GROWTH RATE AND LONGEVITY OF *DREISSENA POLYMORPHA* (PALLAS): A REVIEW AND RECOMMENDATIONS FOR FUTURE STUDY

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ABSTRACT We review the variety of methods that have been used over the last 50 y in the Former Soviet Union, Eastern and Western Europe, and recently in North America to determine growth rate and longevity in zebra mussels (*Dreissena polymorpha* [Pallas]). These methods include: counting annual rings, analysis of size-frequency distributions, following growth under experimental conditions and monitoring marked mussels under natural conditions, without removing them from substrate. The last method provides the most reliable data, however this is the least common method used. *Dreissena polymorpha* growth rates depend on water temperature, season of the year, location in the water column, food availability, oxygen concentrations, water velocity and various other environmental factors. However, it is very difficult to separate the independent effects of each of these factors, especially in natural waterbodies. Several factors may overlap and have additive or synergistic effect that makes it difficult to determine the effects of a single factor. When comparing among studies that used the same methods, we found that zebra mussels grow faster in reservoirs than in lakes. The reported longevity of *D. polymorpha* varies from 2–19 y and it is not clear to what extent this variation is caused by biological variability and environmental conditions and what amount of the variation is caused by the methods used to assess age and longevity.

KEY WORDS: zebra mussels, *Dreissena polymorpha*, growth, growth rate, methods, longevity

INTRODUCTION

The zebra mussel, *Dreissena polymorpha* (Pallas), is one of the most pervasive invaders in freshwaters of the northern hemisphere. However, many aspects of the basic biology of *D. polymorpha* that are necessary for understanding and predicting the population dynamics and ecological impacts of this invader are still not well known. In addition, much of the research on the biology of *D. polymorpha* that has been conducted in the former Soviet Union (FSU), has not been published in English, and therefore it is not available to most scientists currently studying *D. polymorpha*. Growth rate and longevity are particularly important for understanding the population biology and ecological impacts of zebra mussels, especially because fecundity and filtering capacity increase with body size. Most of the published research has been conducted with the invasive subspecies *Dreissena polymorpha polymorpha*, which is capable of living in totally fresh water and has been the major invader in most places where dreissenids have been introduced. Less work has been conducted with *Dreissena bugensis* (Zhuravel 1951, MacIsaac 1994, Baldwin et al. 2002), *Dreissena polymorpha andrusovi* (Karpevich 1952, 1964, Lvova et al. 1983, 1994) and *Dreissena caspia* (Karpevich 1952, 1964).

Here we review the variety of methods used to estimate growth and longevity of zebra mussels over the last 50 y (Table 1, Table 2), discuss limitations of each and recommend the most appropriate methods for measuring growth and longevity in the field. We also synthesize the impacts of a range of environmental factors on growth and longevity in zebra mussels.

METHODS TO ESTIMATE GROWTH RATE

Rings on Shells

One of the oldest and most common methods for estimating the growth rate of zebra mussels is by counting annual rings on shells

of different sizes, and then calculating the average length of each age group of *Dreissena* in a population (Karpevich 1952, 1964, Kachanova 1963, Stanczykowska 1964, Lyakhov & Mikheev 1964, Mikheev 1964, Kornobis 1977, Karatayev & Tishchikov 1979, Kirpichenko & Antonov 1982, Dorgelo & Gorter 1984, Draulans & Wouters 1988, Miroshnichenko 1990). Plotting the average size of each age group against their age provides a growth rate curve. The advantage of this method is that by measuring individuals at a single point in time estimates of growth over several years can be made. However, counting growth rings is very subjective as it is difficult to distinguish annual rings from rings formed because of other factors that slow growth. Morton (1969a) found that two rings are formed annually: when growth slows during the winter and during spawning. Lvova (1980) found in the Uchinskoe Reservoir, 3–9 rings on the shells of 3-y-old mussels grown in cages for 2 y. In Czos Lake Lewandowski (1983) found from 1–3 rings on the shells of 1-y-old *D. polymorpha*, and from 2–5 rings on 2-y-old mussels.

Many other authors have also reported difficulties in distinguishing annual rings (Karpevich 1964, Kirpichenko 1965, Morton 1969a, Wiktor 1969, Lvova-Kachanova 1972, Lvova 1980, Lewandowski 1982a, Karatayev 1983, bij de Vaate 1991, Lvova et al. 1994). Often mussels with distinct rings can be found side by side with mussels without rings (Lvova 1980, Lvova et al. 1994, Jantz 1996). Moreover, 1-mm zebra mussels that settle at the end of the growing season do not produce a first annual ring. Therefore, these mussels would be incorrectly identified as young-of-the-year the following year.

