirs.

The other metapopulation model (Stoekel et al, 1997) acknowledges that upstream source populations are critical, and that all larvae are carried a considerable distance downstream. The difference from the source-sink model is that *D. polymorpha* in the river itself reproduce, permitting further downstream invasion, until physiological limits come into effect (Strayer, 1991; Baker et al., 1993a). Horvath et al. (1996), in fact, acknowledge this possibility. The evidence for this model comes mainly from estimates of larval drift rate (an apparently complex problem), calculated by Neumann et al. (1993) and Stoekel et al. (1996). If these estimates are correct, and reproduction does occur in rivers, part of the *D. polymorpha* range in certain large rivers may be maintained from in-stream source population, rather than a lake population.

Both of these are metapopulation models; their difference is whether there is reproduction in rivers. It is possible that the more realistic model is one with in-stream reproduction, though not as much as reproduction in lakes. Thus, the question is quantitative rather than qualitative: what is the relative contribution of reproduction in rivers and lakes to the overall recruitment in the rivers.

A confounding factor, when comparing *D. polymorpha* demographics in large and small rivers, is that large rivers often have backwater lakes or connecting navigation canals, which can sustain *D. polymorpha* larval growth in the plankton (Biryukov et al., 1968). This difference is certainly true of the two river systems studied by Horvath et al. (1996) and Stoekel et al. (1997). It is possible that at least some of the larvae in the lower 30% of the Illinois River were generated within such backwater areas along the Illinois, with overflowed into the main river system, while retaining enough larvae to maintain their *D. polymorpha* populations. Such backwater areas also exist in the Mississippi River, but there are not many of them in the lower Ohio river.

Neither of the above models accounts for postlarval movement. Postlarval movement is known to exist in lakes, where lake circulation is sufficient to transport postlarvae for considerable distances and times beyond that set by the larval planktonic phase (Martel, 1993). It is not known whether postlarval drifting occurs in rivers; however, the considerably stronger currents in rivers may move not only large numbers of drifting postlarvae, but possibly adults as well.

A final problem encountered by *D. polymorpha* demographers in rivers is the extreme temporal (inter-annual) variability in population density and size (Bij de Vaate and Greijdanus-Klaas, 1993; Miller and Payne, 1997). Populations can decline dramatically even many years after invasion (Bij de Vaate and Greijdanus-Klaas, 1993), or after having attained very high densities (Miller and Payne, 1997).

V. Study Areas

Data on *D. polymorpha* population density and size structure have been provided by USACE from several systems, including the Illinois River, the upper Mississippi River, and the lower Ohio River. Each has a different source for recruitment.

The Illinois River was connected in 1910, artificially, to Lake Michigan, via the Chicago Sanitary and Ship Canal, and is navigable for its entire length. Lake Michigan is normally higher than the head of the Illinois River, and water from Lake Michigan flows into the Illinois system. Stoekel et al. (1997) have estimated that Lake Michigan and associated Chicago-area canals are the primary source of recruitment for at least the upper 70% of the Illinois River, although this is

based on assumptions of mean planktonic phase duration. The Great Lakes are subject to seiching (cross-basin tilting of the water level due to wind and air pressure), which could, in theory, affect discharge rates into the Illinois River independent of the rest of the Illinois River flow rates. However, there is no evidence of this effect. In the USACE data set, *Dreissena polymorpha* densities were sampled at River Mile 113 in 1995 and 1996.

The upper Mississippi River is defined as that portion of the river upstream of its confluence with the Ohio River, its largest tributary. This waterway is navigable to Minneapolis, via numerous locks and impoundments. Some of these impoundments, such as Lake St. Croix and Lake Pepin, are natural, while others are artificial. Lake Pepin, which is invaded by *D. polymorpha* (USACE), is the largest lake on this system; the second largest, Lake St. Croix, is off the main channel and not yet heavily invaded (U.S. Natl. Park Serv., unpubl. data). Lake Pepin is several orders of magnitude smaller than Lake Michigan, but unlike Lake Michigan, water flow from Lake Pepin to portions downstream always occurs at a rate constant with overall river discharge. *Dreissena polymorpha* populations were sampled at River Mile 551 (UMR 551) from 1994 to 1996; at or very near UMR 635 in 1995 and 1996; UMR 752 from 1994 to 1996; and UMR 766 in 1994 and 1995. Several other sites between these were sampled in 1995 only.

The lower Ohio River is defined as that portion downstream of its confluence with the Tennessee, its largest tributary. This portion of the river is navigable. Impoundments on the Ohio are few and small, but just upstream of their near-simultaneous confluence with the Ohio, the Tennessee and Cumberland rivers are both impounded to form the large Kentucky (Tennessee River) and Barkley (Cumberland River) lakes. These lakes are at the same elevation; they are joined by a canal and are invaded by *D. polymorpha*, hence serving as a single source for *D. polymorpha* recruits downstream. These impoundments are larger than those on the upper Mississippi River, and discharge rate may be artificially manipulated independently of river flow rates. A native unionid bivalve bed in the lower Ohio River was sampled from 1993 to 1997.

VI. Annual Growth Estimates for *Dreissena* in the Mississippi

Data Analysis

Estimates of daily growth rate of *Dreissena polymorpha* in Pool 10 (River Mile 635) were provided by A. Miller, U.S. Army Corps of Engineers (hereafter this data will be referred to as USACE). Cohorts of various sizes were followed at approximately biweekly intervals from June 1 to October 1, and the difference in mean shell length between intervals was divided by the number of days since last measured. The size classes measured were 10-15 mm, 15-20 mm, 20-25 mm, and 25-30 mm. It should be noted that although each size class sample was followed independently throughout the study, individuals from each size class grew beyond the original size class limits, often within several weeks. Thus, growth rates reported were for samples, not size classes.

