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Comparative Biology of Zebra Mussels in Europe and North America: An Overview¹

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SYNOPSIS. Since the discovery of the zebra mussel, *Dreissena polymorpha*, in the Great Lakes in 1988 comparisons have been made with mussel populations in Europe and the former Soviet Union. These comparisons include: Population dynamics, growth and mortality rates, ecological tolerances and requirements, dispersal rates and patterns, and ecological impacts. North American studies, mostly on the zebra mussel and a few on a second introduced species, the quagga mussel, *Dreissena bugensis*, have revealed some similarities and some differences. To date it appears that North American populations of zebra mussels are similar to European populations in their basic biological characteristics, population growth and mortality rates, and dispersal mechanisms and rates. Relative to European populations differences have been demonstrated for: (1) individual growth rates; (2) life spans; (3) calcium and pH tolerances and requirements; (4) potential distribution limits; and (5) population densities of veligers and adults. In addition, studies on the occurrence of the two dreissenid species in the Great Lakes are showing differences in their modes of life, depth distributions, and growth rates. As both species spread throughout North America, comparisons between species and waterbodies will enhance our ability to more effectively control these troublesome species.

INTRODUCTION

The zebra mussel was first discovered in the Great Lakes in 1988 and is believed to have been introduced in 1985/86 (Hebert *et al.*, 1989; Griffiths *et al.*, 1991). Mackie *et al.* (1989) reviewed the European literature on the biology, impact, and control of the zebra mussel to try to predict the consequences of its introduction into North American waters. Since that review, numerous studies have been performed on several North American populations. The

objectives of this paper are to review the results of existing biological research on zebra mussels in North America and to compare them to the European experiences. This paper examines recent advances in the classification, taxonomy, general anatomy and morphology, mode of life and habitat, physiology, biochemistry, genetics, dispersal mechanisms, geographic and habitat distribution, predators, parasites, productivity, life history, age and growth, and feeding. Recent research on a second dreissenid, *Dreissena bugensis*, discovered in the Great Lakes in 1989 (Dermott, 1993), has shown differences in many biological traits compared to the zebra mussel. Many of the research findings for both species have resulted in modifications of predictions on dispersal rates, potential distribution range,

¹ From the Symposium *Biology, Ecology and Physiology of Zebra Mussels* presented at the Annual Meeting of the American Society of Zoologists, 4–8 January 1995, at St. Louis, Missouri.

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and the types of habitats that the species will invade. This review adds the experience of the North American invasion to the European literature review by Mackie *et al.* (1989). Early invasion characteristics in North America are described in Nalepa and Schloesser (1993). To avoid excessive citations, information from these two sources have been used liberally without specific citations.

CLASSIFICATION

As many as seven systems of classification have been described for the Mollusca (Mackie *et al.*, 1989), the most recent by Nuttall (1990). Nuttall's (1990) classification is used because it conforms to that commonly used for North American Bivalvia (*e.g.*, Turgeon, 1988).

Recent research by May and Marsden (1992) on the genetics of zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis* (Rosenberg and Ludyanskiy, 1994)) show that we have two species. Readers are encouraged to refer to Rosenberg and Ludyanskiy (1994) in their exhaustive review of the *Dreissena* species, and to Spidle *et al.* (1994) and Marsden (1996) for convincing evidence that *bugensis* is a distinct species. The classification of the two *Dreissena* species in North America can be summarized as follows: CLASS BIVALVIA Linnaeus, 1758; Subclass HETERODONTA Neumayr, 1884; Order VENEROIDA H. & A. Adams, 1856; Suborder DREISSENACEA Gray, 1840; Superfamily DREISSENIOIDEA Gray, 1840; Family DREISSENIDAE Gray, 1840; Genus *Dreissena* van Beneden, 1835; Subgenus *Dreissena* s.l. van Beneden, 1835; *D. polymorpha* (Pallas, 1771); Subgenus *Pontodreissena* Logvinenko and Starobogatov, 1966; *D. (P.) bugensis* (Andrusov, 1897).

TAXONOMY

The taxonomy of *Dreissena* has received considerable attention since the discovery of two species in the Great Lakes. Taxonomic keys and descriptions of European species are numerous (Mackie *et al.*, 1989). Although the shells of all three species of North American Dreissenidae

lack a nacre and instead are composed of aragonite with crossed-lamellar, complex crossed-lamellar and pallial myostracal structures, there are distinct differences in the internal and external shell morphologies (Pathy and Mackie, 1993). The dreissenid species can be differentiated on the basis of easily observable shell traits, as indicated below and in Table 1:

- | | |
|---|------------------------------|
| 1(a) When viewed in cross-section, the ventral margin is convex with a rounded ventrolateral shoulder (Fig. 1a) | 2 |
| 1(b) When viewed in cross-section, the ventral margin is flattened, arched or concave, ventrolateral shoulder is acute (Fig. 1b); freshwater, usually lives attached to solid substrates or in clumps (druses) in mud | <i>Dreissena polymorpha</i> |
| 2(a) Internally, myophore plate is broad and well developed and lacks an apophysis (Fig. 1c); freshwater, lives attached to solid substrates, in clumps or as individuals in mud | <i>Dreissena bugensis</i> |
| 2(b) Internally, myophore plate is narrow and well developed and has an apophysis (Fig. 1c); brackish water | <i>Mytilopsis leucophaea</i> |

Kinzelbach (1992) reviews the phylogeny and speciation of *Dreissena* in Europe but readers should consult Spidle *et al.* (1994) and Marsden (1996) for the phylogenetic relationships between North American and European *Dreissena* on the basis of allozyme characteristics.

