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Variations in the Reproductive Cycle of *Dreissena Polymorpha* in Europe, Russia, and North America[1]

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SYNOPSIS. The reproductive cycle of the zebra mussel (*Dreissena polymorpha*) is highly variable throughout its range in Europe, Russia[2], and North America. The environmental factors influencing this variation are poorly understood, but successful reproduction is occurring in areas where it was initially believed that adult zebra mussels could not survive (*i.e.*, southern United States). The differences in mussel reproduction occurring from site-to-site make it difficult to predict timing of specific events, such as the start of larval production, that are important in initiating containment or control procedures. For example, the amount of time required for a fertilized egg to develop into a juvenile mussel can be as short as 8 days, or as long as 240 days. Release of gametes by adults can be a highly synchronized event, focused over a 1–2 week period, or it can be completely non-synchronized, occurring throughout the year. Zebra mussels in some localities start spawning at water temperatures of 12–13°C, but do not start until water temperatures reaches 22°C at other sites. While some of this variability in reproductive behavior stems from mussel adaptation to local conditions, part is due to difficulties in sampling these events. It is difficult to determine reproductive success of a specific population because of the problems in separating locally produced larvae from larvae drifting in from other areas. Further research is needed not only on the relationship between reproduction and environment at the community level, but also on the variability in response of individual mussels.

INTRODUCTION

Zebra mussels (*Dreissena polymorpha* Pallas) have spread across North America faster and farther than originally predicted (Strayer, 1991). This rapid invasion has been aided by the ability of adult mussels to adapt to a wide range of habitats and by the flexibility of their reproductive cycle. This reproductive flexibility has hindered our ability to predict how zebra mussel populations will respond to different environmental conditions. Even minor changes in environmental conditions can lead to substantial differences in the timing of production of larvae and ripe gametes. This variation, combined with the fact that water currents can carry larvae some distance away from their parent populations, makes it difficult to correlate environmental conditions at a specific site with larval development or mortality rates. Thus, although zebra mussel larvae were first identified in the 1890s (Blockmann, 1891; Korschelt, 1891) and the entire developmental cycle documented by 1901 (Meissenheimer, 1901), the conditions needed for survival of larvae are still poorly understood and difficult to document under field conditions.

The invasion of zebra mussels into North America has increased the need to be able to predict where mussel densities will reach nuisance levels. In order to do this, we need specific information concerning the interaction between zebra mussels and their environment. The purpose of this paper is to

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[2] As used in this paper, the term Russia covers all the zebra mussel range in the former USSR.

review existing knowledge about the basic aspects of zebra mussel reproduction and how this reproductive cycle responds to different environmental conditions in Europe, Russia, and North America. This review focuses on the conditions known to affect the development, growth, settlement, and survival of larvae, the production and release of gametes by the adults, and some of the problems in accurately sampling these events.

BASIC LIFE HISTORY EVENTS

The zebra mussel life cycle consists of a relatively sessile adult phase and a planktonic, free-living larval phase. Most adult mussels are dioecious, with occasional hermaphrodism reported (Antheunisse, 1963; Tourari *et al.,* 1988; Nichols, 1993). Mussels usually become sexually mature when they reach a shell length of ≥5 mm (range 5–12 mm) (Stanczykowska, 1977; Lewandowski, 1982*b*; Afanasyev and Protasov, 1988; Garton and Haag, 1993). In some locations, zebra mussels are 2 years old before they become large enough to be sexually mature (Sprung, 1992). Such results suggest that maturity in *D. polymorpha* is size dependent, with slower growing individuals and populations taking a longer time to reach the size required for maturity. Mussels are sequential spawners, with each mussel releasing gametes over a period of 6 to 8 weeks (Walz, 1978*a*; Borcherding, 1992). Gametes are expelled directly into the water column, and all fertilization and embryological development occurs in the water. The number of eggs carried by an individual female was originally estimated at 30,000–40,000 eggs/female/year (Stanczykowska, 1977). More recent estimates using computer enhancement of gonadal sections place the number at over 1.5 million eggs/female/year (Borcherding, 1991; Neumann *et al.,* 1993). Embryological development follows the typical bivalve pattern (see Ackerman *et al.,* 1994 and Nichols and Black, 1994 for description of developmental stages), progressing through swimming blastula, trochophore, straight-hinge larva, umbonal larva, pediveliger, plantigrade (settlement stage), and juvenile. The plantigrade is the settling or metamorphosis stage, which marks the transition between the planktonic larval stage and the benthic adult stage. During this time period, the shell changes from a round to a more rhomboidal form, with subsequent realignment of internal body structures, loss of the velum, and formation of the siphons. The ability to attach to a substratum (settle) exists by the pediveliger stage, although only a weak, single thread is formed during this time (Ackerman *et al.,* 1994). The number of byssus threads increases during the plantigrade and juvenile stages, although the mussel does not permanently attach to a substratum at this age. The gland at the base of the foot that forms the byssus threads can also produce an enzyme that dissolves these threads, allowing the mussel to move. Migration, or translocation, of young mussels into deeper waters in the fall and into shallower waters in the spring has been documented (Stanczykowska, 1977). However, Lewandowski (1982*b*) believes that such mussel migration is a passive, rather than active process, relying on dislodging of substrata, particularly during vegetation senescence in autumn.