It was assumed that shell length within each sample was distributed normally, with a mean equal to the median. Thus, the initial size classes were expressed as their means (13, 17, 23, and 27 mm, respectively), prior to calculations. This was the length of each cohort at the start of the study (June 1). Two weeks later, the samples were again measured, with a mean shell length somewhat greater than previously. The difference, divided by the number of days after June 1, was the mean daily growth rate, for *D. polymorpha* of 13, 17, 23, or 27 mm in shell length.

The same technique was used to estimate growth rate for the second time period; however, the shell length of each sample was now larger. In the case of the 13-mm sample, mean shell length had increased to nearly 15 mm, for example. Thus, each growth rate for a sample interval was paired with a unique *D. polymorpha* shell length at the start of that interval. The result was 9 sample periods for four initial size-class samples, yielding 36 daily growth rates paired with 36 sizes.

Growth rate was weakly but significantly and negatively related to shell length ($R^2 = 0.29$, $p = 0.00067$; Fig. 1). When combined with temperature in a polynomial relationship, the relationship becomes somewhat stronger, with peak growth rates at 23°C ($R^2 = 0.47$, $p = 0.0001$), as in the following equation:

$$Y = -1.1 + .108X - 0.002X^2 - 0.0265Z \quad (\text{Equation 4})$$

where Y = daily growth (mm), X = water temperature (degrees Celsius), and Z = shell length (mm). The difficulty with this equation is that it predicts that growth does not begin until the temperatures attain 14-15°C, which is contrary to field data. According to Schneider (1992), growth rate peaks at 12-14°C, which is well below the water temperature throughout this study. In addition, the European literature indicates near-linear growth for the majority of the growth season (Bij de Vaate, 1991; Jantz and Neumann, 1992). Finally, daily temperature regime was not available as a variable for some of the USACE demographic data. For this analysis, therefore, estimates of growth rates will be modeled on initial shell length only.

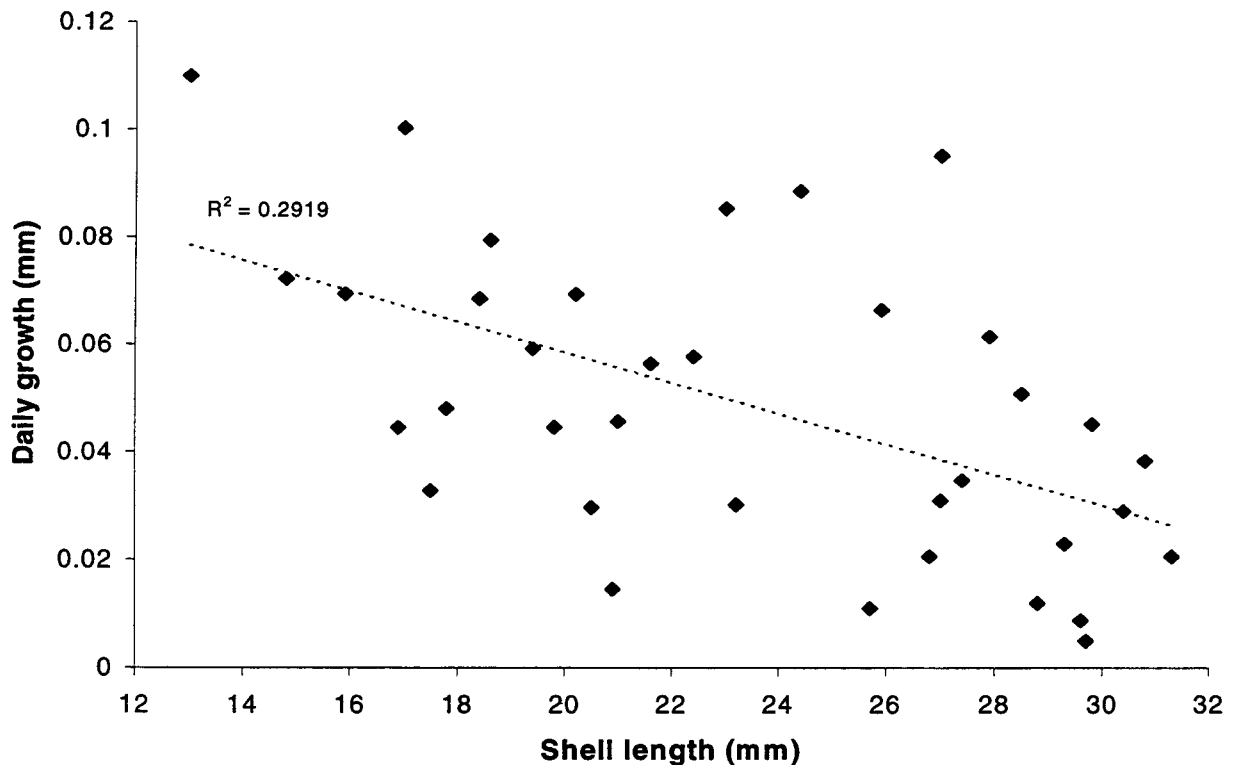


Figure 1. Daily growth increment of *D. polymorpha* regressed on mean water temperature of the growth interval.

