

Primary Research Paper

Changes in the distribution and abundance of *Dreissena polymorpha* within lakes through time

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Received 22 December 2005; in revised form 19 April 2006; accepted 26 April 2006; published online 23 August 2006

Key words: zebra mussels, *Dreissena polymorpha*, density, biomass, dynamics, substrate

Abstract

Dreissena polymorpha population densities and biomass were followed in three Belarusian lakes with different trophic status over a 12-year period subsequent to initial colonization. In all three lakes zebra mussel population densities did not change once they reached a maximum. Application of the Ramcharan et al. [1992. Canadian Journal of Fisheries and Aquatic Sciences 49: 2611–2620] model for predicting population dynamics of zebra mussels was accurate for two of the three lakes studied. Population density appears to depend on the time since initial colonization, relative abundance of substrate available for colonization, lake morphometry and trophic type. Zebra mussel distribution within lakes was highly patchy, but the degree of dispersion decreased over time after initial colonization, which may be a result of saturation of suitable substrates by zebra mussels as populations increase and reach carrying capacity. In lakes where submerged macrophytes are the dominant substrate for zebra mussel attachment, populations may be less stable than in lakes with a variety of substrates, which will have a more balanced age distribution, and be less impacted by year to year variation in recruitment. *Dreissena polymorpha* usually reach maximum population density 7–12 years after initial introduction. However, the timing of initial introduction is often very difficult to determine. Both European and North American data suggest that zebra mussels reach maximum density in about 2–3 years after populations are large enough to be detected.

Introduction

Understanding the population dynamics of invaders is critical for predictions about their effects on ecosystems. Several hypotheses have been proposed for the dynamics of populations of new invaders. One hypothesis is that invader populations will develop very slowly initially (invisible development), and then increase rapidly and steadily (boom) until some equilibrium density is reached (stabilization) (Zenkevich, 1940;

Stanzykowska, 1978; Ramcharan et al., 1992). A second hypothesis, “boom and bust” dynamics, predicts a collapse following very high density, however, recent work suggests that this type of pattern may be a minor phenomenon in invasion biology (Simberloff & Gibbons, 2004). The third hypothesized type of dynamics is oscillatory behavior or dramatic temporal variation in population dynamics among invaders (reviewed in Parker et al., 1999). At present, we have limited information on the population dynamics of

invaders through time, preventing generalizations about which of these hypotheses is most common among invader types or habitats.

Zebra mussels (*Dreissena polymorpha* (Pallas)) are important invaders in aquatic systems, can become enormously abundant, and have caused significant ecological and economic impacts both in Europe and North America (reviewed in Nalepa & Schloesser, 1993; Karatayev et al., 1997, 2002). The extent and magnitude of these impacts are often directly related to mussel abundance, however, population densities are often not stable and can fluctuate widely (Ramcharan et al., 1992; Stanczykowska & Lewandowski, 1993) and densities do not always correlate with total biomass (Young et al., 1996). Based on literature reports of European populations of zebra mussels and the characteristics of lakes they invade, Ramcharan et al. (1992) generated a statistical model to predict population dynamics of zebra mussels. They found that the best predictors of patterns of population dynamics were the log of the lake area and concentrations of phosphates and calcium. To date this model has not been tested. To test their model and other predictions about zebra mussel (or other aquatic invader) population dynamics, populations must be followed at single locations through time. However, there are extremely few studies that have followed zebra mussel populations from initial invasion through time within a single waterbody. In addition, population estimates are frequently based on small sample sizes, or on samples taken from single or few places within a waterbody, making it difficult to estimate whole population abundance or distribution among habitats. Finally, densities alone are inadequate measures for understanding the dynamics of populations or estimating impacts, especially for zebra mussels, as both filtering and reproduction increase with body size (Young et al., 1996; Stoeckel et al., 2004).

In addition to temporal fluctuations of a population within particular waterbody, the average population density and biomass of zebra mussels is strikingly variable among different waterbodies (e.g., Stanczykowska, 1975; Ramcharan et al., 1992; Stanczykowska & Lewandowski, 1993; Karatayev et al., 1998). The abundance of *D. polymorpha* in a waterbody may depend on many factors including time since initial coloni-

zation, bottom substrate type, trophic state, and water quality (reviewed in Karatayev et al., 1997; 1998), among many other factors. However, it is still not known to what extent each of these factors controls zebra mussel population densities, and our inability to predict population size in a waterbody limits our ability to predict the magnitude of impact on the ecosystems they invade. We hypothesize that the major factors affecting the size of population will be (1) time since initial colonization; (2) relative abundance of different substrates for zebra mussel attachment; and (3) waterbody morphometry and trophic type.

To test these hypotheses, we conducted long-term research on the Narochanskie Lakes in Belarus, including mesotrophic Lake Naroch, eutrophic Lake Myastro and highly eutrophic Lake Batorino, which were colonized with zebra mussels in mid-1980s. These lakes are among the best-studied lakes in the former Soviet Union (Winberg, 1985; Ostapenya et al., 1993, 1994a,b) thus provide an excellent opportunity to address hypotheses about the patterns of population dynamics of *D. polymorpha* and test the predictions of the Ramcharan et al. (1992) model.

Materials and methods

Study area

We examined the population density and dynamics of zebra mussels in the Narochanskie Lakes, lakes Naroch, Myastro and Batorino, in the Republic of Belarus (Table 1, Fig. 1).