One problem in comparing various studies on zebra mussel larvae is that the terminology used is not consistent. For example, the term "settlement stage" is often equally applied to pediveligers, plantigrades, and/or young juveniles. This inconsistent terminology combined with the fact that many studies merely present larval size, with no mention of developmental stage (*e.g.,* see studies by Hillbricht-Ilkowska and Stanczykowska, 1969; Lewandowski and Ejsmont-Karabin, 1983; Skalskaya, 1985; Zhdanova and Gusynskaya, 1986; Borcherding and De Ruyter Van Steveninck, 1992), leads to difficulties in interpreting and comparing the information presented. Ideally, both larval size and developmental stage should be recorded. This is critical since the size of each developmental stage can vary between years and between sites. Ackerman *et al.* (1994) reviewed published sizes of the various developmental stages of *D. polymorpha* and found that straight-hinge larvae can range in height from 70 to 160 μm, umbonal larvae from 120 to 280 μm, pediveligers from

167 to 300 μm, and plantigrades from 158 to 500 μm. No information presently exists addressing the causes of variation in larval size in zebra mussels. However, among marine bivalves, adult body condition determines larval size (Gallager and Mann, 1986), and larval size determines survival (Kraeuter *et al.*, 1982). Such mechanisms probably influence zebra mussel larvae as well.

The amount of time required for development of a fertilized egg to a completely formed juvenile varies inversely with water temperature. Mussels in warmer waters develop faster than those in cooler waters, although no models have been developed that directly relate water temperatures to developmental times. A wide variety of developmental times have been reported, ranging from: 8 days (Hillbricht-Ilkowska and Stanczykowska, 1969); 12 days (Kirpichenko, 1964); 17 days (Borcherding and De Ruyter Van Steveninck, 1992); 18, 23, and 33 days (Sprung, 1989); 21 days for laboratory populations (Nichols, 1993); 35 days (Walz, 1978*a*); 180 days (Nichols and Kovalak, 1995); 240 days (Kirpichenko, 1964). (Unfortunately, few of these studies discuss size or developmental stage.) Considering the amount of time spent in the plankton and the increase in size from about 100 microns to about 350 microns, larvae grow rather quickly. Growth rates of individual larvae have been measured at 1–4 microns/day (Sprung, 1993), 7.6 microns/day (Borcherding and De Ruyter Van Steveninck, 1992), and up to 20 microns/day for those larvae that spend only 8 days in the plankton (Sprung, 1993). Sprung (1993) notes that larval growth rates are more curvilinear, than linear, with different stages of larvae (*i.e.*, umbonal or pediveliger) growing at different rates even under the same conditions.

An important question concerning larval populations is the number or percentage of larvae that successfully complete development and become reproductive adults. However, due to the planktonic nature of zebra mussel larvae, obtaining quantitative data on mortality rates of a single larval cohort throughout its development can be challenging. Planktonic larvae are not randomly distributed in the water column and can rapidly change distribution patterns. Vertical distribution of larvae changes in response to diurnal cycles (Kachalova and Sloka, 1964; Lewandowski, 1982*a*; Zhdanova and Gusynskaya, 1986) and horizontal distribution can be altered by water currents, wind, and storm events (Stanczykowska, 1964; Lewandowski and Ejsmont-Karabin, 1983; Martel *et al.*, 1993; Stanczykowska and Lewandowski, 1993). This results in a patchy distribution of planktonic populations leading to uneven distribution of settling stages, with settlement often occurring some distance from the parent mussels (Lewandowski, 1982*b*; Bij de Vaate, 1991). The distribution of juvenile and adult zebra mussels is further complicated because newly-settled juveniles move, or translocate by primary and secondary settlement mechanisms (Ackerman and Claudi, 1991; Ackerman *et al.*, 1994). The problem of tracking the settlement success of a particular larval cohort can be further aggravated depending on types of sampling gear used. Certain types of sampling gear are biased toward collecting a certain stage of mussel, or are ineffective under specific water flow regimes (Nichols and Kovalak, 1993).

Since the recruitment success of a single larval cohort is difficult to track, data based on the number of dead larval/juvenile shells counted at a particular point in time is generally the technique used to estimate mortality rates. This technique is limited in that it cannot estimate the number of larvae/juveniles that were produced in the area and migrated (translocated) elsewhere. The estimates of mortality rates obtained using this technique are variable, ranging from 20 to 100% (Wiktor, 1963; Stanczykowska, 1977; Lewandowski, 1982*a*, *b*; Lewandowski and Ejsmont-Karabin, 1983; Sprung, 1989). Most of these studies indicate that most larval mortality occurs late in the cycle during metamorphosis and settlement. Sprung's study (1989) is one of the few that found high mortality rates at the straight-hinge stage, but this work was done using caged larvae. Mortality at the straight-hinge stage is common among larvae raised in the laboratory and usually indicates food prob-

lems, either in type or amount (Nichols, 1993). Overall, mortality in larvae and newly-settled juveniles in field populations has been attributed to a variety of causes, such as problems in finding settlement substratum, specific environmental conditions, and to a degree, predation.

