

## The Physiological Ecology of the Zebra Mussel, *Dreissena polymorpha*, in North America and Europe<sup>1</sup>

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**SYNOPSIS.** The zebra mussel, *Dreissena polymorpha* (Pallas), was introduced into North America in 1986. Initial North American (N.A.) studies suggested that physiological responses varied between N.A. and European populations. However, literature review indicates agreement on most aspects of physiological adaptation including: respiratory responses; hypoxia/anoxia tolerance; salinity limits; emersion tolerance; freezing resistance; environmental pH limits; calcium limits; starvation responses; and bioenergetic partitioning. The main differences among N.A. and European mussels appear to be elevated upper thermal limits and temperatures for optimum growth among N.A. populations. N.A. zebra mussels probably originated from the northern shore of the Black Sea in the warmest portion of the mussel's European range. However, most European physiological data come from northern Europe where populations may be adapted to colder temperatures. Alternatively, N.A. research suggests that mussels may have a capacity for seasonal temperature acclimatization such that responses recorded in warmer N.A. waters may be different from those recorded in northern Europe even after short-term laboratory acclimation. Studies of genetic variation and physiological response among European and N.A. *D. polymorpha* populations are required to elucidate the basis for physiological differentiation. Recently evolved *D. polymorpha* has poor resistance adaptations compared to unionacean and sphaeriid bivalves with longer freshwater fossil histories. Poor resistance adaptations make it less suited for stable habitats, instead, its high fecundities, early maturity, and rapid growth are adaptations to unstable habitats where extensive resistance adaptations are of little value.

### INTRODUCTION

The European, freshwater, zebra mussel, *Dreissena polymorpha* (Pallas, 1771) was introduced into the Lake St. Clair-Detroit River region of the Laurentian Great Lakes of North America (N.A.) in 1986 (Hebert *et al.*, 1989; Mackie *et al.*, 1989). The likely source population was the lower Dnieper or Bug River, both opening on the northern shore of the Black Sea near the Ukrainian port cities of Kherson and Nikolayev (Spidle *et al.*, 1994; McMahon *et al.*, 1994). Its dispersal through N.A. freshwaters has been

remarkable. It is now in all of the Great Lakes, the Finger Lakes, Oneida Lake and Lake Champlain, the St. Lawrence, Hudson, Seneca, Mohawk, Susquehanna, Illinois, Mississippi, Ohio, Tennessee, Cumberland, Arkansas, Atchafalaya, Allegheny, St. Croix, Kanawha, White and Neosho Rivers and New York's Erie Barge Canal (Zebra Mussel Information Clearing House, 1995; United States National Biological Service, 1995). It has also invaded smaller, isolated inland rivers and lakes, 54 populations recorded from isolated lakes in six states bordering the Great Lakes (United States National Biological Service, 1995).

The zebra mussel has colonized N.A. aquatic environments of widely varying physico-chemical characteristics, suggest-

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ing capacity for physiological compensation and/or toleration. Preliminary estimates of its resistance and capacity adaptations suggest that it will eventually colonize the majority of permanent inland freshwater in the U.S. and southern Canada (Strayer, 1991; Electric Power Research Institute, 1992; McMahon, 1992; Claudi and Mackie, 1993).

Because it is both an ecological (Hebert *et al.*, 1991; MacIsaac *et al.*, 1991, 1992; Mackie, 1991; Nalepa *et al.*, 1991; Haag *et al.*, 1993; Gillis and Mackie, 1994; Schloesser *et al.*, 1996) and macrofouling threat (McMahon, 1990; McMahon and Tsou, 1990; Electric Power Research Institute, 1992; Miller *et al.*, 1992; Claudi and Mackie, 1993), N.A. biologists, environmentalists, government officials, and industrial and agricultural managers are assessing their waters' susceptibility to zebra mussel colonization. Development of accurate colonization risk analyses requires a thorough understanding of the mussel's physiological resistance and capacity adaptations as will future studies of its ultimate impact on N.A. freshwater and development of nonchemical mitigation/control strategies for its macrofouling (Electric Power Research Institute, 1992; Miller *et al.*, 1992; Claudi and Mackie, 1993).

Early studies indicated that the resistance and capacity adaptations of N.A. zebra mussels were divergent with those of northern Europe, particularly thermal responses (Iwanzki and McCauley, 1992; McMahon *et al.*, 1994; Nichols, 1996). If differences exist, they may result from the majority of European studies being carried out on mussels from waters which are colder (for a review of European research see Mackie *et al.*, 1989) than those colonized by mussels in N.A. Their suspected origin from just north of the Ukrainian Black Sea in the warmest portion of *D. polymorpha's* European range (Spidle *et al.*, 1994; Marsden *et al.*, 1996), suggests that N.A. mussels may be adapted to warmer environments.

In order to provide a foundation for further investigation of physiological adaptation in *D. polymorpha*, and assess possible differences between N.A. and European populations, I have reviewed available lit-

erature on the physiological adaptation of *D. polymorpha* on both continents. Topic areas include: temperature responses; respiratory responses; hypoxia/anoxia tolerance; salinity tolerance; emersion and freezing resistances; pH and Ca<sup>2+</sup> concentration limits; starvation resistance; and bioenergetic partitioning.

#### TEMPERATURE RESPONSES

Temperature responses among European and N.A. zebra mussels initially appear incongruent. However, analysis of published results suggests general similarity with a few notable exceptions. In Europe, spawning temperatures, usually recorded as temperature of first appearance of eggs or larval stages in the plankton, range from 10°C to 17°C (Sprung, 1992). In German lakes, oöcyte number and ovary volume decreased markedly after initiation of spawning at 12°C (Borcherding, 1991). A spawning threshold of 12°C has also been recorded in the Rhine River, Germany (Neumann *et al.*, 1992). In contrast, initial spawning temperatures in N.A. have been greater than 12°C. Weekly to biweekly examination of male and female gonad sections in mussels from western Lake Erie indicated that spawning first occurred at 22–23°C even though veliger larvae were first observed at 18°C. Veliger abundance declined sharply in the fall at water temperatures below 18°C (Garton and Hagg, 1992). Veligers were first recorded at 22°C near the southern shore of western Lake Erie (Nichols, 1996) and at 18°C in western and central Lake Erie, veliger density again declining rapidly after water temperatures fell below 18°C (Fraleigh *et al.*, 1992). A similar 18°C threshold for first veliger appearance occurred throughout eastern Lake Erie in 1990 (Rieszen *et al.*, 1992). In contrast, on the southern shore of the Lake Ontario, veligers were present in 1993 in low densities (<300 m<sup>-3</sup>) at water temperatures as low as 3.4°C, and increased markedly (>3,000 m<sup>-3</sup>) only after 18°C was reached (R. F. Green, personal communication). These data suggest that spawning in *D. polymorpha* may start at 12°C, but is maximized above 17–18°C. Similarly, in a Polish lake, veligers occurred in minimal densities at temperatures

as low as 8°–10°C, but reached peak levels only above 20°C (Kornobis, 1977). Thus, it appears that limited spawning may occur below 17–18°C in both N.A. and European populations. When minimal veliger densities prevent effective sampling at low temperatures, it may appear that spawning is initiated above the 17–18°C threshold where spawning activity is maximized. Thus, initial spawning temperatures of 17–21°C are also reported among a number of European populations (Sprung, 1992). Spawning temperatures therefore appear to be similar in Europe and N.A., being initiated at ~12°C and maximized above 17–18°C. The 17°–18°C peak spawning threshold corresponds to the optimum temperature (18°C) for larval development (Sprung, 1987) and peak pediveliger settlement (18°C) (Piesik, 1983; Afanas'yev and Protasov, 1988).

Occurrence of veliger larvae in Lake Ontario at 3.5–11°C (R. F. Green, personal communication), below the 12°C threshold for gamete maturation and spawning among both European (Borcherding, 1991) and N.A. zebra mussel population (Garton and Haag, 1992), suggests that they were not the result of a winter spawning event, particularly as fertilization is impossible below 10°C (Sprung, 1987). Instead, declining fall water temperatures may have arrested veliger development, causing them to remain in the plankton during winter months. Winter arrest of veliger settlement and metamorphosis has been reported in both Europe (Kirpichenko, 1964; Lewandowski, 1982) and N.A. (Nichols, 1996) and probably accounts for appearance of veligers during periods when spawning and fertilization are impossible (<12°C) in both N.A. (R. F. Green, personal communication) and Europe (Sprung, 1992).

Temperature influences larval development and adult growth rates. European data suggest that 10°–26°C is required for successful fertilization (Sprung, 1987) and 12°–24°C, for larval development with 17.3°C being optimal (Sprung, 1987). Development time declines with increased temperature; metamorphosis to the D-shaped veliger requiring 90 hr at 12°C, but only 31 hr at 24°C (Sprung, 1987). Rapid

development at higher temperatures is associated with increased larval growth rates (Sprung, 1989). Temperature effects on larval development have not been investigated in N.A.

Zebra mussel growth rates are temperature dependent. The threshold for initiation of adult shell growth in English and Russian reservoirs was 11°–12°C (Morton, 1969). In European mussels, ingestion rates are maximized at this temperature (Walz, 1978a). Temperature for maximum adult growth also falls within the 10°–15°C range optimal for tissue growth (Walz, 1978b) and 10°–22°C range for maximal filtration rate (Reeders and Bij de Vaate, 1990).

Temperature effects on shell or tissue growth rate have not been investigated in N.A. zebra mussels. However, population age/size structures indicate that shell growth rates were >1 cm/yr in Lake Erie (Griffiths *et al.*, 1991) where temperatures remain for long periods above the 10°–15°C range considered optimal for shell growth in Europe (Walz, 1978b). Surface water temperatures fell within 10°–15°C an average of only 50 days per year (range = 34–61 days) over 1992–1994 in Lake Erie at Buffalo, NY, yet mussels maintained high rates of summer growth in this area (G. L. Dye, personal communication). They also maintained rapid shell growth rates in the lower Mississippi River at Baton Rouge, LA (T. H. Dietz, personal communication), in waters which fall below 15°C for only a few winter months (Hernandez *et al.*, 1995). Further studies of temperature effects on N.A. zebra mussel shell and tissue growth are clearly required.

European and N.A. estimates of zebra mussel thermal tolerance limits also disagree. Northern European data indicate an incipient upper lethal limit of 27°–28°C based primarily on field studies (Afanas'yev and Protasov, 1987; Testard, 1990; Jenner and Janssen-Mommen, 1992). In contrast, N.A. Great Lakes mussels could be held indefinitely in the laboratory at 30°C, 31°C being the incipient upper lethal limit (Iwanyzki and McCauley, 1992; McMahon *et al.* 1994) (Fig. 1A). Observations in the lower Mississippi River suggest that mussel populations thrive where tempera-

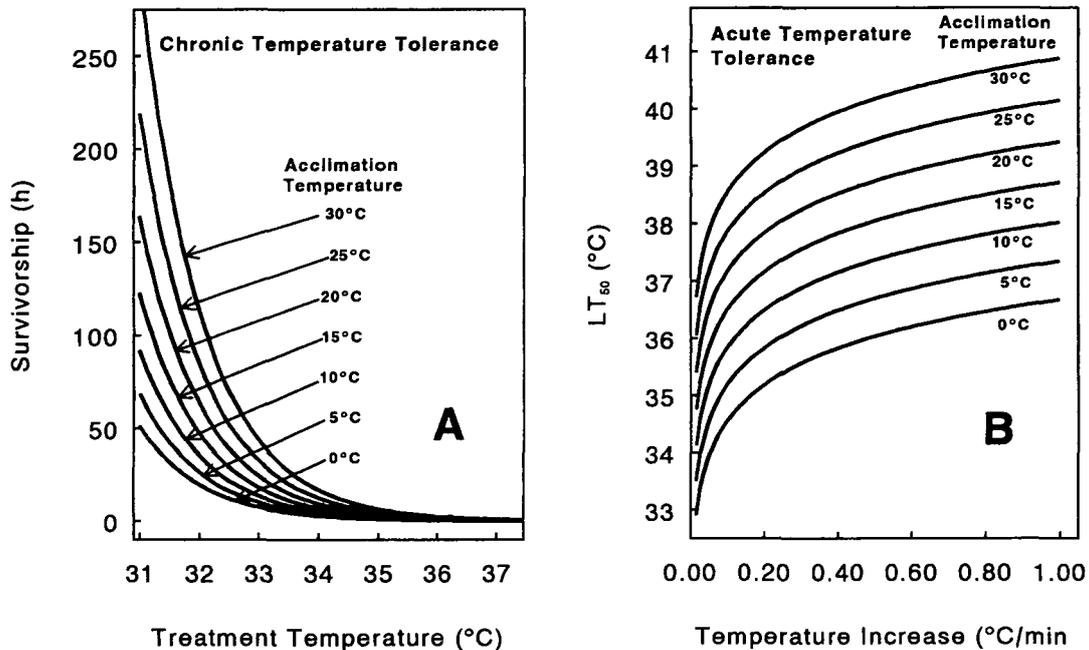


FIG. 1. Chronic and acute upper thermal limits of the zebra mussel, *Dreissena polymorpha*. A. Hours survived (vertical axis) during chronic (long-term) exposure to constant lethal temperatures (horizontal axis) after prior temperature acclimation (labeled on response curves). Response curves derived from a multiple linear regression model presented in the text (after McMahon *et al.*, 1994). B. Effects of acute exposure to temperatures increasing at different rates (horizontal axis) and after prior temperature acclimation (as labeled on response curves) on the temperature of 50% sample mortality (vertical axis, LT<sub>50</sub> as estimated from the method of probits). Curves derived from a multiple linear regression model presented in the text (after McMahon *et al.*, 1993).

tures reach or exceed 30°C (Hernandez *et al.*, 1995), conditions which would extirpate European populations (Afanas'yev and Protasov, 1987; Testard, 1990). However, other European studies report holding zebra mussels for long periods at 30°C (Tourari *et al.*, 1988), indicating an upper thermal limit equivalent to N.A. mussels (McMahon *et al.*, 1994).