ANATOMY AND MORPHOLOGY

Mackie *et al.* (1989) provide references that give details on different organ systems. Additional general descriptions have been provided recently by Morton (1993) and Claudi and Mackie (1994), but the most significant advancement in our knowledge of anatomy and morphology has been on byssus structure. Ekrodt *et al.* (1993), using scanning electron microscopy, have provided new information on byssal structure and the byssal secreting process. They described two types of threads produced by the mussels; temporary and permanent at-

TABLE 1. Summary of diagnostic shell features of North American dreissenids.*

| Shell features | <i>Dreissena polymorpha</i> | <i>Dreissena bugensis</i> | <i>Mytilopsis leucophaeata</i> |
|--|--|---|---|
| Exterior | | | |
| Shape, colour | Mytiliform, striped, all black or white | Mytiliform, striped, light colored, white in deep water | Mytiliform, some stripes, all black or dark |
| Ventral margin | Arched, flattened, acute ventro-lateral shoulder | Convex, rounded ventro-lateral shoulder | Convex, rounded ventro-lateral shoulder |
| Dorsal margin | Rounded | Rounded, often wing-like | Flattened |
| Umbone | Pointed | Pointed | Rounded |
| Posterior margin | Angled ventro-posteriorly | Rounded ventro-posteriorly | Rounded ventro-posteriorly |
| Interior | | | |
| Myophore plate | Broad and well developed | Broad and well developed | Narrow and well developed |
| Apophysis | Absent | Absent | Present |
| Position of AAMS ^a and ABRMS ^b | Both on myophore plate | Both on myophore plate | AAMS on myophore, ABRMS on apophysis |
| Pallial line | Entire, rounded | Entire, rounded | Indented posteriorly as pallial sinus |

* Modified from Pathy and Mackie, 1993.

^a Anterior adductor muscle scar.^b Anterior byssal retractor muscle scar.

tachment threads. The types are differentiated by length, thickness, number, arrangement and plaque morphology. Permanent attachment threads are formed in clumps or are arranged in rows and make up the majority of a byssal mass. Temporary attachment threads are few in number (1–6), arranged in a tripod pattern, originate individually, and are separated spatially from the main byssal mass of permanent threads. Temporary threads are secreted before or after the initial byssal mass attachment. Adult mussels (2 to 2.5 mm shell length) secrete about 23 threads per mussel per week but the rate of thread formation varies considerably, depending on size, temperature and water quality. The total numbers of threads secreted can be estimated from the regression, No. threads = $-8.59 + 19.26(\text{shell length, mm})$ (Claudi and Mackie, 1994). The threads are composed of DOPA (3,4-dihydroxyphenyl-alanine), a prominent amino acid present in the byssus of marine mollusks, but the precursors differ considerably in sequence (Rzepecki and Waite, 1993). The adhesive strength of the zebra mussel byssal thread varies with the composition of materials on which it is attached (Ackerman *et al.*, 1992).

MODE OF LIFE AND HABITAT

Mackie (1991) described the mode of life of *D. polymorpha* in the Great Lakes as an epifaunal one but recent research by Claxton (University of Guelph, Guelph, Ontario, pers. comm.) indicates that *D. bugensis* has an ability for an epibenthic habit in deeper waters. He collected benthic samples and settlement data from plexiglass plates at 1 to 36.6 m and found that recruitment rates (No./m²) decreased significantly ($P \leq 0.05$) with increasing depth, the greatest recruitment occurring at 14.3 m and the least at 36.6 m. Benthic samples showed that the ratio of quagga to zebra mussels increased significantly with increasing depth. Only quagga mussels were taken in Ekman grab samples at 36.6 m. Claxton (personal communication) suggested that quagga mussels may be altering their shell allometry for an epibenthic existence; quagga mussels are thinner and lighter in weight in soft profundal sediments than on firm inshore substrates, whereas zebra mussels exhibit little or no changes in shell allometry on firm or soft substrates.

