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The Impact of *Dreissena polymorpha* (Pallas) Invasion on Unionid Bivalves

key words: *Dreissena polymorpha*, zebra mussel, Unionidae, unionids, impacts

Abstract

Dreissena polymorpha, the zebra mussel, is one of the most aggressive and important invading aquatic species world wide. Its spread has followed the path of human activity, initially following human constructed canals connecting the Black Sea and Baltic Sea basins. One consequence of this invasion is the impact of zebra mussels on native bivalves. Overgrowth by *Dreissena* can cause a dramatic decrease in unionid density. The extent of this effect is determined by several factors including *Dreissena* density, time since invasion by *Dreissena*, biomass of attached *Dreissena*, and type of bottom sediments (sand versus silt). We found a correlation between overall *Dreissena* density and the number of zebra mussels per overgrown unionid, and between *Dreissena* density and the ratio of the mass of attached zebra mussels to the mass of the host unionid. The extensive overgrowth of unionids by *Dreissena*, resulting in mass mortality, is characteristic of periods of rapid population growth*,* when *Dreissena* invade a new waterbody.

1. Introduction

Dreissenids, especially *Dreissena polymorpha*, can become enormously abundant in freshwater, where they are the only bivalves which attach to hard substrates and have a planktonic larval stage. Within a short period of time they can obtain an order of magnitude higher biomass than that of all other native benthic invertebrates (Sokolova *et al*., 1980a; Kharchenko, 1983; Karatayev *et al*., 1994; Sinitsyna and Protasov, 1994). The zebra mussel is frequently competitively dominant over native freshwater fauna, and has large impacts on all parts of the ecosystem, especially benthic animals (Wiktor, 1969; Sokolova *et al*., 1980b; Karatayev and Burlakova, 1995a; Karatayev *et al*., 1997). Often the most direct and severe impact of zebra mussels is on unionid bivalves (Sebestyen, 1937; Mackie, 1991; Karatayev *et al.*, 1997).

Prior to the zebra mussel invasion, the major bivalves in freshwater benthic communities were unionids. Unionids have a very different lifestyle and life history than zebra mussels. They live in soft sediment, crawl through the sediment with a large foot, and live solitary or in groups, but not in as extreme densities as zebra mussels. Unionids have slow growth, low fecundity, are long lived, and have parasitic glochidia larvae. Unionids can provide the most abundant source of hard substratum for colonization by *D. polymorpha* in many lakes, reservoirs, and rivers (Lewandowski, 1976; Karatayev, 1983; Hebert *et al*., 1989; Lyakhnovich *et al*., 1994).

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Overgrowth by zebra mussels can have negative effects on the host unionids (reviewed in SCHLOESSER *et al.*, 1996; KARATAYEV *et al.*, 1997). By attaching to their valves, *D. polymorpha* can make it more difficult for unionids to burrow and move through sediment, and the added mass of *Dreissena* can weigh down unionids, resulting in burial in very soft or unconsolidated sediments (SEBESTYEN, 1937; KARATAYEV, 1983; MACKIE, 1991; GILLIS and MACKIE, 1994; SCHLOESSER and NALEPA, 1994). Mussel attachment to unionid shells can increase drag and the likelihood of dislodgment by water motion for species living near shore (SEBESTYEN, 1937; KARATAYEV, 1983; TUCKER, 1994). Zebra mussel attachment can occlude the openings in unionid valves, preventing opening for respiration, feeding and reproduction, or preventing the closing the valves (RICCIARDI *et al.*, 1996). *D. polymorpha* may directly compete with unionids for food (HAAG *et al.*, 1993), occupy otherwise available space (TUCKER, 1994), and induce shell deformities (LEWANDOWSKI, 1976; HUNTER and BALEY, 1992).

We measured the zebra mussel abundance and unionid fouling rates in a wide range of waterbodies in Belarus with different characteristics. We tested whether fouling by zebra mussels has negative impacts on unionids. We examined whether the mass of unionids was negatively correlated with the mass of zebra mussels attached to them, and whether the extent of mortality seemingly caused by zebra mussel fouling was associated with substrate type and time since invasion. We contrasted these results with similar data from two lakes in North America and literature information for other lakes. Finally, we use these date to test whether we can use zebra mussel densities in the environment to predict the fouling rate and impact of zebra mussels on unionid bivalves.