A regression equation modeling effects of acclimation temperature (AT), exposure temperature (ET) and shell length (SL) as independent variables on the chronic thermal tolerance of N.A. zebra mussels has been developed (McMahon *et al.*, 1994):

$$\begin{aligned} \ln \text{ Survivorship (h)} &= 33.982 + 0.0579(\text{AT in } ^\circ\text{C}) \\ &\quad - 0.944(\ln \text{ ET in } ^\circ\text{C}) \\ &\quad - 0.0517(\text{SL in mm}). \end{aligned}$$

Thus, tolerance times increase with increased acclimation temperature and decrease exponentially with increased expo-

sure temperature. Temperatures  $\geq 36^\circ\text{C}$  were nearly instantaneously lethal regardless of acclimation state. In contrast, at a threshold of 31°C, they ranged from 50–300 hr in 0°C to 30°C acclimated specimens, respectively (Fig. 1A). The negative slope for SL indicates that larger specimens are less tolerant than smaller individuals, opposite that reported for European mussels (Afanas'yev and Protasov, 1987). Survivorships predicted by this model are generally greater than reported for European mussels. European mussels tolerated 33°C for less than 1.5 hr (Jenner and Janssen-Mommen, 1992) while N.A. mussels tolerated it for 10–50 hr depending on acclimation state (Fig. 1).

Acute upper lethal limits have been modeled for N.A. adult zebra mussels exposed to constant warming rates ranging from 0.0167°C to 0.2°C min<sup>-1</sup> (McMahon *et al.*, 1993). Values of LT<sub>50</sub> (estimated temperature for 50% sample mortality) were af-

ected by temperature increase rate (TIR) and prior acclimation temperature (AT) as follows:

$$\begin{aligned} \ln LT_{50} \text{ in } ^\circ\text{C} \\ = 3.603 + 0.026(\ln \text{TIR in } ^\circ\text{C}/\text{min}) \\ + 0.0036(\text{AT in } ^\circ\text{C}). \end{aligned}$$

$LT_{50}$  increases exponentially with increasing warming rate and linearly with increasing acclimation temperature (Fig. 1). Slower warming rates induce mortality at lower temperatures, warming rates of  $0.05^\circ\text{C min}^{-1}$ – $0.0333^\circ\text{C min}^{-1}$  inducing 50% sample kills at temperatures of  $33.5$ – $38^\circ\text{C}$  depending on acclimation state (Fig. 1B).

The basis for elevated thermal tolerance among N.A. zebra mussels has been debated. Differences may be due to different European and N.A. experimental protocols. Alternatively, they could be genetic and/or ecophenotypic. Because N.A. zebra mussels are likely to have originated from the warmest portion of the species' European range (Marsden *et al.*, 1996), they could have a genetically elevated thermal tolerance (McMahon *et al.*, 1994) relative to Northern European populations. Capacity for rapid temperature adaptation has been demonstrated for a zebra mussel population in a thermal discharge, which, within 8–10 years, developed allele frequencies at four of seven loci significantly different from those of a thermally unaffected source population (Fetisov *et al.*, 1991). Similarly, zebra mussels from the much warmer lower Mississippi River ( $30$ – $31^\circ\text{C}$  during summer months) tolerated  $33^\circ\text{C}$  longer than did more northern Niagara River mussels, suggesting that they were a thermally tolerant physiological race (Hernandez *et al.*, 1995). The apparent capacity of *D. polymorpha* for thermal selection supports the contention that N.A. mussels may be genetically more thermally tolerant than northern European mussels.

The thermal tolerance of zebra mussels drawn from the lower Mississippi River also had a seasonal component resistant to laboratory temperature acclimation. After laboratory acclimation to  $5^\circ$ ,  $15^\circ$  or  $25^\circ\text{C}$ , their thermal tolerance remained positively correlated with ambient water temperature

at time of collection (Fig. 2, Hernandez *et al.*, 1995), indicative of longer-term, seasonal "acclimatization" of thermal tolerance (acclimatization is defined as a longer-term, reversible, phenotypic adjustment of physiological response to an environmental variable that is not readily influenced by shorter-term laboratory acclimation to that variable). Thus, mussels seasonally acclimatized to cooler ambient conditions have lower thermal tolerances than those seasonally acclimatized to warmer ambient conditions even after standard laboratory temperature acclimation (Fig. 2). There is circumstantial evidence for seasonal acclimatization in European mussels. In the Volga River where downstream veliger dispersal precludes genetic race formation, mussels from warmer, southern river reaches were more thermally tolerant than those from cooler, northern reaches (Smirnova *et al.*, 1992). Temperature acclimatization could partially account for thermal tolerance variation among European and N.A. populations, particularly as northern European specimens were likely to have been drawn from seasonally cooler waters than N.A. mussels (Iwanyzki and McCauley, 1992; McMahon *et al.*, 1994). Recent evidence that the upper thermal limits of European mussels (Tourari *et al.*, 1988) and N.A. mussels are similar at  $30^\circ\text{C}$  (McMahon, *et al.*, 1994) suggests that seasonal acclimatization may account for the majority of variation among N.A. and European studies of thermal tolerance.

Temperature also affects zebra mussel hemolymph osmolarity, ion concentrations and ion flux. At  $4$ – $5^\circ\text{C}$  for 51 days, mussels decreased hemolymph  $\text{Na}^+$ ,  $\text{Cl}^-$  and osmotic concentrations and increased  $\text{Ca}^{2+}$  concentration compared to those held at  $20$ – $25^\circ\text{C}$  (Scheide and Boniaminio, 1994). Hemolymph ion concentrations in individuals acclimated to  $20$ – $25^\circ\text{C}$  changed less relative to fresh caught individuals than they did in cold-acclimated individuals. Similar responses occurred in cold-acclimated unionids (Scheide and Boniaminio, 1994). Transferral of  $20$ – $25^\circ\text{C}$  acclimated mussels to  $4$ – $5^\circ$  initially resulted in a net efflux of  $\text{Na}^+$  and  $\text{Cl}^-$ , perhaps due to metabolic reduction in capacity for active up-

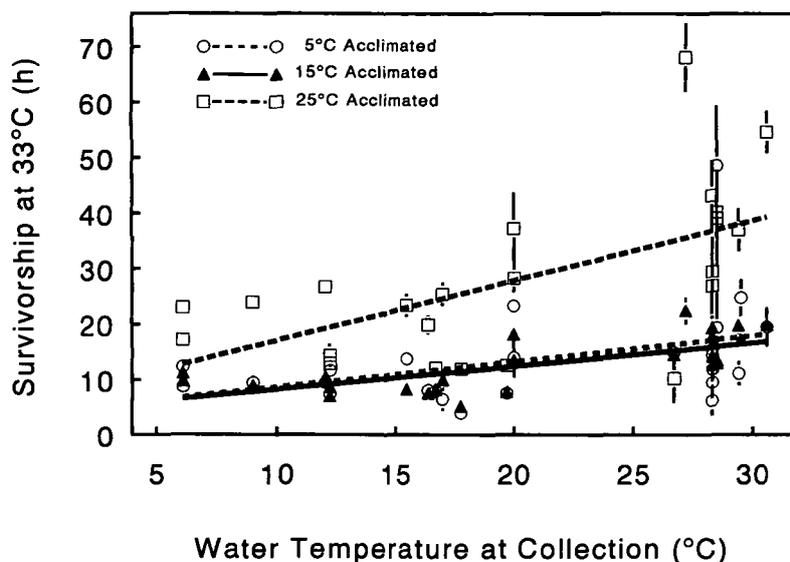


FIG. 2. Effects of water temperature at time of collection (horizontal axis) and laboratory acclimation temperature (5°C acclimated = open circles, 15°C = solid triangles, 25°C = open squares) on mean hours survived (vertical axis) on exposure of zebra mussels (*Dreissena polymorpha*) to a lethal temperature of 33°C. Vertical bars about means are standard errors. Lines represent best fits of least squares linear regressions relating mean survival times to ambient water temperature at collection (5°C acclimated = short dashes, 15°C = solid line and 25°C = long dashes). Intercepts and slopes of regressions for 5°C and 15°C acclimated individuals are not significantly different ( $P < 0.05$ ), while the regression slope for 25°C acclimated mussels is greater ( $P > 0.05$ ) than that of 5° and 15°C acclimated individuals (after Hernandez *et al.*, 1995).

take. However, after 51 days, net  $\text{Na}^+$  and  $\text{Cl}^-$  losses approached zero, suggesting that new, lower equilibrium  $\text{Na}^+$ ,  $\text{Cl}^-$  and osmotic concentrations had been reached (Scheide and Boniaminio, 1994). Zebra mussel osmotic and ionic regulation is reviewed in this volume by Dietz *et al.* (1996).

#### RESPIRATION AND METABOLISM

Zebra mussel  $\text{O}_2$  consumption rates are essentially similar to those of freshwater unionid and sphaeriid bivalves (Alimov, 1975), suggesting these groups have similar metabolic maintenance demands. Oxygen consumption rates ( $\dot{V}\text{O}_2$ ) are related to individual dry tissue mass ( $M$ ) as follows:

$$\dot{V}\text{O}_2 = aM^b,$$

where “a” and the exponent, “b”, are constants relating dry tissue mass to  $\dot{V}\text{O}_2$ . Values of “b” in this equation model increase in  $\dot{V}\text{O}_2$  with unit increase in tissue mass. They ranged from 0.66–0.84 in European zebra mussel populations from February

through October (Lyashenko and Karchenko, 1969). An average “b” of 0.63 was computed for zebra mussel based on combined data of several European authors (Alimov, 1975). A value of 0.82 can be computed from the data of Quigley *et al.* (1992) for N.A. mussels. Zebra mussel “b” values fall among those of other freshwater molluscs. Alimov (1975) recorded an average “b” of 0.721 ( $\pm 0.026$ ) for freshwater bivalves in the former U.S.S.R. Hornbach (1985) reported “b” to range from 0–1.24 among 28 sphaeriid species while “b” values ranging from 0.25 to 1.45 occur among a wide variety of freshwater bivalves (Burky, 1983).

Respiratory responses to acute temperature change and prior temperature acclimation have been recorded in N.A. and European zebra mussels. Mussels from the western basin of Lake Erie displayed partial respiratory temperature compensation such that  $\dot{V}\text{O}_2$  recorded over 5°–30°C was significantly decreased in 25°C relative to 5°C and 15°C acclimated individuals (Fig. 3, Al-

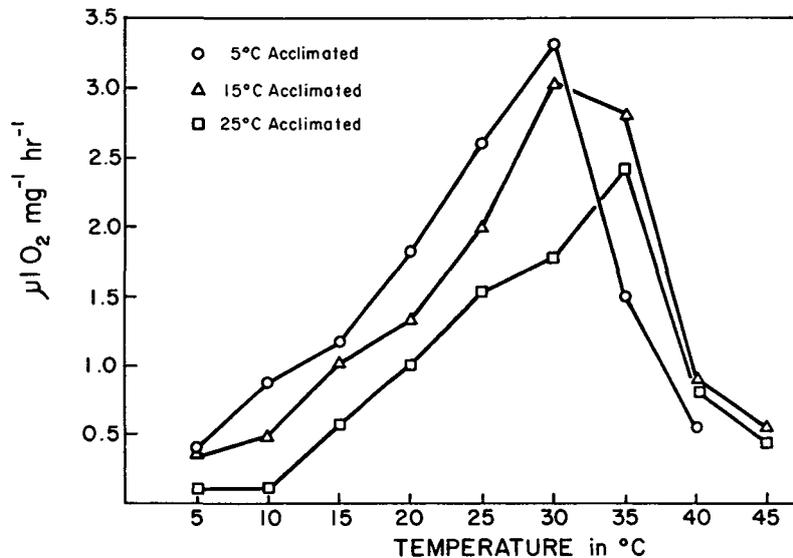


FIG. 3. The effect of exposure temperature (horizontal axis) and prior acclimation temperature (5°C = circles, 15°C = triangles, 25°C = squares) on the oxygen consumption rate of standard sized individual of zebra mussel, *Dreissena polymorpha*, in microliters of oxygen per mg dry tissue weight per hour ( $\mu\text{l O}_2 \text{ mg}^{-1} \text{ hr}^{-1}$ ) (vertical axis) (J. E. Alexander, Jr. and R. F. McMahon, unpublished data).

exander and McMahon, unpublished data). Among 5°C acclimated specimens, maximal  $\dot{V}\text{O}_2$  occurred at 30°C, between 30° and 35°C in 15°C acclimated individuals, and at 35°C in 25°C acclimated individuals (Fig. 3). Temperatures of maximum  $\dot{V}\text{O}_2$  (Fig. 3) and acute upper lethal temperatures on exposure to slow warming (*i.e.*, 0.0167°C/60 min, Fig. 1B) correspond, suggesting that declines in  $\dot{V}\text{O}_2$  at higher temperatures (Fig. 3) are due to acute thermal stress.