Lake Batorino, the first (upper) lake in the system, is highly eutrophic, and connected to Lake Myastro by a narrow (5–6 m width) stream overgrown by macrophytes (Fig. 1). Lake Batorino has the largest watershed of the three lakes (Table 1) (Ostapenya et al., 1994b). The lake shoals are silted to the shoreline; sandy sediments are quite rare. Emergent macrophytes (dominated by *Scirpus lacustris*, *Phragmites australis* and two species of *Typha*) are found down to 1.6 m. Greater than 60% of the bottom area is covered with silt (Ostapenya et al., 1994b).

Eutrophic Lake Myastro is the second lake in the Narochanskie Lakes system and is connected to Lake Naroch by the stream Skema (0.2–1.5 m

Table 1. Physical and chemical characteristics of the Narochanskie Lakes (Ostapenya et al. 1993, 1994a, b)

	Surface area (km ²)	Volume (10 ⁶ m ³)	Maximum depth (m)	Average depth (m)	Secchi depth (m)	pH	Ca (mg l ⁻¹)	PO ₄ (mg P l ⁻¹)	% of lake area in the littoral zone	Watershed area (km ²)	% of watershed that is agricultural land
Lake Naroch	79.6	710.4	24.8	9.0	6.0	8.2	32.9	0.0016	30	58.8	47
Lake Myastro	13.1	70.0	11.3	5.4	3.9	8.4	32.9	0.0032	18	34.6	36
Lake Batorino	6.3	18.7	5.5	3.0	1.3	8.5	43.0	0.0029	22	86.6	20

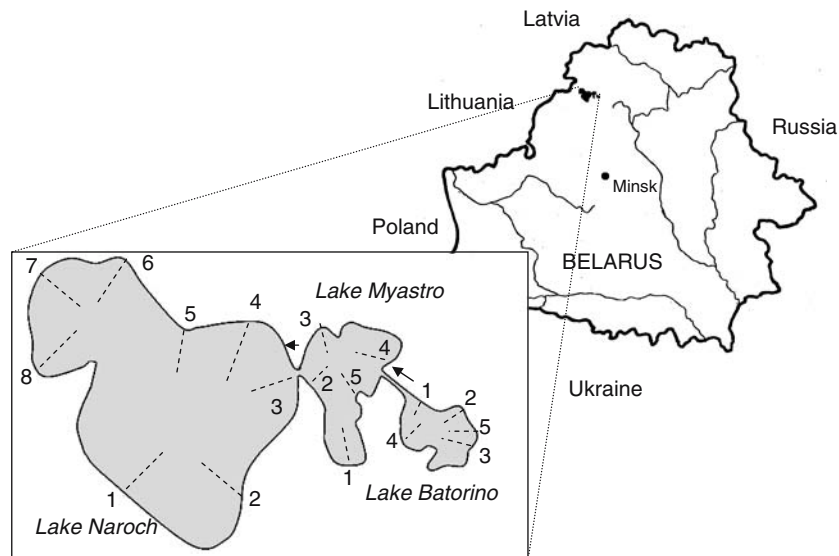


Figure 1. Map of Belarus and the Narochanskies Lakes system. For each lake, the locations of sampled transects are indicated.

deep, up to 10 m wide) (Fig. 1). The littoral zone of the lake is covered with silty sand; rocky substrates are less common. Emergent macrophytes occur up to 1.3 m depth, while submerged macrophytes form a belt 5–30 m wide down to 4.5 m depth (Gigevich, 1985).

Mesotrophic Lake Naroch is the largest lake in Belarus (Table 1, Fig. 1). A large portion of the lake is shallow. Submerged macrophytes, mainly *Chara* and *Elodea*, are very abundant in the littoral zone, are found down to 8 m, and are responsible for >90% of total annual primary production in this lake (Winberg, 1985). The main substrate in the littoral zone is sand, with rocky areas on the northern part of the lake.

Lake Myastro was the first lake where *D. polymorpha* was found in 1984; most likely, adult mussels were transported to this lake on fishing tackle from commercial fisheries (Burlakova, 1998). Zebra mussels were found in Lake Batorino around the same time, in the mid-1980s (Ostapenya et al., 1994b). A few years later, in 1989, zebra mussels were found in Lake Naroch (Ostapenya et al., 1993).

As all of the lakes belong to the same system, they have similar chemical composition (Ostapenya et al., 1993, 1994a, b; Table 1), and all are suitable for zebra mussels in terms of calcium and pH (Burlakova, 1998).

Sampling protocol

All samples used to determine the distribution and abundance of *D. polymorpha*, were collected in July or August. In Lake Naroch, we collected samples from eight permanent transects in 1990, 1993, 1994, 1995 and 1997 (Fig. 1). We sampled five permanent transects in lakes Myastro and Batorino in 1993 and 1995 (Fig. 1). For all years for all lakes, transects were initiated on the shore and ran perpendicular to the shore toward the center of the lake. Transects were distributed around each lake based on bathymetric maps, maps of bottom sediments, and distribution of macrophytes such that they included all major habitat types within each lake and covered all regions of the lake. For each transect, up to 10 replicate samples were collected at 0.5, 1, 1.5, 2, and 3 m depth and then at an interval of 1 or 2 m down to the maximum depth where *D. polymorpha* was found. For all samples in all lakes collected from 1990–1995, 0.25 m² quadrat samples were collected by hand down to 2 m depth; however in Lake Naroch in 1997, quadrat samples were collected down to 7 m with the aid of a surface supplied air diving system (Pioneer 230 X, Brownie's Third Lung). Within each quadrat, the surface sediment down to 5 cm was collected, except for pure sand sediments when the visibility was

sufficient to determine that there were no mussels within a quadrat. Deeper water benthic samples were collected with an Eckman grab on soft sediments or a Peterson grab on hard sediments (both 0.025 m²). In 2002, due to time limitations, samples were collected from 1 and 2 m depth only from five of the eight permanent transects in Lake Naroch and three of five permanent transects in lakes Myastro and Batorino. Densities were estimated per unit area of the lake bottom rather than per unit area of substrate, as this allows the best estimates of total population size and ecological impacts.