2. Methods

To determine the impact of zebra mussels on unionids, we studied nine lakes from the Naroch region, Lake Lepelskoe, the Svisloch River, and two reservoirs (Drozdy and Chizhovskoe) on this river in Belarus, and Lakes Clark and Vineyard in Michigan, USA (Table 1). The Svisloch River flows through Minsk, the capital of Belarus. The Drozdy reservoir is upstream of Minsk, is subject to low levels of industrial and urban pollution, is well oxygenated, and has an abundance of sand and rubble substrates; silts are rare. The Chizhovskoe Reservoir is downstream of the main industrial regions of the city and is heavily polluted with industrial and metropolitan sewage and petroleum waste. Lake Lepelskoe is 120 km northeast and Lake Naroch 110 km northwest of Minsk. Vineyard and Clark Lakes are both in Jackson County, Michigan, U.S.A., approximately 100 km west-southwest of Detroit.

The waterbodies we studied differed in a number of limnological parameters, time since zebra mussel colonization, and *Dreissena* density (Table 1). *D. polymorpha* was first reported from Lake Lepelskoe in 1929 (OVCHINNIKOV, 1933) but probably colonized this lake much earlier, shortly after construction of the Dnieper-Zapadnaya Dvina Canal in 1805. This canal connects the Dnieper River (Black Sea basin) and the Zapadnaya Dvina River (Baltic Sea basin) and was the route through which zebra mussels colonized northern Belarus (BURLAKOVA, 1998). The Svisloch River, Chizhovskoe and Drozdy reservoirs and the rest of the Belarussian lakes studied were colonized with zebra mussels in the 1980s. In North America, zebra mussels were first detected in Lakes Vineyard and Clark in 1994.

In each waterbody, we hand collected unionids at approximately 1.5–2.5 m depth by diving. Every unionid within a 1 m wide transect (100 or 500 m, depending on unionid density) was collected. In the Svisloch River, unionids were collected from 9 separate transects. All bivalves were identified to species. Before dissection, we cleaned *Dreissena* and other fouling organisms from the surface of the shell. Unionid shell lengths (maximum linear dimension) were measured with calipers (±1 mm). Then unionids and zebra mussels were cut open with a scalpel, to remove water from mantle cavities, and weighed.

Table 1. Physical and chemical characteristics of the waterbodies studied, *Dreissena* density (in entire waterbody), and unionid bivalve species composition. n.r. = data not reported.

Waterbody	Surface area (km^2)	Volume (10^6 m^3)	Max. depth (m)	Secchi depth (m)	pH	Permanganate oxidizability (mg OL^{-1})	Hydro-carbonate (mg L^{-1})	*Dreissena* density (m^{-2})	Unionid bivalve species
Belarus									
Lakes:									
Lepelskoe, 1997	9.2	41.2	26.8	2.0	8.6	6.8	162	n.r.	*Unio pictorum, U. tumidus, Anodonta anatina, Pseudanodonta complanata*
Naroch, 1990	79.6	710.4	24.8	6.0	8.2	3.3	140	7.4	*U. pictorum, U. tumidus, A. cygnea, A. piscinalis, A. anatina, P. complanata*
Bolduk, 1998	0.8	11.9	39.7	4.5	8.5	8.7	159	274	*U. tumidus*
Dolzha, 1998	1.0	5.4	13.7	2.6	8.4	13.3	168	183	*U. pictorum, U. tumidus, P. complanata*
Myadel, 1998	16.4	102.0	24.6	4.8	8.7	6.7	163	762	Only dead unionids were found
Malye Shvakshty, 1998	1.9	2.9	3.2	2.5	8.0	11.8	137	<1	*U. pictorum, A. piscinalis, P. complanata*
Bolshiye Shvakshty, 1998	9.6	22.3	5.3	3.1	8.6	8.9	167	112	*U. pictorum, U. tumidus, A. anatina*
Spory, 1998	0.7	3.3	20.8	2.6	8.8	7.9	213	25	*U. pictorum, U. tumidus, A. anatina*
Svir, 1998	22.3	104.3	8.7	1.8	8.7	9.2	171	430	*U. pictorum, U. tumidus, A. anatina*
Volchin, 1998	0.5	7.9	32.9	3.8	8.5	7.2	167	195	*U. pictorum, U. tumidus, A. anatina*
Reservoir Drozdy, 1995	2.1	5.7	6.0	0.7	8.2	8.6	195	838	*U. pictorum, U. tumidus, A. anatina*
Reservoir Chizhovskoe, 1995	1.6	2.9	4.7	0.5	8.3	8.6	195	81	*U. pictorum, U. tumidus, A. anatina*
River Svisloch, 1995	n.r.	n.r.	2.0	0.2	8.1	8.6	195	2500	*U. pictorum, U. tumidus, U. crassus, A. anatina, A. cygnea*
United States									
Lake Clark, 1996	2.35	n.r.	15.4	4–6	8.1–8.3	n.r	n.r.	1835	*Lampsilis cardium, Pyganodon grandis, Anodontoides ferussacianus, Villosa iris, Strophitus u. undulatus*
Lake Vineyard, 1996	2.05	n.r.	12	2–4	8.1–8.3	n.r.	n.r.	41825	*Eliptio dilatata*