European and N.A. data on zebra mussel respiratory responses to acute temperature variation are similar.  $\dot{V}\text{O}_2$  in freshly field collected European mussels was maximized at 25°–35°C (Mikheev, 1964; Lyashenko and Karchenko, 1989). Respiratory response to temperature was similar at different times of the year (Mikheev, 1964; Lyashenko and Karchenko, 1989), suggesting little capacity for metabolic temperature compensation, a result contradicting observations in N.A. mussels (Fig. 3). Alexander *et al.* (1994) also found little evidence of respiratory compensation in Lake Erie zebra mussels acclimated to 10°, 18° or 26°C. Further study of respiratory temperature ac-

climation is required in zebra mussels in order to resolve such contradictory data.

$Q_{10}$  values relating increase in  $\dot{V}\text{O}_2$  to temperature ( $Q_{10}$  is a computed value indicating the factor by which  $\dot{V}\text{O}_2$  increases with a 10°C increase in temperature. It can be calculated over any temperature range) have been reported for zebra mussels in Europe and N.A. (Table 1). Both European and N.A.  $Q_{10}$  data indicate that  $\dot{V}\text{O}_2$  increases more rapidly with increasing temperature in the lower portion of the mussel's ambient range (5°–20°C) than at higher temperatures (20°C–30°C) (Alimov, 1975; Dorgelo and Smeenk, 1988; Quigley *et al.*, 1992; Alexander and McMahon, unpublished data) (Table 1). From 5° to 20°C,  $Q_{10}$  values are generally greater than 2.0 (Table 2), suggesting active metabolic augmentation. Active increase in metabolic rate up to 20°C may be responsible for the marked increase in mussel metabolic demand during increasing spring water temperature in Europe (Lyashenko and Karchenko, 1989) and N.A. (Quigley *et al.*, 1992).

Seasonal studies of respiration rate have been carried out among European and N.A.

TABLE 1.  $Q_{10}$  values estimating the relative increase in oxygen consumption rate over a 10°C ambient temperature increase computed over different temperature ranges and for different levels of temperature acclimation in the zebra mussel, *D. polymorpha*.

Temperature range	Respiratory $Q_{10}$ value			
	Alexander and McMahon, unpublished data			Other observations <sup>a-d</sup>
	5°C Acc.	15°C Acc.	25°C Acc.	
5°–10°C	4.79	1.53	0.81	3.24 <sup>a</sup>
10°–15°C	1.81	4.80	4.15	3.47 <sup>a</sup>
15°–20°C	2.45	1.67	3.03	2.23 <sup>a</sup>
20°–25°C	2.03	2.28	2.29	1.59 <sup>a</sup>
25°–30°C	1.63	2.29	1.37	1.46 <sup>a</sup>
30°–35°C	0.21	0.85	1.84	—
35°–40°C	0.15	0.10	0.05	—
10°–26°C	—	—	—	1.96 <sup>b</sup>
7.5°–19°C	—	—	—	2.3 <sup>c</sup>
10°–20°C	—	—	—	3.5 <sup>d</sup>

<sup>a</sup> Alimov, 1975.

<sup>b</sup> Quigley *et al.*, 1992.

<sup>c</sup> Dorgelo and Smeenk, 1988.

<sup>d</sup> Alexander *et al.*, 1994.

zebra mussels. The  $\dot{V}O_2$  of European mussels from the Dnieper-Donbass Canal, Ukraine, reached maximal levels during peak temperature periods (Lyashenko and Karchenko, 1989), a response similar to that of N.A. mussels from Lake St. Clair (Quigley *et al.*, 1992). Interestingly, at both sites, peak  $\dot{V}O_2$  occurred after spring water temperatures rose rapidly from 7°–10°C to 19°–20°C, suggesting that metabolic demand was being partially driven by onset of maximal spawning activity above 17°–18°C (see section on “Temperature Responses”).

Turbidity also affects zebra mussel  $\dot{V}O_2$ . Acute exposures to 0, 5, 20 and 80 NTU (nephelometric turbidity units) induced a progressive decline in  $\dot{V}O_2$ . Thereafter,  $\dot{V}O_2$  stabilized over 80 to 160 NTU at 40–70% of the rate at 0 NTU (Alexander *et al.*, 1994). Zebra mussels thrive in the lower Ohio River (Zebra Mussel Information Clearinghouse, 1995) where turbidities can exceed 145 NTU (Alexander *et al.*, 1994), suggesting that turbidity induced suppression of  $\dot{V}O_2$  is transitory with mussels capable of compensating  $\dot{V}O_2$  to ambient turbidities over naturally occurring exposure periods (Alexander *et al.*, 1994).

Temperature may also affect protein ver-

sus nonprotein catabolism in zebra mussels. During early spring and fall at temperatures below 16°C, molar ratios of  $O_2$  consumed to nitrogen excreted (O:N ratio) in Lake St. Clair mussels ranged between 29.7 and 48.3 (Quigley *et al.*, 1992), indicative of 20%–39% of metabolic demands being supported by nonprotein catabolism (*i.e.*, carbohydrate and lipid catabolism, computation based on Bayne, 1973). During May through August at temperatures above 18°C when spawning was likely to be maximized, O:N ratios fell to 16.0–22.2, indicative of increased dependence on protein catabolism (Quigley *et al.*, 1992) (7%–13% of catabolism dependent on nonprotein metabolites, computation based on Bayne, 1973). Mid-summer decreases in tissue mass and nonprotein catabolism also occur in European zebra mussels. During winter, low food availability may prevent mussel catabolism from being completely supported by assimilation, leading to increasing dependence on nonprotein, carbohydrate energy stores (Walz, 1979), thus accounting for the high O:N ratios of 30–48 recorded in Lake Erie below 8°C (Quigley *et al.*, 1992).

As in a naturally spawning zebra mussel population from Lake St. Clair (Quigley *et al.*, 1992), artificially spawned European mussels had lower O:N ratios than non-spawning individuals (Sprung, 1991), suggesting that post-spawning individuals increased dependence on protein catabolism for maintenance energy. During starvation, freshwater bivalves deplete carbohydrate and lipid stores, marked by a decrease in O:N ratio with increasing dependence on protein catabolism (Burky, 1983). Thus, reduction in O:N ratios of Lake St. Clair mussels above the 18°C peak spawning threshold (Quigley *et al.*, 1992) may have been due to massive allocation of nonprotein energy stores to gametogenesis. Reductions in tissue ash free dry weight, and lipid content during July through September among Lake St. Clair zebra mussels (Nalepa *et al.*, 1993) are evidence of post-spawning reduction in nonprotein energy stores. During this period, tissue organic carbon to nitrogen ratios (C:N) fell from 6–7 to approximately 3.5–4 (Nalepa *et al.*, 1993). As average protein C:N is 3.25, post-spawning mussels had re-

duced carbohydrate and lipid energy reserves. Resulting increased dependence on protein catabolism would yield the low O:N ratios recorded during post-spawning periods (Quigley *et al.*, 1992).

Metabolic and shell growth rates are positively correlated with degree of individual multiple locus heterozygosity in marine bivalves (for a review see Garton and Haag, 1991). When tested against seven polymorphic enzyme loci, the shell length of western Lake Erie zebra mussels was positively correlated with increasing multiple locus heterozygosity, but not with  $\dot{V}O_2$ . Increased growth rate in highly heterozygous individuals may be a manifestation of their increased energetic efficiency (Garton and Haag, 1991). However, lack of correlation between metabolic rate and degree of heterozygosity suggested that increased tissue growth rates were due to increased assimilation rates in highly heterozygous individuals rather than to reduction in maintenance metabolism (Garton and Haag, 1991).

#### RESPONSES TO HYPOXIA/ANOXIA

European and N.A. studies indicate that zebra mussels are relatively intolerant of hypoxia or anoxia. Held in sealed chambers depleted of  $O_2$  by mussel respiration, European zebra mussels experienced 100% mortality within 144 hr at 17°–18°C, 96 hr at 20°–21°C and 72 hr at 23°–24°C (Mikheev, 1964). When anoxic for 37 hr at 22°C, mortality was greatest (100%) among smaller mussels (shell length = 1–4.9 mm), survivorship increasing in larger size classes (0% mortality at a shell length = 20–24.9 mm) (Mikheev, 1964). Similarly, mean survival times of N.A. Niagara River mussels held in media depleted of  $O_2$  by  $N_2$  bubbling ranged from 907–1005 hr 228–428 hr and 53–83 hr at 5°, 15°C and 25°C, respectively (Fig. 4). These values were somewhat greater than reported by Mikheev (1964). More rapid mortality in Mikheev's (1964) study may have been due to effects of toxic anaerobic end-products accumulated in sealed test chambers. At test temperatures of 15° and 25°C, zebra mussel anoxia tolerance increased with increasing acclimation temperature (Fig. 4), perhaps due to a reduction in metabolic rate among warm-

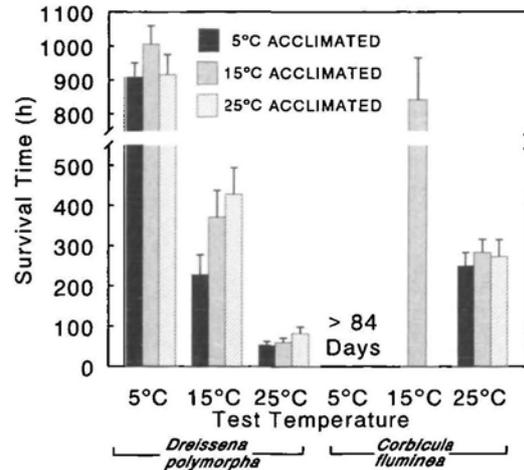


FIG. 4. Effects of test temperature (horizontal axis) and prior acclimation temperature (5°C acclimated = solid histograms, 15°C = finely cross-hatched histograms, 25°C = coarsely cross-hatched histograms) on mean survivorship in hours (vertical axis) of specimens of *Dreissena polymorpha* and *Corbicula fluminea* exposed to extreme hypoxia ( $PO_2 < 3$  torr). Mean hypoxia survival times on the left side of the horizontal axis are for specimens of *D. polymorpha* and on the right-hand side, for *C. fluminea*. Vertical bars above histograms are standard errors of the means. There were no significant differences among mean survival times of different acclimation groups of *C. fluminea* at a test temperature of 25°C, therefore, only 15°C and 5°C acclimated specimens were exposed to test temperatures of 15° and 5°C, respectively. Extreme hypoxia at 5°C produced no mortality among specimens of *C. fluminea* during 84 days of exposure (after Matthews and McMahon, 1994).

acclimated individuals (Fig. 3). Congruent with Russian results (Mikheev, 1964), larger individuals were more anoxia tolerant than smaller individuals (Matthews and McMahon, 1994 and unpublished data). Asian clams, *Corbicula fluminea* (Müller), among the most anoxia intolerant of all freshwater bivalves (McMahon, 1983a), are approximately twice as anoxia tolerant as zebra mussels (Fig. 4, Matthews and McMahon, 1994), making zebra mussels among the least anoxia/hypoxia tolerant of all freshwater bivalves. In contrast, freshwater unionacean and sphaeriid bivalves are relatively anoxia/hypoxia tolerant (McMahon, 1991). The chronic, lower lethal  $PO_2$  for N.A. adult zebra mussels is approximately 32–40 Torr at 25°C (Johnson and McMahon, unpublished data), a value sim-

ilar to the minimum of 32 Torr required for larval development at 18°–20°C (Sprung, 1987). Recently transformed juvenile unionids are also anoxia intolerant (Dimock and Wright, 1993).

Most freshwater unionacean and sphaeriid bivalves highly regulate O<sub>2</sub> consumption, maintaining  $\dot{V}O_2$  at or near air O<sub>2</sub> saturation levels even at very low PO<sub>2</sub> (McMahon, 1991). In contrast, *D. polymorpha*, like *C. fluminea* (McMahon, 1979), is a poor to nonregulator of  $\dot{V}O_2$ . Lake St. Clair mussels displayed no regulatory capacity (Quigley *et al.*, 1992). We have shown that both test temperature and prior temperature acclimation significantly affect regulatory ability in *D. polymorpha* (Fig. 5). Degree of O<sub>2</sub> regulation can be estimated by fitting standardized  $\dot{V}O_2$  values (*i.e.*,  $\dot{V}O_2$  expressed as a fraction of that at air O<sub>2</sub> saturation) as the dependent variable to a quadratic equation against PO<sub>2</sub> in Torr. The quadratic coefficient or “b<sub>2</sub>” value of this equation estimates degree of O<sub>2</sub> regulation, becoming increasingly negative as regulatory ability increases (Mangum and Van Winkle, 1973). Based on “b<sub>2</sub>” analysis, zebra mussels were good to nonregulators of oxygen consumption dependent on test and prior acclimation temperatures, regulation increasing with decreasing acclimation temperature and increasing test temperature. Thus, among 5°C, 15°, and 25°C acclimated mussels, those acclimated to 5°C and tested at 25°C displayed the best (but still mediocre) capacity for oxygen regulation, while those acclimated to 25° had essentially no regulatory ability at 5°C (Fig. 5, Alexander and McMahon, unpublished results). Increased O<sub>2</sub> regulation when cold-acclimated (Fig. 5) may allow overwintering mussels to survive hypoxia resulting from surface ice formation in lentic habitats as occurs in some freshwater unionids and pulmonate gastropods (McMahon, 1991, 1983b).