Zebra mussels are known to inhabit especially large freshwater lakes and rivers

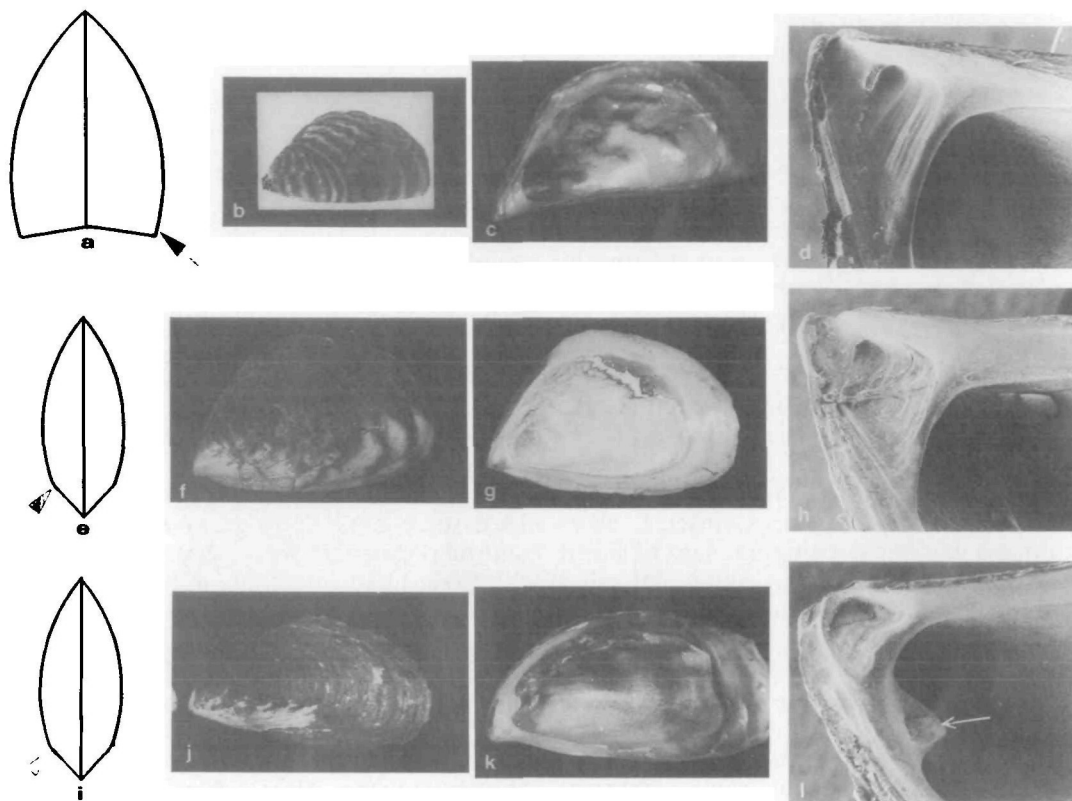


FIG. 1. Shell characteristics of dreissenids in North America. (a)–(d) *Dreissena polymorpha*: (a) schematic drawing of end view showing carinate ventro-lateral margin (arrow) and concave ventral margin; (b) outer view of right valve; (c) inner view of right valve; (d) myophore plate; (e)–(h) *Dreissena bugensis*: (e) schematic drawing of end view showing rounded ventro-lateral margin (arrow) and convex ventral margin; (f) outer view of right valve; (g) inner view of right valve; (h) myophore plate; (i)–(l) *Mytilopsis leucophaea*: (i) schematic drawing of end view showing rounded ventro-lateral margin (arrow) and convex ventral margin; (j) outer view of right valve; (k) inner view of right valve; (l) myophore plate showing apophysis (arrow).

(Strayer, 1991) but the mussels also do well in cooling ponds, quarries, and irrigation ponds of golf courses as well. Recent research in North America has also demonstrated that zebra mussels are capable of living in brackish water or estuaries where the salinity does not exceed 8 to 12 ppt (Naplepa and Schloesser, 1993; Kilgour *et al.*, 1994). Temperature, the relative amounts of sodium and potassium (Deitz *et al.*, 1996) and the rate of acclimation to salinity greatly affect the tolerance of larval and adult mussels to salinity; at higher temperatures (18–20°C) the optimum salinity for adult mussels is about 1 ppt but at lower temperatures (3–12°C) the optimum salinity for adults is 2–4 ppt (Kilgour *et al.*, 1994). The

incipient lethal salinity for post-veligers is near 2 ppt and for adults (5–15 mm) it is between 2 and 4 ppt (Kilgour *et al.*, 1994).

PHYSIOLOGY, BIOCHEMISTRY, GENETICS

Several aspects of the physiology, biochemistry, and genetics of zebra mussels have been described in the European literature. These include osmotic and ionic regulation, desiccation resistance, filtration characteristics, resistance to metabolites, karyotypes, polymorphic systems, DNA characteristics, and protamine descriptions, uric acid composition, anerobic fermentation products, and carotenoid content (see Mackie *et al.*, 1989 for literature review). Recent, significant advances in our knowl-

edge of physiology and genetics of North American dreissenids are provided elsewhere in this symposium. Many of these advances have improved our abilities to predict the potential distribution range of zebra mussels in North America, the potential biotic and abiotic impacts of dreissenids on North American waters, and our understanding of the regulatory processes mechanisms that control reproduction and recruitment of zebra and quagga mussels.

DISPERSAL MECHANISMS

Mackie *et al.* (1989) and Carlton (1993) review numerous potential dispersal mechanisms of larval and adult dreissenids, many of them being natural mechanisms (*e.g.*, water currents, birds, insects, other animals) but most being human-mediated (*e.g.*, artificial waterways, ships and other vessels, fishing activities, amphibious planes, and recreational equipment, to mention a few). The planktonic veliger stage is probably the most effective natural dispersal phase, with intracontinental dispersal occurring quickly via downstream movement of the veligers. Artificial canals enhanced the dispersal of zebra mussels in Europe, especially in the USSR and Britain (Kerney and Morton, 1970). Not all mechanisms have been verified, especially for the planktonic stage, which are usually not the first life stage found in a newly established mussel population (Nalepa and Schloesser, 1993). In general, natural dispersal of zebra mussels is believed to occur primarily by currents carrying planktonic veligers. However, sedentary mussels attached to floating debris may also distribute mussels. In addition, juvenile and adult mussels can possibly be dispersed by extending mucous threads (up to 15 mm long) from the surface of the water by capillary action and drifting with surface water currents (Martel, 1993). Dispersal caused by turtles, crayfish, and birds may occur but is not well documented (Carlton, 1993).

Human-mediated dispersal mechanisms are believed to be the most common means of distributing zebra mussels, especially between continents and unconnected water bodies (Table 2). Carlton (1993) describes three lines of evidence which lead to the

conclusion that freshwater ballast in transoceanic vessels transported zebra mussels from Europe to the Laurentian Great Lakes: (1) the common presence of veligers in ballast water combined with patterns of vessel traffic in the Great Lakes; (2) the introduction of other exotics (*e.g.*, crustaceans) transported in ballast water; and (3) the inability to identify other probable mechanisms. However, desiccation studies by Usery and McMahon (1994) suggest that it is also possible that adult mussels may have attached to anchors or their chains of vessels in European harbors and survived the transoceanic voyage. This is probable if the anchors and chains were stored on board with sufficient moisture content to allow at least some mussels to survive the voyage and then drop off when ships anchored in the Great Lakes (McMahon, personal communication).

GEOGRAPHIC DISTRIBUTION

The range of zebra mussels before the 19th century occurred primarily over small areas of the Black, Caspian, and Azov seas (Stanczykowska, 1977). The limited distribution of zebra mussels in 1800 was a result of thousands of years of natural processes. Between 1800 and 1900, zebra mussels more than doubled their range in Europe (Schloesser, 1995). The doubling of the range of mussels in only 100 years is attributed to human-mediated dispersal mechanisms (Kinzelbach, 1992; Morton, 1993).