Not all growth occurs between June and October, the period of the USACE data collection. Schneider (1992) predicted that maximum tissue growth in the Great Lakes would occur prior to June, although those predictions were not compared to actual North American field data. In Europe, *D. polymorpha* exhibits a sigmoidal shell length growth curve from Mid-April to early October, but the transition to and from zero growth is very brief (Bij de Vaate, 1991; Jantz and Neumann, 1998). Effectively, shell length increase is linear between March or April and September or October, occasionally as early as August (Bij de Vaate, 1991; Smit et al., 1992; Sprung, 1992. Jantz and Neumann, 1998). After omitting the extremes, the mean length of the shell growth season in rivers, calculated from the above sources, is 182 days. Thus, growth from June 1 to October 1 is about 67% (122 days) of the total annual growth (182 days), based on European seasons. A similar growth season, based on data for the end of the growth period, appears to be indicated for North America (Bitterman et al., 1994; Martel, 1995; Stice, 1997), but precise dates were not available from these studies.

Having determined that shell length was a significant predictor of growth, we were able to use the total growth, April-October, for the four size-class sample, to predict growth of larger and smaller size classes. Regressing total growth against sample shell length gave the relationship:

$$Y = 16.3 - 0.343X \quad (\text{Equation 5})$$

where Y = annual growth increment (mm), and X = shell length (mm) at the beginning of the growth interval ($R^2 = 0.94$). This equation permitted an estimate of growth for the same time period for any size class, up to a maximum of 16.2 mm in one year for newly-settled juveniles (shell length < 1 mm). This is a mean growth rate for the population, with an unknown level of variability in individual growth. Inter-annual variability in growth rate may arise from variations in the length of the growth season (Table 2). This assumes, however, that during a longer growth season temperatures do not exceed physiological tolerance for growth (McMahon, 1996).

Discussion of annual growth

The available information suggests that shell length increase is linear throughout most of the growing season (Bij de Vaate, 1991; Smit et al., 1992; Sprung, 1992. Jantz and Neumann, 1998), and is about 184 days in European rivers. Thus, growth from June 1 to October 1 (the period of the USACE data collection) is about 66% (122 days) of the total annual growth (182 days), based on European seasons. A similar growth season, based on data for the end of the growth period, appears to be indicated for North America (Martel, 1995; Stice, 1997), but precise dates were available from neither study.

The above calculations indicate modest growth of *Dreissena polymorpha* in the upper Mississippi River, compared to some other estimates (Morteaux and Khalanski, 1994; Stice, 1997). For larger individuals, the growth rates are comparable to those reviewed for *D. polymorpha* from a number of lake sites in Europe, but for smaller individuals, Mississippi River Pool 10 growth rates are faster (Bij de Vaate, 1991). Growth rates of 65-75 μ per day for newly metamorphosed juveniles was reported for Lake Erie (Martel et al., 1995), slightly lower than the 88 μ predicted by Equation 5 (assuming 184 growing days) for new recruits in the upper Mississippi River. Growth rates integrated over the entire year in Lake St. Croix were 51 μ per day for individuals starting at 4.2 mm (Bitterman et al., 1994), compared to 80 μ per day predicted by Equation 5.

The Mississippi growth rate is considerably lower than those reported in some other flowing systems. Using the same growth season as above (184 days), annual growth rate estimates range from 32 mm (calculated from Morteaux and Khalanski, 1994) to 34 mm (calculated from Stice, 1997). The Mississippi River growth rates (16.2 mm for new recruits) are nearly equal to the 16.9 predicted from Martel (1995) (Table 3). If growth rate is indeed negatively exponentially related to initial size, as predicted by some authors (Bij de Vaate, 1991; Smit et al., 1992; Morteaux and Khalanski, 1994), Equation 5 provides a slight underestimation of growth for the smallest size class. The large sample size in the USACE data, and the fact that the study was designed to study growth rate in the field, and the near-agreement with Martel (1995) suggest that the USACE-based growth interval is the most reliable of the various data sets available for the present analysis.

Increased temperature may not translate into increased growth for *D. polymorpha*. Deitz et al. (1994) suggested that high temperatures were lethal to *D. polymorpha* larvae. Schneider (1992) and McMahon (1996) have extensively reviewed the upper thermal limits of *D. polymorpha*; depending of the function measured, optimal temperature varies between about 18 and 22°C, with lethal temperatures at about 31°C. Although there are errors associated with it, a quadratic model using the USACE data (Equation 5), using both temperature and shell length, also predicts a peak growth rate, at about 23°C. Water temperatures in the upper Midwest frequently exceed 22°C, but seldom exceed 30°C. Unfortunately, many thermal tolerance studies took place in still water; the interactions of flowing water and temperature are not understood. Quantification of the annual growth interval, therefore, should be done separately for each site for which population models are desired.

The growth model developed from the USACE data (Equation 5) can be used to approximately divide populations into year classes, based on shell length. *Dreissena polymorpha* recruiting in July in Pool 10 (USACE) should be about 17 mm in shell length by the following July, about 28 mm in two years, and about 35 mm in three years. The relative scarcity of specimens in the USACE data above 28 mm in shell length indicates very low survival past the 2nd year. If the USACE data represent an underestimation of growth (caused by, for example, handling effects), then there may be virtually no survival past the first year in the systems examined. In either case, the population would be extremely responsive to annual variations in recruitment.