Size-Frequency Distributions

Size-frequency distributions have been used in a number of studies of *D. polymorpha* growth rates (Morton 1969a, Jantz & Neumann 1992, Martel 1993, 1995, Smit et al. 1993, Dall & Hamburger 1996, Chase & Bailey 1999a, Orlova & Panov 2004), and can be useful if there is highly synchronized spawning and settlement and low interindividual variation in growth. Newly settled

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TABLE 1.

Impact of environmental factors on the growth rate of *Dreissena polymorpha*.

Factor	Impact	References
Temperature increase	Accelerates growth if maximum temperature <30°C	Mikheev 1964, Morton 1969a, Spiridonov 1969, Yaroshenko & Naberezhnyi 1971, Lvova-Kachanova 1972, Skalskaya 1976a, 1976b, Stanczykowska 1976a, Kornobis 1977, Elagina et al. 1978, Walz 1978b, 1978c, Karatayev & Tishchikov 1979, Lvova 1980, Karatayev 1983, 1984, 1988, Smit et al. 1992, 1993, MacIsaac 1994, Jantz 1996
Season of a year	Maximum growth is usually at the beginning of the growing season	Mikheev 1964, Lovova 1980, Karatayev 1983, Sprung 1995a, Jantz 1996, Burlakova 1998
Location in the water column	Growth is faster in the water column than on the bottom	Kachanova 1963, Spiridonov 1971, Kornobis 1977, bij de Vaate 1991, Yu & Culver 1999
Trophic conditions	Growth is faster in eutrophic than oligotrophic waters	Walz 1978a, Dorgelo & Gorter 1984, Smit et al. 1992, 1993, Dorgelo 1993, Sprung 1992, 1995a, Jantz 1996, Burlakova 1998, Jantz & Neumann 1998, Schneider et al. 1998, Horvath & Lamberti 1999
Water current	Moderate current accelerates growth	Kachanova 1963, Mikheev 1964, bij de Vaate 1991, Smit et al. 1992, 1993, Dorgelo 1993, Burlakova 1998
Depth	Growth decreases with depth	Mikheev 1964, Garton & Johnson 2000
Wave action	Inhibits growth rate	Mikheev 1964
Turbidity	High amount of suspended matter inhbits growth rate	Reeders et al. 1989, Noordhuis et al. 1992, Alexander et al. 1994, Summers et al. 1996, Madon et al. 1998, Schneider et al. 1998
Year-to-year variation	Growth varies significantly	Lvova 1980, Dorgelo 1993, Chase & Bailey 1999b

mussels form a distinct size class maintain distinct size structure for all age/size classes (Golikov 1970). However, in many water bodies *D. polymorpha* spawn throughout the entire summer, producing several peaks in veliger densities during the year (Lvova 1977, 1980, Karatayev 1983, Lvova et al. 1994, Burlakova 1998) and a wide size range (up to 16 mm difference in size) by the end of their first growing season (Wesenberg-Lund 1939, Mikheev 1964, Kirpichenko 1971, Szlauer 1974, Lvova 1977, Lewandowski 1983, Neumann et al. 1993, Martel 1995). Therefore, age classes will not form distinct size classes (Karatayev 1983, bij de Vaate 1991, Jantz & Neumann 1992, Lvova et al. 1994). This method is most effective when *D. polymorpha* spawn synchronously, have fast growth and are short lived, such as the shallow areas of the Svisloch River (Burlakova 1998). In this river *D. polymorpha* settle in the summer and grow during the following year, producing two distinct size classes of mussels (0+ and +) because the majority of older mussels die over winter because of fluctuating water levels and predation by ducks. At deeper depths mussels survive longer, producing many age classes, which are less distinct as cohorts, making this method less useful (Burlakova 1998). This method could also be used for studies that follow growth on experimental substrates when the time of settlement is known (Lvova 1977, Sprung 1992).

Growth Under Experimental Conditions

Many studies have been used to estimate *D. polymorpha* growth under experimental conditions, especially in cages. In the FSU this method was used in Kuybyshevskoe (Mikheev 1964), Uchinskoe (Lvova-Kachanova 1972, Lvova 1980) and Tsimlyanskoe (Lvova et al. 1983) reservoirs, in Lake Lukomskoe (Karatayev 1983), the Narochanskie lakes and the Svisloch River (Burlakova 1998). More recently, this method has been used by East European (Stanczykowska & Lewandowski 1995), West Eu-

ropean (Smit et al. 1992, 1993, Sprung 1992, 1995a, Dorgelo 1993, Dall & Hamburger 1996) and North American scientists (Bitterman et al. 1994, MacIsaac 1994, Allen et al. 1999, Horvath & Lamberti 1999, Yu & Culver 1999, Garton & Johnson 2000).