The relationship between substratum, larval settlement, and larval mortality varies from site to site. Most studies indicate that zebra mussel larvae must attach to hard substrata in order to complete metamorphosis and survive as juveniles (*e.g.,* Wiktor, 1963; Stanczykowska, 1977; Lewandowski, 1982*b*; Sprung, 1989; Smit *et al.,* 1993). Larval and juvenile mussels demonstrate considerable selectivity over the orientation, size and type of hard substrata colonized (Kilgour and Mackie, 1993; Yankovich and Haffner, 1993; Mellina and Rasmussen, 1994). Such substratum selectivity is commonly reported among marine bivalve larvae (Bayne, 1965). However, other studies indicate that hard substratum is not critical for larval metamorphosis, and that all types of soft or hard substrata are colonized by zebra mussels, including aquatic plants (Lewandowski, 1983; Stanczykowska and Lewandowski, 1993) and soft sediments (Stanczykowska and Lewandowski, 1993; Berkman *et al.,* 1995). Further studies by Stanczykowska and Lewandowski (1993) indicated that substratum stability, not type, was more important in gauging the survival of newly-settled juveniles. In their study area, larvae colonized everything, actually preferring macrophytic plant surfaces over hard substrata. However, those animals settling on soft sediments showed a higher mortality rate because they were buried during storm activity when sediments shifted position. Hard substrata are obviously an important factor in providing habitat for the settling larvae and juveniles. However, the absence of such substrata does not necessarily mean that settlement will fail. For example, in Lake Erie, zebra mussels are successfully colonizing areas where 99% of the actual substratum is a soft, muddy sediment (Berkman *et al.,* 1995). Initial attachment does occur on a small piece of hard substratum, such as a pebble. Further colonization builds on the shells of the first set of mussels, resulting in the formation of a "floating mat" of zebra mussels, that appears to be able to overwinter.

Habitat quality other than substratum type have been correlated with increases in larval mortality rates. Stanczykowska (1977) indicated that conditions such as calcium levels <50 mg/liter (measured as CaO), low oxygen, fast water currents, and large amounts of sediment in the water column would kill larvae. Sprung's (1989) work with caged veligers found that larvae required water temperatures of 12–24°C, pH of 7.4–9.4, and calcium concentrations of 40–60 mg/liter for optimum survival. Sprung (1987) found that similar conditions were required for zebra mussel eggs to develop. However, in both studies, mortality rates were 99.3–100%, indicating that optimum conditions for larvae were not being met. In some areas of North America, zebra mussel larvae are commonly found and settle under conditions that do not meet the above criteria, particularly with regard to water temperatures. For example, larvae are able to complete metamorphosis and reach juvenile densities of over 300,000/m^2 in Baton Rouge, Louisiana (Tom Dietz, Louisiana State Univ., personal communication), where water temperatures are consistently over 27°C during the summer months (Fig. 1), and calcium concentrations are usually below 40 mg/liter. The ability of zebra mussel larvae to settle and metamorphose successfully in the lower Mississippi River under ambient conditions falling outside the range previously considered necessary for larval development and settlement suggests that larvae are capable of acclimatizing to local conditions to a much greater extent than previously considered possible or that there has been natural selection for larvae with increased tolerances of elevated ambient temperatures or lower calcium levels.

As mentioned above, calcium levels are very important for larval survival. Unfortunately, differences in reporting results and in lab techniques used in the analysis leads to confusion as to exactly what calcium levels are required. Stanczykowska (1977) analyzed CaO, not $CaCO_3$ (these units are not