Table 3. Estimates of daily and annual growth increments (mm) for *Dreissena polymorpha*, calculated from the literature. Standardized annual growth (mm/yr) is based on standard growing seasons: 151 days for lakes and 184 days for rivers (see text). Pool 10 predicted growth intervals are the predicted growth rate (mm/yr), given the initial shell length (2nd column), and assuming growing conditions as those in Pool 10 of the Mississippi River (growth season = 184 days, growth rate predicted by Equation 5).

Locality	shell length	daily growth	actual annual growth	standardized annual growth	Pool 10 predicted
Ijsselmeer, 1983 ¹	5.5	0.070	8.5	10.5	14.4
Ijsselmeer, 1984 ¹	6	0.064	7.6	9.7	14.2
Markermeer, 1984 ¹	6	0.039	6.4	5.9	14.2
Heider Bergsee, 1987 ²	2.3	0.072	10.9	10.8	15.5
Lake St. Clair, 1991 ³	4.2	0.051	NA	9.4	14.9
Lake Erie, 1992 ⁴	0.2	0.07	NA	12.9	16.3
upper Rhine, 1992 ⁵	10	0.041	7.2	7.5	12.9
upper Rhine, 1993 ⁵	10	0.083	7.0	15.3	12.9
Moselle R., 1992/1993 ⁶	7.5	0.171	NA	31.5	13.7
Rideau River, 1994 ⁷	0.2	0.092	NA	16.9	16.3
Mississippi R., 1996 ⁸	13	0.066	NA	12.1	11.8
Mississippi R., 1996 ⁸	17	0.053	NA	9.8	10.5
Mississippi R., 1996 ⁸	23	0.048	NA	8.9	8.4
Mississippi R., 1996 ⁸	27	0.037	NA	6.8	7.0

1. Bij de Vaate, 1991

2. Sprung, 1992

3. Bitterman et al., 1994

4. Martel et al., 1995

5. Jantz & Neumann, 1998

6. Morteaux and Khalanski, 1994

7. Martel, 1995

8. USACE, Pool 10

VII. Mississippi River Invasion Trends

The St. Paul District of the U.S. Army Corps monitored abundance of adult (>10 mm) *Dreissena polymorpha* on fixed structures at various pools (defined as regions between Army-Corps maintained navigation dams) on the upper Mississippi River (Yager, 1992, 1993a, 1993b, 1994a,

1994b, 1995). Although incomplete, when combined with some additional data (Cope et al., 1997), this provides some ideas of abundance trends for *D. polymorpha* in this region. Measurement of *D. polymorpha* density on fixed structures (usually, navigation locks) is significant, because there is no opportunity for the substrate—with the attached fauna—to be moved by ice rafting or floods.

D. polymorpha population trends are plotted for select sites in the upper Mississippi River (Fig. 2). *D. polymorpha* was first discovered in the Mississippi River in Pool 8, near LaCrosse, Wisconsin. By the end of 1992, it had been recorded to the head of navigation, in Minneapolis, with no overall trend in abundance. Subsequent sampling of Pools 1-10 in 1993, 1994, and 1995, however, revealed a faster *D. polymorpha* density increase in downstream pools; by 1995, *D. polymorpha* was classified as "layered" on all lock structures from Pool 4 (Lake Pepin) downstream, and quantitative sampling ceased at most sites (Yager, 1992, 1993b, 1994b, 1995).