Poor anoxia/hypoxia tolerance (Fig. 4) and O<sub>2</sub> regulatory ability (Fig. 5) may restrict zebra mussels to well oxygenated habitats (Stańczykowska, 1977), account for their poor colonization success in eutrophic lakes (Stańczykowska, 1984), and prevent populations from extending into hypoxic, hypolimnetic waters (Mackie *et*

*al.*, 1989). In contrast, the second dreissenid species introduced into North America, *Dreissena bugensis* Andrusov (quagga mussel), occurs in hypolimnetic waters and inhabits soft substrata from which *D. polymorpha* is generally excluded (McDermott, 1993). Their profundal habitat suggests that quagga mussels are more hypoxia tolerant and better O<sub>2</sub> regulators than zebra mussels, hypotheses supported by preliminary experimentation (Birger *et al.*, 1978). However, further research is required to confirm this speculation.

#### SALINITY TOLERANCE

European information on zebra mussel salinity tolerance is primarily based on field observations and is somewhat divergent (for a review see Strayer and Smith, 1992). In the tidal reaches of the Rhine River, Netherlands, maximal salinities for mussel occurrence were 0.6‰ (Wolff, 1969). That for completion of the entire life cycle was 0.75‰ to 1.29‰ (2.1–3.7% of sea water at 35‰) (Smit *et al.*, 1992). Such data suggest that 0.5–2.0‰ is this species' chronic, upper salinity limit, which corresponds to the salinity limits for mussel occurrence in northern Europe and the Black Sea region (Strayer and Smith, 1992 and references therein). In contrast, zebra mussels occur in North-Baltic Sea estuaries at salinities up to 3.8‰–6.2‰ and, in the Caspian and Aral Seas, up to 6–10.2‰ (Strayer and Smith, 1992 and references therein). Higher mussel salinity tolerances in the Caspian, Aral and North Baltic Seas may be due to their reduced tidal fluctuations. In more tidally influenced Dutch estuaries, mussel populations are subjected to extended tidal emersion. As *D. polymorpha* is intolerant of emersion (McMahon *et al.*, 1993), mussels may be restricted to low salinity, upper portions of Dutch estuaries where tidal fluctuations are dampened, leading to an underestimate of their salinity tolerance (Strayer and Smith, 1992). A human mediated increase in Aral Sea salinity to 14‰ extirpated its zebra mussel population in 1976–77 (Aladin and Potts, 1992). Thus, 14‰ may be the mussel's incipient upper salinity limit. Recent laboratory studies suggest that N.A. juvenile and adult zebra mussels do

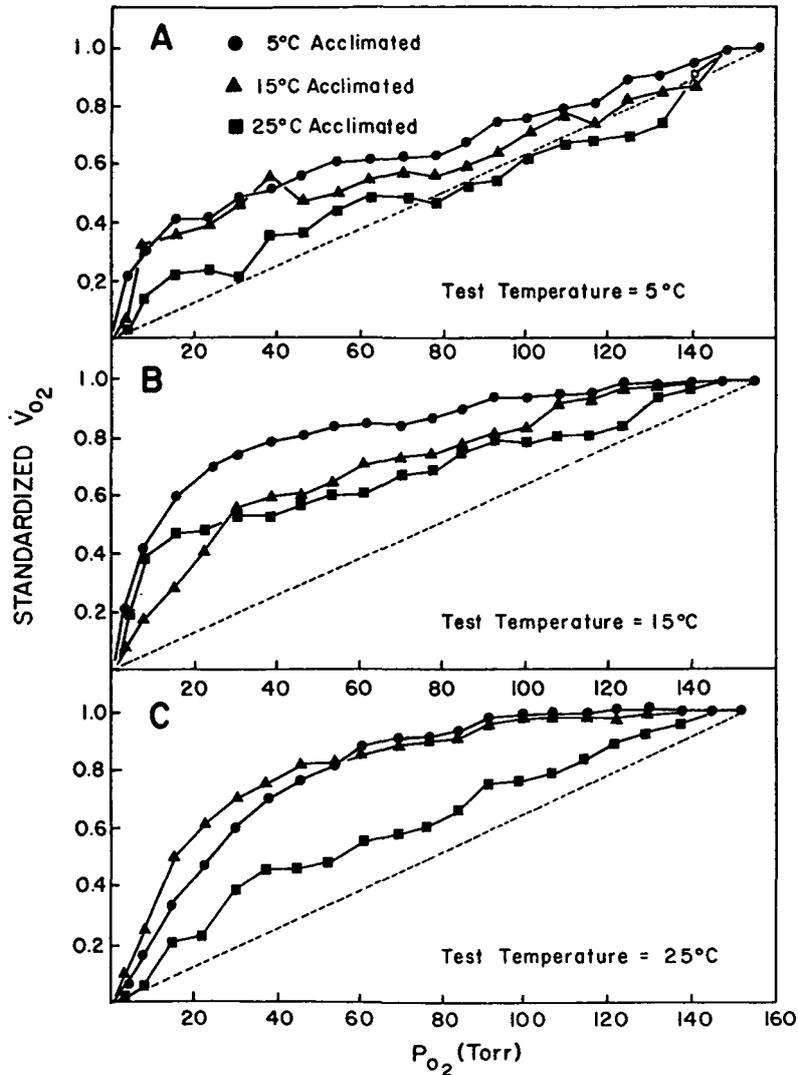


FIG. 5. Respiratory response of *Dreissena polymorpha* to progressive hypoxia. In all three figures, medium  $P_{O_2}$  is indicated as Torr on the horizontal axis versus mean standardized oxygen consumption rate ( $\dot{V}_{O_2}$ ) in which  $\dot{V}_{O_2}$  at any one  $P_{O_2}$  is expressed as a fraction of the rate recorded at full air  $O_2$  saturation ( $P_{O_2} = 159$  torr) on the vertical axis. Solid circles are mean  $\dot{V}_{O_2}$  values for 5°C acclimated individuals, triangles, for 15°C acclimated individuals, and squares, for 25°C acclimated individuals. The dashed line in each figure represents the respiratory response to progressive hypoxia of a completely oxygen dependent individual ( $\dot{V}_{O_2}$  directly proportional to  $P_{O_2}$ ). The greater the divergence of a respiratory response curve above the dashed line, the greater the degree of  $\dot{V}_{O_2}$  regulation. A. Respiratory response to hypoxia at a test temperature of 5°C, B., at a test temperature of 15°C, and C., at a test temperature of 25°C (J. E. Alexander, Jr. and R. F. McMahon, unpublished data).

not tolerate salinities above 4‰, with quagga mussels (*D. bugensis*) being even less tolerant (Kilgour and Kepple, 1993; Kennedy *et al.*, 1995).

Even with a salinity tolerance of 6–10‰, the zebra mussel is still considered to be a

freshwater species because upper limits of 3–8‰ are typical of most freshwater species (Remane and Schlieper, 1971; Green, 1968), while upper limits of 8–10‰ are typical of most freshwater bivalves (Fuller, 1974; Gainey and Greenberg, 1977). Upper

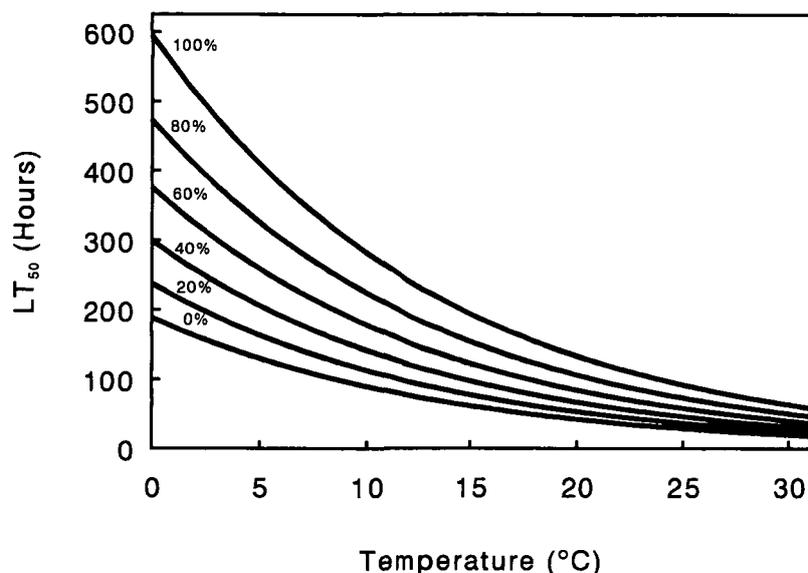


FIG. 6. Effects of temperature (horizontal axis) and relative humidity (as indicated on individual response curves) on the emersion tolerance of zebra mussels, *Dreissena polymorpha*, expressed as  $LT_{50}$  values (*i.e.*, estimated time in hours for 50% sample mortality, vertical axis) as computed from the multiple regression model described in the text (after McMahon *et al.*, 1993).

salinity limits of truly estuarine species are well above 10‰ (Remane and Schlieper, 1971; Green, 1968; Gainey and Greenberg, 1977).

When acclimated to freshwater, Lake St. Clair zebra mussels could be induced to spawn by external serotonin application in media  $\leq 3.5\%$  at 12–27°C, but successful fertilization required  $\leq 1.75\%$  (Fong *et al.*, 1996). Acclimation to 1.75, 3.5 or 7‰ allowed spawning to be induced up to 7‰ and successful fertilization up to 3.5‰ (Fong *et al.*, 1996). Early zebra mussel embryonic development occurs in salinities <6‰, and, at <4‰ in quagga mussels (Kennedy *et al.*, 1995). Less than 8‰ was required for development of zebra mussel larvae to D-hinge veligers and <6‰ for successful pediveliger settlement. Quagga mussels required <4‰ for development of D-hinge veligers and pediveliger settlement (Wright *et al.*, 1995). Thus, early *D. polymorpha* developmental stages have the same or slightly lower maximum salinity limits as adults with salinities below  $\approx 6\%$  required for successful spawning, fertilization, settlement and transformation to the juvenile and below  $\approx 7\text{--}10\%$ , for successful

adult colonization. Salinity limits appear somewhat lower for *D. bugensis*, with below  $\approx 4\%$  required for successful life cycle completion and maintenance of adult populations.

#### DESICCATION AND FREEZING RESISTANCE

European zebra mussels are relatively emersion intolerant, incipient mortality occurring after four days in air at 20–22°C. Anaerobic, hemolymph respiratory acidosis during emersion was buffered by shell  $\text{CaCO}_3$  (Alyakrinskaya, 1978). Our studies indicate that emersion tolerance (computed as  $LT_{50}$  values, *i.e.*, time for 50% sample mortality estimated by probit analysis) in Lake Erie zebra mussels decreased exponentially with increasing air temperature and decreasing R.H. as modeled by the following multiple regression equation:

$$\ln LT_{50} = 5.243 - 0.074(^{\circ}\text{C}) + 0.011(\% \text{R.H.})$$

(Fig. 6) (McMahon *et al.*, 1993). Water loss rates in emersed mussels increased exponentially with increasing temperature and decreasing R.H. At 5°, 15°C and 25°C, percent of total water lost at death (total water

= tissue plus extracorporeal mantle cavity water) ranged between 58% and 71% in <5% to 75% R.H., levels of lethal desiccation similar to that of other freshwater bivalves (Byrne and McMahon, 1994). However, at >95% R.H., mean percent of total water lost at death was much lower at 35–40%, suggesting that death resulted from lethal accumulation of metabolic end-products (McMahon *et al.*, 1993). Similar levels of N.A. zebra mussel desiccation resistance have been reported by Ricciardi *et al.* (1995).

Based on  $LT_{50}$  values, zebra mussel emersion tolerance times above 25°C were less than 100 hr regardless of R.H., increasing to 100–400 hr at 5°C depending on R.H. (Fig. 6) (McMahon *et al.*, 1993). These levels of emersion tolerance are far less than recorded among other freshwater bivalve species, many of which tolerate emersion for many months (for reviews see McMahon, 1991; Byrne and McMahon, 1994). Poor desiccation tolerance may be the reason that juvenile zebra mussels settling at depths <1 m migrate into deeper waters (Mackie *et al.*, 1989). However, extended emersion tolerance in mussels at low temperatures and high R.H. (Fig. 6) suggest that mussels could be transported long distances on anchor chains of ocean-going vessels, trailered pleasure craft, or aquatic macrophytes snagged on boat trailers. Extensive mussel anchor chain colonization occurred within 24 hr on a vessel anchored in Lake Ontario (R. F. Green, personal communication), making anchor chains a possible vector for this species' introduction to N.A. (McMahon *et al.*, 1993) in addition to larval transport in ship ballast water (Mackie *et al.*, 1989).

At 15°C, N.A. quagga mussels (*D. bugensis*) had emersion tolerances very similar to zebra mussels between <5%, and 33% R.H., but tolerance was reduced at R.H.  $\geq$ 53% (Ussery and McMahon, 1994). Similarly, N.A. quagga mussels were found to be less emersion tolerant than zebra mussels at 10°C and 95% R.H. (Ricciardi *et al.*, 1995). Reduced quagga mussel emersion tolerance in elevated R.H. was associated with reduced evaporative water loss rates relative to zebra mussels, suggesting that

emerged quagga mussels expose mantle tissues for aerial gas exchange less frequently than zebra mussels (Ussery and McMahon, 1994). Reduction in aerial gas exchange at high R.H. by quagga mussels could lead to their more rapid accumulation of anaerobic end-products to lethal levels. In contrast, Ricciardi *et al.*, (1995) found that evaporative water loss rates in *D. bugensis* were greater than those of *D. polymorpha* when emersed at 20°C in 10%, 50% or 95% R.H. The quagga mussel's profundal habit (McDermott, 1993) exerts little selection pressure for emersion tolerance (Ussery and McMahon, 1994), thus its poorer emersion tolerance relative to epilimnetic zebra mussels is not unexpected.