Other methods for studying mussel growth under experimental conditions include growing mussels on artificial substrates (Dorgelo & Gorter 1984, Sprung 1992, Martel 1993), and in the laboratory (Walz 1978a, 1978b, Jantz & Neumann 1992, 1998, Dorgelo 1993, Neumann et al. 1993, Jantz 1996, Baldwin et al. 2002). All of these methods could produce different types of artifacts, which may influence observed growth rates. Mesh, usually 3–5 mm, may prevent normal water flow through the cage, particularly for smaller mesh sizes (e.g., 1.2 mm, Garton & Johnson 2000). Cages can also be overgrown by periphyton, further reducing water flow (Kachanova 1963, Karatayev 1983, Stanczykowska & Lewandowski 1995, Burlakova 1998). However, the effects of caging artifacts on growth rates are usually not well tested or quantified (see Burlakova 1998 later).

Marked Mussels Under Natural Conditions

Following tagged mussels under natural conditions has been used in very few studies (e.g., Stoeckman & Garton 1997, Burlakova 1998) although this method could provide the most realistic estimates of zebra mussel growth rates. Burlakova (1998) found that the growth rate of mussels on stones in the Svisloch River was greater than that for caged mussels in the same environment (Fig. 1A). Early in the spring (April), when macrophytes and periphyton abundances were low, the difference between caged and uncaged mussels was small (~30%). This difference increased to almost 400% in the middle and especially by the end of the growing season when the quantity of drifting plants in the water increased and periphyton densities were high (Burlakova 1998). The disadvantage of this method is that zebra mussels can move, form

TABLE 2.

Estimates of the longevity of *Dreissena polymorpha* from different methods.

Waterbody	Longevity (years)	Maximum Length (mm)	Reference
Counts of annual rings on shells			
Volga River	18	32–33	Karpevich 1952
Volga River	17–19	30–32	Karpevich 1964
Uchinskoe Reservoir	11	32	Kachanova 1963
Pyalovskoe Reservoir	10–12	29–33	Mikheev 1964
Mazurian lakes	5–7, max 10	n.r.	Stanczykowska 1963
Firth Szczecin	5–6	30–35	Wiktor 1969
Volgogradskoe Reservoir	7–9	30	Spiridonov 1971
Masurian lakes	5	n.r.	Stanczykowska 1975
Koninskie lakes	4	29	Kornobis 1977
Lukomskoe Lake	6–8	32–34	Karatayev & Tishchikov 1979
Jorzec Lake	7	n.r.	Lewandowski 1982b
Glebokie Lake	5	n.r.	Lewandowski 1982b
Bartag Lake	5	n.r.	Lewandowski 1982b
Otow Lake	5	n.r.	Lewandowski 1982b
Majcz Wielki Lake	5	n.r.	Stanczykowska et al. 1983
Inulec Lake	5	n.r.	Stanczykowska et al. 1983
Zelwazek Lake	5	n.r.	Stanczykowska et al. 1983
Plas Leblance Pond	5	29.9	Draulans & Wouters 1988
Laguno Pond	4	25.7	Draulans & Wouters 1988
Tsimlyanskoe Reservoir	7	31–33	Miroshnichenko 1990
Average ± SE	7.4 ± 0.9		
Analysis of size-frequency distributions			
n.r.	3	31–34	Clarke 1952
Reservoir #2 Walthamstow	5	40	Morton 1969a
River Rhine	3	31	Jantz & Neumann 1992
Lake Esrom	4	32	Dall & Humburger 1996
River Svisloch	3	30	Burlakova 1998
Lake Ontario:			
Stoney Point	2	n.r.	Chase & Bailey 1999a
Whealtey (2 and 6 m)	2–3	n.r.	Chase & Bailey 1999a
Port Dalhousie (2 and 6 m)	≥4	n.r.	Chase & Bailey 1999a
Average ± SE	3.3 ± 0.3		
Growth in experimental cages			
Uchinskoe Reservoir	4	36	Lvova 1980
Lukomskoe Lake	8	30	Karatayev 1984
Lake Wawasee	3	n.r.	Garton & Johnson 2000
Svisloch River	3	30	Burlakova 1998

n.r. = not reported

druses or be consumed by predators, making it difficult to follow individuals through time.

IMPACT OF ENVIRONMENTAL FACTORS ON GROWTH RATE

The growth rate of *Dreissena* depends on water temperature, season of the year, location in the water column, trophic conditions, which affect food availability, and water velocity as well as other environmental factors (Table 1).