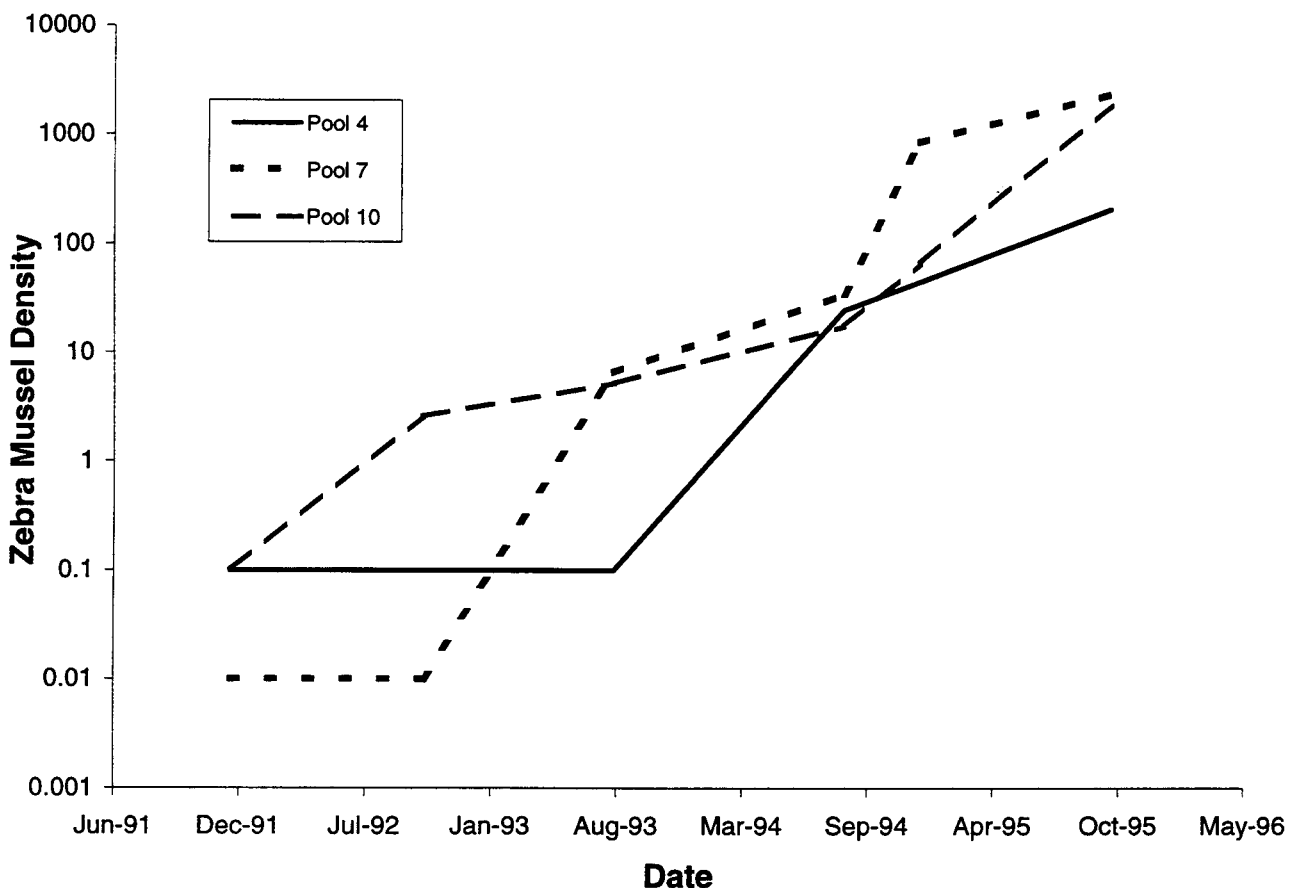


Figure 2. Zebra Mussel densities (m^{-2}) on fixed structures in the upper Mississippi River.

At most sites, there is also an exponential population growth increase, with temporally varying growth rate (Fig. 2; note the logarithmic scale). Although *D. polymorpha* densities at Pool 3 were low in 1995 (the last year of sampling at that site), even at this site, the proportional increase is greater than in the previous year. At Pool 10, this trend continued into 1996. Thus, USACE and NBS data for 1994-1996 appear to span a period of explosive population growth in the upper Mississippi River, based on *D. polymorpha* densities on fixed structures.

At other sites, the exponential growth seems to have come to a stop. In the Illinois River, *D. polymorpha* densities peaked in 1994, and have declined dramatically since then (Stoekel et al., 1997). In the lower Ohio River (Miller and Payne, 1997), *D. polymorpha* densities in 1994-1996 varied greatly from year to year, without a continuation of the exponential population increase seen on fixed structures in the upper Mississippi River.

In all sites, whether the populations are growing exponentially or have declined, there seems to be substantial inter-annual variability in growth rates. For example, the pool populations depicted in Fig. 2 are growing exponentially (as evidenced by generally linear growth curves when plotted on logarithmic scale), with an average growth rate of about 9-fold per year. However, the growth rate in each year (the slope of each segment of the lines) shows substantial variation. In this model, high inter-annual variability may be accounted for by differences in recruitment, differences in mortality, or both. Stoekel et al. (1997) reported extreme variability in larval abundance at a fixed sampling point in the Illinois River, sampling on a weekly basis. Martel et al. (1994) were able to correlate settlement with veliger density; such a study could be modified for Midwest river systems to compare larval availability with subsequent juvenile density. Marine studies on mortality of juvenile bivalves (Osman et al., 1989; Roegner, 1991) could also be modified, to examine inter-annual mortality of *D. polymorpha* in an experimental manner.

Another possible source of the extreme inter-annual variations in the river populations is static sampling combined with adult *D. polymorpha* downstream migration. The benthic sampling schemes used for *D. polymorpha* are similar to those used for native unionid clams, which have a long evolutionary history in rivers (Miller et al., 1993). Replicate quadrats in approximately the same locations are sampled each year; although the quadrats may not be in precisely the same location each year (because of sampling artifacts), they are quite close. This may be reasonable for interannual comparisons of unionid bivalve populations; unionids are burrowing, can reburrow if dislodged (McMahon, 1991), and the adults of most species weigh several hundred grams. For zebra mussels, it may be unsafe to assume that the population stays in the same location over time, once they have settled from the plankton. *Dreissena polymorpha* cling tightly to substrate with byssal threads, but this is of no help if the substrate itself (e.g. wood or pebbles) is dislodged. If the adult *D. polymorpha*, which weigh about a gram, are dislodged, they are unable to burrow into the sediment to prevent downstream transport. Population-scale bedload transport as a common event has been recorded even for burrowing bivalves (Emerson and Grant, 1991; Roegner et al., 1995). Thus, inter-annual variability of *D. polymorpha* in natural sediments in rivers may be dependent upon random sediment transport events, a form of involuntary migration, which can either remove or deposit large densities of juveniles and adults. This phenomenon would not occur on fixed structures, such as navigation locks.

VIII. *Dreissena* Mortality and Migration in Rivers

Data Analysis

Data on *Dreissena polymorpha* size frequency distributions and overall density at specific sites were provided by USACE. For some sites, multiple density levels, each expressed as a range (e.g. 500-1000 *D. polymorpha*·m⁻²), were provided. For purposes of analysis, such ranges were converted to their median; e.g., 500-1000 becomes 750. These values were then used to estimate size-specific density, multiplying median density by the proportion of the sample within each size class.

The relative area covered by each density was not recorded. In such cases (Upper Mississippi River Mile 635, in Pool 10; Lower Ohio River), size-specific density was estimated by taking the mean from the three highest-density samples, on the assumption that high density sites accounted for the majority of *D. polymorpha* in an area, and hence drove size distributions. For other sites only one overall density was reported. Size frequencies were converted to actual size-specific *D. polymorpha* densities at each site. The frequency distributions of size-specific densities in consecutive years were compared as described below to estimate age-specific survival rates. An example of two consecutive frequency distributions of size-specific densities is given in Fig. 3.