Zebra mussels were discovered in North America in June 1988 in Lake St. Clair of the Laurentian Great Lakes (Hebert *et al.*, 1989). Length-frequency analysis of known populations in 1988 and review of studies performed before 1988 indicate that mussels became established in Lake St. Clair and the most western portion of Lake Erie downstream from Lake St. Clair in 1986 (Griffiths *et al.*, 1991) (Fig. 2). This initial founding population occurred in a range about 75 km north to south (N-S) by 25 km east to west (E-W). By 1990, zebra mussels occurred primarily downstream of the founding population in a range extending to the extreme eastern and western ends of the Great Lakes—600 km N-S by 1,400 km

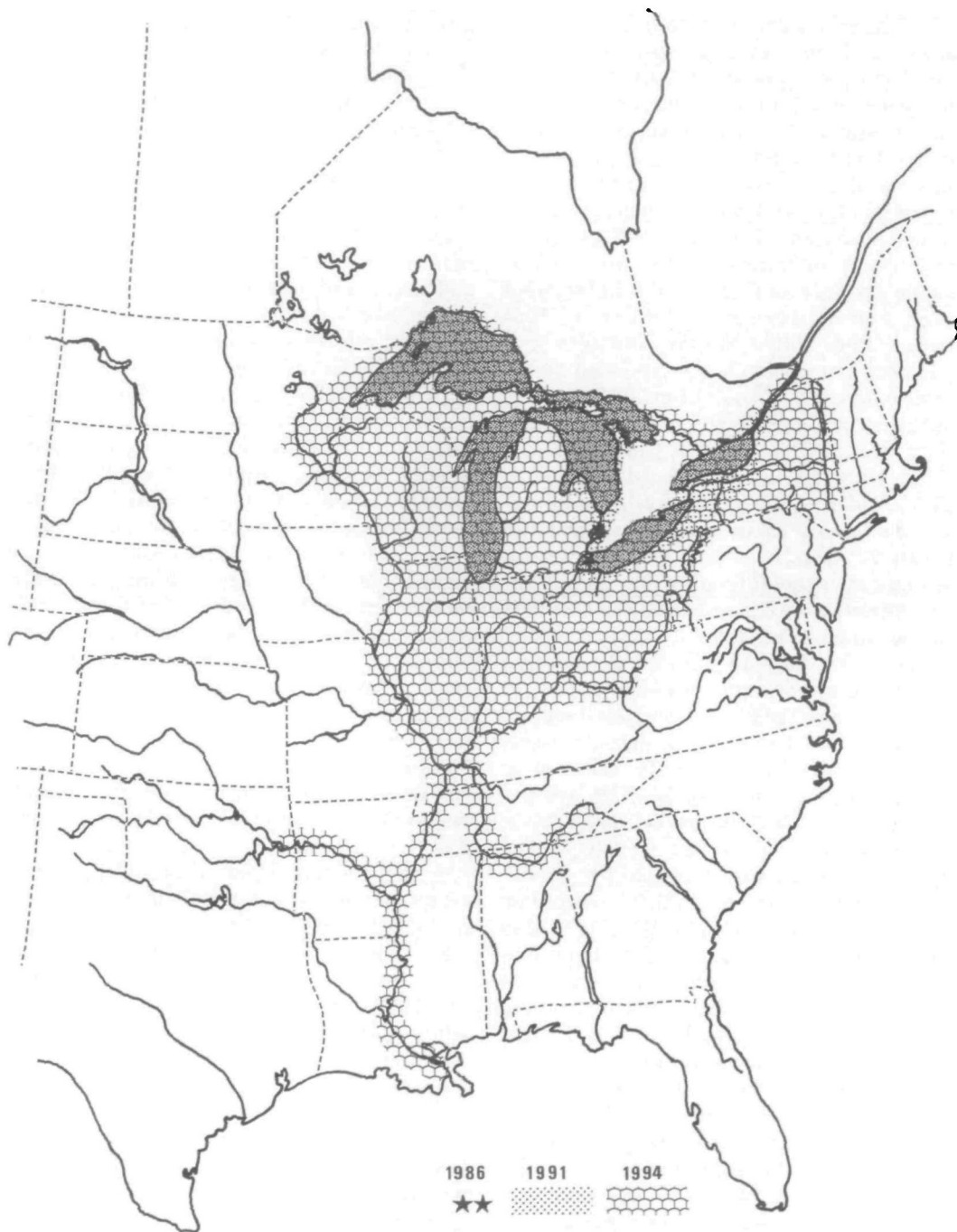


FIG. 2. Distribution of *Dreissena polymorpha* in four-year intervals from 1986 (Lake St. Clair and western basin of Lake Erie = stars), to 1991 (mainly all the Great Lakes = stippled areas), and 1994 (most major tributaries of Mississippi River and many inland areas = hatched areas) as described in text.

E-W. Mussels were also found at several harbors and river mouths upstream of the founding mussel population. In 1991, mussels were found outside the Great Lakes water basin. In 1992, mussels occurred as far south as Vicksburg, Mississippi, west to Minneapolis, Minnesota, and north and east to Quebec. By 1994 mussels were found in a range extending 1,900 km N-S by 1,700 km E-W. To date most of the infested waters are connecting rivers of the Mississippi River such as the upper Mississippi, Tennessee, Ohio, and Arkansas, although several lakes not connected to infested rivers are also infested. In addition, live mussels attached to trailered boats have been found as far west as Los Angeles, California. Zebra mussels are also well established in Lake Simcoe, Ontario, where most unionids have 2 to 8 zebra mussels per unionid (Trevor Claxton, personal communication), and appear to be following the same patterns reported for Lake St. Clair unionids (Gillis and Mackie, 1994).