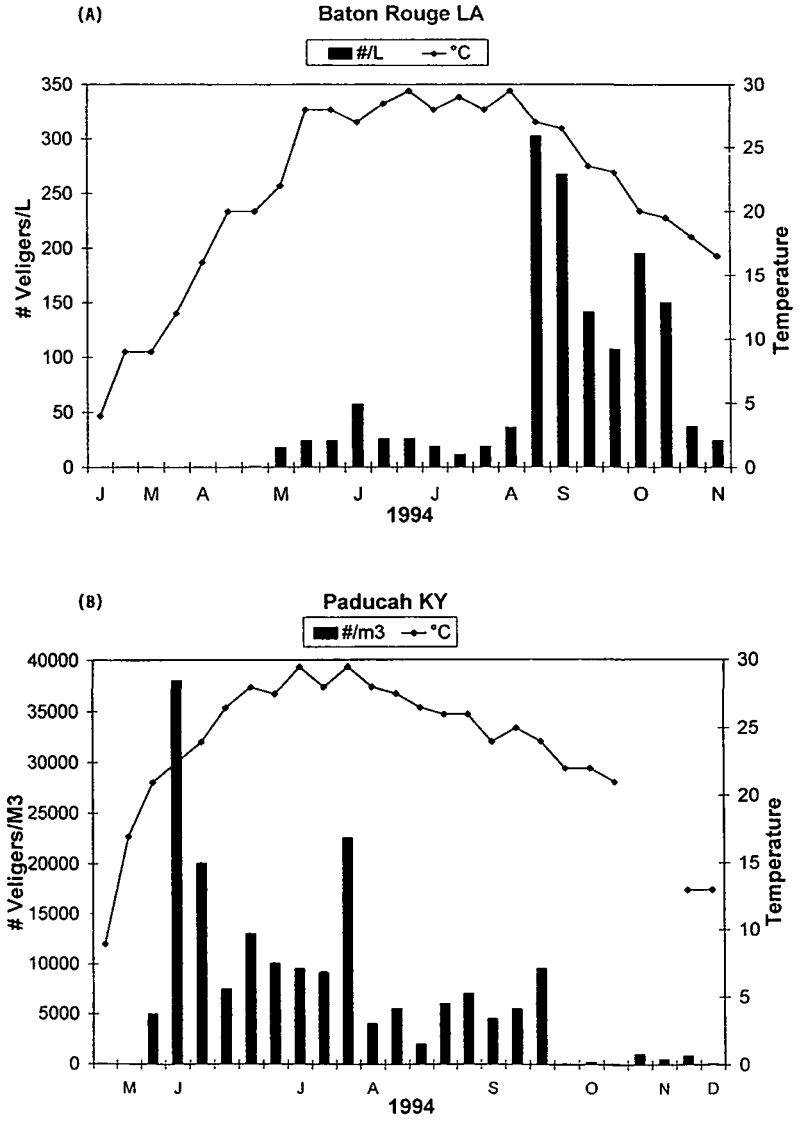

FIG. 1. Densities of zebra mussel larvae at various water temperatures at: (A). Baton Rouge, Louisiana (Tom Dietz, Louisiana State Univ); and (B). Paducah, Kentucky (Bennie Kerley, Tennessee Valley Authority) in 1994.

necessarily interchangeable). Sprung (1987) indicated that while a few zebra mussel larvae would survive at 12 Ca mg/liter, survival was better at calcium levels above 24 mg/liter. However, his experiment was based on a standardized salt solution bioassay ($CaCO_3$), with no testing to determine the actual amount of calcium salt that went into solution. Strayer's (1991) review of zebra mussel habitats lists calcium as meq/liter. Unfortunately, this variation in reporting results makes it difficult to make predictions on zebra mussel calcium requirements. There is also the possibility that zebra mussels, like other bivalves (see Pynnönen, 1991) can obtain calcium from their food supply, and therefore would not be totally dependent on dissolved calcium ions in the water (unit most commonly measured).

The water temperatures reported at Baton Rouge, Louisiana, regularly exceed what

European and Russian studies consider lethal limits for veligers (*e.g.,* Lewandowski and Ejsmont-Karabin, 1983; Sprung, 1987, 1989). An examination of live/dead larval ratios at Baton Rouge showed that at times in the summer of 1994, the number of dead larvae in the water column outnumbered the number of live larvae (Hernandez *et al.,* 1995). The highest percentages of dead larvae occurred during July and August, 1994, when water temperatures exceeded 28–31°C (46–70% dead) and again during late November (88% dead) at 16°C. However, larval production and settlement continued throughout the summer months when water temperatures were high and population densities of newly settled juveniles in the area exceeded 300,000/m^2 by the end of the year.

Zebra mussels are known to survive in estuaries and brackish waters throughout their range in Europe and Russia (Strayer and Smith, 1993). Adult populations are surviving and reproducing in the Caspian Sea in salinities up to 10 ppt (Ludyansky *et al.,* 1993) and remained in the Aral Sea until salinities rose above 11 ppt (Aladin and Potts, 1992). However, these water bodies, particularly the Caspian Sea, have a much different ionic content than oceanic waters which may alter the mussel's ability to survive (Ludyansky *et al.,* 1993). The actual salinity levels tolerated by zebra mussel larvae differs with larval age and larval stages appear to be more tolerant of salinity than adults (Kennedy *et al.,* 1995; Kilgour *et al.,* 1994). Fong *et al.* (1995) reports that zebra mussel eggs did fertilize at salinities as high as 7 ppt (with minimal success) but that acclimation of the adults to saline waters improved fertilization success. This research indicates that reproduction will be very limited in brackish waters, although adults may be capable of surviving in such areas.

Reproduction in estuaries is not necessary for adults to be present due to drifting of larvae from nearby freshwater rivers. For example, Borcherding and De Ruyter Van Steveninck (1992) and Neumann *et al.* (1993) found that larvae produced throughout the lower part of the Rhine River generally do not settle in the river. The water retention time in this part of the river (before reaching the ocean) was less than the 17 days required for complete larval development and the entire production of larvae was being discharged into the esturaries of the North Sea. Situations of this type should occur in North America, particularly in portions of the lower Mississippi and St. Lawrence rivers. However, at this time there are no confirmed records of zebra mussel populations colonizing brackish waters in North America (Kilgour *et al.,* 1994).

Predation is another reported cause of larval mortality, although its impact on larval densities is not known (Lewandowski, 1982*b*). A number of animals feed on veligers, including fish and eels (Wiktor, 1963; Kornobis, 1977), zooplankton (Karabin, 1978), and even adult zebra mussels (Mikheev, 1967; MacIssac and Sprules, 1991). At this time, there has not been any documentation of predators of any type sharply reducing larval densities. MacIssac and Sprules' (1991) model predicts that predation rates by adult zebra mussels on veligers may be sufficient to control population numbers, but this has not been documented under field conditions.

Without question, there are a number of factors affecting larval mortality rates during development and metamorphosis. Certainly, metamorphosis is a physiologically expensive process for zebra mussel larvae, as they must stop feeding, realign internal body structures, and alter shell growth patterns (Ackerman *et al.,* 1994). With this added stress, any health problems existing in the larvae will be magnified. Unfortunately, there are presently no reliable techniques for measuring health or condition of zebra mussel larvae.