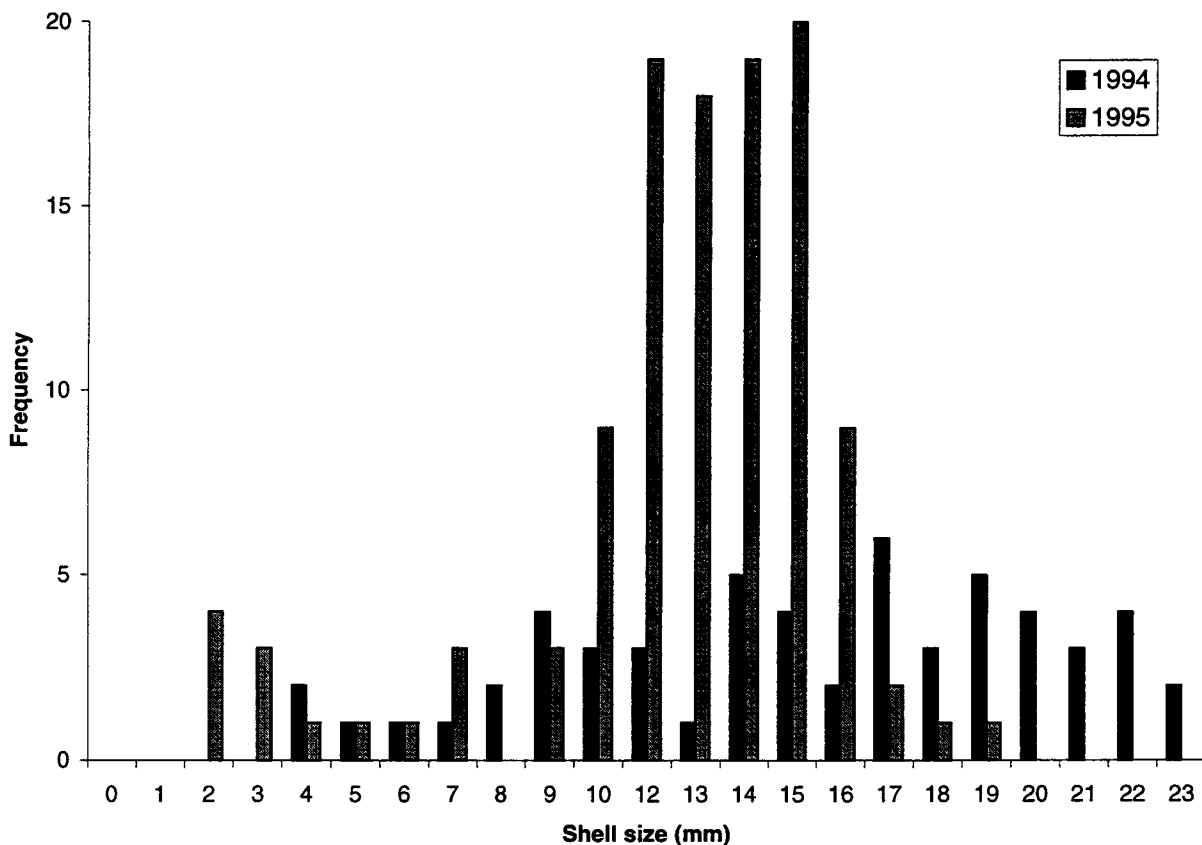


Figure 3. Size distribution of Zebra Mussels at Illinois river mile 113 in 1994 and 1995.

For this analysis, it is necessary to first group the frequency distributions to age classes. Age classes were based on mean annual growth estimates (Equation 5), producing cohorts of 0-16 mm in shell length, 17-27 mm, and 28-34 mm. Although the growth model predicts that *D. polymorpha* above 34 mm shell length will be in their 4th year, no such individuals were reported in USACE data.

Size-specific growth rates (Equation 5) were used in two ways to estimate cohort survival rates. Both methods assume a closed population (i.e., no immigration or emigration). Apparent cohorts, based on peaks in size-specific density, were ignored, because more than one seasonal cohort can be produced in a year (Haag and Garton, 1992; Stoekel et al., 1997), yet collectively fall into a single year-class cohort. Survival estimates were not statistically analyzed for reasons explained below.

The first method (S1 in Table 4) assumes stationary and stable population, with constant survival rates from year to year. The survival rate is calculated as the ratio of density of a size class to density of the previous size class in the same year. For example, the density of 17-27 mm class, divided by that of 0-16 mm class in the same year, gives an estimate of the survival rate of 0-16 mm class, with the above assumptions.

The second method (S2 in Table 4) assumes a population at the stable age distribution. The survival rate is calculated as the ratio of density of a size class to density of the previous size class *one year ago*. For example, the density of 17-27 mm class in 1995, divided by the density of 0-16 mm class in 1994 gives an estimate of the survival rate of 0-16 mm class. An asterisk for S1 or S2 values indicates that the estimated survival rate is above 1.0, due to sampling variation, measurement error, or migration. Truncating these to 100%, the average survival rate for 0-16 mm class is about 35%, with a standard deviation of 45%. The average survival rate for 17-27 mm class is about 3%, with a standard deviation of 11%.