3. Results

Lake Naroch – We studied Lake Naroch from 1990–1995. Since Lake Naroch was invaded by zebra mussels in the mid–1980s, our study was during the initial stage of colonization. The average density and biomass of zebra mussels across the whole lake dramatically increased from 1990 to 1995 (Table 2).

The percent of unionids infested with zebra mussels increased from 60% in 1990 (n = 93), to 100% in 1993 (n = 100) and 1995 (n = 50). The average number and mass of mussels per host unionid also increased, as did the ratio of mass of *D. polymorpha* to host unionid (Table 2). In 1990, all unionids found were alive. However, in 1993 the majority of the host-unionids were dead; only 3% of unionids collected were alive. In 1995 all unionids were still fouled by *D. polymorpha* and only 8% were alive.

In 1990 zebra mussels were most abundant on unionids near a stream, Skema, which flows into Lake Naroch from Lake Myastro. Lake Myastro was colonized by zebra mussels before Lake Naroch, and the connecting stream provided the route for the zebra mussel invasion (BURLAKOVA, 1998). The percentage of unionids fouled with *D. polymorpha* and the abundance of *Dreissena* attached to unionids decreased with increasing distance from the outflow of this stream (Figure 1).

Lake Myadel – Lake Myadel was colonized at the same time as Lake Naroch. By 1998 zebra mussels had reached very high densities (Table 1) and we found no live unionids, only empty shells.

Lake Lepelskoe – In contrast, unionids are still abundant in Lake Lepelskoe, where zebra mussels were first reported in 1929 (OVCHINNIKOV, 1933) but probably colonized shortly after construction of the Dnieper-Zapadnaya Dvina Canal in 1805. Divers readily collected hundreds of unionids within an hour. Although 92% were infested with zebra mussels, the average ratio of mass of *D. polymorpha* to host unionid was lower than that in Lake Naroch (Table 2) and only 12% of infested unionids were dead.

Lake Volchin – Unionids in Lake Volchin on sandy sediments were completely overgrown with *Dreissena*. The number of zebra mussels per unionid host was significantly higher than on silty sediments ($P = 0.049$, ANOVA) and zebra mussels were found only on the posterior third of unionid shells. The ratio of mass of *D. polymorpha* and host unionid was not significantly higher on sand than on silt ($P = 0.054$, ANOVA), but due to unequal sample sizes our statistical analysis has relatively low power.

Svisloch River – The highest densities of zebra mussels were found in the Svisloch River (Table 1). In this river, sand and rubble sediments alternate with silt. In sandy and rubble

Table 2. The overgrowth of unionids by zebra mussels in Lake Naroch. Means ± standard errors.

	1990	1993	1995
The number of sites sampled (n)	(37)	(45)	(80)
Average density of *D. polymorpha* in the lake (m^{-2})	7.4 ± 3.0	763 ± 149	1521 ± 451
Average biomass of *D. polymorpha* in the lake (gm^{-2})	1.5 ± 0.6	99 ± 30	107 ± 44
% of all unionids colonized by *D. polymorpha*	60	100	100
% of unionids found dead	0	97	92
Average number of *D. polymorpha* per living infested unionid bivalve	9.5 ± 6.2	135 ± 35	36 ± 11
Biomass of *D. polymorpha* per living infested unionid bivalve (g)	1.8 ± 0.9	34.0 ± 8.4	14.4 ± 3.7
Ratio of mass of *D. polymorpha* and living host unionid bivalve	0.3 ± 0.2	2.8 ± 1.4	1.1 ± 0.4