At a lethal temperature of 35°C, zebra mussel emersion tolerance times were greatly reduced (10–40 hr depending on R.H.) relative to nonlethal temperatures (<30°C), but increased with decreasing R.H., a result opposite that recorded at nonlethal temperatures. In lethal air temperatures such as 35°C, inhibition of evaporative cooling at high R.H. may have reduced capacity for evaporative cooling causing tissues to more rapidly reach lethal temperatures (McMahon *et al.*, 1993).

Juvenile zebra mussels settling in shallow water may migrate to greater depths to avoid emersion in freezing winter air (Mackie *et al.*, 1989). Adult, N.A. zebra mussels proved highly intolerant of aerial freezing (Clarke 1993; Clarke and McMahon, 1993). Single (separate) individuals experienced 100% mortality within 2–15 hr at  $-10^{\circ}$  to  $-1.5^{\circ}\text{C}$  (Fig. 7). Among clusters of 10 mussels, representing conditions in dense populations, the maximal temperature for mortality was  $-3^{\circ}\text{C}$ . Survival times of clustered mussels were double that of single mussels at all tested temperatures ( $-3.0^{\circ}$  to  $-10^{\circ}\text{C}$ ) (Fig. 7). Clustering increased relative tissue mass, and therefore, time required for tissues of clustered individuals to freeze. Tissue super cooling points were high ( $\approx -0.37^{\circ}$  to  $-2.03^{\circ}\text{C}$ ), suggesting lack of the tissue or hemolymph antifreeze agents characteristic of truly freeze resistant organisms (Clarke, 1993). Fifty percent sample mortality occurred when 22% of body water was frozen (Clarke, 1993), sug-

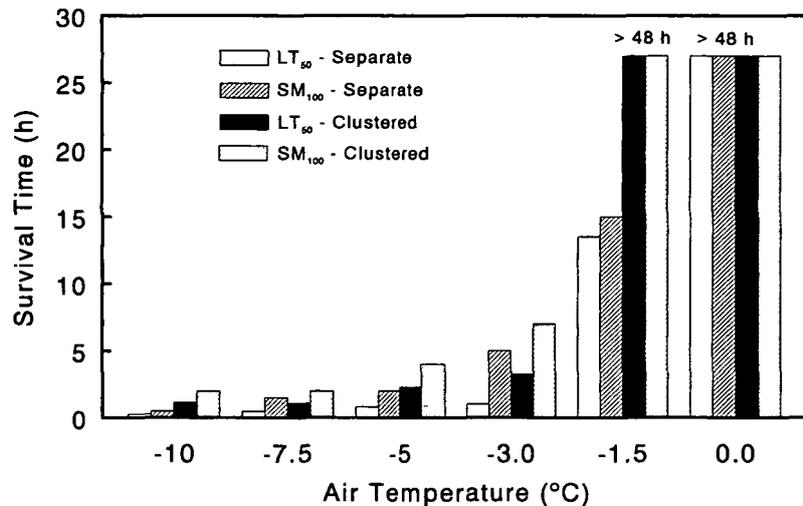


FIG. 7. The effect of subfreezing air temperatures (horizontal axis) on survival times in hours (vertical axis) of the zebra mussel (*Dreissena polymorpha*). Histograms represent survival of individuals either singly exposed (separate) or exposed in a group of 10 clustered mussels (clustered) expressed as either hours for 50% sample mortality (LT<sub>50</sub> estimated by the method of probits) or as hours required for actual 100% subsample mortality (SM<sub>100</sub>). Single individuals at 0°C and clustered individuals at 0°C and -1.5°C survived emersion more than 48 h (after Clarke, 1993; McMahon *et al.* 1993).

gesting a lack of cryoprotectants that allow tolerance of extensive tissue freezing in intertidal mytilid mussels (Williams, 1969).

#### CALCIUM CONCENTRATION AND pH LIMITS

Zebra mussels are less tolerant of low calcium concentration and low pH than other freshwater bivalves (McMahon, 1991). Most unionaceans grow and reproduce at a pH of 5.6 to 8.3 and at Ca<sup>2+</sup> concentrations above 2.0 to 2.5 mg Ca<sup>2+</sup>/liter. Many sphaeriid species are adapted to acidic, low calcium habitats (McMahon, 1991 and references therein). Minimum pH limits are 6.5 for adult zebra mussels and 7.4 for veligers. Those for moderate and maximal adult growth are 7.4 and >8.0, respectively (Claudi and Mackie, 1993). European mussels were absent from lakes with pH <7.3 and Ca<sup>2+</sup> concentrations <28.3 mg Ca<sup>2+</sup>/liter. Population density was positively correlated with Ca<sup>2+</sup> concentration and negatively correlated with PO<sub>4</sub><sup>3-</sup> and NO<sub>3</sub><sup>-</sup> concentrations (Ramcharan *et al.*, 1992). In N.A., mussels inhabit waters ≥15 mg Ca<sup>2+</sup>/liter, with dense populations developing ≥21 mg Ca<sup>2+</sup>/liter (Mellina and Rasmussen, 1994). North American zebra mus-

sel Ca<sup>2+</sup> tolerances are somewhat lower than reported for European populations (Ramcharan *et al.*, 1992) and correspond with lower limits of 10–11 mg Ca<sup>2+</sup>/liter for initiation of shell growth and 25–26 mg Ca<sup>2+</sup>/liter for maintenance of moderate shell growth (Claudi and Mackie, 1993).

The bases for the relatively high lower pH and Ca<sup>2+</sup> concentration limits of zebra mussels have received little study. Adult mussels cannot regulate hemolymph Ca<sup>2+</sup> at <12–14 mg Ca<sup>2+</sup>/liter. Hemolymph Ca<sup>2+</sup> regulatory capacity declines below pH 6.8–6.9 (Vinogradov *et al.*, 1992). Both values correspond with the lower Ca<sup>2+</sup> concentration and pH thresholds for zebra mussels (see above). In contrast, two unionids, *Anodonta cygnea* (L.) and *Unio pictorum* (L.), were much more tolerant of low pH and Ca<sup>2+</sup> concentration, regulating hemolymph Ca<sup>2+</sup> at 3 mg Ca<sup>2+</sup>/liter and 6–7 mg Ca<sup>2+</sup>/liter, respectively, as well as regulating hemolymph Ca<sup>2+</sup> in media of much lower pH than could zebra mussels (Vinogradov *et al.*, 1992). Apparent inability of zebra mussels to regulate hemolymph ion and acid/base levels in waters of even moderate acidity and calcium concentration may be

associated with their restriction to waters of greater pH and hardness relative to most other freshwater bivalves (McMahon, 1991).

Zebra mussel veliger larvae have pH and calcium limits similar to those of adults. Successful rearing requires media  $\leq 12$  mg  $\text{Ca}^{2+}$ /liter. Rearing success is positively correlated with  $\text{Ca}^{2+}$  concentration, production of deformed larvae being minimized above 34 mg  $\text{Ca}^{2+}$ /liter (Sprung, 1987). A pH of 7.4–9.4 is required for successful veliger development, optimal rearing success and minimal larval deformation occurring at pH = 8.4 (Sprung, 1987). Further studies of pH and calcium concentration effects on *D. polymorpha* are required.

#### RESPONSES TO STARVATION

Zebra mussels are highly starvation tolerant. Among starving N.A. mussels, 50% mortalities ( $\text{LT}_{50}$ ) occurred after 118 days at 25°C and 352 days at 15°C, corresponding 100% mortalities ( $\text{SM}_{100}$ ) occurring at 143 and 545 days, respectively (Chase and McMahon, 1995). A 67% mortality occurred after 774 days starvation at 5°C (R. Chase, personal communication). Estimated for a 20 mm shell length (SL) standard individual, dry tissue mass loss at death was 74% at 25°C and 69% at 15°C (Chase and McMahon, 1995), similar to a 76% loss reported for European mussels on a submaintenance ration for 700 days at 4.5–5.5°C (Walz, 1978c). Similar levels of starvation tolerance and dry tissue mass loss have been reported for *C. fluminea* (Cleland *et al.*, 1986). Mussel dry tissue weight decreased linearly with time of starvation, loss rate increasing with increased temperature (Fig. 8). Based on tissue energy content, metabolic rates of starving mussels were 22%, 11% and 10% those of fed individuals at 25°C, 15° and 5°C, respectively (Chase and McMahon, 1995). In contrast,  $\dot{V}\text{O}_2$  was not reduced in European mussels during a much shorter, 31 day starvation period (Sprung and Borcharding, 1991). Metabolic depression during prolonged starvation, particularly at low temperatures ( $\leq 5^\circ\text{C}$ ), could allow mussels to overwinter without significant loss of reproductive energy stores (Chase and McMahon, 1995).

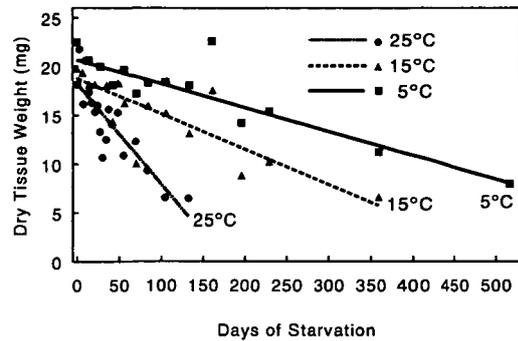


FIG. 8. Effect of prolonged starvation on dry tissue weight in the zebra mussel, *Dreissena polymorpha*. Horizontal axis is days of starvation. Solid squares are the estimated dry tissue weight of a 20 mm shell length standard sized mussel starved at 5°C. Triangles represent these same values in mussels starved at 15°C and squares, in mussels starved at 25°C. Lines represent best fits of Least Squares Linear Regressions relating dry tissue weight of a standard individual as the dependent variable to days of starvation at 5°C (dot-dashed line), 15°C (dashed line) and 25°C (solid line) (after Chase and McMahon, 1995).

Dry shell mass in a 20 mm SL standard specimen remained constant during prolonged starvation at 25°C, but declined at 5°C and increased at 15°C (Chase and McMahon, 1995). Shell mass increase at 15°C was likely due to nacre deposition without corresponding increase in shell length while decrease in shell mass at 5°C was likely due to dissolution of shell mineral components at greater rates than metabolic capacity for secretion (Chase and McMahon, 1995).

During the first 10 days of a 31 day starvation period, tissue mass reduction was greatest in the digestive diverticula of zebra mussels. Thereafter, gonadal degradation accounted for the majority of weight loss (Sprung and Borcharding, 1991). In starving mussels, tubules of the digestive diverticulum either condensed or degraded completely. Gonads of starving individuals may degenerate with gametes being reabsorbed. Gonad degeneration was more pronounced in post-reproductive individuals than in reproductive individuals (Bielefeld, 1991). Even after starvation for up to 21 days at 20°C, N.A. zebra mussels could still be induced to spawn by external serotonin application (Fong *et al.*, 1996). In nonstarved mussels, carbohydrates made up <11% and

lipids <18% of total dry tissue mass. Lipid stores were depleted during the first seven days of a 31 day starvation period, while carbohydrate content remained stable. Thus, the majority of maintenance energy during the latter stages of starvation was derived from protein catabolism (Sprung and Borcharding, 1991) which, in nonstarved individuals, makes up 62% of dry tissue mass (Walz, 1979).

Algal food concentrations required to prevent tissue loss (*i.e.*, maintenance rations) range from 0.1–0.3 mg C liter<sup>-1</sup> (*i.e.*, mg algal organic carbon/liter) in 1 yr old, and 0.1–0.7 mg C liter<sup>-1</sup> in 2 yr old mussels at 4°–18°C (Walz, 1978c). Maintenance rations increase with increasing temperature (Walz, 1978b) as metabolic demands increase (Fig. 3). Major reductions in tissue protein content ( $\approx 67\%$ ) occurred in mussels fed submaintenance rations for 700 days (Walz, 1978c). Above 20°C, elevated metabolic demands (Fig. 3) cause maintenance rations to exceed maximal assimilation rates, leading to loss of tissue and protein mass (Walz, 1978b). Inability to support maintenance demands above 20°C may, in part, cause the tissue mass reductions reported among zebra mussels during summer months (see section on Temperature Responses) and suggests that mussel maintenance above 20°C could cause rapid physiological deterioration.

*D. polymorpha* veliger larvae feed on algal particles 1–4  $\mu\text{m}$  in diameter and may starve when phytoplankton is dominated by larger or smaller algal species (Sprung, 1989). Starving veligers generally continue to swim, experiencing 100% mortality within 11–15 days at 12°–24°C (Sprung, 1989).

#### BIOENERGETICS

Studies of bioenergetics have only been published for European zebra mussel populations, although several N.A. studies were in progress at the writing of this article. Walz (1978a) showed that filtration rates remained constant in media with algal concentrations up to 2 mg C liter<sup>-1</sup> (*i.e.*, mg algal organic carbon/liter), but proportionately declined at higher concentrations such that consumption rate was constant over 2–

8.5 mg C liter<sup>-1</sup>. Pseudofeces were first produced at 0.2 mg C liter<sup>-1</sup>. Pseudofeces production rate increased with further increase in algal concentration such that it remained constant at 67% of filtered algal carbon above a ration of 2 mg C liter<sup>-1</sup>. Consumption rate for a 40 mg C mussel at 15°C peaked at 75  $\mu\text{g C hr}^{-1}$  ( $=1.9 \mu\text{g algal C mg}^{-1} \text{ hr}^{-1}$ ), decreasing at higher or lower algal concentrations. Assimilation efficiency [(assimilation rate/ingestion rate)(100)] was 40.7% in terms of algal organic carbon or 35.2% in terms of total algal organic mass. This value falls within that reported for other freshwater molluscs (Aldridge, 1983; Burky, 1983; McMahon, 1983b) and is bracketed by summer and fall assimilation efficiencies of 6–95% recorded for a Polish zebra mussel population (Stańczykowska, 1977).