For all quadrat and grab samples, sediments were washed through a 550 μ m mesh, and within 48 h of sampling all zebra mussels larger than 1 mm maximum dimension were counted, opened with a scalpel to remove water from the mantle cavity, and the total sample was weighed to the nearest 0.01 g after being blotted dry on absorbent paper (wet weight, soft tissue plus shell). For zebra mussels, because of their thin shell and seasonal changes in soft mass due to spawning, total wet weight has been determined to be the most stable measure of mass for both reproductive potential and filtering impact (Karatayev, 1983).

Statistical analysis

Population dynamics

To test among different hypotheses about population dynamics of invader, we analyzed the changes in density and biomass of *D. polymorpha* populations in Narochanskies lakes through time. For this analysis, we used the density and biomass data from 1 and 2 m depth samples for all three lakes that were from transects resampled in 2002. Because many samples contained no zebra mussels (density = 0), we used the Friedman test, a non-parametric alternative to a one-way repeated measures analysis of variance (Zar, 1996).

To estimate the average density and biomass of *D. polymorpha* for the total area of each lake, we calculated weighted averages for each transect (using averages for each depth), and then calculated the average from all transects sampled. In addition, we calculated the percentage of all samples in each lake that contained zebra mussels.

To compare the variability in density and biomass of zebra mussels, we used modified variance-ratio test for difference between variances in two correlated populations (Zar, 1996) on all pooled data for each lake and on annual average data from Lake Naroch.

To test if the type of substrate in a lake determines the zebra mussel population size, we used data on density and biomass of *D. polymorpha* on different substrates in each of the lakes. To compare density and biomass of *D. polymorpha* on different substrates within and among lakes, we used Kruskal–Wallis tests separately for each lake and multiple comparisons of mean ranks for all groups (Zar, 1996). To determine how substrate type affects the mass of *D. polymorpha*, we compared the average mass of mussels on different substrates using 2-way ANOVA on log-transformed average mass following with HSD test. The average mass of *D. polymorpha* individuals in a sample was calculated by dividing the total mass of *D. polymorpha* by the number of mussels in each sample.

To determine the dispersion pattern of zebra mussels in each lake, we calculated the Green's coefficient of dispersion from our quadrat samples across depths. This index has been shown to be relatively unaffected by population density and sample size, and ranges from -1.0 (uniform) to $+1.0$ (clumped); random patterns yield zero values (Krebs, 1999).

Predictions of Ramcharan, Padilla & Dodson model

Lake area and multi-annual averages of concentrations of phosphates and calcium in lakes Naroch, Myastro and Batorino (Ostapenya, 1993; 1994a, b) were used in the discriminant function analysis developed by Ramcharan et al. (1992) to predict population fluctuations. To calculate the canonical discriminant function, we used coefficients given by Ramcharan et al. (1992) (-0.115 for Ca, 12.783 for PO₄, 0.666 for log (surface area), and 3.788 as a constant).

Time since initial colonization to maximum population size

To compare the population dynamics in the Narochanskies Lakes with published data, we collected all available data from literature. We found only two other waterbodies where the time of

Table 2. The abundance of *Dreissena polymorpha* on different substrate types in the three Narochanskies Lakes

Lake	Sand	Rocks	Semi-submerged macrophytes	Submerged macrophytes	Shells*	Silt	Average for the lake
<i>Lake Naroch</i>							
1990	<i>N</i> 14 ± 8	34 ± 6	n.r.	27 ± 19	Absent	0	7.4 ± 3.0
	<i>B</i> 3 ± 2 (31)	11 ± 2 (2)		4 ± 3 (15)		0 (6)	1.5 ± 0.6 (54)
1993	<i>N</i> 812 ± 371	964 ± 236	n.r.	2681 ± 550	Absent	40 ± 40	763 ± 149
	<i>B</i> 208 ± 95 (20)	156 ± 52 (2)		259 ± 57 (21)		5 ± 5 (6)	99 ± 30 (49)
1994	<i>N</i> 104 ± 45	1165 ± 567	n.r.	2794 ± 947	2340 ± 2180	0	758 ± 240
	<i>B</i> 24 ± 8 (81)	1348 ± 916 (3)		293 ± 99 (33)	554 ± 542 (2)	0 (7)	115 ± 30 (126)
1995	<i>N</i> 159 ± 53	2128 ± 372	n.r.	7050 ± 1951	n.r.	152 ± 103	1521 ± 451
	<i>B</i> 33 ± 12 (72)	787 ± 255 (5)		366 ± 91 (29)		26 ± 18 (10)	107 ± 44 (116)
1997	<i>N</i> 190 ± 31	2647 ± 559	n.r.	3199 ± 408	1296 ± 147	0	922 ± 238
	<i>B</i> 52 ± 9 (134)	609 ± 126 (12)		286 ± 31 (115)	371 ± 34 (3)	0 (21)	99 ± 20 (285)
<i>Lake Myastro</i>							
1993	<i>N</i> 2105 ± 1088	n.r.	n.r.	1499 ± 808	n.r.	133 ± 133	747 ± 300
	<i>B</i> 1393 ± 863 (14)			501 ± 326 (12)		82 ± 82 (15)	402 ± 187 (41)
1995	<i>N</i> 947 ± 297	1644 ± 806	n.r.	2593 ± 942	1640	0	645 ± 147
	<i>B</i> 452 ± 245 (25)	1024 ± 567 (4)		330 ± 187 (8)	2324 (1)	0 (7)	288 ± 118 (45)
<i>Lake Batorino</i>							
1993	<i>N</i> 987 ± 414	n.r.	1300 ± 700	n.r.	n.r.	0	227 ± 54
	<i>B</i> 446 ± 214 (18)		245 ± 155 (2)			0 (18)	79 ± 13 (38)
1995	<i>N</i> 127 ± 98	n.r.	1751 ± 622	n.r.	n.r.	78 ± 75	262 ± 88
	<i>B</i> 56 ± 46 (13)		679 ± 335 (8)			24 ± 23 (16)	100 ± 36 (37)