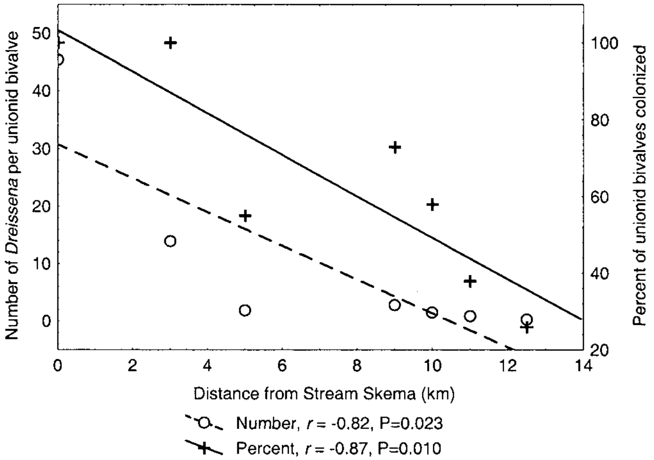

Figure 1. The percent of unionids colonized by *Dreissena* and density of *D. polymorpha* attached to unionids at different distances from the outflow of the Stream Skema.

areas the unionids had high numbers of attached zebra mussels (up to 100 per unionid). In contrast, unionids burrowed in silt were completely free of zebra mussels, even though at several of these sites the density of unionids was around 100 m^{-2}.

Reservoirs Drozdy and Chizhovskoe – High densities of zebra mussels were found in the upstream Reservoir Drozdy, but not as high as in the Svisloch River (Table 1). Zebra mussels were most abundant in the shallow areas, at 0.5 m depth, on sandy-rubble substrate. Half of the 54 unionids collected from this reservoir were dead and all had attached zebra mussels. Zebra mussels were found in low densities in the lower reservoir, Chizhovskoe (Table 1), and primarily at the mouth of an inflowing stream. Unionids were abundant in this reservoir, and none of approximately 100 unionids collected from silty sediments had attached zebra mussels.

Lakes Clark and Vineyard – We found similar results in North America. In Lake Clark unionids were found on the surface of sandy sediment and were completely overgrown with zebra mussels. In Lake Vineyard, the unionids were partly burrowed in silty sediments and zebra mussels were found only on the posterior half to one third of their shells. The average number of infested unionids and the ratio of mass of *D. polymorpha* and host unionid

Table 3. Percent of unionids fouled by zebra mussels in different waterbodies. Intact druses do not have additional remains of damaged byssal threads. Damaged druses have additional remains of byssal threads, indicating that more zebra mussels were previously attached. The remains of just byssal threads on a unionid indicates that zebra mussels were attached at some time in the past.

Lake	Sample size	% Intact druses	% Damaged druses	% With byssal threads only	% No zebra mussels or byssal threads
Bolshye Shvakshty	147	11	29	37	23
Dolzha	31	71	16	13	0
Spory	26	23	8	31	38
Bolduk	25	53	27	12	8

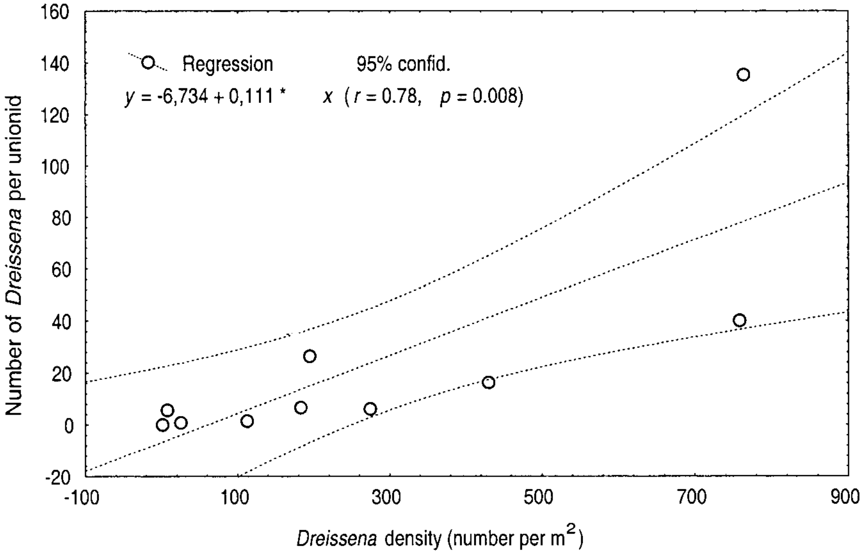

Figure 2. The number of *Dreissena* per unionid bivalve for Belarussian lakes with different densities of *Dreissena*.