Ration, temperature and body size effect zebra mussel tissue growth rates (Walz, 1978b). Maximum gross growth efficiencies [(tissue growth rate/consumption rate)(100)] of  $\approx 60\%$  occurred at moderate levels of consumption (algal carbon consumption = 1–2% of mussel tissue carbon mass/d) at 8–10°C. It declined at higher temperatures and greater ration levels. Assimilation efficiencies were essentially similar over a wide size range and across 8°C to 20°C (Table 2; Walz, 1978b). Smaller mussels allocated greater assimilation to growth, particularly at elevated temperatures. Larger individuals (*i.e.*, 20 or 40 mg total tissue C) had no or negative growth at 20°C as maintenance demands approached or surpassed assimilation rates (Table 2; Walz 1978b). The percentage of assimilated carbon allocated to tissue growth in smaller individuals (*i.e.*, 5 and 20 mg tissue C) at  $\leq 15^\circ\text{C}$  (range = 30.8–71.5%) was high compared to other freshwater bivalves (Burky, 1983; McMahon, 1991), accounting for the rapid growth of juvenile and subadult mussels below 20°C. In contrast, reduced carbon allocation to growth in larger mussels (>20–40 mg tissue C) may account for their low growth rates (Walz, 1978b and references therein). Lack of tissue growth in larger mussels above 20°C needs further confirmation because N.A. zebra mussels sustain substantial summer

growth in Lake Erie (Griffiths *et al.*, 1991) and the lower Mississippi River (T. H. Dietz, personal communication) where waters are >20°C throughout the summer. Thus, they appear to be accumulating new tissue mass at temperatures well above the upper 20°C threshold for maintenance of tissue growth in European mussels.

High growth rates and short life spans allow zebra mussels to rapidly reach high densities in favorable habitats (Claudi and Mackie, 1993). Capacity for population growth is measured by P/B ratios (*i.e.*, annual productivity rate/average standing crop biomass) equivalent to the fraction of population standing crop biomass produced annually by new tissue growth. The greater population productivity, the higher the P/B ratio (Russell-Hunter and Buckley, 1983). P/B ratios were not density dependent among zebra mussel populations in 21 Polish lakes (density range = 16–2,000 mussels m<sup>-2</sup>) (Stańczykowska, 1977). Population mean P/B ratio was 0.568 (SD = ±0.074, range = 0.42–0.71), a value lower than recorded for most freshwater sphaeriids (mean P/B = 5.07, range = 0.2–13.5) (Burky, 1983) and *C. fluminea* (P/B = 2.6–4.1) (Aldridge and McMahon, 1978), but greater than that of 0.2 determined for the long-lived unionid, *Anodonta anatina* (L.) (Negus, 1966). Low P/B values suggest that Polish populations were slow growing and unproductive as evidenced by their relatively low population densities. In contrast, N.A. zebra mussels are faster growing and reach greater densities (>100,000 m<sup>-2</sup>) (Claudi and Mackie, 1993 and references therein), suggesting that they are more productive than European populations. The bioenergetics of N.A. zebra mussels clearly require experimental attention.

Reproductive costs have not been extensively analyzed for *D. polymorpha*. Gamete release in males and females is associated with tissue mass reduction. Post-spawning females lose 30% of original body weight, associated with release of up to 10<sup>6</sup> eggs during a spawning event (Sprung, 1991). Presence of ripe oocytes did not increase Vo<sub>2</sub> relative to post-spawning individuals nor did spawning induce changes in protein catabolism, suggesting that maintenance en-

TABLE 2. Effects of temperature and tissue mass on parameters of individual carbon budgets for the zebra mussel, *Dreissena polymorpha*, in which parameters are expressed in terms of organic carbon and as a percentage of total tissue organic carbon (modified from the data of Walz, 1978b).

Ambient temperature °C	Tissue mass in mg carbon											
	5 mg C				20 mg C				40 mg C			
	8°	15°	20°	8°	15°	20°	8°	15°	20°	8°	15°	20°
Maximum consumption rate as mg carbon animal <sup>-1</sup> day <sup>-1</sup>	0.243	0.296	0.196	0.724	0.788	0.582	1.248	1.360	1.004	1.248	1.360	1.004
as a % of tissue carbon day <sup>-1</sup>	4.86%	5.29%	3.91%	3.62%	3.94%	2.91%	3.12%	3.40%	2.51%	3.12%	3.40%	2.51%
Assimilation efficiency (%)	40.1%	56.5%	69.8%	45.6%	50.8%	46.7%	48.7%	46.2%	44.6%	48.7%	46.2%	44.6%
Assimilation (growth + respiration) as mg carbon animal <sup>-1</sup> day <sup>-1</sup>	0.098	0.150	0.137	0.333	0.400	0.272	0.608	0.628	0.448	0.608	0.628	0.448
as a % of tissue carbon day <sup>-1</sup>	1.95%	2.99%	2.73%	1.65%	2.00%	1.36%	1.52%	1.57%	1.12%	1.52%	1.57%	1.12%
% assimilation respired	33.8%	43.1%	69.2%	28.5%	44.5%	97.8%	25.7%	49.0%	100%	25.7%	49.0%	100%
% assimilation allocated to growth	66.2%	56.9%	30.8%	71.5%	54.5%	2.2%	74.3%	51.0%	-30.4%	74.3%	51.0%	-30.4%
Maintenance ration as mg carbon animal <sup>-1</sup> day <sup>-1</sup>	0.022	0.035	0.043	0.064	0.136	0.440	0.120	0.340	1.640	0.120	0.340	1.640
as a % of tissue carbon day <sup>-1</sup>	0.44%	0.70%	0.85%	0.32%	0.68%	2.20%	0.30%	0.85%	4.10%	0.30%	0.85%	4.10%
as % of max. consumption rate	9.1%	13.2%	21.7%	8.8%	17.3%	75.6%	9.6%	25.0%	163.3%	9.6%	25.0%	163.3%

TABLE 3. Summary of the resistance adaptations of the zebra mussel, *Dreissena polymorpha*, and the quagga mussel, *D. bugensis*, to the major physico-chemical parameters likely to influence their capacity to colonize North American freshwaters based on research reports reviewed in the body of this paper.

Parameter	Species	Life cycle stage	Environmental tolerance limits	
			Parameter	Species
Temperature tolerance	<i>D. polymorpha</i>	Adult	Cannot survive above 30°C	
		Veliger larva	Fertilization, 10°–26°C; Development 12°–24°C	
	<i>D. bugensis</i>	Adult	Unknown, upper limit likely < <i>D. polymorpha</i>	
Respiratory response		Veliger larva	Unknown	
	<i>D. polymorpha</i>	Adult	O <sub>2</sub> uptake rate maximized at 30–35°C	
	<i>D. bugensis</i>	Veliger larva	Unknown, requires further study	
Anoxia/hypoxia tolerance		Adult	Unknown, requires further study	
	<i>D. polymorpha</i>	Veliger larva	Unknown, requires further study	
	<i>D. bugensis</i>	Veliger larva	Unknown, requires further study	
Salinity tolerance	<i>D. polymorpha</i>	Adult	PO <sub>2</sub> ≥ 32–40 torr at 25°C, poor O <sub>2</sub> regulator	
		Veliger larva	PO <sub>2</sub> ≥ 32 torr at 18–20°C	
	<i>D. bugensis</i>	Adult	Unknown, likely > tolerance than <i>D. polymorpha</i>	
Emersion tolerance		Veliger larva	Unknown, requires further study	
	<i>D. polymorpha</i>	Adult	Variable, <4–8%, may acclimatize to higher levels	
	<i>D. bugensis</i>	Veliger larva	<7% for spawning, <6% for development	
Freezing air temperature tolerance		Adult	<4%, requires further study	
	<i>D. polymorpha</i>	Veliger larva	<4%, requires further study	
	<i>D. bugensis</i>	Veliger larva	Unknown, likely to be highly intolerant	
Ph limits	<i>D. polymorpha</i>	Adult	Dependent on temp. and R.H., <8 days above 25°	
		Veliger larva	Unknown, likely to be highly intolerant	
	<i>D. bugensis</i>	Adult	Similar to <i>D. polymorpha</i> , reduced at high R.H.	
Calcium concentration limits		Veliger larva	Unknown, likely to be highly intolerant	
	<i>D. polymorpha</i>	Adult	Single mussels < -1.5°C, when clustered < -3.0°C	
	<i>D. bugensis</i>	Veliger larva	Unknown, likely to be highly intolerant	
Starvation tolerance		Veliger larva	Unknown, likely to be highly intolerant	
	<i>D. polymorpha</i>	Adult	Unknown, likely to be highly intolerant	
	<i>D. bugensis</i>	Veliger larva	Unknown, likely to be highly intolerant	
Starvation tolerance		Adult	≥6.5, >8 for maximal growth	
	<i>D. polymorpha</i>	Veliger larva	7.4–9.4 for successful development, optimum = 8.4	
	<i>D. bugensis</i>	Veliger larva	Unknown, requires study	
Starvation tolerance		Adult	Unknown, requires study	
	<i>D. polymorpha</i>	Veliger larva	lower limit = 15 mg/l, ≥25 mg/l for good growth	
	<i>D. bugensis</i>	Adult	lower limit = 12 mg/l, optimum ≥34 mg/l	
Starvation tolerance		Veliger larva	Unknown, requires study	
	<i>D. polymorpha</i>	Adult	Unknown, requires study	
	<i>D. bugensis</i>	Veliger larva	Unknown, requires study	
Starvation tolerance		Veliger larva	LT <sub>50</sub> = 118 d at 25°, 352 d at 15°, >500 d at 5°C	
	<i>D. polymorpha</i>	Adult	100% mortality in 11–15 days at 12°–24°C	
	<i>D. bugensis</i>	Veliger larva	Unknown, requires study	
		Veliger larva	Unknown, requires study	

TABLE 3. Continued.

Parameter	Species	Life cycle stage	Environmental tolerance limits
Turbidity tolerance	<i>D. polymorpha</i>	Adult	Upper limit unknown, > 160 NTU
	<i>D. bugensis</i>	Veliger larva	Unknown, requires study
Organic enrichment		Adult	Unknown, requires study
	<i>D. polymorpha</i>	Veliger larva	Unknown, requires study
	<i>D. polymorpha</i>	Adult	Density declines with $PO_4^{3-}$ and $NO_3^-$ enrichment
	<i>D. bugensis</i>	Veliger larva	Unknown, requires study
Food particle size limitations		Adult	Unknown, requires study
	<i>D. polymorpha</i>	Veliger larva	Unknown, requires study
	<i>D. polymorpha</i>	Adult	< 1 $\mu$ m up to planktonic rotifers and crustaceans
	<i>D. bugensis</i>	Veliger larva	Algae 1–4 $\mu$ m in diameter
		Adult	Unknown, requires study
		Veliger larva	Unknown, requires study

ergy demands are similar in zebra mussels regardless of reproductive state (Sprung, 1991). Instead, reduction in tissue mass during spawning is indicative of diversion of a large proportion of nonrespired assimilation away from tissue growth into gametogenesis. Reproductive costs require further assessment in N.A. and European mussels.

The short life-spans, early maturity, small gametes, high fecundities, and rapid growth rates of zebra mussels are life history characteristics associated with adaptation to unstable habitats where unpredictable environmental disturbance results in periodic massive population reductions (McMahon, 1991). These characteristics allow *D. polymorpha* to reach high densities rapidly after introduction to a favorable habitat or recolonization of an unstable habitat from which they were extirpated by environmental disturbance.

#### CONCLUSIONS

On the whole, there is general European and N.A. agreement on the resistance and capacity adaptations of *D. polymorpha* (summarized in Table 3). Temperatures of initial and maximal spawning, respiratory responses, seasonal respiratory variation, responses to anoxia/hypoxia, salinity limits, calcium concentration limits, pH limits, and responses to starvation are relatively similar among N.A. and European mussels, indicative of a single species. Discrepancies remain in European and N.A. data regarding temperature effects on growth rate and thermal tolerance limits. Maximal growth rates of northern European populations occur at much lower temperatures (10°–15°C, Walz, 1978b) than in Lake Erie (Griffiths *et al.*, 1991) or the lower Mississippi River (T. H. Dietz, personal communication). Chronic upper thermal tolerance limits determined for northern European mussels are 27–28°C while they are 30°–31°C among N.A. mussels (McMahon *et al.*, 1993, 1994). However, other European studies suggest the zebra mussel's thermal tolerance limits are similar to that of N.A. mussels (Tourari *et al.*, 1988). Differences are likely to result from either genetic variation and/or non-genetic, ecophenotypic differences induced

by differences in populations' thermal regimes.

Evidence exists for both hypotheses. North American zebra mussels probably originated from the northern shore of the Black Sea, the warmest region of this species' European range. Thus, they may have evolved greater thermal tolerance than mussels from the colder northern waters on which European physiological studies of mussels have almost exclusively centered. Conversely, the thermal tolerance limits of N.A. mussels appear to be positively correlated with ambient water temperature even after laboratory temperature acclimation. This result suggests that differences in thermal tolerance and temperature/growth responses in N.A. and northern European mussels may result from ecophenotypic seasonal acclimatization of N.A. mussels to higher average ambient water temperatures. Elucidation of the bases for variation in the thermal responses of N.A. and European mussels will require rigidly controlled, comparative isozyme and/or DNA analyses of interpopulation genetic variation. Divergence of the population genetics of northern European and Black Sea region mussels and genetic similarity between Black Sea region and N.A. mussels would strongly support a genetic basis for thermal response differences in northern European and N.A. mussels. In contrast, lack of genetic divergence would support nongenetic, seasonal temperature acclimatization as of the basis for these differences.