N = density (mussels m⁻²), and *B* = biomass (g m⁻²). Cell values are means ± SE, sample size in parentheses, n.r. – not recorded. The data are for all depths and transects sampled in 1990–1997. *A substrate formed of dead zebra mussel shells that appeared in the lakes subsequent to zebra mussel invasion.

introduction was known, and the whole lake was sampled using similar sampling methods in multiple years: Lake Lukomskoe, Belarus (Karatayev, 1983), and Uchinskoe Reservoir, Russia (Lvova, 1980). Although there are several published studies from Europe and North America, they only include the dynamics of zebra mussel populations after they reach some detectable level, and populations are growing exponentially; the time of invasion is either not known or not reported.

Lake morphometry and trophic type

To compare the depth distribution of *D. polymorpha* among lakes, we calculated the proportion of the total population of mussels within each lake at each depth and then tested for differences with a Fisher–Freeman–Halton test (a generalization of the Fisher's exact test for *r* by *c* contingency table) with asymptotic *p*-value to test for homogeneity in contingency tables (Freeman & Halton, 1951).

For all statistical tests we used Statistica software (STATISTICA version 6, StatSoft, Inc. 2001) and StatXact-4 (version 4.0.1, Cytel Software Corp.). Effects were considered statistically significant at *p* < 0.05. When multiple tests were conducted on the same data, we used a sequential Bonferroni correction to adjust the critical alpha considered for statistical significance (Rice, 1989). Where appropriate, we present the critical alpha (α) with the results of each statistical test.

Results

Population dynamics

Lake Naroch

When Lake Naroch was first sampled, in 1990, the average density of *D. polymorpha* was only 7.4 m⁻², average biomass 1.5 g m⁻², and mussels were found in only 22% of all samples collected.

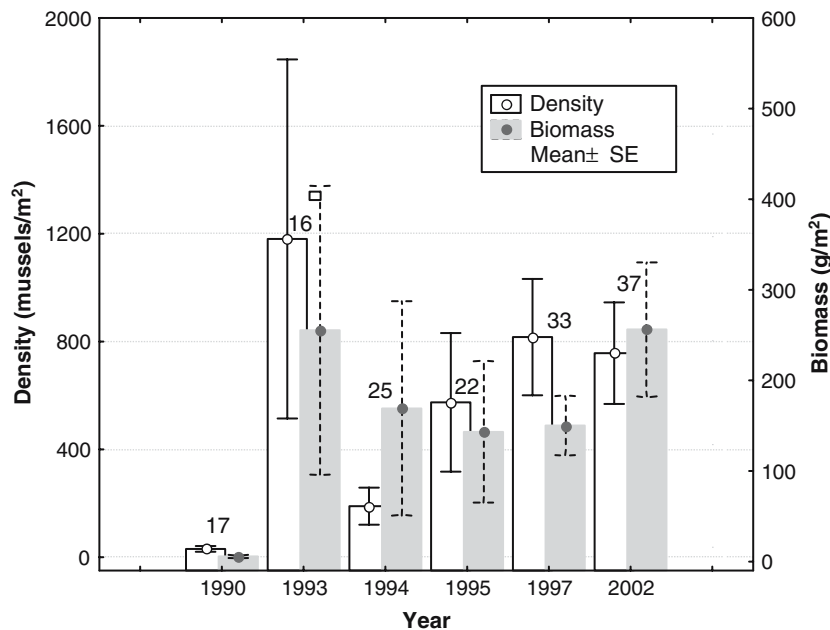


Figure 2. Density (open bar) and biomass (gray bar) of zebra mussels in Lake Naroch at 1 and 2 m depth for transects monitored in 1990, 1993, 1994, 1995, 1997 and 2002. Means \pm standard error. Number of samples are above bars.

By 1993 the average density across the whole area of the lake increased 100 times and biomass increased 68 times (Table 2). From 1993 to 2002 zebra mussels were found in 46–80% of all samples taken. The increase in density and biomass of *D. polymorpha* at 1 and 2 m depth in Lake Naroch from 1990 to 1993 was significant (density: $p < 0.006$, critical $\alpha = 0.0125$; biomass: $p < 0.015$, critical $\alpha = 0.0167$, Friedman test) (Fig. 2). However, there were no significant changes in the density and biomass of *D. polymorpha* at 1 and 2 m depth from 1993 to 2002 (density: $p > 0.35$; biomass: $p > 0.60$, Friedman test) (Fig. 2). Variability in zebra mussel density was significantly larger than in biomass ($p \ll 0.001$ for all raw data and annual averages, modified variance-ratio test).