Table 4. Size-class densities (m^{-2}) and annual survival rate estimates (%) for *D. polymorpha*. S1 is survival estimate (%) assuming stationary and stable population: it is the ratio of density of a size class to density of the previous size class in the same year (i.e., 3rd column divided by 2nd column, or 6th column divided by 3rd column). S2 is survival estimate (%) assuming stable population: it is the ratio of density of a size class to density of the previous size class *one year ago* (e.g., 3rd column for 1995 divided by 2nd column for 1994). An asterisk for S1 or S2 values indicates that the estimated survival rate is above 1.0.

Site/Month/Year	0-16 mm	17-27 mm	S1	S2	28-34 mm	S1	S2
Illinois RM 113; Oct 1994	209.4	125.5	59.9		0	0	
Illinois RM 113; Oct 1995	8646	154.4	1.79	73.73	0	0	0
Lower Ohio River; Aug 1993	10.3	69.8	*		0	0	
Lower Ohio River; Aug 1994	134958.9	0	0	0	0	0	0
Lower Ohio River; Aug 1995	635.9	3110	*	2.30	4.1	0.13	0
Lower Ohio River; Aug 1996	3394.2	0	0	0	0	0	0
Lower Ohio River; Aug 1997	44	205.8	*	6.06	0	0	0
UMR 551 Oct. 1994	432	68	15.73		0	0	
UMR 551 Oct. 1995	2600	400	15.38	92.58	0	0	0
UMR 551 Sept. 1995	789	11	1.42		0	0	
UMR 551 Sept. 1996	15500	0	0	0.0	0	0	0
UMR 635 July 1995	167	426	*		0	0	
UMR 635 July 1996	3781	2899	76.67	*	151	5.20	35.36
UMR 752 Oct. 1994	46	0	0		0	0	
UMR 752 Oct. 1995	106	224	*	*	0	0	0
UMR 752 Aug. 1995	155	0	0		0	0	
UMR 752 Aug. 1996	73.5	8.5	11.63	5.51	0	0	0
UMR 766 Sept. 1994	1600	0	0		0	0	
UMR 766 Sept. 1995	8645	154.4	1.79	9.65	0	0	0

Discussion

The size-specific densities on natural substrates in Midwest rivers are frequently higher than those possible by growth of a cohort from the preceding year, and occasionally exceed those of the smaller size class within a sample year (Table 4). Moreover, in 1/3 of cases, all individuals sampled were within the 0-year-class cohort (0-16 mm). The observed density patterns indicate that the *Dreissena polymorpha* population at a given sampling site are determined by factors other than (or in addition to) densities in the previous year.

The results of this analysis may have three possible explanations. One possibility is that adult *D. polymorpha* are transported downstream wholesale, between one sample date and the next. Even if some survive, the juvenile population of last year will be this year's adult population an unknown distance downstream. If surviving *D. polymorpha* are sorted by river currents as sediment particles are, then different sizes of Zebra Mussels may be sorted differentially (accumulate in different locations, due to currents), resulting in size-class concentrations that have nothing to do with biological mechanisms. In addition, rate of byssal drifting of juveniles in rivers is an unknown quantity. Marine bivalves up to several millimeters in length may be transported by byssal drifting (Baker and Mann, 1997); the strong currents in rivers may permit even larger individuals to move in this manner.

Several experimental or sampling options may be adapted to test the above hypothesis. Downstream transport of juveniles can be sampled using fixed nets (Ellertsen, 1977; McIvor and Odum, 1989; Lipcius et al., 1990), and the relatively large size (> 1 mm) of the juveniles permits a relatively large net mesh, reducing clogging difficulties. Filamentous settlement substrate (Lipcius et al., 1990; Martel, 1992) may capture drifting juveniles that cannot attach to hard sampling substrates in strong currents. Sediment traps (Butman, 1989) may be affective at capturing other individuals. If a low-cost, low-impact marking technique can be developed for *D. polymorpha*, large-scale marking can also be used in mark-recapture studies (Brower et al., 1990).

A second hypothesis to explain the results is that individual (shell) growth rates are significantly under-estimated, which is possible, given data by Morteaux and Khalanski (1994), Martel (1995) and Stice (1997). If this is the case, all individuals seen at all sites may be 0-year-class individuals, and survival from one year to the next is approximately zero at all sites. This hypothesis is not consistent, however, with modest proportions of individuals > 28 mm in shell length (predicted to be 2nd-year-class individuals in this study), sampled in July in the upper Mississippi River at Mile 635 (Table 2). July is well before the end of the growing season for *D. polymorpha*, and even the most optimistic growth rates do not predict that new recruits will attain that size by July. Thus, while mortality beyond the first year appears high, some survival to further year classes occurs at least some years. The mortality hypothesis could be tested by further growth and survival studies, using marked individuals on fixed structures.

A third explanation is that survival rates have a very high temporal and spatial variation. For example, the zebra mussel data on the Olmsted bed shows extreme spatial variability, which is due in part to the extreme variability in substratum conditions, which change from bedrock to cobble, to sand/gravel, to shifting sand. Combined with sampling error (in estimating densities, or identifying sampling locations from previous years), the high variability of survival rates makes the estimation of a population mean very difficult. Sampling error in estimating densities

could be caused by (1) errors in subsampling or counting in the laboratory, and (2) improper field method in which the collected sample does not allow for an accurate estimate of benthic density.

IX. A Preliminary Model

In this section, we briefly discuss the implications of the results of the analysis, and of the information from the literature, for modeling the dynamics of Zebra Mussel metapopulations.