Comparative studies of European and N.A. zebra mussel thermal responses should be carried out with the same experimental protocols or within the same laboratories, assuring that differences do not result from varying methodologies. Responses could also be studied in mussels reciprocally transferred between European and N.A. populations for long enough to allow acclimatization to local conditions. Thus, intercontinental, collaborative, studies should be of high priority in future zebra mussel physiological research. Other areas of potentially valuable physiological research include: effects of seasonal acclimatization and geographic distribution on physiological variables; salinity tolerance

of European and N.A. mussels; effects of pH and calcium concentration; respiratory and protein/nonprotein catabolic responses to season and long-term starvation; and bioenergetic analyses of fast growing, highly productive N.A. populations, particularly with regard to reproductive costs and temperatures of optimal energetic efficiency relative to European populations (Walz, 1978a, b, c). Physiological studies at all levels are required for *D. bugensis*, for which little data presently exist (Table 3). This species may be replacing *D. polymorpha* in some N.A. habitats (e.g., Lake Ontario and the St. Lawrence River). Knowledge of its physiological responses is needed to predict its eventual N.A. distribution.

This review indicates that *D. polymorpha* is relatively less tolerant of environmental stress (Table 3) and a poorer hyperosmotic regulator compared to native N.A. sphaeriid and unionid bivalves (Dietz *et al.*, 1996). In this regard, it is similar to the nonindigenous, freshwater Asian clam, *Corbicula fluminea* (McMahon, 1991). *Dreissena* and *Corbicula* are both heterodont bivalves relatively recently evolved from marine ancestors, *Dreissena*, inhabiting freshwater since the late Miocene ( $\sim 13 \cdot 10^6$  yr, Nuttall, 1990) and *Corbicula*, since the late Cretaceous ( $\sim 70 \cdot 10^6$  yr, Keen and Casey, 1969). In contrast, the super family, Unionacea, has occupied freshwater since the Triassic ( $\sim 245 \cdot 10^6$  yr, Haas, 1969) and the family, Sphaeriidae, since the upper Jurassic ( $\sim 150 \cdot 10^6$  yr, Dance, 1969). With much longer freshwater histories, unionaceans and sphaeriids appear to have become better adapted to the stresses of freshwater life than either *Corbicula* or *Dreissena*. McMahon (1991) has argued that unionaceans and sphaeriids display life history characteristics adapting them for life in stable, predictable habitats including: long life spans, extensive iteroparity, low effective fecundities, large offspring, delayed maturity, and reduced growth rates. These traits prevent both groups from rapid habitat recolonization after extirpation by environmental disturbance; thus, they have evolved extensive resistance adaptations that allow survival of environmental extremes.

Dreissenids and corbiculaceans, as rela-

tively recent colonizers of freshwaters, retain some of the primitive characteristics of their marine ancestors including planktonic larvae, and reduced resistance to environmental stress. Poor stress tolerance makes them less competitive than sphaeriids and unionaceans in stable habitats (exception is zebra mussel colonization of unionacean shells). Instead, they have become specialized for life in unstable habitats, their planktonic larvae, elevated fecundity, fast growth, early maturity, and attenuated life-spans allowing rapid reinvasion and recolonization of unstable habitats after extirpation by unpredictable environmental disturbance. In unstable habitats, selection pressures for resistance or capacity adaptations are reduced, as they will not prevent extirpation by periodic massive disturbance. Adaptation to unstable habitats and lack of natural biotic checks have allowed *D. polymorpha* and *C. fluminea* to be extremely successful invaders of N.A. freshwaters. They have also made them of the most economically damaging aquatic species ever introduced to North American freshwaters (McMahon, 1983a, 1991; Claudi and Mackie, 1993).

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## REFERENCES

- Afanas'yev, S. A. and A. A. Protasov. 1987. Characteristics of a *Dreissena* population in the periphyton of a nuclear power plant cooling pond. *Hydrobiol. J.* 23:42-49.
- Aladin, N. V. and W. T. W. Potts. 1992. Changes in the Aral Sea ecosystems during the period 1960-1990. *Hydrobiologia* 237:67-79.
- Aldridge, D. W. 1983. Physiological ecology of freshwater prosobranchs. In W. D. Russell-Hunter (ed.), *The Mollusca*, Vol 6, *Ecology*, pp. 330-358. Academic Press, Inc., Orlando, Florida.
- Aldridge, D. W. and R. F. McMahon. 1978. Growth, fecundity, and bioenergetics in a natural population of the Asiatic freshwater clam, *Corbicula manilensis* Philippi, from north central Texas. *J. Moll. Stud.* 44:49-70.
- Alexander, J. E., Jr., J. H. Thorp, and R. D. Fell. 1994. Turbidity and temperature effects on oxygen consumption in the zebra mussel (*Dreissena polymorpha*). *Can. J. Fish. Aquat. Sci.* 51:179-184.
- Alimov, A. F. 1975. The rate of metabolism in freshwater bivalve molluscs. *Soviet J. Ecol.* 5:6-13.
- Alyakrinskaya, I. O. 1978. Biochemical adaptations to drying conditions in bivalves in the Kruski Zaliv Baltic Sea USSR. *Zool. Zh.* 57:136-138.
- Bayne, B. L. 1973. Physiological changes in *Mytilus edulis* L. induced by temperature and nutritive stress. *J. Mar. Biol. Ass. U.K.* 53:39-58.
- Bielefeld, U. 1991. Histological observation of gonads and digestive gland in starving *Dreissena polymorpha* (Bivalvia). *Malacologia* 33:31-42.
- Birger, T. I., A. Ya. Malarevskaja, O. M. Arsan, V. D. Solomatina, and Yu. M. Gupalo. 1978. Physiological aspects of adaptations of mollusks to abiotic and biotic factors due to blue-green algae. *Malacol. Rev.* 11:100-102.
- Borcherding, J. 1991. The annual reproductive cycle of the freshwater mussel *Dreissena polymorpha* Pallas in lakes. *Oecologia* 87:208-218.
- Burky, A. J. 1983. Physiological ecology of freshwater bivalves. In W. D. Russell-Hunter (ed.), *The Mollusca*, Vol. 6, *Ecology*, pp. 281-327. Academic Press, Inc., Orlando, Florida.
- Byrne, R. A. and R. F. McMahon. 1994. Behavioral and physiological responses to emersion in freshwater bivalves. *Amer. Zool.* 34:194-204.
- Chase, R. and R. F. McMahon. 1995. Starvation tolerance of zebra mussels, *Dreissena polymorpha*. In *Proceedings of the fifth international zebra mussel and other aquatic nuisance species conference 1995*, pp. 31-38. Ontario Hydro, Toronto, Ontario.
- Clarke, M. 1993. Freeze sensitivity of the zebra mussel (*Dreissena polymorpha*) with reference to dewatering during freezing conditions as a mitigation strategy. Masters Thesis, The University of Texas at Arlington, Arlington, Texas.
- Clarke, M., R. F. McMahon, A. C. Miller, and B. S. Payne. 1993. Tissue freezing points and time for complete mortality on exposure to freezing air temperatures in the zebra mussel (*Dreissena polymorpha*) with special reference to dewatering during freezing conditions as a mitigation strategy. In J. L. Tsou and Y. G. Mussalli (eds.), *Proceedings, third international zebra mussel conference, 1993*, pp. 4-120-4-145. EPRI TR-102077, Electric Power Research Institute, Palo Alto, California.
- Claudi, R. and G. L. Mackie. 1993. *Practical manual for zebra mussel monitoring and control*. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Cleland, J. D., R. F. McMahon, and G. Elick. 1986. Physiological differences between two morphotypes of the Asian clam, *Corbicula*. *Amer. Zool.* 26:103A.
- Dance, P. 1969. Family Pisidiidae Gray, 1857. In R. C. Moore (ed.), *Treatise on invertebrate paleon-*

- ology, Part N, Vol. 2, pp. N669–N670. Geological Society of America, Inc., Boulder, Colorado.
- Dietz, T. H., S. J. Wilcox, R. A. Byrne, J. W. Lynn, and H. Silverman. 1996. Osmotic and ionic regulation of North American zebra mussels. *Amer. Zool.* 36:364–372.
- Dimock, R. V., Jr. and A. H. Wright. 1993. Sensitivity of juvenile freshwater mussels to hypoxic, thermal and acid stress. *J. Elisha Mitchell Sci. Soc.* 109: 183–192.
- Dorgelo, J. and J-W. Smeenk. 1988. Contribution to the ecophysiology of *Dreissena polymorpha*: Growth, filtration rate and respiration. *Verh. Internat. Verein. Limnol.* 23:2202–2208.
- Electric Power Research Institute. 1992. *Zebra mussel monitoring and control guide*. EPRI 101782, Electric Power Research Institute, Palo Alto, California.
- Fetisov, A. N., A. V. Rubanovich, T. S. Slipchenko, and V. A. Shevchenko. 1991. Effect of the temperature factor on the genetic structure of populations of *Dreissena polymorpha* (Bivalvia). *Soviet Genetics* 26:1159–1162.
- Fong, P. P., K. Kyoizuka, J. Duncan, S. Rynkowski, D. Mekasha, and J. L. Ram. 1996. The effect of salinity and temperature on spawning and fertilization in the zebra mussel, *Dreissena polymorpha* (Pallas) from North America. *Biol. Bull* (Woods Hole, Mass.) 189:320–329.
- Frleigh, P. C., P. L. Klerks, G. Gubanich, G. Matisoff, and R. C. Stevenson. 1992. Abundance and settling of zebra mussel (*Dreissena polymorpha*) veligers in western and central Lake Erie. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 129–142. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Fuller, S. H. L. 1974. Clams and mussels (Mollusca: Bivalvia). In C. W. Hart, Jr. and S. L. H. Fuller (eds.), *Pollution ecology of freshwater invertebrates*, pp. 215–273. Academic Press, Inc., Florida.
- Gainey, L. F., Jr. and M. J. Greenberg. 1977. Physiological basis of the species abundance-salinity relationship in molluscs: A speculation. *Mar. Biol.* (Berlin) 40:41–49.
- Garton, D. W. and W. R. Haag. 1991. Heterozygosity, shell length, and metabolism in the European mussel, *Dreissena polymorpha*, from a recently established population in Lake Erie. *Comp. Biochem. Physiol.* 99A:45–48.
- Garton, D. W. and W. R. Haag. 1992. Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in western Lake Erie. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: biology, impacts, and control*, pp. 111–128. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Gillis, P. L. and G. L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. *Can. J. Zool.* 72:1260–1271.
- Green, J. 1968. *The biology of estuarine animals*. University of Washington, Seattle, Washington.
- Griffiths, R. W., D. W. Schloesser, J. H. Leach, and W. P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 48: 1381–1388.
- Haag, W. R., D. J. Berg, D. W. Garton and J. L. Farris. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. *Can. J. Fish. Aquat. Sci.* 50:13–19.
- Haas, F. 1969. Superfamily Unionacea Fleming, 1828. In R. C. Moore (ed.), *Treatise on invertebrate paleontology*, Part N, Vol. 1, pp. N411–N467. Geological Society of America, Inc., Boulder, Colorado.
- Hebert, P. D. N., B. W. Muncaster, and G. L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): A new mollusc in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 46:1587–1591.
- Hebert, P. D. N., C. C. Wilson, M. H. Murdoch, and R. Lazar. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. *Can. J. Zool.* 69:405–409.
- Hernandez, M. R. 1995. Thermal response and tolerance in the introduced freshwater bivalve, *Dreissena polymorpha* (zebra mussel). Masters Thesis, The University of Texas at Arlington, Arlington, Texas.
- Hernandez, M. R., R. F. McMahon, and T. H. Dietz. 1995. Investigation of geographic variation in the thermal tolerance of zebra mussels, *Dreissena polymorpha*. In *Proceedings of the fifth zebra mussel and other aquatic nuisance organisms conference 1995*, pp. 195–209. Ontario Hydro, Toronto, Ontario.
- Hornbach, D. J. 1985. A review of metabolism in the Pisiidiidae with new data on its relation to life history traits in *Pisidium casertanum*. *Am. Malacol. Bull.* 3:187–200.
- Iwanzyki, S. and R. W. McCauley. 1992. Upper lethal temperatures of adult zebra mussels (*Dreissena polymorpha*). In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 667–673. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Jenner, H. A. and J. P. M. Janssen-Mommen. 1992. Monitoring and control of *Dreissena polymorpha* and other macrofouling bivalves in the Netherlands. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 537–554. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Keen, M. and R. Casey. 1969. Superfamily Corbiculacea Gray, 1847. In R. C. Moore (ed.), *Treatise on invertebrate paleontology*, Part N. Vol. 2, pp. N664–N669. Geological Society of America, Inc., Boulder, Colorado.
- Kennedy, V., S. McIninch, D. Wright, and E. Setzler-Hamilton. 1995. Salinity and zebra and quagga mussels. Abstract of a paper presented at *The fifth international zebra mussel and other aquatic nuisance organisms conference 1995*, p. 66. Held 21–24 February, 1995, Toronto, Ontario.