In 1990, just after initial colonization, both zebra mussel density and biomass were low and did not vary among substrates (density: $p = 0.056$, critical $\alpha = 0.0167$; biomass: $p = 0.039$, $\alpha = 0.025$, Kruskal–Wallis test) (Table 2). Later in the invasion, from 1993 to 2002, the density and biomass of zebra mussels were always significantly different on different substrates ($p < 0.001$, $\alpha = 0.01$, Kruskal–Wallis test), with the highest densities found on submerged

macrophytes ($p < 0.001$, $\alpha = 0.0083$, multiple comparisons of mean ranks). The lowest average mass of Naroch mussels was found on submerged macrophytes ($p < 0.0001$, $\alpha = 0.0063$, unequal n HSD test).

The dispersion pattern of zebra mussels changed as populations grew: Green's coefficient of dispersion decreased with time indicating that zebra mussels became less clumped (all lakes: $p = 0.014$, $\alpha = 0.017$, Kruskal–Wallis test; Naroch Lake: Spearman $r = -0.51$, $p = 0.0015$, $\alpha = 0.0125$).

Lake Myastro

Dreissena polymorpha was first found in Lake Myastro in 1984. The density and biomass of *D. polymorpha* in Lake Myastro at 1 and 2 m depth did not change significantly from 1993 over the following 9 years (density: $p > 0.30$; biomass: $p > 0.95$, Friedman test) (Table 2). As with Lake Naroch, variability in zebra mussel density was significantly larger than in biomass (all raw data: $p = 0.0003$, modified variance-ratio test). The density and biomass of *D. polymorpha* were significantly different among substrates (1993: density $p = 0.0042$, biomass $p = 0.0034$, $\alpha = 0.025$; 1995, density $p = 0.0035$, biomass $p = 0.0017$,

$\alpha = 0.025$, Kruskal–Wallis test), with the highest average density and biomass on sand and sandy-rocky sediments (Table 2).

Lake Batorino

Zebra mussels were found in Lake Batorino in the mid-1980s. From 1993 to 2002 the density and biomass of *D. polymorpha* at 1 and 2 m depth did not significantly change in Lake Batorino ($p > 0.20$; biomass: $p > 0.05$, Friedman test). Again, variability in zebra mussel density was significantly larger than in biomass (all data: $p < 0.001$, modified variance-ratio test). The density and biomass of *D. polymorpha* were significantly different among substrates (1993: density $p = 0.0001$, biomass $p = 0.0002$, $\alpha = 0.025$; 1995: density $p < 0.0001$, biomass $p < 0.0001$, $\alpha = 0.025$, Kruskal–Wallis test), with the highest densities and biomass on submerged portion of semi-submerged macrophytes (Table 2). There was no significant difference in the average mass of *D. polymorpha* among substrates in Lake Batorino, which lacked submerged macrophytes (year $p = 0.53$, substrate $p = 0.60$, year \times substrate $p = 0.89$, 2-way ANOVA).

Predictions of Ramcharan, Padilla & Dodson model

The discriminant function Ramcharan et al. (1992) developed to distinguish between lakes with variable and constant zebra mussel populations uses the log surface area of a lake, phosphate concentration (PO) and calcium. The centroid value of the canonical discriminant function for the group of lakes with constant zebra mussel populations was 0.928, and -0.591 for the group of lakes with variable zebra mussel populations. The values of the discriminant function for lakes Naroch (1.29) and Myastro (0.79) predicted constant populations. For Lake Batorino the value was negative (-0.59), predicting a variable zebra mussel population.

Time since initial colonization to maximum population size

Zebra mussels were first noticed in Lake Naroch in 1989. The largest mussel found in 1990 was about 4-years-old (Burlakova, 1998), indicating the lake was invaded ~ 1986 . Thus, the latency period for

the *D. polymorpha* population (the time between initial colonization and initial detection) in Lake Naroch was ~ 3 years, and the time to maximum population density (1983) was 7 years (Fig. 3). In general, zebra mussels reached maximum population density and biomass 7–12 years after their initial invasion in the other Narochanskies Lakes, Lake Lukomskoe, and Uchinskoe Reservoir (Fig. 3). However, in contrast to the date of initial detection, the time of initial invasion is rarely known. Using comparable data from different waterbodies on different continents, we found that time from initial detection to maximum population density of zebra mussels was 2–3 years (Table 3).

Lake morphometry and trophic type

For all three lakes the depth-density distribution (for 0–5 m depth, the maximum depth of Lake Batorino) was significantly different in 1993 and 1995 ($p < < 0.001$, $\alpha \geq 0.0056$, Fisher–Freeman–Halton test). For Lake Naroch the depth distribution of *D. polymorpha* was significantly different among all sampled years when all years were considered together ($p < 0.001$, $\alpha = 0.0056$), but was similar in 1995 and 1997 ($p = 0.38$, Fisher–Freeman–Halton test).

The depth-distribution of *D. polymorpha* in mesotrophic Lake Naroch and eutrophic Lake Myastro was bell-shaped, with the highest densities and biomass between 4 and 6 m depth (Figs. 4 and 5), the depths with maximum abundance of submerged macrophytes. This pattern was different in highly eutrophic Lake Batorino, where there were no submerged macrophytes. In this lake semi-submerged macrophytes (the main substrate for zebra mussels) were abundant only to 1.6 m depth, and the rest of the bottom was covered with mud (Fig. 5).