The factors that will limit the distribution and abundance of zebra mussels appear to be temperature, pH, and calcium content. Predictions for the spread of zebra mussels in North America are currently based on an upper thermal tolerance of 26–32°C (Strayer, 1991), a calcium threshold for survival of 12 mg/liter (Neary and Leach, 1991), and a pH and calcium threshold for growth and reproduction of 7.3 and 28.3 mg/liter, respectively (Ramcharan, 1992a, b). These criteria are largely based on European laboratory studies which showed particularly highly variable response levels to calcium (Mackie *et al.*, 1989). However, Hincks (1994), using both laboratory and field studies, examined the effects of pH levels less than 7.0 and calcium levels lower than 12 mg/liter on survival, growth and reproduction of zebra mussels and found: 100% mortality in water with pH less than 7.1, mortality decreasing with increasing pH above 7.1; positive growth at levels above pH 7.1 and 8.5 mg Ca/liter; and reproduction in waters with calcium levels above 20 mg/liter. Mackie and Kilgour (1995) found a pH threshold limit of survival for veligers at 7.4–7.5. Therefore, it appears that although zebra mussels may survive and

grow in waters with pH as low as 7.3 and calcium levels between 8 and 20 mg/liter, infestation levels of abundance probably will not occur until pH exceeds 7.5–8.0 and calcium levels exceed 15–20 mg/liter.

HABITAT DISTRIBUTION

Mackie *et al.* (1989) reviewed the European literature for information on the vertical distribution of zebra mussel veligers and the abundance of adults in relation to depth. North American research is providing new information on the vertical distribution of veligers of *D. polymorpha* and *D. bugensis*. Fraleigh *et al.* (1993) reported that wind driven currents have a profound effect on the vertical distribution of zebra mussel veligers; significant depth effects were found only at wind velocities <8 km/h when 5% of the population was found at 0–2 m, 30% at 2–4 m, and 64% at 4–6 m. Veligers are found deeper in the water column when NOT mixed vertically by wind. Smylie (1994) examined the depth distribution of *D. polymorpha* on calm days (waves less than 10 cm high) and found peaks in abundance between 2 and 6 m at sites ranging from 6 to 20 m in Hamilton Harbour (Lake Ontario) and at 18 m at a site deeper than 35 m in Lake Erie, but always at temperatures between 16.7 and 17.8°C at all sites.

Perhaps wind driven currents have less effect on the vertical distribution of veligers in lakes with small surface areas than in lakes with large surface areas, like Lake Erie. Based on European data, Fraleigh *et al.* (1993) showed that the maximum densities of larvae tend to decrease with increasing surface area and depth of lakes. However, Lake Erie, almost twice as large as the largest reservoirs (*e.g.*, Kuibyshev Reservoir and Lake Ladoga) or lake studied in Europe (Lake Constance), does not fit the pattern and has the largest density of larvae in lakes reported to date (Fraleigh *et al.*, 1993).

Dreissena bugensis first settled in the eastern basin of Lake Erie in August, 1989 (Riessen *et al.*, 1993). By summer, 1990 the quagga mussel had been dispersed to the mouth of the Niagara River and by December 1990 to the eastern end of Lake Ontario

(Dermott, 1993). The quagga mussel had succeeded in occupying the entire eastern and most of the central basin of Lake Erie and occurred at several sites along the southern shores (U.S.) of Lake Ontario by July, 1992 (Dermott, 1993). The species has displaced the zebra mussel at many sites in Lake Erie and is the only dreissenid found in waters exceeding 40 m deep (Dermott, 1993). The quagga mussel has been found in depths exceeding 150 m and is reported to grow and reproduce in profundal sediments where the temperature never exceeds 12°C (Dermott, 1993; Mills *et al.*, 1995).

In spite of these differences, many similarities in horizontal and depth distributions of zebra mussels exist between European and North American lakes. For veligers, the depth of maximum abundance typically varies between 3 and 7 m, but maxima at 11 to 12 m are common (Mackie *et al.*, 1989). Similar depths of maximum abundance are described for veligers in European lakes (Mackie *et al.*, 1989) but as a "belt of shore waters" around the perimeter of the lake. The width of the belt depends on the bathymetry of the lake, the widest belts occurring in lakes with a shallow slope.

Few veligers occur below the thermocline in temperate lakes (Mackie *et al.*, 1989; Fraleigh *et al.*, 1993; Smylie, 1994). Variations in the vertical distribution of veligers can usually be attributed to wind driven currents. However, there are numerous other factors. Secchi depth visibility and temperature are two factors commonly attributed to variations in maximum densities (Mackie *et al.*, 1989). Moreover, there appears to be a diurnal movement of veligers, with maximum densities occurring near the surface during early morning and at 5–7 m during the day (Mackie *et al.*, 1989).

Veligers are usually contagiously distributed, though the factors responsible for this are not yet well understood. Mackie *et al.* (1989) describe studies that show the patchiness is not due to prevailing winds in Polish lakes, but Martel (1993) has demonstrated that prevailing winds plays a major role in the patchiness of veliger abundance in Lake Erie. Smylie (1994) found few differ-

ences in veliger abundance between inshore and offshore waters, but when differences appeared, offshore waters had greater densities of than inshore waters. Doka (1994) showed that while wave height, wind velocity, and fetch hours did not correlate strongly with recruitment rates, all three were significant variables in multiple regression models for predicting size of recruitment of *Dreissena* populations in Lake Erie.

Different patterns of distribution have been reported for adults than for larvae. For adults the depth of maximum density is highly variable among lakes and varies seasonally. However, the reasons for the seasonal shifts appear to differ between European and North American studies. Mackie *et al.* (1989) reported smaller, younger specimens migrating from shallow water in the summer to deep water in the winter. This resulted in a seasonal shift of the age structure in the main belt of occurrence, from an increase in the proportion of young specimens during summer to a decrease in the winter. In North American populations seasonal differences tend to be attributed to differences in size-selected "loss rates," the losses representing both mortality and translocation. Smaller mussels translocate at higher rates than larger mussels (Martel, 1993), probably because larger mussels have greater numbers of byssal threads from neighboring individuals holding them in place (Claudi and Mackie, 1994). Bishop and DeGaris (1976) found that dreissenids tend to occur independently of other molluscan species. However, this may be because dreissenids have displaced other mollusks (Gillis and Mackie, 1994; Schloesser *et al.*, 1996).