LARVAL PRODUCTION

Zebra mussels are believed to be sequential spawners, capable of releasing gametes over a 6–8 week period, with the first release of gametes being the largest (Borcherding, 1991; Walz, 1978*a*). Field data indicate that most of the individuals in a population will develop ripe gonadal tissue at the same time (Antheunisse, 1963; Borcherding, 1991; Garton and Haag, 1993). Water temperature is believed to be a major factor in triggering gamete release. Finally, laboratory experiments indicate that expo-

sure to ripe eggs and sperm in the water column often triggers gamete release by other zebra mussels (Walz, 1978*a*; Nichols, 1993; Ram and Nichols, 1993). These factors should lead to highly synchronized larval production in field populations, with peak larval densities being reached very rapidly and then larval numbers gradually declining over a 6–8 week period. This highly-synchronized pattern has been documented (*e.g.,* Haag and Garton, 1992), but is not common.

The most common pattern of larval production reported in Europe, Russia, and northern North America shows less synchrony. (Note: in Europe and Russia, zebra mussel populations are usually found between the 40th and 60th parallel. The term northern North America refers to areas above the 40th parallel, which runs above St. Louis, Missouri). Larval numbers are very low at the beginning of production, requiring 4–8 weeks to reach the first of usually two peaks in larval densities (peaks in densities are usually separated by a week or so, but this also varies greatly) (Fig. 2). Larval numbers then gradually decline over the next 6–10 weeks (*e.g.,* Kirpichenko, 1964; Kachalova and Sloka, 1964; Hillbricht-Ilkowska and Stanczykowska, 1969; Lewandowski, 1982*a*; Lewandowski and Ejsmont-Karabin, 1983; Skalskaya, 1985; Sprung, 1989; Fraleigh *et al.,* 1993; Leach, 1993; Nichols and Kovalak, 1995). There is also a great deal of variation in the duration of larval production, with estimates ranging from 6 to 52 weeks (see reviews by Lewandowski, 1982*b,* and Sprung, 1993).

Initial reports from Europe, Russia and northern North America indicated that reproduction was initiated when water temperatures rose above 12°C (*e.g.,* Sprung, 1993). However, different populations will begin larval production at different temperatures (>12°C). The majority of the populations in Europe, Russia, and northern North America start producing larvae when water temperatures are between 16 and 19°C (see review in Lewandowski, 1982*b*; Sprung, 1993). Some populations start production below 16°C, usually around 12°C, while others will not produce larvae until water temperatures are over 20°C. Large bodies of water may contain separate populations that start spawning at different water temperature. For example, in Lake Erie, populations producing larvae at 16–18°C have been reported from the middle of the western basin (Garton and Haag, 1993), at 22°C from a nearshore region of the western basin (Nichols and Kollar, 1991), and at 12°C from the eastern basin (Cameron Lange, Acres International personal communication). The reasons behind different populations starting production at different water temperatures have not been investigated. However, studies done by McMahon *et al.* (this volume) indicate that even though 18°C is a physiologically optimum temperature for these animals, mussels will adapt rapidly to ambient temperature regimes.

Larval production supposedly stops once water temperatures drop below 10–12°C, even in populations that start spawning at 12°C (Kirpichenko, 1964; Kachalova and Sloka, 1964; Lewandowski, 1982*a,* Skalskaya, 1985; Sprung, 1989; Fraleigh *et al.,* 1993; Garton and Haag, 1993). One reason for this is that zebra mussel eggs reportedly will not fully ripen at temperatures less than 11°C (Morton, 1969; Lyashenko and Karchenko, 1989). In areas where water temperatures do not drop below 12°C, such as thermally heated reservoirs or laboratory conditions, larval production has been documented year round (Stanczykowska, 1977; Lewandowski, 1982*a*; Stanczykowska *et al.,* 1988; Nichols, 1993). However, in many areas, larval production basically stops before water temperatures drop to 12°C (*e.g.,* Fraleigh *et al.,* 1993; Leach, 1993). One problem is that it is not always easy to determine if, or when, larval production has actually ceased and the larvae present are inputs from other areas, or if local larval production is continuing at very low levels.

One of the main difficulties in determining when larval production has stopped is that zebra mussel larvae produced in the fall are capable of overwintering. Straight-hinge larvae are frequently collected both in Russia (Kirpichenko, 1964; Lewandowski, 1982*b*; Zhdanova and Gusynskaya, 1986) and North America (Nichols and Ko-