General model structure

If any (or a combination) of the above hypotheses is correct, the implication is that attempts to predict future densities of *D. polymorpha* at a given site in a river, on a non-fixed substrate may be very difficult. This suggests that a risk-based, medium-term approach may be more appropriate than attempts to predict the exact density and distribution of Zebra Mussels from one year to the next.

Similar considerations apply to the spatial structure of the model. The scale of spatial variability in rivers suggests a regional metapopulation model, with major sections of the rivers, as well as lakes with connection to the rivers, modeled as separate but connected subpopulations. Within each of these subpopulations, the dynamics may be modeled with an age-structured model with 3 age classes: 0-1 year (0-16 mm), 1-2 year (17-27 mm) and 2-3 year (>27 mm). The survival rates (and their variation) for each age class may be crudely estimated from Table 4, but a more precise model would require further fieldwork (see Recommendations below).

Recruitment

If large-scale downstream movements of adults occurs, in-stream larval production (Stoekel et al., 1997) is not required to maintain *D. polymorpha* populations at any of the sites in this study. This makes it impossible to reject the source-sink model of *D. polymorpha* in rivers (Horvath et al., 1996) without additional data. Examination of larval production in rivers is suggested to test this model. As a start, researchers could look for trochophore or very early veliger *D. polymorpha* larvae (Ackerman et al., 1994) in the river at a site where they could not have come from a lake population, based on drift rates. In conclusion, *Dreissena polymorpha* may not be doing as well in rivers as the high densities suggest, and that lakes and estuaries will remain the critical habitat for this species. A preliminary metapopulation model for Zebra Mussels in rivers may be based on the assumption of lower reproduction in rivers than in lakes. The reproduction rate (fertility) in lakes may be set so as to give, when combined with survival estimates, the observed exponential growth rate of 9-fold per year. The fertility in rivers may be set so as to give a declining population, without the inflow of larvae from upstream (lake or river) populations.

To estimate fertility more accurately would require further fieldwork on settlement rates, veliger density and factors that affect reproduction. For example, Martel et al. (1994) have shown that in lakes, settlement is related to veliger density, and Stoekel et al. (1997) have quantified variability in veliger density in the Illinois River. Another study may be done to relate veliger densities in rivers with a causative factor, such as seiching in Lake Michigan, which may affect the rate of flow into the Illinois River.

Dispersal

All larval Zebra Mussels from a river population may be assumed to drift to one or more downstream populations. In such a metapopulation model, the major recruitment source in such a model would be lakes with Zebra Mussel populations. The available data suggest that such recruitment may have high temporal (year-to-year) variation. It may even be zero in certain years. The estimates of rate of dispersal are closely linked with those of recruitment from upstream sources. Studies designed to estimate recruitment should also give clues about dispersal.

Variability, uncertainty and model utility

As discussed above, many aspect of a potential Zebra Mussel are poorly known. Carefully designed field studies would decrease this kind of uncertainty, originating from lack of information. However, there is another source of uncertainty, which originates from natural variability in physical and biological factors affecting the Zebra Mussel populations, that cannot be reduced (but can be better understood) with additional of fieldwork. This natural variability has both spatial and temporal components, and necessitates a risk-based, medium-term (5-10 years) large scale (at the level of rivers, or river sections) model.

Such a model can be used to address questions about the effect of various factors on the risk of a Zebra Mussel population explosion. The factors may include the frequency and amount of recruitment from lakes, down-stream dispersal in rivers, in-stream reproduction, and mortality rates.

X. Summary and Recommendations

(1) Zebra Mussel densities on fixed structure in the upper Mississippi River from 1992 to 1995 showed an exponential growth, while the densities on natural substrates surveyed in rivers varied more unpredictably over some of the same period.

It is recommended that population studies on fixed substrates, such as navigation locks, be resumed, in addition to studies on adjacent river beds. The sampling locations on river beds should be marked, with permanent structures, if possible. If spatial variation in densities is high, identification of locations based on river miles or GPS coordinates may not be sufficiently accurate. Following individually marked cohorts, in addition to the census techniques currently used, would provide much data under these conditions.

(2) Growth data combined with a literature survey suggest that *D. polymorpha* can be broken into age classes based on size of individuals. These growth rates are intermediate for those reported in the European literature, but slower than those reported for American rivers. These classes are used as the basis of estimating survival rates, so their accurate estimation is important.

It is recommended that site-specific annual growth be estimated by use of marked cohorts.

(3) Densities of size/year classes bore little relationship to each other within sites. This may be due to large-scale downstream movement of adults and juveniles, high mortality of older *D. polymorpha*, high spatial and temporal variation in survival rates (combined with sampling error), or a combination of these factors.

It is recommended that studies be conducted to

- (a) examine downstream movement of juvenile and adult *D. polymorpha*,
 - (b) compare survival of *D. polymorpha* in river beds to survival on fixed structures, and
 - (c) quantify in-stream *D. polymorpha* reproduction.
- (4) Ideally, fieldwork and modeling should proceed in coordination. In this report, initial fieldwork results were used to develop a model. Next, this model should be used to determine the factors that are most influential in population dynamics of Zebra Mussels, and to identify the types of data that would improve the model most. It is important to emphasize that the above recommendations are based on the analysis of currently available data. More precise identification of data needs can be accomplished by a comprehensive, risk-based sensitivity analysis. Such an analysis can also be used to answer questions such as the conditions under which high Zebra Mussel densities are likely in river populations. The first step for the proposed sensitivity analysis should be the estimation of a range (interval or bound) for each parameter in the model.

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