Temperature

It is well established that the growth rate of *D. polymorpha* is accelerated by increased water temperature (Table 1). Especially convincing are data from studies in different temperature zones of cooling water reservoirs for thermal power plants in the FSU (Yaroshenko & Naberezhnyi 1971, Skalskaya 1976a, 1976b, Elagina et al. 1978, Karatayev & Tishchikov 1979, Karatayev 1983,

1984, 1988) and other areas of Eastern Europe (Stanczykowska 1976a, Kornobis 1977). In these studies *D. polymorpha* growth rates were compared among the various temperature zones of the same waterbody or lakes within same lake system. Therefore, environmental conditions other than temperature were similar, allowing a direct estimate of thermal effects.

However, when the maximum temperature is >30°C, *D. polymorpha* growth decreases, and at temperatures >32°C most mussels die. In the hottest zone of Lukomskoe Lake, where maximum summer temperature exceeds 32°C, more than 90% of the *D. polymorpha* in experimental cages died, whereas in the moderately heated zone (maximum summer temperature ≤30°C) mortality was less than 10% and did not differ from the control, ambient zone (Karatayev 1983). Similar upper maximal temperature limits for *D. polymorpha* survival have been found by other authors in different regions of the FSU: 31.5°C in Zaporozhskoe Reservoir and 32°C in a canal of the Pridnieprovskaya Power Station in
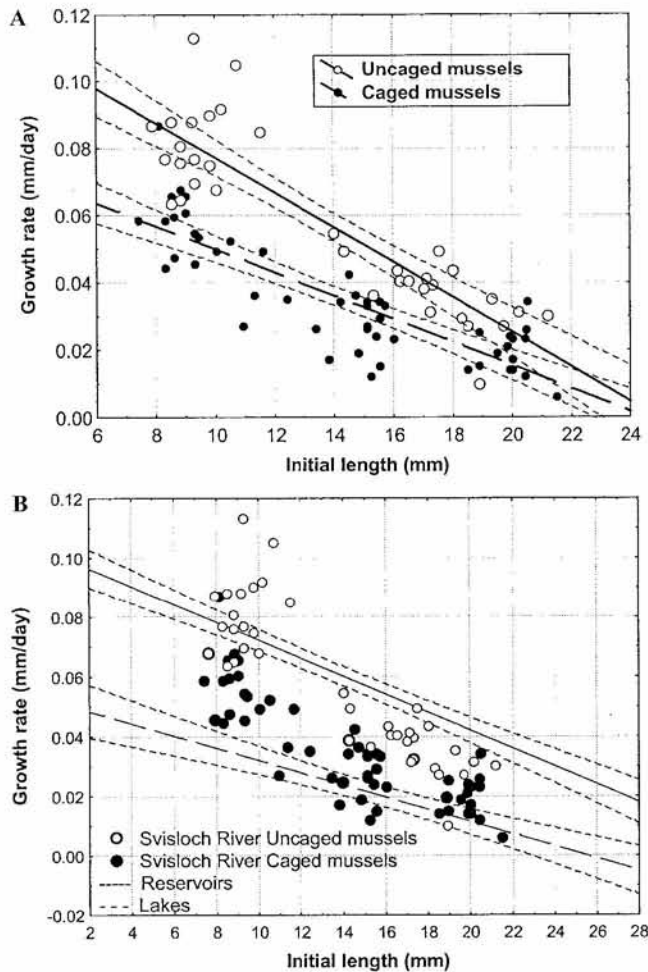
Figure 1. A. Growth rate (mm/day) of caged (filled circles) and uncaged (open circles) *Dreissena polymorpha* in the Svisloch River in 1995 (from Burlakova 1998). Data points are the growth rates of individual mussels. Regression lines (uncaged – solid line, Y = 0.129–0.005*X, R^2 = 0.78, $P < 0.001$; caged – dashed line, Y = 0.084–0.003*X, R^2 = 0.71, $P < 0.001$) and 95% confidence intervals are shown. Uncaged mussels grew faster than caged mussels. The two regression lines differ significantly in slope ($P = 0.003$). B. Growth rate of caged and uncaged *D. polymorpha* in the Svisloch River with the regression lines for size-specific growth of *D. polymorpha* in cages in lakes (dashed line) and reservoirs (solid line). Caged mussels in the river grew at rates more similar to those caged in lakes, whereas uncaged mussels grew at rates more similar to those caged in reservoirs.

Ukraine (Lyakhnovich et al. 1994), 32°C in Kuchurganskiy Liman in Moldova (Vladimirov 1983), 33°C in a cooling reservoir of the South-Ukrainian Nuclear Power Station (Sinitsina & Protasov 1993) and 34°C in a cooling reservoir of the Chernobyl Nuclear Power Station (Protasov et al. 1983).