bivalve in Lake Clark were significantly higher than in Lake Vineyard (P = 0.026, ANOVA) (Table 4). In addition, the unionids in Lake Vineyard were significantly larger ($P \ll 0.001$, ANOVA) and heavier (73.1 ± 4.4 g vs. 18.8 ± 2.2 g, $P \ll 0.001$, ANOVA) than in Lake Clark. The average length of unionids from Belarus lakes was significantly smaller ($P < 0.001$, *t*-test) than in North American lakes Clark and Vineyard (56.6 ± 0.56 mm in Belarus, 74.5 ± 3.2 mm in North America).

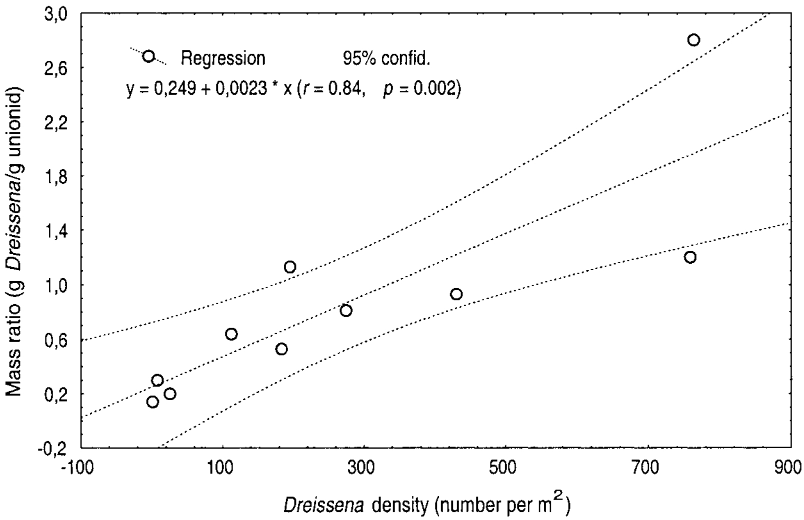

Figure 3. The mass ratio of attached *Dreissena* and host unionid bivalve (mass of zebra mussels attached per mass of unionid bivalve), for different densities of zebra mussels in Belarussian lakes.

Byssal Thread Remains – We frequently found unionids with the remains of *Dreissena* byssal threads on their shells (Table 3). In all lakes, the majority of unionids had at least the remains of byssal threads attached to their shells (Table 3). The number of *D. polymorpha* per unionid with intact druses (without additional remains of byssal threads) was higher, than on those with druses and byssal remains (damaged druses). In the Lake Bolshye Shvakshty the average number of zebra mussels per host unionid with intact druses (7.2 ± 1.3, n = 17) was significantly higher ($P < 0.001$, *t*-test) than for those with damaged druses (1.8 ± 0.2, n = 42). In Lake Dolzha we found an average of 8.9 ± 1.5 (n = 6) zebra mussels per unionid with intact druses and 2.6 ± 0.8 (n = 20) on unionids with damaged druses.

Zebra Mussel Density and Unionid Overgrowth – To determine if there was a relationship between zebra mussel density and degree of overgrowth of unionids in a waterbody, we used data from Lake Naroch (1990 and 1993) and eight lakes in the Naroch region studied in 1998 (Table 1). Both the number of zebra mussels and the ratio of mass of *D. polymorpha* and host unionid were correlated with zebra mussel density (Figure 2 and 3).

4. Discussion

We found a positive correlation between *Dreissena* density in a waterbody and number of zebra mussels attached to unionids, and between *D. polymorpha* density and the ratio of the mass of attached mussels to the mass of the host unionid bivalve. LEWANDOWSKI (1976) found similar correlations for lakes in Poland, as did RICCIARDI *et al.* (1995) for the St. Lawrence River. RICCIARDI *et al.* (1995) also found that unionid mortality (reflected by the proportion of dead unionids) correlated with *Dreissena* field density, and a significant relationship between the ratio of mass of *D. polymorpha* and host living unionid and the proportion of freshly killed unionids.