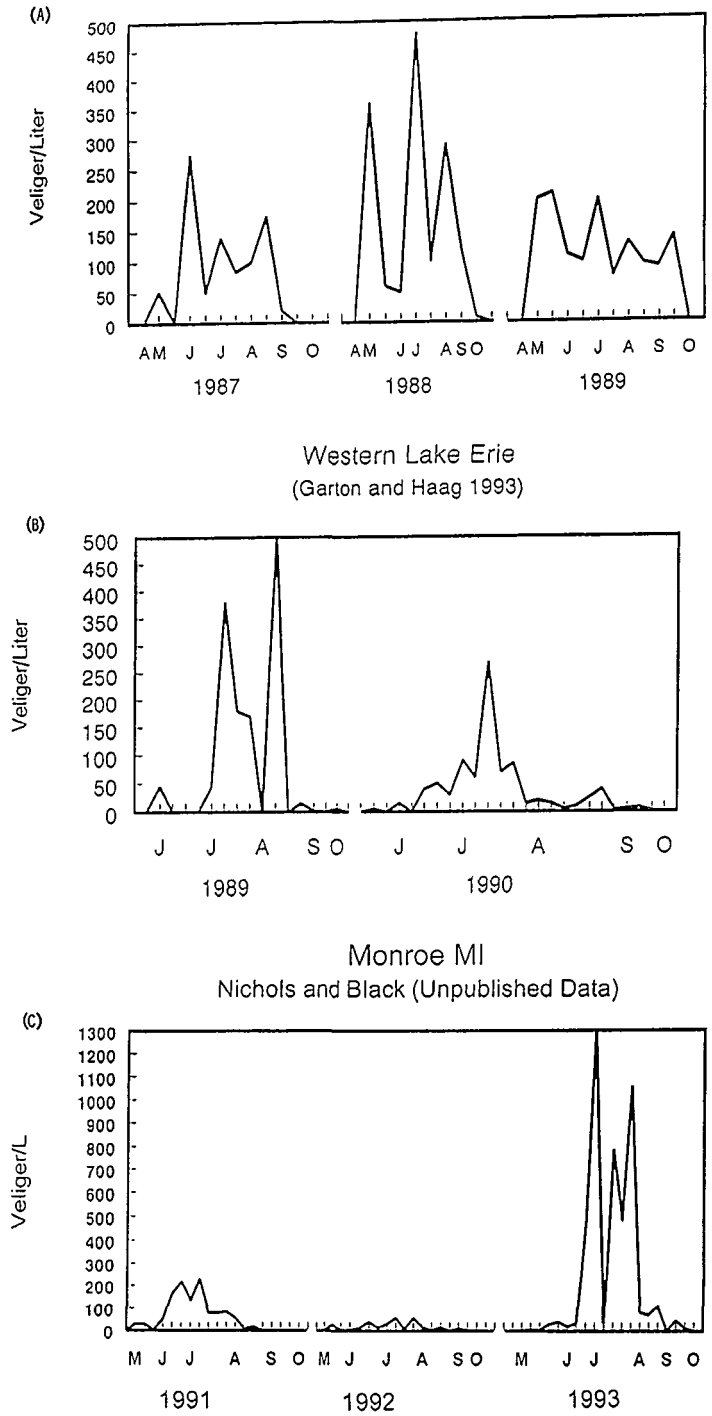

FIG. 2. Annual and seasonal variations in densities of zebra mussel larvae reported from: (A) River Rhine at the German/Dutch border, at Lobith (Smit *et al.* 1993); (B) western basin of Lake Erie, U.S.A. (Garton and Haag 1993); and (C) Monroe Michigan, in the western basin of Lake Erie, U.S.A. (Nichols and Black, Unpubl. data).

valak, 1995; Cameron Lange, Acres International personal communication) when water temperatures are <5°C. It is theoretically possible, of course, that a small part of the population is capable of producing larvae when water temperatures are <10°C. However, Kirpichenko (1964) and Lewandowski (1982*b*) believe that these winter larvae were actually produced in the fall and that their development was delayed or very slow due to the colder winter temperatures. A few of these larvae will continue developing throughout the winter and will settle in early spring (Kirpichenko, 1964; Nichols and Kovalak, 1995). Kirpichenko (1964) states that overwintering larvae took 8 months to reach a developmental stage that took other larvae 14 days to reach during the summer. In the western basin of Lake Erie, larvae collected throughout the winter gradually increased in developmental stage and completed metamorphosis after about 6 months (Nichols and Kovalak, 1995).

The overall duration of larval production is responsive to water temperature regimes. Even minor fluctuations in ambient water temperatures will alter the length of time larvae are produced at a particular site from one year to the next. When water temperatures were 4–5°C warmer than normal during the summer (*e.g.,* 28°C rather than 23°C), the number of weeks that larvae were produced decreased, with peak larval densities occurring rapidly after production began (Hillbricht-Ilkowska and Stanczykowska, 1969; Lewandowski, 1982*a*; Adrian *et al.,* 1994). While the adult mussels may start spawning at their normal temperature (*e.g.,* 17°C), larval production will cease up to 2–3 months earlier (*e.g.,* August instead of October; Lewandowski, 1982*a*). In at least one study, this rapid decline in production was due to the lack of ripe eggs in the females by August (Fig. 3). When water temperatures ran 3–4°C cooler than normal (*e.g.,* 19°C rather than 23°C), the number of weeks during which larvae were produced increased, sometimes extending the season by more than 2 months, with peak larval densities being suppressed (Hillbricht-Ilkowska and Stanczykowska, 1969; Adrian *et al.,* 1994).

The patterns seen in larval production, particularly the delay between the first appearance of larvae and the time of peak densities, indicate that at least initially, many mussels in the population are not involved in spawning, even though they may be carrying ripe eggs. Thus, while water temperatures may have to reach a certain threshold level, temperature by itself may not actually trigger reproduction in most of the ripe mussels in a population, or temperature may have a cumulative effect (degree days). There are many other factors that could also influence reproduction, including food supply or light regimes (see Dorgelo and Kraak, 1993 and Ram and Nichols, 1993 for a discussion of factors influencing bivalve spawning in general). Areas that need further study are: (1) determining the number of individual zebra mussels spawning at any given time, and (2) factors that trigger spawning.