The upper temperature limit for *D. polymorpha* in European cooling reservoirs is similar to that found in the Lower Mississippi River, where maximum temperature in the summer exceeds 30°C (Allen et al. 1999). In this river *D. polymorpha* growth rate is highest during spring and fall when temperatures ranged from 16°C to 28°C, however, shell growth ceases during the summer when temperatures remain 29°C to 31°C (Allen et al. 1999). Mihuc et al. (1999) found that in the Atchafalaya River system (Louisiana) *D. polymorpha* grow throughout the winter and growth in-

creases in late spring (April and May). Adult mortality occurs from May to August because dissolved oxygen levels decline and minimum daily temperatures warm above 29°C in the floodplain and 32.5°C in riverine sites. Thus, the maximum upper temperature limit for *D. polymorpha* survival is similar in both Europe and North America.

Season

In temperate regions, zebra mussel growth stops in the winter and resumes in the spring after water temperatures warm. Although Smit et al. (1992) assumed that the lower temperature limit for shell growth should be set by the lower temperature limit for filtering (3°C; Mikheev 1967a, 1967b, Kondratiev 1969, Reeders & bij de Vaate 1990), a majority of studies have found that the threshold temperature for mussel growth is 10°C to 12°C (12°C, Kachanova 1961; 11°C, Morton 1969a, 1969b; 10°C, Alimov 1974, Karatayev 1983, Jantz & Neumann 1992; 10°C to 12°C, Mackie 1991). bij de Vaate (1991) did report a lower temperature limit of 6°C, however in North America MacIsaac (1994) found that small mussels incubated at 6°C experienced shell degrowth and mass loss, whereas large individuals experienced shell degrowth but weight gain. These differences among studies may be the result of local effects, but clearly call for further study.

Maximum growth in *D. polymorpha* is usually found early in the growing season (Karatayev 1983, 1984, Smit et al. 1992, Lvova et al. 1994, Burlakova 1998, Garton & Johnson 2000), and corresponds with a peak in phytoplankton abundance (Walz 1978a). In midsummer growth rate often decreases (Spiridonov 1971, Walz 1978a, Smit et al. 1992, Stanczykowska & Lewandowski 1995, Allen et al. 1999) and has been attributed to low food concentrations (Walz 1978a), blooms of dinoflagellates (e.g., *Ceratium hirundinella*) that impede filter feeding (Stanczykowska & Lewandowski 1995), high water temperatures (Allen et al. 1999) and spawning (Spiridonov 1971, Lvova 1977, 1980, Karatayev 1983, 1992, Allen et al. 1999). In the autumn, when water temperatures decrease, growth stops (Morton 1969a). In the Uchinskoe Reservoir growth stops when temperatures fall to 10°C (Lvova 1977, 1980) and in the River Rhine at 10° to 15°C (Jantz & Neumann 1992).

Based on a bioenergetics model of zebra mussel growth in the Laurentian Great Lakes, Schneider (1992) predicted positive growth in the spring and fall when high phytoplankton biomass associated with spring and fall turnover coincides with temperatures near the optimum for growth. Even under conditions of high food availability, growth rates in his model typically decline in the beginning of summer and increase again in August and September as temperature begins to decline. Schneider (1992) used Walz's bioenergetic estimates of metabolic parameters for zebra mussels from Lake Constance (Walz 1978d), where the optimal temperature range for growth is 8°C to 15°C. This temperature range is much lower than optimum found by other authors, and therefore more empirical tests of this model are needed before we can assess the generalizability of its predictions.

Location in the Water Column

Dreissena polymorpha grow faster in the water column above the bottom (e.g., on buoys, cages, submerged constructions, floating objects) than on the bottom (Kachanova 1963, Mikheev 1964, bij de Vaate 1991, Smit et al. 1992, 1993, Dorgelo 1993, Burlakova 1998). Yu and Culver (1999) tested the effect of cage loca-

tion in stratified Hargus Lake (Ohio), and found highest growth at their pelagic site (2.5–4 m depth) and in the littoral zone at 2.5 m depth. All mussels held below the thermocline (5-m depth) died before the end of experiment (163 days).

Trophic Conditions

Trophic conditions also affect zebra mussel growth (Table 1). Dorgelo (1993) found that zebra mussels growth rates in Dutch eutrophic lakes Mararsseveen II and Vechten was higher (0.54– 0.59 mm wk^{-1}) than of those grown in mesooligotrophic Lake Masrsseveen I (0.35 mm wk^{-1}), even though there was no difference in mean temperature between these lakes. Jantz and Neumann (1992) found a significant strong correlation ($r_s = 0.80$) between the rate of shell length growth and chlorophyll *a* concentration and between shell growth and temperature ($r_s = 0.82$). However, because these two environmental factors are highly correlated, it is impossible to determine the relative contribution of each of these factors on growth (Jantz & Neumann 1992). In a later study (Jantz & Neumann 1998) they found that shell growth rate and the duration of the growing season were correlated with the quantity of available algal food.