Discussion

Population dynamics

Our data showed that populations of zebra mussels were fairly stable after they reached maximum in all three lakes. The average density of *D. polymorpha* in all lakes varied significantly more than biomass. Although most researchers use density (numbers of mussels per area) as the only popu-

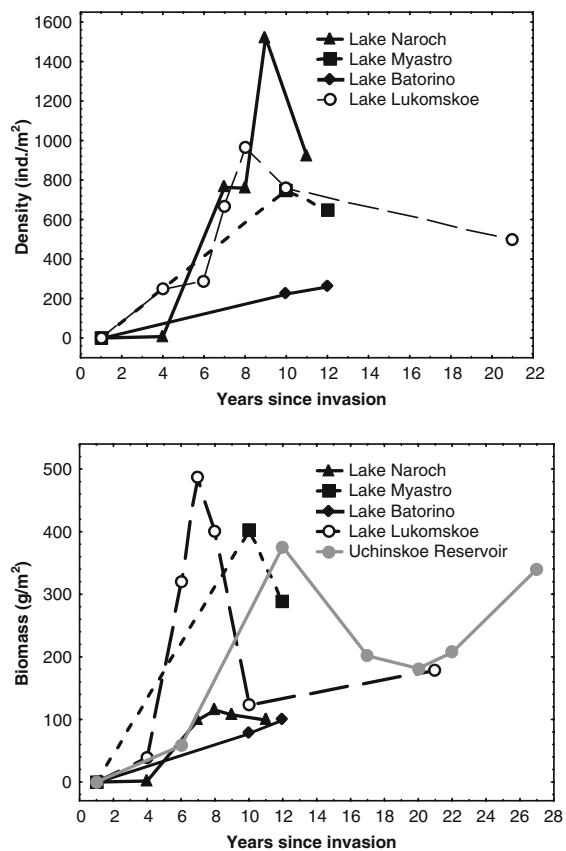


Figure 3. Average density and biomass of zebra mussels in the Narochanskies Lakes, Lake Lukomskoe (from Karatayev, 1983) and Uchinskoe Reservoir (Lvova, 1980) in different years since initial invasion.

lation parameter, the impacts of zebra mussels are more likely to be tied to biomass than numbers of mussels. Biomass and density are often decoupled

because of differences in size frequency distributions among populations (Young et al., 1996). For example, in Lake Naroch the density of *D. polymorpha* was highest in 1995, but the average biomass was highest in 1994. The high densities in 1995 were due to a large number of young mussels in the population: the average mass of a mussel in 1995 was smaller than in all other years (153 vs. 180–265 in other years). As a population parameter, biomass is probably a better indicator of ecological effects and population reproductive capacity, and will dampen transient fluctuations among year classes of mussel.

In all three lakes, mussel populations did not change significantly after they reached maximum population densities and biomass, indicating that they may be at carrying capacity. In contrast, in the Hudson River Strayer and Malcom (2006) reported 2–4 year cycles in zebra mussel abundance over 13 years. However, it is likely that zebra mussel population dynamics in rivers will be different than in lakes as they are open, receiving larvae from upstream and losing larvae through outflow.

The Narochanskies lakes differ in trophic status, and as a result, in the amount of food available to *D. polymorpha* populations. In addition, densities were found to be highest in meso-oligotrophic Lake Naroch and the lowest in eutrophic Lake Batorino (Table 2). These patterns suggest that carrying capacity was set by substrate availability rather than food. In terms of numbers, the densest populations were found in Lake Naroch, especially on submerged macrophytes, where the density was

Table 3. The number of years from first detection to maximum population density of zebra mussels in different waterbodies

Waterbody	First found	Reached maximum	Years	Author
Lake Balaton, Hungary	1932	1934	2	Sebestyen (1937)
Kuybyshevskoe Reservoir, Russia	1956	1958	2	Lyakhov & Mikheev (1964)
Kamskoe Reservoir, Russia	1960	1962	2	Gromov (1965)
Lake Lukomskoe, Belarus	1972	1975	3	Karatayev (1983)
Lake Naroch, Belarus	1989	1993	4	This study
Long Point Bay, Lake Erie	1990	1992	2	Petrie & Knapton (1999)
Saginaw Bay, Lake Huron	1990	1992	2	Nalepa et al. (1995)
Hudson River, New York	1990	1992	2	Strayer et al. (1996)
Seneca River, New York	1991	1993	2	Effler & Siegfried (1994)
Oneida Lake, New York	1991	1992	1	Mellina et al. (1995)
St. Lawrence River sites, Canada	1992	1994–1995	2–3	Ricciardi et al. (1997)