In Lake Naroch, shortly after invasion, zebra mussels caused a dramatic decline in unionid bivalve density. In contrast, in Lake Lepelskoe, where zebra mussels have been for far longer, unionids coexist with *D. polymorpha*. Although overgrowth by zebra mussels has caused some host mortality, unionids not only persist, but also maintain high densities. Unionids and zebra mussels also coexist in Lake Lukomskoe (KARATAYEV, 1983) and the Tsimlyanskoe Reservoir (Russia) (MIROSHNICHENKO *et al.*, 1984; MIROSHNICHENKO, 1987). There have been detectable negative impacts of zebra mussels on unionid populations in other lakes, including Lake Balaton (Hungary) (PONYI, 1992). However, the decline in abundance of unionids in Lake Hallwil (Switzerland) from the 1910s to the 1980s was caused by a decrease in the number of host fish for unionid larvae and an increase in eutrophication in addition to the influence of *D. polymorpha* which colonized in the 1970s (ARTER, 1989). Similarly, the drop in the number of unionid species in Mikolajskie Lake from 1972 to 1987 was not a direct result of zebra mussel impact, but was due to increased eutrophication and pollution (LEWANDOWSKI, 1991).

Extensive overgrowth of unionids by *D. polymorpha*, resulting in mass mortality can be characteristic of periods of rapid population growth of zebra mussels, when they invade a new waterbody. The dramatic decline of unionids after zebra mussel invasion is well documented both in Europe (SEBESTYEN, 1937; KARATAYEV and BURLAKOVA, 1995b; BURLAKOVA, 1998) and North America (HAAG *et al.*, 1993; NALEPA, 1994; RICCIARDI *et al.*, 1996). However, *D. polymorpha* coexist with native bivalves in European waters with established zebra mussels populations (LEWANDOWSKI, 1976; KARATAYEV, 1983; PONYI, 1992; BURLAKOVA, 1998).

In sandy and rubble areas of the Svisloch River, we found that unionids were heavily overgrown with *D. polymorpha*. In silty areas unionids were very abundant, were buried in sediments, and were completely free of zebra mussels. Similar results were found in Lake

Table 4. Impact of zebra mussels on unionids. (means ± SE). n.r. = data not reported.

Waterbody	Sample size of unionids	% of unionids colonized	Number of *Dreissena* per unionid bivalve	Ratio of mass of *Dreissena* and host unionid bivalve	References
Europe:					
Mikolajskie Lake, 1972	395	85	20	0.43–1.93	LEWANDOWSKI, 1976
Mikolajskie Lake, 1974	47	92	52	n.r.	LEWANDOWSKI, 1976
Lake Lukomskoe, 1978	80	75	40 ± 9	1.2	KARATAYEV, 1983
Lake Myastro, 1993	16	94	9.6 ± 2.05	0.60 ± 0.10	BURLAKOVA, 1998
Lake Naroch, 1990	93	60	5.7 ± 3.7	0.3 ± 0.2	This study
Lake Naroch, 1993	4	100	135 ± 35	2.8 ± 1.35	This study
Lake Naroch, 1995	4	100	107 ± 44	1.1 ± 0.18	This study
Lake Lepelskoe, 1997	37	92	28.7 ± 8.7	0.73 ± 0.21	This study
Lake Volchin, 1998	17	100	26.5 ± 5.6	1.13 ± 0.21	This study
Lake Spory, 1998	26	31	0.85 ± 0.33	0.20 ± 0.06	This study
Lake Svir, 1998	51	90	16 ± 2.1	0.93 ± 0.17	This study
Lake Bolduk, 1998	25	80	6.1 ± 1.2	0.81 ± 0.18	This study
Lake Bolshye Shvakshty, 1998	147	48	1.5 ± 0.24	0.64 ± 0.12	This study
Lake Malye Shvakshty, 1998	9	10	0.1	0.14 ± 0.05	This study
Lake Dolzha, 1998	30	87	6.7 ± 1.2	0.53 ± 0.09	This study
Reservoir Drozdy, 1995	15	100	38	1.8	This study
North America:					
Lake St. Clair, 1988 (average from 11 sites)	221	0–93	0–17.1 ± 4.7	n.r.	HEBERT *et al.*, 1989
Lake St. Clair, 1989	n.r.	n.r.	300	n.r.	MACKIE, 1991
Lake St. Clair, 1989 (site # 13 with the highest infestation of unionids)	n.r.	n.r.	5,496	2–3	HEBERT *et al.*, 1991
Lake St. Clair, 1990 (14 lightly infested sites)	112	14	<1	n.r.	NALEPA, 1994
Lake St. Clair, 1992 (14 lightly infested sites)	99	97	32	n.r.	NALEPA, 1994
Lake St. Clair, 1990 (15 highly infested sites)	136	97	0–1,360	1.2	NALEPA, 1994