Sprung (1995a) found a strong correlation between zebra mussel shell growth and food conditions (seston concentration). He suggested that this correlation will exist when seston concentrations stay below those at which the intestine is filled to capacity when the animal filters at a maximum rate (Sprung 1995b). Similarly, Schneider et al. (1998) found that the scope for growth under laboratory conditions had a strong positive relationship with food quality.

Water Motion

In areas with constant water current *D. polymorpha* grow faster than in still water (Table 1). Kachanova (1963) found that *D. polymorpha* grow faster on the concrete walls of the canal flowing from Uchinskoe Reservoir than in the reservoir. Mikheev (1964) found that in Kuybyshevskoe Reservoir moderate water currents (up to 0.8 m s^{-1}) facilitate mussel feeding and respiration and *D. polymorpha* grown in water currents reached 27–28 mm, whereas same aged mussels at the same depth out of currents were only 19–20 mm in length. Smit et al. (1993) suggested that water movement seems to have a larger influence on growth than the amount of algal food in the water column. They found that the young-of-the-year zebra mussels in the Rhine River were almost 3 times longer (16 mm) that in Lake Ijsselmeer (6 mm) in spite of lower chlorophyll *a* concentrations in the river (10–42 µg L^{-1} in the river, 34–106 µg L^{-1} in lakes).

However, strong water currents may inhibit *Dreissena* growth. The maximum length of 2-y-old zebra mussels in waterways of the Kuybyshevskaya hydroelectric power plant with constant water currents <0.5 m s^{-1} was 18 mm, and in places with water currents >1.5 m s^{-1} was 13–14 mm (Mikheev 1964).

Wave action can also inhibit *D. polymorpha* growth. Mikheev (1964) found that in the littoral zone of Kuybyshevskoe Reservoir exposed to waves, the average (4–5 mm) and maximum (8–10 mm) length of yearling mussels was almost half that of mussels at the same depth but without waves (7.2 mm mean, 14 mm maximum). He also found that the average length of the young-of-the-year *D. polymorpha* in parts of the Tsimlyanskoe Reservoir exposed to strong waves was 9 mm (maximum 12.5 mm), whereas in

quiet areas at the same depth the average length was 12 mm (maximum 19.2 mm).

Depth

Dreissena polymorpha grow faster in shallow than in the deep parts of a waterbody (Table 1). In Kuybyshevskoe Reservoir the maximum length of yearling mussels at 1–1.5 m depth was 13.7– 14 mm, and at 20 m depth, only 6–7 mm (Mikheev 1964). Similarly, Garton and Johnson (2000) found that in Lake Wawasee zebra mussel growth rate declined 15% per meter between 1–4 m depth. They hypothesized that this decrease was caused by lower temperature and reduced food with depth.

Turbidity

High concentrations of suspended matter in the water negatively affects filtration, ingestion, assimilation and growth potential of zebra mussels (Reeders et al. 1989, Noordhuis et al. 1992, Alexander et al. 1994, Summers et al. 1996, Madon et al. 1998, Schneider et al. 1998). In Dutch lakes, clearance rates of adult 20-mm zebra mussels declined exponentially as dry suspended matter increased from 5–90 mg L^{-1} (Reeders et al. 1989, Noordhuis et al. 1992).

Madon et al. (1998) found that concentrations of suspended inorganic sediment above 1 mg L^{-1}, and a ratio of inorganic to organic fraction of seston higher than 1.71 may cause negative growth. Similar limits were found by Schneider et al. (1998): the scope for growth declined with decreasing food quality and fell below 0 cal mg^{-1} h^{-1} at an organic/inorganic ratio of 0.5. They suggested that high concentrations of suspended inorganic sediment in large turbid rivers represents a difficult growth environment for zebra mussels and that populations in turbid rivers may not stabilize at the very high densities typical of lentic environments.

Year-to-year Variation

The growth rates of *D. polymorpha* in the same waterbody vary significant among years (Lvova 1980, Dorgelo 1993, Chase & Bailey 1999b). Zebra mussels in the Uchinskoe Reservoir with initial shell lengths of 8 mm grew to 21.2 ± 0.29 mm by the end of the growing season in 1967, to 19.5 ± 0.27 mm in 1968, and to 16.8 ± 0.18 mm in 1969 (Lvova 1980). Dorgelo (1993) found the growth rate of *D. polymorpha* in lakes Maarsseveen I and II was significantly lower in the summer of 1986 than in 1985. In a study of growth and production of *D. polymorpha* in lakes St. Clair, Erie and Ontario, Chase and Bailey (1999b) estimated shell production as a part of total production (total production = shell + somatic + gamete production). They found that the site by year interaction (among 5 populations) explained >80% of the variation; differences between sites in production depended on the year examined. Variation in total production depended on variation in somatic and shell production only, as gamete production was relatively constant among years. Chase and Bailey (1999b) hypothesized that, in response to poor environmental conditions, *D. polymorpha* shifts the allocation of resources from growth (somatic and shell) to reproduction. As individuals cannot predict how long adverse conditions will persist, investment in growth may be unprofitable (Chase & Bailey 1999b).