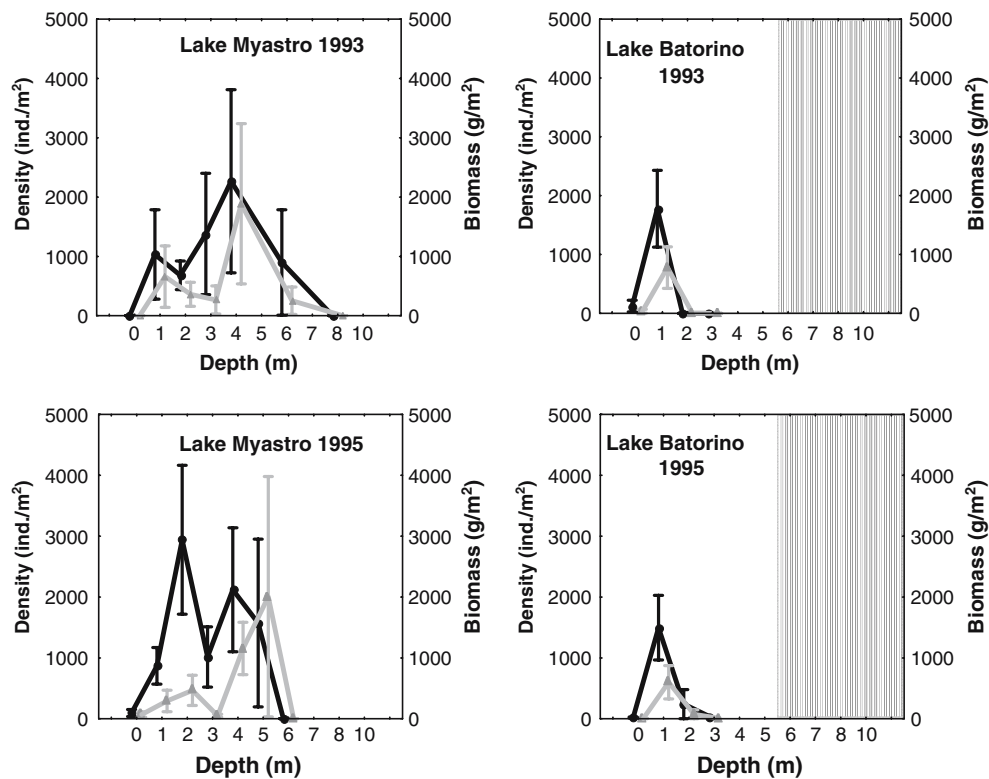


Figure 4. Density (black line) and biomass (gray line) of zebra mussels at each depth sampled in Lake Myastro and Lake Batorino in 1993 and 1995. Means \pm standard error. Lake Batorino has a maximum depth of 5.5 m.

dominated by small mussels, providing a relatively low biomass. Macrophytes die back annually, and attached zebra mussels fall to the bottom and usually die as they are covered by mud and suffer periods of low oxygen (Lewandowski, 1983; Karatayev et al., 1998). The highest average biomass was found in eutrophic Lake Myastro (Table 2), which provided more stable substrates for mussel attachment, and thus a more stable population of larger mussels. The main substrate for zebra mussel attachment in Lake Batorino was semi-submerged macrophytes growing up to 1.5 m depth. Therefore *D. polymorpha* occupied only a narrow zone in the littoral area. Semi-submerged macrophytes are considered to be one of the best substrates for zebra mussel attachment (reviewed in Karatayev et al., 1998) as their stems persist for several years allowing attached mussels to survive. Most of the bottom in deeper area of the lake (60% of the whole bottom) is covered by silt, the poorest substrate for zebra mussels (Zhadin, 1946; Karatayev et al., 1998), and no zebra mussels were

found in this area. Therefore, although in Lake Batorino zebra mussels were limited to a narrow belt along the shore line, the average biomass in the lake was quite high.

The notion that zebra mussels are primarily substrate limited and reached carrying capacity is supported by our finding that the degree of dispersion decreased over time after initial colonization. This decrease in patchiness is likely a result of saturation of suitable substrates as populations increase. These data illustrate the importance of extensive sampling throughout a lake, especially early during an invasion. The more patchy the population, the more difficult it will be to obtain accurate estimates of population density and size. As populations of zebra mussel develop, they also generate new substrate – dead zebra mussel shells, which are subsequently colonized. By 1994–1995 mussel shells had accumulated in lakes Naroch and Myastro at depths of 4–7 m, providing mussels with a new, more stable substrate for attachment (Table 2).

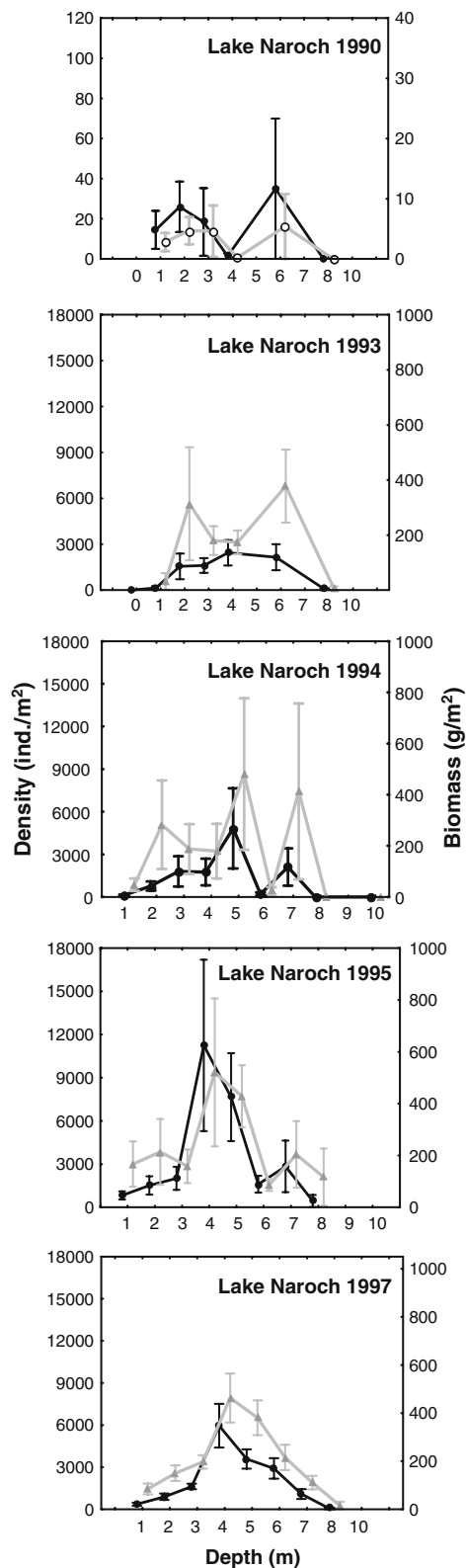


Figure 5. Density (black line) and biomass (gray line) of zebra mussels at each depth sampled in Lake Naroch in 1990, 1993, 1994, 1995 and 1997. Means \pm standard error.