The relationship between larval production and water temperature in southern North America (south of the 40th parallel) is even more ambiguous. First, most of the data available for these southern populations indicate that spawning does not begin until water temperatures are above 20°C. More importantly, as in northern areas, there is a delay between the onset of larval production and the date when peak larval densities occur. This delay is much longer in southern regions, lasting over 10 weeks, resulting in larval production beginning in May but reaching peak densities in the fall (*e.g.,* Fig. 1). Larval production continues throughout the summer, when water temperatures are at levels, which, according to European and Russian experience (*e.g.,* Walz, 1978; Lewandowski and Ejsmont-Karabin, 1983; Strayer, 1991) would be lethal to adult zebra mussels as well as larvae.

However, even in this southern region, larval production is variable and since this is a riverine situation, difficult to interpret. For example, in the lower Ohio River, at Paducah, Kentucky, larvae first appear in May (at 20°C), reach peak densities within 2 weeks, and then gradually decline, a decline that continues through at least December (13°C; Bennie Kerley, Tennessee Valley

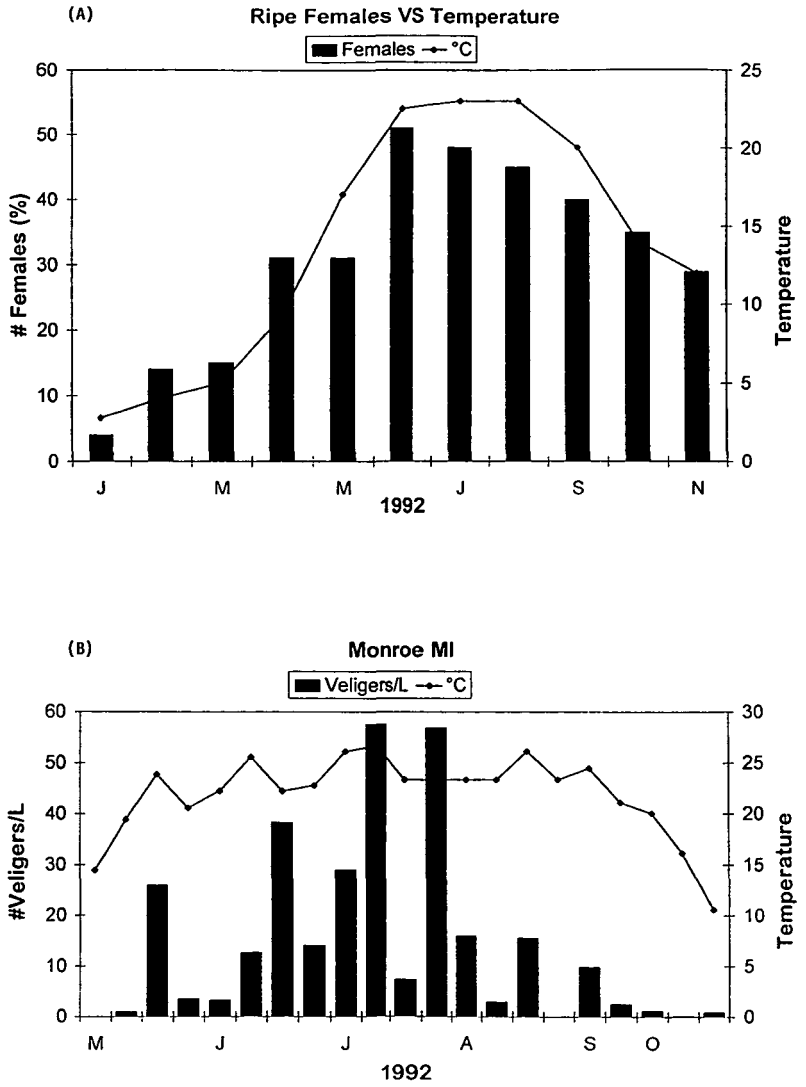

FIG. 3. Comparison of when zebra mussel larvae were found in the water column, to when female mussels contained ripe eggs. Plankton net data collected in 1992, from Monroe, Michigan, U.S.A. (Nichols and Black, unpublished data).

Authority, personal communication, Fig. 1). At Memphis, Tennessee (Ibid.) zebra mussel larvae were present from June, 1994, when sampling started, through December 1994, with peak densities occurring in August and another peak in December, when temperatures were 13°C. The pattern of larval densities at Baton Rouge, Louisiana, on the Mississippi River, shows larvae first appear in May (20–22°C) with highest larval densities occurring over 12 weeks later in September and October when water temperatures were 27°C (Fig. 1; Tom Dietz, Louisiana State Univ., personal communication). After October, densities started to decline, but even by the end of November densities had not fallen below 1/liter.

Interpretation of larval density information from the Mississippi River highlights the problems in dealing with planktonic larvae under riverine conditions. Larval numbers can be reported and larval age esti-

TABLE 1. *Occurrence of* Dreissena polymorpha *larvae recorded by various authors.**