Lakes versus Reservoirs

Although environmental factors that affect mussel growth such as temperature, food availability and other conditions can differ

greatly among waterbodies and among years within the same waterbody, when we compared size-specific growth rates of zebra mussels among studies that all used a similar method (following caged mussels), some patterns emerged. We compared the data for size specific zebra mussel growth from three studies in reservoirs (two different reservoirs, two different years in one reservoir) and six studies conducted in 5 different lakes (4 in Eastern Europe, 1 in North America). We found that the size-specific growth of mussels in reservoirs was consistently higher than that of mussels grown in lakes (Fig. 2). Surprisingly, given the range of likely conditions among water bodies and among years, growth in reservoirs was very consistent ($R^2 = 0.92$). For lakes there was more spread ($R^2 = 0.72$), but the patterns and rates were similar among studies. Data for the growth of uncaged mussels in the Svisloch River are much more similar to mussels in reservoirs, whereas those grown in cages were more similar to mussels in lakes (Fig. 1 B).

LIFE SPAN

Methods to Estimate Longevity

Most of the methods used to estimate longevity of *D. polymorpha* are similar to those used to estimate growth rate: counting annual rings on shells, analysis of the size-frequency distributions and growth under experimental conditions (Table 2).

Counting Annual Rings on Shell

The maximum longevity reported using this method has decreased through time from 17–19 y (Karpevich 1964) to 4–5 y
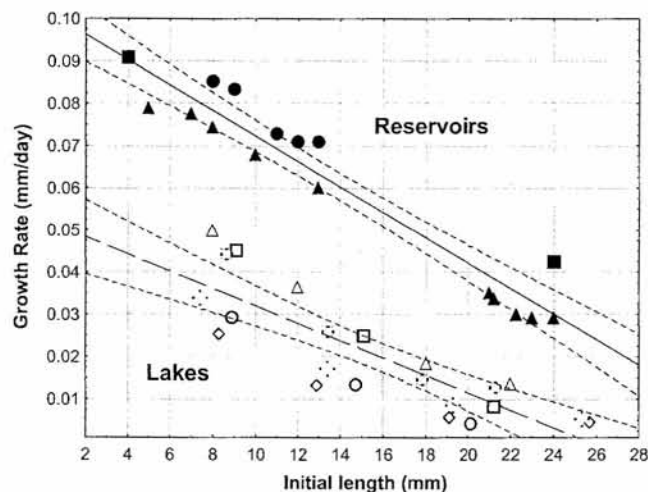

Figure 2. Growth rates of *Dreissena polymorpha* in reservoirs (filled symbols) and lakes (open symbols, stars and crosses). In all studies, zebra mussels were kept in cages and followed through time. Regression lines are for size-specific growth rate in reservoirs (solid line, Y = 0.102 − 0.003*X, $R^2 = 0.92$, $P < 0.001$) and lakes (dashed line, Y = 0.053 − 0.002*X, $R^2 = 0.72$, $P < 0.001$) with 95% confidence intervals. The two regression lines significantly differ in slope ($P = 0.013$) and their 95% confidence intervals do not overlap. Data sources are: ● Uchinskoe Reservoir, 1967 and ▲ Uchinskoe Reservoir, 1968 (Russia)—Lvova (1980), ■ Tsimlyanskoe Reservoir (Russia)—Miroshnichenko (1990), ○ Lake Lukomskoe, unheated zone and □ Lake Lukomskoe, heated zone (Belarus)—Karatayev (1983), △ Mikolajskie Lake (Poland)—Stanczykowska & Lewandowski (1995), ◇ Lake Naroch (Belarus) —Burlakova (1998) and + Lake Myastro (Belarus)–Burlakova (1998), * Lake Wawasee (US)—Garton & Johnson (2000).

(Draulans & Wouters 1988). Through time some authors have revised their earlier estimates of zebra mussel longevity. Stanczykowska (1964) initially reported a maximum longevity for *D. polymorpha* of 10–12 y; 11 y later she revised her estimates from these same data to 5 y (Stanczykowska 1975, 1976b). Kachanova (1963) (this author published later under the name Lvova-Kachanova and Lvova) reported that the maximum life span of zebra mussels in the Uchinskoe Reservoir was 6–11 y, and later revised this estimate to 4 y (Lvova 1980, Table 2). Although the advantage of this method is that it allows an estimate of the age structure of a population by measuring *D. polymorpha* at a single point in time, as discussed earlier, it is very difficult to separate annual rings formed during winter from other rings.