PREDATORS

Larval stages of mussels appear to be consumed mainly by crustacean zooplankton (*e.g.*, copepods) and larval fish, but the relative importance of these prey groups to the total mortality of larval stages is unknown (Mackie *et al.*, 1989). In North America, Conn and Conn (1993) reported predation of larval stages by the cnidarian, *Hydra americana*.

Adult zebra mussels have a very high nu-

tritional value of the tissues, with 60.7% protein, 12.0% lipid, 19.0% carbohydrate, and 5.9% ash (Cleven and Frenzel, 1992) and are consumed in large quantities by crayfish, fish, and waterfowl (Mackie *et al.*, 1989). The nutritional value changes seasonally. In Europe, Mackie *et al.* (1989) describe several European predation studies. Several species of fish consume zebra mussels but the roach seems to have the most significant impact on mussel densities. The roach has strong pharyngeal denticles and can consume large shells. In some Polish lakes, the diet of roach consists almost exclusively (*i.e.*, 95–100%) of zebra mussels, although feeding on mussels may be seasonal (*e.g.*, autumn and winter). In general, it appears that fish do not limit the densities of *D. polymorpha* in European lakes.

In North America, zebra mussels have been found in the stomachs of walleye, yellow perch, freshwater drum, white suckers, and a few others. The relative contribution of the fish species to predation of zebra mussels in North America is unknown. Only the freshwater drum, *Aplodinotus grunniens*, has been investigated in some detail (Nalepa and Schloesser, 1993); predation on zebra mussels increases as drum size increases, with large drum feeding almost exclusively on zebra mussels. The freshwater drum is the only species in the Great Lakes that has molariform pharyngeal teeth for crushing shells of mollusks. The only other significant predator of zebra mussels is waterfowl and MacIsaac (1996) examines the recent literature and describes the effects of predators on dreissenids in North America.

PARASITES

Freshwater bivalve mollusks are common intermediate hosts of parasites, particularly trematodes, whose definitive hosts are fish, waterfowl, and sometimes humans (Mackie, 1976). Mackie *et al.* (1989) concluded from their European literature survey that *D. polymorpha* is not a common vector of parasites. Protists and digeans were the most common parasites found, with Nematoda observed sporadically. Many protists are common parasites but

they do not seem to “affect the numbers” of the zebra mussel.

The survey of the European literature of Mackie *et al.* (1989) also concluded that trematodes are less common parasites of zebra mussels than protists, the greatest infestation rate observed being 10%. The most dangerous protists are ciliates of the family Ophryoglenidae which parasitize the digestive gland and may kill the mussel. The trematodes, *Phyllodistomum folium* and *Bucephalus polymorphus* are also important parasites in Netherland lakes where the infestation prevalence is usually about 1% and may go as high as 10% (Nalepa and Schloesser, 1993). Infestation apparently lowers the resistance of mussels to metal accumulation, infested mussels having higher levels of Zn, Cu, Cd, and Pb than noninfested mussels. The effects of parasites on European populations of *D. polymorpha* appear to be minimal, at least until high emissions of cercariae of *B. polymorphus* occur (Mackie *et al.*, 1989). Intensity of parasitism by *P. folium* was directly correlated to shell size of *D. polymorpha*, the maximum number recorded being 200 at a shell size of 24–28 mm.

Similar results have been reported in North America by Toews *et al.* (1993). They reported a 2.9% prevalence of plagioglychid metacercariae in mussels and 2.7% prevalence of adults and juvenile aspidogastriids in mussels from two sites in Lake Erie. The ciliate, *Ophryoglena*, was also found, with 1.3% prevalence at a site in Lake St. Clair and 2.7 to 4.3% prevalence at two sites in Lake Erie. Toews *et al.* (1993) concluded that although parasites do not significantly affect changes in densities of *D. polymorpha*, there is a great probability that mass development of zebra mussels may increase the infection rate in definitive hosts, especially fish and waterfowl. The oligochaete, *Chaetogaster limnaei*, and the chironomid *Paratanytarsus*, have also been reported as commensals in zebra and quagga mussels (Conn *et al.*, 1994).

PRODUCTIVITY

Densities of veligers and adults in the Great Lakes are among the highest reported to date. Fraleigh *et al.* (1993) tabulated

mean monthly densities of veligers in eight European lakes and reservoirs and found that the western basin and its island region averaged 126–268 individuals/liter in July and August (Leach [1993] reported means near 400/liter), whereas European waters averaged about 10–100/liter, the Konin Lakes being an exception with 22–320/liter in the same period. Mean densities (No./m²) of adult range from about 54,000 (Dermott *et al.*, 1993) to 779,000 (Pathy, 1994) in Lake Erie to 43,000 in Lake St. Clair (Pathy, 1994). Average densities of adult mussels in European lakes range from about 5,000 to about 115,000/m² (Mackie *et al.*, 1989).

The abundance of *D. polymorpha* has been related to trophic type, the largest populations occurring in eutrophic waters (Mackie *et al.*, 1989). However, Stanczykowska (1964) found no relationship between abundance of *D. polymorpha* and trophic status of lakes.

Biomass of *D. polymorpha* in a given water body is usually related to the density but the average biomass of populations is highly variable among lakes (e.g., 0.13 to 20 kg/m²) and within lakes (e.g., 0.05–10.5 kg/m²) (Mackie *et al.*, 1989). Some of this variation is due to variations in body condition of mussels and in length-weight relationships. Several indices of condition have been used; length, height and/or width or “size” of shells; wet and dry weight of whole animals, shell only and dry tissue only; length:width ratio or slenderness; length:height ratio or flatness; and the ratio of wet weight to dry weight (Mackie *et al.*, 1989). Of these, slenderness, flatness, and ratio of wet to dry weight showed the least variation within and among lakes; average size and weight varied considerably among lakes but tended to vary only slightly within lakes; body (tissue) weight and shell weight tended to vary in the same manner among lakes (i.e., lakes with high shell weights also had high body weights) (Mackie *et al.*, 1989).