- Kilgour, B. and R. Kepple. 1993. Effects of salinity on the survival of zebra mussel veliger larvae. Abstract of a paper presented at the *Third International Zebra Mussel Conference '93*. Held 23–26 February, 1993, Toronto, Ontario.
- Kirpichenko, M. Ya. 1964. Phenology, population dynamics, and growth of *Dreissena* larvae in the Northern Dvina River. In B. K. Shtegman (ed.), *Biology and control of Dreissena*, pp. 15–24. Academy of Sciences of the U.S.S.R., Institute of Biology of Inland Waters, Moscow, Russia.
- Kornobis, S. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Dreissenidae, Bivalvia) in lakes receiving heated water discharges. *Pol. Arch. Hydrobiol.* 24: 531–545.
- Lewandowski, K. 1982. The role of early developmental stages, in the dynamics of *Dreissena polymorpha* (Pall.) (Bivalvia) populations in lakes. II. Settling of larvae and the dynamics of numbers of settled individuals. *Ekol. Pol.* 30:223–286.
- Lyashenko, A. V. and T. A. Karchenko. 1989. Annual dynamics of energy metabolism in *Dreissena*. *Hydrobiol. J.* 25:34–41.
- MacIsaac, H. J., W. G. Sprules, and J. H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): Can cannibalism on larvae influence population dynamics? *Can. J. Fish. Aquat. Sci.* 48:2051–2060.
- MacIsaac, H. J., W. G. Sprules, O. E. Johannsson, and J. H. Leach. 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Oecologia* 92:30–39.
- Mackie, G. L. 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia* 219:251–268.
- Mackie, G. L., W. N. Gibbons, B. W. Muncaster, and I. M. Gray. 1989. *The zebra mussel, Dreissena polymorpha: A synthesis of European experiences and a preview for North America*. Ontario Ministry of the Environment, Water Resources Branch, Queen's Printer for Ontario, Toronto, Ontario.
- Mangum, C. P. and W. Van Winkle. 1973. Responses of aquatic invertebrates to declining oxygen conditions. *Amer. Zool.* 13:529–541.
- Marsden, J. E., A. P. Spidle, and B. May. 1996. Review of genetic studies of *Dreissena* sp. *Amer. Zool.* 36:259–270.
- Matthews, M. A. and R. F. McMahon. 1994. The survival of zebra mussels (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) under extreme hypoxia. In *Proceedings: Fourth international zebra mussel conference '94*, pp. 231–249. Wisconsin Sea Grant Institute, Madison, Wisconsin.
- McDermott, R. M. 1993. Distribution and ecological impact of quagga mussels in the lower Great Lakes. In J. L. Tsou and Y. G. Mussalli (eds.), *Proceedings, third international zebra mussel conference, 1993*, pp. 2-1–2-21. EPRI TR-102077, Electric Power Research Institute, Palo Alto, California.
- McMahon, R. F. 1979. Response to temperature and hypoxia in the oxygen consumption of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Müller). *Comp. Biochem. Physiol.* 63A:383–388.
- McMahon, R. F. 1983a. Ecology of an invasive pest bivalve: *Corbicula*. In W. D. Russell-Hunter (ed.), *The Mollusca*, Vol. 6, *Ecology*, pp. 505–561. Academic Press, Inc., Orlando, Florida.
- McMahon, R. F. 1983b. Physiological ecology of freshwater pulmonates. In W. D. Russell-Hunter (ed.), *The Mollusca*, Vol. 6, *Ecology*, pp. 359–430. Academic Press, Inc., Orlando, Florida.
- McMahon, R. F. 1990. *The zebra mussel—U.S. utility implications*. EPRI GS-6995, Electric Power Research Institute, Palo Alto, California.
- McMahon, R. F. 1991. Mollusca: Bivalvia. In J. H. Thorp and A. P. Covich (ed.), *Ecology and classification of North American freshwater invertebrates*. Academic Press, Inc., Orlando, Florida.
- McMahon, R. F. 1992. The zebra mussel—the biological basis for its macrofouling and potential for distribution in North America. In *Corrosion '92: Proceedings of the 47th NACE Annual Conference*, reprint no. 342, pp. 342-1–342-14. National Association of Corrosion Engineers, Houston, Texas.
- McMahon, R. F., T. A. Ussery, and M. Clarke. 1993. *Use of emersion as a zebra mussel control method*. Technical report No. EL-93-1, U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi.
- McMahon, R. F., T. A. Ussery, A. C. Miller, and B. S. Payne. 1993. Thermal tolerance in zebra mussels (*Dreissena polymorpha*) relative to rate of temperature increase and acclimation temperature. In J. L. Tsou and Y. G. Mussalli (eds.), *Proceedings, third international zebra mussel conference, 1993*, pp. 4-97–4-118. EPRI TR-102077, Electric Power Research Institute, Palo Alto, California.
- McMahon, R. F., M. A. Matthews, T. H. Ussery, R. Chase, and M. Clarke. 1994. Further studies of heat tolerance in zebra mussels: Effects of temperature acclimation and chronic exposure to lethal temperatures. In *Proceedings: Fourth international zebra mussel conference '94*, pp. 251–272. Wisconsin Sea Grant Institute, Madison, Wisconsin.
- Mellina, E. and J. B. Rasmussen. 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physicochemical factors. *Can. J. Fish. Aquat. Sci.* 51:1024–1036.
- Mikheev, V. P. 1964. Mortality rate of *Dreissena* in anaerobic conditions. In B. K. Shtegman (ed.), *Biology and control of Dreissena*, pp. 65–68. Academy of Sciences of the U.S.S.R., Institute of Biology of Inland Waters, Moscow, Russia.
- Miller, A. C., B. S. Payne, F. Neilsen, and R. F. McMahon. 1992. *Zebra mussel: Control strategies for zebra mussel infestations at public facilities*. Technical report EL-92-95, U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi.
- Morton, B. S. 1969. Studies on the biology of *Dreis-*

- senae polymorpha* Pall. III. Population dynamics. Proc. Malacol. Soc. Lond. 38:471-482.
- Nalepa, T. F., B. A. Manny, J. C. Roth, S. C. Mozley, and D. W. Schloesser. 1991. Long-term decline in freshwater mussels (Bivalvia: Unionidae) of the western basin of Lake Erie. J. Great Lakes Res. 17:214-219.
- Nalepa, T. F., J. F. Cavaletto, M. Ford, W. M. Gordon, and M. Wimmer. 1993. Seasonal and annual variation in weight and biochemical content of the zebra mussel, *Dreissena polymorpha*, in Lake St. Clair. J. Great Lakes Res. 19:541-552.
- Neumann, D., J. Borcharding, and B. Jantz. 1992. Growth and seasonal reproduction of *Dreissena polymorpha* in the Rhine River and adjacent waters. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 95-109. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Nichols, S. J. 1996. Variations in of the reproductive cycle of *Dreissena polymorpha* in Europe, Russia and North America. Amer. Zool. 36:311-325.
- Nuttall, C. P. 1990. Review of the Caenozoic heterodont bivalve superfamily Dreissenacea. Paleontology, 33:707-737.
- Piesik, Z. 1983. Biology of *Dreissena polymorpha* (Pall.) settling on stylon nets and the role of this mollusc in eliminating the seston and the nutrients from the water course. Pol. Arch. Hydrobiol. 30: 353-361.
- Quigley, M. A., W. S. Gardener, and W. M. Gordon. 1992. Metabolism of the zebra mussel (*Dreissena polymorpha*) in Lake St. Clair of the Great Lakes. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 295-306. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Ramcharan, C. W., D. K. Padilla, and S. I. Dodson. 1992. Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. 49:2611-2620.
- Reeders, H. H. and A. Bij de Vaate. 1990. Zebra mussels (*Dreissena polymorpha*): A new perspective for water quality management. Hydrobiologia 200/201:437-450.
- Remane, A. and C. Schlieper. 1971. *Biology of brackish water*. Wiley (Interscience), New York.
- Ricciardi, A., R. Serrouya, and F. G. Whoriskey. 1995. Aerial exposure tolerance of zebra and quagga mussels (Bivalvia: Dreissenidae): Implications for overland dispersal. Can. J. Fish. Aquat. Sci. 52: 470-477.
- Riessen, H. P., T. A. Ferro, and R. A. Kamman. 1992. Distribution of zebra mussel (*Dreissena polymorpha*) veligers in eastern Lake Erie during the first year of colonization. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 143-152. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Russell-Hunter, W. D. and D. E. Buckley. 1983. Actuarial bioenergetics of nonmarine molluscan productivity. In W. D. Russell-Hunter (ed.), *The Mollusca*, Vol. 6, Ecology, pp. 463-503. Academic Press, Inc., Orlando, Florida.
- Scheide, J. L. and P. N. Bonaminio. 1994. Effect of low water temperature on ion balance in the zebra mussel, *Dreissena polymorpha*, and the unionid mussel, *Lampsilis radiata*. Nautilus 107:113-117.
- Schloesser, D. W., T. F. Nalepa, and G. L. Mackie. 1996. Zebra mussel infestation of unionid bivalves (Unionidae) in North America. Amer. Zool. 36:300-310.
- Smirnova, N. F., G. I. Biochino, and G. A. Vinogradov. 1992. Some aspects of the zebra mussel (*Dreissena polymorpha*) in the former European USSR with morphological comparisons to Lake Erie. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 217-226. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Smit, H., A. Bij de Vaate, H. H. Reeders, E. H. Van Nes, and R. Noordhuis. 1992. Colonization ecology, and positive aspects of zebra mussels (*Dreissena polymorpha*) in the Netherlands. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 55-77. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Spidle, A. P., J. E. Marsden, and B. May. 1994. Identification of the Great Lakes quagga mussel as *Dreissena bugensis* from the Dnieper River, Ukraine, on the basis of allozyme variation. Can. J. Fish. Aquat. Sci. 51:1485-1489.
- Sprung, M. 1987. Ecological requirements for developing *Dreissena polymorpha* eggs. Arch. Hydrobiol. Suppl. 79:69-86.
- Sprung, M. 1989. Field and laboratory observations of *Dreissena polymorpha* larvae: Abundance, growth, mortality, and food demands. Arch. Hydrobiol. 115:537-561.
- Sprung, M. 1991. Costs of reproduction: A study on metabolic requirements of the gonads and fecundity of the bivalve *Dreissena polymorpha*. Malacologia 33:63-70.
- Sprung, M. 1992. The other life: An account of present knowledge of the larval phase of *Dreissena polymorpha*. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 39-53. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Sprung, M. and J. Borcharding. 1991. Physiological and morphometric changes in *Dreissena polymorpha* (Mollusca; Bivalvia) during a starvation period. Malacologia 33:179-191.
- Stańczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pall.) in lakes. Pol. Arch. Hydrobiol. 24: 461-530.
- Stańczykowska, A. 1984. The effect of various phosphorus loadings on the occurrence of *Dreissena polymorpha* (Pall.). Limnologica (Berlin): 15: 535-539.
- Strayer, D. L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. Can. J. Fish. Aquat. Sci. 48:1389-1395.
- Strayer, D. L. and L. C. Smith. 1992. Distribution of the zebra mussel (*Dreissena polymorpha*) in estuaries and brackish waters. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology,*

- impacts, and control*, pp. 715–727. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Testard, P. 1990. Elements d'écologie du lamellibranche invasif *Dreissena polymorpha* Pallas. Doctoral dissertation, Université Pierre et Marie Curie, Paris, France.
- Tourari, A. L., C. Crochard, and J. C. Pihan. 1988. Action de la température sur le cycle de reproduction de *Dreissena polymorpha* (Pallas) étude "in situ" et au laboratoire. *Haliotis* 18:85–98.
- United States National Biological Service. 1995. Zebra mussel distribution update. Newsletter, United States National Biological Service, Southeastern Biological Science Center, Gainesville, Florida.
- Ussery, T. A. and R. F. McMahon. 1994. Comparative study of the desiccation resistance of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*). In *Proceedings: Fourth international zebra mussel conference '94*, pp. 351–369. Wisconsin Sea Grant Institute, Madison, Wisconsin.
- Vinogradov, G. A., N. F. Smirnova, V. A. Sokova, and A. A. Bruznitsky. 1992. Influence of chemical composition of the water on the mollusk *Dreissena polymorpha*. In T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 283–293. Lewis Publishers, CRC Press, Boca Raton, Florida.
- Walz, N. 1978a. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. I. Pattern of activity, feeding and assimilation efficiency. *Arch. Hydrobiol.* 55:83–105.
- Walz, N. 1978b. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. III. Growth under standard conditions. *Arch. Hydrobiol.* 55:121–141.
- Walz, N. 1978c. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. IV. Growth in Lake Constance. *Arch. Hydrobiol. Suppl.* 55:142–156.
- Walz, N. 1979. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. V. Seasonal and nutritional changes in biochemical composition. *Arch. Hydrobiol.* 55:235–254.
- Williams, R. J. 1969. Freezing tolerance in *Mytilus edulis*. *Comp. Biochem. Physiol.* 35:145–161.
- Wolff, W. J. 1969. The mollusca of the estuarine region of the Rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. II. The Dreissenidae. *Basteria* 33:93–103.
- Wright, D. A., E. M. Setzler-Hamilton, J. A. Magee, and V. S. Kennedy. 1995. Development of *Dreissena polymorpha* and *D. bugensis* larvae in salt water. Abstract of a paper presented at *The fifth international zebra mussel and other aquatic nuisance organisms conference 1995*, p. 67. Held 21–24 February, 1995, Toronto, Ontario.
- Zebra Mussel Information Clearinghouse. 1995. North American range of the zebra mussel as of 1 September 1995. *Dreissena!* 6(3):6–7.