Western Lake Erie, 1989 September	29	100	6,805 ± 623	2.57	SCHLOESSER and NALEPA, 1994
Western Lake Erie, 1990 May, June	9	100	346 ± 95	0.47	SCHLOESSER and NALEPA, 1994
Lake Erie, Power Plant Canal, 1989 February	9	100	24 ± 3.9	n.r.	SCHLOESSER and KOVALAK, 1991
Lake Erie, Power Plant Canal, 1989 August	10	100	6,777 ± 811	0.74	SCHLOESSER and KOVALAK, 1991
Mississippi River, 1993	743	100	37.4	n.r.	TUCKER, 1994
Lake St. Louis, 1992–1995 (1st site)	n.r.	58	0.8 ± 0.2–7.7 ± 1.2	0.03 ± 0.005–0.21 ± 0.04	RICCIARDI *et al.*, 1995, 1996
Lake St. François, 1992	n.r.	55	1.2 ± 0.04	0.06 ± 0.02	RICCIARDI *et al.*, 1995, 1996
Lake St. François, 1995	n.r.	n.r.	26.4 ± 5.2	0.24 ± 0.07	RICCIARDI *et al.*, 1996
Lake St. Pierre, 1995 (Sites 1–3)	n.r.	n.r.	0.7 ± 0.3–47.7 ± 4.0	0.04 ± 0.02–0.07 ± 0.01	RICCIARDI *et al.*, 1996
Port of Montréal, 1994	n.r.	100	23.1 ± 2.8	0.58 ± 0.08	RICCIARDI *et al.*, 1995, 1996
Soulanges Canal, 1992–1994	n.r.	74–100	3.1 ± 0.6 –52.1 ± 10.3	0.04 ± 0.01–0.87 ± 0.18	RICCIARDI *et al.*, 1996
Hudson River, 1993*	301	38	1.0	n.r.	STRAYER and SMITH, 1996
Hudson River, 1994*	189	23	0.6	n.r.	STRAYER and SMITH, 1996
Hudson River, 1995*	162	30	4.7	n.r.	STRAYER and SMITH, 1996
Lake Clark, 1996	21	100	219.6 ± 24.5	0.40 ± 0.06	This study
Lake Vineyard , 1996	14	100	117.6 ± 12.9	0.22 ± 0.03	This study

* Recalculated from figure 2 (STRAYER and SMITH, 1996)

Hallwil, where *Unio tumidus* is usually buried in the sediments and is rarely overgrown by zebra mussels, however, *Anodonta cygnea* is often only partly buried and is colonized more often by zebra mussels (ARTER, 1989). Based on these findings and data from reservoirs with different levels of pollution (Dr. V. VINOKUROV, pers. comm.), we hypothesize that under certain circumstances unionids, being more resistant to low oxygen and pollution than zebra mussels, may survive in waters unsuitable for *Dreissena*. In addition, some unionids may be capable of removing zebra mussels from their valves. In lakes where we found unionids heavily fouled by *D. polymorpha*, we found some individuals completely free of zebra mussels, but with byssal threads still attached.