Mackie *et al.* (1989) examined the European literature and concluded that variations in length-weight relationships correlated highly with variations in environmental conditions. Regressions of shell length

and shell and body weight follow the power function, $\text{Weight} = a \times \text{Length}^b$, where b varies between 1.937 and 3.284 for European populations, depending on lake type and time of year. Zebra mussel populations in the Great Lakes fall within this range; Nalepa and Scloesser (1993) give studies that report slope values of 2.612 for total dry weight and 2.198 for dry tissue weight (vs. shell length); Mackie (1991) reports 2.996 and 2.982, respectively for the same variables. Neumann and Jenner (1994) provide studies that evaluate the use of shell length, shell height, and shell volume for accurately predicting biomass of zebra and quagga mussels. Both shell height and shell weight are good predictors of ash free dry weight (AFDW) for both species; volume measurements do not provide as good an estimate of AFDW as did shell length and height.

Estimates of annual production of *D. polymorpha* in European waters are uncommon but vary between 0.1 and 29.8 g/m²/yr dry body weight and 3.3 and 525.9 g/m²/yr total dry weight (Mackie *et al.*, 1989). In the Great Lakes annual production of zebra mussels is higher than most European populations, about 150 g/m²/yr dry body weight (Dermott *et al.*, 1993). Cleven and Frenzel (1992) reported annual production for River Seerhein, the outlet of Lake Constance, as 138 g C_{org}/m², including organic shell content. In European waters the P/B ratio varies between 0.42 and 0.65 for dry body weight and 0.47 and 0.81 for total dry weight (Mackie *et al.*, 1989). The highest P/B ratio recorded is 6.8 for Lake Constance (Mackie *et al.*, 1989), but the population was still in its exponential phase of growth and the P/B ratio may have dropped when the population stabilized. Dermott *et al.* (1993) reported a P/B ratio of 4.7 for a population in Lake Erie.

LIFE HISTORY

The life history of *D. polymorpha* and its variations are well known, especially for European waters (Mackie *et al.*, 1989). Ackerman *et al.* (1994) have reviewed the early life history of dreissenids and have standardized the terminology with that used for marine mussels. Variations in life his-

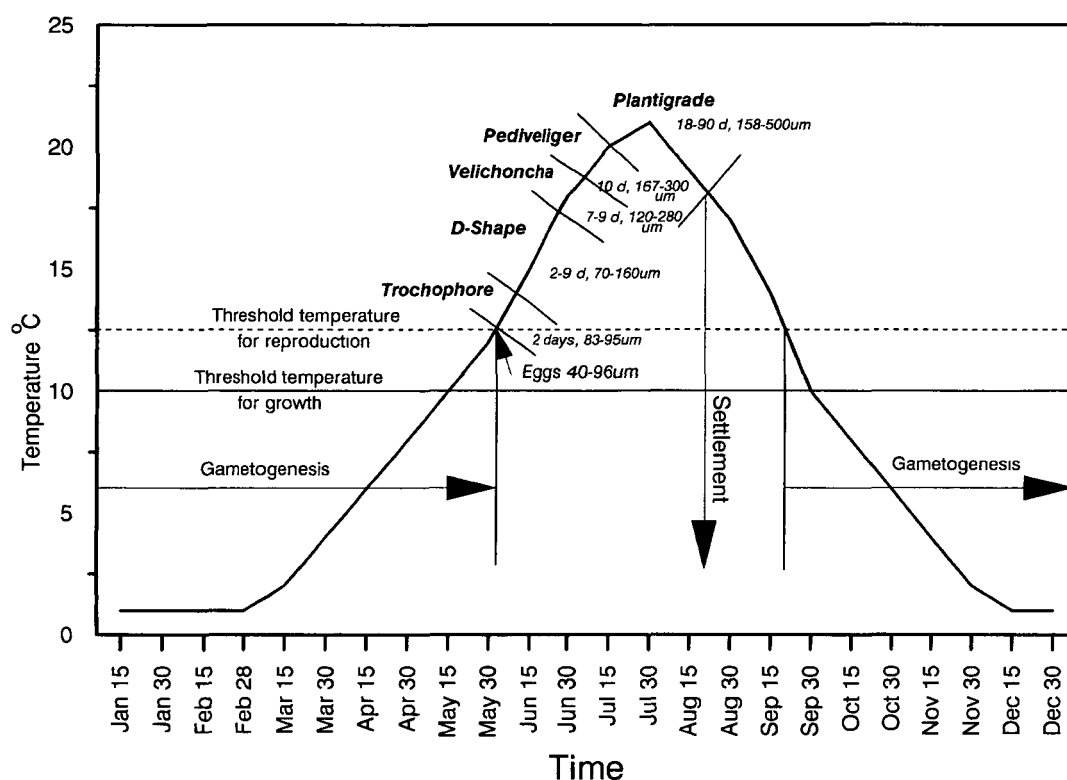


FIG. 3. Life cycle of *Dreissena polymorpha* in relation to annual temperature cycle in Great Lakes region. Threshold temperatures for growth and reproduction are also shown. Life cycle is based on maximum development times reported by Ackerman *et al.* (1994) in relation to typical settlement periods in Great Lakes reported by Doka (1994). At least one settlement event is possible based on maximum development times but some years may have two or more, depending on durations of each stage shown in bold italics. Size ranges are for heights of shells, as reported by Ackerman *et al.* (1994).

tory of North American zebra mussels have been described by Mackie (1991, 1993), Haag and Garton (1992), Garton and Haag (1993), Claudi and Mackie (1994), and Pathy (1994) but the variations are somewhat different from European populations. In Europe, adults become sexually mature in their second year of life (Mackie *et al.*, 1989); in North America, zebra mussels become sexually mature in their first year of life, usually by 8 to 10 mm in shell length. Zebra mussels have exceedingly high fecundities, varying from 30,000 to 1,610,000 eggs/female (Mackie *et al.*, 1989; Borchering, 1992). Typically, gametogenesis begins in the fall after all gametes are spent, continues through winter, with intensive growth of oocytes and spermatozoa in spring when mussels attain a shell length of 8–9 mm or larger (Pathy, 1994). Fig. 3

summarizes the annual life cycle of zebra mussels in the Great Lakes in relation to temperature. Additional details are provided by Nichols (1996).