Predictions of Ramcharan, Padilla & Dodson model
Data for Lake Naroch and Lake Myastro support the prediction of the Ramcharan et al. (1992) that these lakes should have stable populations. However, contrary to the predictions of the Ramcharan et al. model, the zebra mussel population in Lake Batorino did not change significantly from 1993 to 2002. This discrepancy could be due to several factors. The model was built without lakes similar to Lake Batorino (small area), and therefore may not be accurate for such lakes. Alternatively, the population of zebra mussels in Lake Batorino may be buffered by its water and dispersal connection to the two other lakes. Continued monitoring of these populations will be required to determine if these patterns persist in the long term.

Lake morphometry and trophic type

The three lakes studied differed in morphometry and trophic status: deep mesotrophic Lake Naroch, more shallow eutrophic Lake Myastro, and very shallow highly eutrophic Lake Batorino (Table 1). The area of maximum *D. polymorpha* density was at shallower depths in more eutrophic lakes (Fig. 4). The maximum depth of zebra mussels within a lake also decreased with increasing of lake trophic status from 8 m in Lake Naroch to 3 m in Lake Batorino. This pattern could be explained by decreased water transparency with increased lake eutrophication and a reduction in the depth of submerged macrophytes, which are an important substrate for zebra mussels. In addition, increased eutrophication leads to increased siltation, reducing the area of suitable substrates for *D. polymorpha*. However, morphometry and trophic type are often correlated (Horne & Goldman, 1994). As we had only a single lake of each trophic type and morphometry and trophic type were correlated, these patterns need to be tested on other lakes to determine if the generalizations hold.

Change in populations through time

It is well known that there is a lag time between when zebra mussels first invade a new waterbody

and when they are abundant enough to detect and have ecologically relevant effects (Zhadin, 1946; Lvova, 1980). This type of lag time has been found for many other invaders (Williamson, 1996; Crooks & Soulé, 1999; Mack et al., 2000; Kiritani & Yamamura, 2003), and the lag may range from dozens of years to less than one year depending on the individual species and habitats they invade (Kiritani & Yamamura, 2003; Simberloff & Gibbons, 2004). As with most other invaders, there are very few studies that actually document this lag-time for zebra mussels (Lvova, 1980; Karatayev, 1983).

We found that it took 7–12 years for zebra mussels to reach maximum population density and biomass after their initial invasion in the Narochanskies Lakes, Lake Lukomskoe and Uchinskoe Reservoir. However, this period may vary depending on lake size, morphometry, food and substrate availability. In Lake Balaton zebra mussels were found in 1932 and reached maximum densities by 1934 (Sebestyen, 1937). Zhadin (1946) hypothesized that *D. polymorpha* was introduced to this lake by a flat bottom ship that came through a canal in 1927. If we accept his hypothesis, it took 7 years for zebra mussels to reach a maximum after initial colonization, which corresponds very well with our data.

Because it is very difficult to determine the timing of an initial introduction, much more data are available on the dynamics of zebra mussels after populations reach some detectable level and are showing exponential growth (Table 3). For comparable data from different waterbody types and different continents (Europe and North America), the time from initial detection to maximum population density of zebra mussels was similar, usually 2–3 years. Our results fit well with these data for other lakes.

Conclusion

Our data suggest that the total population density of zebra mussels depends on the time since initial colonization, relative abundance of substrate available for colonization, lake morphometry and trophic type. *Dreissena polymorpha* usually reach maximum population density 7–12 years after their

initial introduction. However, the timing of initial introduction is often very difficult to determine. Both European and North American data suggest that zebra mussels reach maximum density in about 2–3 years after populations are large enough to be detected. Substrate limitation can influence the overall densities and the size of zebra mussel population in lakes. As populations develop through time, they generate new substrate – dead zebra mussel shells, which are subsequently colonized, allowing mussel populations to expand to areas of the lake that they otherwise could not use. Although zebra mussel distribution was highly patchy, the degree of dispersion decreased over time after initial colonization, most likely because of saturation of suitable substrates as mussel populations increase and reach carrying capacity. In lakes where submerged macrophytes are the dominant substrate for the zebra mussels attachment, populations may be less stable than populations in lakes with a variety of substrates, which will have a more balanced age distribution, and less impacted by year to year variation in recruitment.

Acknowledgements

In the Republic of Belarus the research was supported by Grant Number 657/65 from Ministry of Education and Science Republic of Belarus and Grant Number 444/50 from Belarusian State University (to AYK & LEB). We thank I. Rudakovsky, Dmitry and Vadim Karatayev, Drs P. A. Mitrakhovich and S. E. Mastitsky, and students of the General Ecology Department of Belarusian State University for assistance in the field and with sample processing. We appreciate the help of the Director of the Naroch Biological Station Dr T. V. Zhukova, and the Staff of the Station, as well as the Director Dr A. P. Ostapenya and Staff of the Laboratory of Hydroecology (Belarusian State University). We are thankful to Dr D. P. Molloy (NYSM) who provided us with the diving system Pioneer 230 X. Support during the manuscript preparation was provided by Stephen F. Austin State University (Faculty Research Grant # 14123 to AYK, LEB & DKP). We thank the Director and Staff of the Center For Limnology, University of Wisconsin – Madison for providing space and facilities during preparation of this manuscript.

Portions of this work were conducted while DKP was a Sabbatical Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0072909), the University of California and the Santa Barbara campus.

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