Analysis of Size-frequency Distributions

For this method the numbers of peaks on a size-frequency histogram are counted, assuming that each peak represents an age class. However, as discussed earlier, age classes may not have distinct sizes, making it difficult to estimate longevity based on size-frequency distributions.

Growth Under Experimental Conditions

Usually authors keep mussels of different initial sizes in cages for a limited period (1–4 y), and then the obtained growth rates are used to estimate the time to reach the maximum size found in the population. However keeping mussels in cages can produce different types of artifacts discussed earlier, which may affect observed growth rates and, therefore, estimates of mussel longevity.

Factors Affecting Longevity

To our knowledge, the first estimates of the longevity of zebra mussels were reported by Karpevich (1952) and Clarke (1952) (Table 2). Karpevich (1952) counted annual rings on shells and estimated zebra mussel longevity in the Volga River as 18 y. In contrast, Clarke (1952) using unpublished data from J. Wilhelmi (study site not mentioned) found three peaks in the size-frequency distribution of *D. polymorpha* and suggested that typical longevity is about three years. Overall, the longevity of *D. polymorpha* estimated by different authors over the last 50 y varies from 2–19 y. However, the maximum sizes of *D. polymorpha* reported by these authors are similar (Table 2). This contradiction supports a hypothesis that the reported differences in longevity may be explained to a large extent by the artifacts of the methods used. This suggestion is also supported by the fact that the average *D. polymorpha* longevity estimated by counting annual rings on shells (7.4 ± 0.9) is significantly different from average longevity estimated by analysis of size-frequency distribution (3.3 ± 0.3, $P < 0.001$, 2-sided *t*-test) (Table 2). Alternatively, zebra mussels may have a fixed maximum size, and local conditions that affect growth rates determine longevity—fast growing mussels will live for shorter periods of time, whereas slow growing mussels will live longer. Therefore, it is unclear how much of this variability in longevity is natural or is caused by the artifacts of the methods used and definitely requires future investigation.

GENERAL FINDINGS AND FUTURE DIRECTIONS

Although many generalizations can be made about the growth rate and longevity of *D. polymorpha*, and the impacts of various environmental factors on these parameters, the answers to many questions are far from clear. The most important questions that

need to be addressed, problems that need to be solved, and targets for future study are:

Methodological Problems

Growth rate and longevity of *D. polymorpha* have been estimated by using four different methods, most of which have serious methodological problems. Thus, different estimates of *D. polymorpha* growth rates and longevity are affected not only by differences in environmental conditions but also by artifacts of the methods used. Following the growth of undisturbed *D. polymorpha* will provide more reliable data on growth potential and variability among different waterbodies with different environmental conditions. Following and subsampling mussels that naturally settle on experimental surfaces through time provides the control and ease found in experimental studies with the growth rates expected from natural populations.

Co-effects of Environmental Factors

Dreissena polymorpha growth rates depend on water temperature, season of the year, location in the water column, food availability, oxygen concentrations, water velocity and various other environmental factors (Table 1). However, it is difficult to separate the independent effects of each of these factors, especially in natural waterbodies where most of these factors will covary. Several factors may have additive or synergistic effects, making it difficult to study the effect of a single factor. Separation of the effects of single and combined factors on growth is essential.

Temperature

The upper temperature limit for zebra mussel growth seems to be 30°C to 32°C, and the lower temperature limit ~10°C to 12°C (Kachanova 1961, Morton 1969a, 1969b, Alimov 1974, Karatayev, 1983, Mackie 1991, Jantz & Neumann 1992). However, some studies have found much lower limits (bij de Vaate 1991, Smit et al. 1992). Differences among studies may be a result of local effects but clearly calls for further study.

Growth in Different Types of Waterbodies

There seems to be substantial differences in growth between mussels in reservoirs and lakes—mussels grow much faster in reservoirs than lakes. Experiments that directly test the relative contributions of environmental factors versus the type of water body and what factors are different between reservoirs and lakes are clearly called for to answer this question. It may be that reservoirs provide a better overall growth environment in terms of temperature, nutrition, and water motion than do natural lakes or rivers.

Longevity

The reported longevity of *D. polymorpha* varies from 2 to 19 y. It is critically important to understand to what extent this variation is caused by biological variability, environmental conditions and what amount of the variation is caused by the methods used. In addition to the basic value of understanding the variability in *D. polymorpha* longevity, it is also important if we are to predict population dynamics, spread or to develop control methods for this important invader.

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