Settling stages are the most sensitive stages and have high mortality rates, usually 90–99% (Mackie *et al.*, 1989; Nalepa and Schloesser, 1993). However, these mortality rates did not consider immigration and emmigration (translocation) of young stages; MacIsaac *et al.* (1991) suggested that when immigration and emmigration are accounted for, mortality could be as low as 70% in the western basin of Lake Erie. They indicated that larval mortality could be lower during the colonization phase and then increase when adults become established and begin to filter their own larvae.

There is often misuse of the terms “settlement” and “recruitment”. Settlement re-

fers to the passage from a pelagic habit to a benthic one and involves not only a change in position in the water column but attachment and certain morphometric changes as well (Doka, 1994). Recruitment is essentially the process of settlement combined with post-settlement mortality. The process is thought to be comprised of three phases; larval supply, settlement, and metamorphosis (Doka, 1994). Newly settled mussels are considered recruits if they have survived to a size or an elapsed period of time set *a priori* by the investigator. Doka (1994) found that peaks in recruitment densities occurred at similar times among her study sites and between years; a peak in recruitment can be expected during the first three weeks in August at most sites in Lake Erie. However, she found variability in the number of recruitment events between sites, probably because of local hydrological conditions delivering larval pulses toward shore. Nevertheless, adult population dynamics appear to be regulated, in part at least, by recruitment fluctuations as “supply-side” ecology suggests (Doka, 1994).

AGE AND GROWTH

The growth rate of larvae in nature is highly variable, depending mainly on temperature (Mackie *et al.*, 1989) and chlorophyll a content (Smylie, 1994). Estimates of larval growth rates of zebra mussels are few; 1 to 4 $\mu\text{m}/\text{d}$ for larvae in two lakes in Germany (Mackie *et al.*, 1989), 6.0 to 11 $\mu\text{m}/\text{d}$ for a drifting population in the River Rhine (Neumann and Jenner, 1994), and 2.4 to 23.7 $\mu\text{m}/\text{d}$ for larvae at several sites in Lake Erie (Smylie, 1994). Smylie (1994) also reared larvae in the laboratory and achieved 4.1 to 4.5 $\mu\text{m}/\text{d}$ at 13.1°C and 6.5 to 8.7 $\mu\text{m}/\text{d}$ at 16.6°C.

The relationship between age and growth of mussels varies considerably, much of the variation being due to the method used to age the mussels. Mackie *et al.* (1989) describe two patterns of growth in European populations, “slow-growing” and “fast-growing” populations. The maximum growth rate for the slow-growing group appears to be less than 1 cm/yr with a maximum shell size of 3.5 cm; the fast-growing group exceeds 1.5 cm/yr with a maximum

shell length >4.0 cm. Populations in the Great Lakes are different still, where most mussels grow quickly (1.5–2.0 cm/yr) but their maximum size is typically only 2.5–3.0 cm (Mackie, 1991).

The growth rate of *D. polymorpha* is dependent on quality and quantity of food, temperature, and body size (Mackie *et al.*, 1989). Growth rates decrease with increasing body size and increase with increasing food concentration up to 2 mg C/liter, with an optimum between 10 and 15°C, although in the Great Lakes growth and settlement rates appear to be optimum between 15 and 17°C (Smylie, 1994). The temperature threshold for growth usually varies between 10 and 12°C (Mackie *et al.*, 1989; Neumann and Jenner, 1994; Smylie, 1994); a value as low as 6°C was reported by Bij de Vaate (1991). The quagga mussel appears to be able to reproduce at temperatures below 8°C, in the hypolimnion of Lake Erie (Trevor Claxton, University of Guelph, Guelph, Ont., personal communication).

The life span of *D. polymorpha* is highly variable, but it appears that North American populations have a shorter longevity than European populations. The average life span of zebra mussels is 3–5 years in most Polish lakes, 5 years in British waters, and 6–9 years in some Russian reservoirs (Mackie *et al.*, 1989). In North America, most zebra mussel populations have a life span of about 1.5 to 2 years (Mackie, 1991). Zebra mussels inhabiting heated waters have life spans truncated by about 1 year compared to unheated lakes in the same area (Mackie *et al.*, 1989).

FOOD AND FEEDING

Food selection is performed by a variety of cilia, including those in the mantle cavity (gills, labial palps and foot) and in the stomach and midgut. Cilia in the mantle cavity and stomach select particles of 15–40 μm for food but can filter out particles as small as 0.7–1.0 μm in diameter from the water (see Mackie *et al.*, 1989 for review). Significant advancements in our knowledge of ciliary filter feeding processes and feeding habits have been made by Silverman *et al.* (1996) MacIsaac (1996)

and should be consulted for a detailed discussion of feeding in dreissenids.

The filtration rate is affected by size, turbidity, temperature, and certain concentrations of specific sizes and kinds of algal cells (e.g., *Chlamydomonas*) and bacterial cells (Mackie *et al.*, 1989; Reeders and bij de Vaate, 1989; Reeders *et al.*, 1993). The filtration capability of *D. polymorpha* in relation to its role as a clarifier of water in an entire lake, epilimnion or littoral zone has been reviewed by Neumann and Jenner (1992); they also describe applications of zebra mussels in water quality management, particularly as water clarifiers. Although mussels are efficient clarifiers, the suspended materials accumulate on the bottom as faeces and pseudofaeces. The size of faecal and pseudofaecal pellets varies with mussel size and the settling velocities and rate of accumulation greatly exceed normal sedimentation processes (Dean, 1994).

ACKNOWLEDGMENTS

Contribution Number 955, National Biological Service, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan 48105.

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