Overgrowth by *D. polymorpha* adversely affects host unionids. The extent of this effect depends on a number of factors including zebra mussel density in a waterbody, time since invasion, and type of bottom sediment. Although the appearance of zebra mussels in the North-American waterbodies has been correlated with negative impacts on the native unionids (HAAG *et al.*, 1993; NALEPA, 1994; SCHLOESSER and NALEPA, 1994), a large decline in biodiversity and abundance of unionids was detected long before the appearance of zebra mussels in the North America (NALEPA *et al.*, 1991; SCHLOESSER and NALEPA, 1994). Since 1989, all unionids in Western Lake Erie have been colonized by zebra mussels (SCHLOESSER and NALEPA, 1994). North American scientists have reported extremely high densities of *D. polymorpha*, greater than several thousand per unionid (HEBERT *et al.*, 1991; SCHLOESSER and KOVALAK, 1991; SCHLOESSER and NALEPA, 1994). These densities are much higher than those reported by European scientists (Table 4). Do these differences constitute a significant difference in the impact of zebra mussels on native unionids? From the perspective of the unionid, the mass of attached *D. polymorpha*, or the ratio of the mass of attached zebra mussels to the mass of the host unionid bivalve is probably more important than density (HEBERT *et al.*, 1991; KARATAYEV *et al.*, 1997). Of the studies which we could compare, the mean ratio of the biomass of attached *D. polymorpha* and the host unionid bivalve was very similar to that found in Europe (Table 4).

Moreover, high densities of zebra mussels on unionids are typical mainly for the Great Lakes. In other waterbodies, average *Dreissena* densities per host unionid bivalve are very similar to those in Europe (Table 4). Differences between the density of attached mussels reported by North American and European scientists could result if the size-frequency composition of zebra mussel populations is different in North America, North American studies include smaller mussels in density estimates than European studies, or North American unionids are larger than European bivalves. In general, European scientists do not include mussels smaller than 1–2 mm in density estimates (LVOVA, 1980; KARATAYEV, 1983; LVOVA *et al.*, 1994), and sometimes they do not include mussels <5 mm (BIJ DE VAATE, 1991) or 8 mm (HAMBURGER *et al.*, 1990). The overwinter mortality of young-of-the-year and one-year-old mussels is very high, and by the spring the number of live mussels is greatly reduced. For example, in western Lake Erie in February 1989 the density of *D. polymorpha* was 24 ± 4 per unionid bivalve, and in August, after larval settlement, the density of mussels averaged $6{,}777 \pm 811$ per unionid (SCHLOESSER and KOVALAK, 1991). In addition, we found that the average length of unionids from Belarussian lakes was significantly smaller than in North American Lakes Clark and Vineyard. The mean unionid bivalve shell length in North America used by RICCARDI *et al.* (1995) was even greater (9.5 cm), and the unionids from western Lake Erie (114 ± 5.6–119 ± 5.6 mm) (SCHLOESSER and KOVALAK, 1991) were more than twice as large as those from Belarussian waterbodies.

Is it possible that zebra mussels will have greater effects on unionids in North America than in Europe? In pre-glaciation Europe, zebra mussels and unionids coexisted. The distribution of zebra mussels was restricted to areas surrounding the Caspian and Black Sea only after the Pleistocene glaciation. Because North American native species have no evolutionary history of coexistence with zebra mussels, we might expect zebra mussels to have a larger impact on North American unionids. The species composition of unionids in the North America is much different than in Europe, and we might expect species-specific differences in response to fouling. The bivalve fauna of North American freshwaters is the most diverse in the world, with >250 native and 6 introduced species**.** Historically, there are records of 297 species, >21 of which are now extinct, and >42 are endangered or threatened, all which belong to the superfamily Unionacea (families Margaritiferidae and Unionidae) (BOGAN, 1993). In contrast, the bivalve fauna in Europe consists of 62 species, and only 14 species in the superfamily Unionacea (JAECKEL, 1967).

Currently, North America is in the early phase of zebra mussel invasion, and populations are growing rapidly. At this stage of invasion, *D. polymorpha* caused a dramatic decline in the abundance of unionids in Europe (SEBESTYEN, 1937; DUSSART, 1966; KARATAYEV and BURLAKOVA, 1995b; BURLAKOVA, 1998). However, to our knowledge, the zebra mussel invasion did not result in the complete elimination of unionids in any European lakes. After initial peaks in zebra mussel abundance, *D. polymorpha* coexist with unionids in all lakes, reservoirs and rivers studied. Will this pattern hold true for North America? With time, perhaps the impact of *D. polymorpha* on unionids will decrease. Our hypothesis may be supported by SCHLOESSER *et al.* (1996) who indicate that some unknown factor(s) reduces the intensity of unionid infestation by zebra mussels, thus decreasing mortality in some North American waterbodies where unionids and zebra mussels coexist.

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