Author	Time span when larvae were found in the plankton	Temperature at the first recording	Locality and year
Kačanova (1961)	June/July–October	15–16°C	Uchinsk reservoir (SU) 1956–1959
Kirpičenko (1964)	June/July–October	15°C	Kujbyshev reservoir (SU) 1960/1961/1963
Ševtsova (1968)	April/May–October	12–15°C	Dnjepr-Krivoj Rog (SU) 1965/1966
Wiktor (1969)	April–September	12–14°C	Firth of Szczecin (PL)
Hillbricht-Ilkowska and Stańczykowska (1969)	June–September	16–21°C	Masurian Lakes (PL) 1963, 1964, 1966
Kornobis (1977)	April/May–August/October	12–13°C	Mikorzynko-Wasoskie-Lake (heated lake near Konin, PL) 1973–1975
Lewandowski (1982)	June–September	17–19°C	7 Masurian Lakes (PL) 1976–1978
Lewandowski and Ejsmont-Karabin (1983)	April–September	?	Heated lakes near Konin (PL) 1970–1978
Breitig (1965)	April/June–August/October	10–15°C	Pohlitzer See and Oder-Spree-Kanal (GDR) 1956–1964
Walz (1973)	June–September	17°C	Gnadensee (FRG) 1971
	July–October	14°C	Überlinger See (FRG) 1971
Einsle (1973)	June–October	14–15°C	Lake Constance (FRG) 1971
Siller (1983)	April–October	10°C	Fühlinger See (FRG) 1981
Sprung (1989)	May–September/October	12°C	Fühlinger See and Heider Bergsee (FRG) 1985–1987
Borcherding (1992)	May–September	17–20°C	Rhine River 1990 (FRG) 1991
Garton and Haag (1993)	June–October	18°C	Lake Erie (USA) 1991
Fraleigh *et al.* (1993)	May–November	18°C	Lake Erie (USA) 1991
Dietz (1994)	April–November	20°C	Mississippi River (USA) (1994)
Nichols (1991)	May–October	22°C	Lake Erie (USA) 1990

* Adapted from Sprung, 1989.

mated, but there is still no way to determine exactly where the larvae originated. Some of the larvae found at sites along the Mississippi River certainly were produced by mussel populations located in upstream areas, while some larvae are undoubtedly the product of local populations. Comparisons between peak larval densities, peak larval settlement, and changes in gonadal ripeness in local adults may be helpful in indicating when local larval production is occurring. For example, peak larval numbers are found at Baton Rouge in September and October (1994), and this corresponds to the increase in gonadal maturity in local adult mussels seen in late August and early September (Tom Dietz, Louisiana State Univ., personal communication). However, even this comparison may not provide sufficient information to determine the origins of the larvae settling at a specific site. The ability of locally produced larvae to remain in a specific part of a river system will be dependent on local water flow regimes and will vary by locality and by season.

Regardless of the exact origins of the zebra mussel larvae drifting in the rivers of the southern United States, settlement is occurring, and adult populations in these areas are reaching sexual maturity. Predictions concerning the future of zebra mussel populations in these areas are premature, as this region is still under invasion with rapidly changing densities of adult zebra mussels. Patterns of larval densities will probably change in response to changes in adult densities. However, considering that water temperatures are not below 10–12°C for much of the year (when zebra mussel eggs stop developing) and adult mussels seem to be adapting to warmer temperatures (see McMahon *et al.* this volume), larval production could easily continue throughout most of the year in this region.

GAMETE PRODUCTION

The seasonal flexibility in larval production patterns indicates that zebra mussels must either develop ripe gametes very quickly or carry ripe (or almost ripe) gametes for long periods of time without releasing them. Both long-term studies (*e.g.*,

Antheunisse, 1963; Borcherding, 1991; Nichols, 1991) and seasonal studies (*e.g.,* Garton and Haag, 1993) show that mussels carry ripe gametes for long periods of time even though larval production may not be occurring and that gamete production is correlated to seasonal changes in water temperatures (Fig. 3).

The physical costs of reproduction can be high. Sprung (1991) and Borcherding (1992) found that gonadal tissue can comprise over half the dry weight of a female zebra mussel, with larger mussels having a higher gonadal/body weight ratio than smaller mussels. These studies, along with that of Dorgelo and Kraak (1993), found that total mussel body weight declined 30–45% just after spawning was completed. Both males and females showed an equal decline in body weight, as both released about the same relative weight of gametes (Sprung, 1991). At some sites, reproductive costs are so high that mussels do not grow or feed during reproduction (Morton, 1969; Stanczykowska, 1977; Smit *et al.,* 1992). Physiological parameters, such as growth rate, feeding rate, number of gametes produced, and body weight, may vary depending on local food and temperature conditions (Borcherding, 1992; Sprung, 1992).

Zebra mussels show tremendous physiological plasticity in response to local conditions and are managing to reproduce in areas of North America that would be considered limiting by European standards. For example, Walz's (1978*b*) work in Lake Constance demonstrates that once water temperatures rise above 24°C, mussels cannot assimilate enough food to maintain body weight, much less reproduce. Most of the areas in North America regularly reach water temperatures above 24°C, and mussels >24 mm in length are found throughout the range. In parts of Russia and Europe, zebra mussels require calcium levels above 50 ppm in order to complete reproduction (Stanzcykowska, 1977). However, parts of southern North America do not have calcium levels this high, and zebra mussels are still colonizing in high densities.

This apparently wider tolerance to habitat parameters in North America makes it difficult to predict the final range of this exotic species. The adaptability to various habitats, in combination with a highly flexible reproductive cycle, will allow zebra mussels to continue their rapid expansion across North America. Certainly, more research is needed on various aspects of the zebra mussel's reproductive cycle, including: the conditions that trigger gamete release in individual mussels; the percentage of spawning adults within a population at any particular time; and the effects of various environmental conditions on gametogenesis, spawning, larval survival, and settlement success.

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