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Endosymbionts of *Dreissena polymorpha* (PALLAS) in Belarus

key words: Dreissena polymorpha, endosymbionts, *Conchophthirus acuminatus*, trematodes

Abstract

Dreissena polymorpha were dissected and examined for endosymbionts from 17 waterbodies in Belarus – the country through whose waterways zebra mussels invaded Western Europe nearly two centuries ago. Fourteen types of parasites and other symbionts were observed within the mantle cavity and/or associated with internal tissues, including ciliates (*Conchophthirus acuminatus*, *Ancistrumina limnica*, and *Ophryoglena* sp.), trematodes (Echinostomatidae, *Phyllodistomum*, *Bucephalus polymorphus*, and *Aspidogaster*), nematodes, oligochaetes, mites, chironomids, and leeches. Species composition of endosymbionts differed among river basins and lake systems. The most common endosymbiont was the ciliate *C. acuminatus*. Its mean infection intensity varied significantly among waterbodies from 67 ± 6 to $3,324 \pm 556$ ciliates/mussel.

1. Introduction

Zebra mussels, *Dreissena polymorpha*, have been spreading throughout European waterbodies since the beginning of the 19th century causing significant ecological impacts in the process (MACISAAC, 1996; KARATAYEV *et al.*, 1997). Only a little more than a decade ago, *Dreissena* spp. were introduced into North American waters. Within a few years after the discovery of *D. polymorpha* in Lake St. Clair in 1988 (HEBERT *et al.*, 1989), these mussels rapidly spread across much of North America (JOHNSON and PADILLA, 1996), causing hundreds of millions of dollars in damage and increased operating expenses at raw water-dependent infrastructures (O'NEILL, 1996, 1997).

The extent of the ecological and economic impact of zebra mussels is directly related to their density within a habitat, and it is well documented that population densities of zebra mussels are not stable and can fluctuate widely (RAMCHARAN *et al.*, 1992). Defining the role endosymbionts play in these density fluctuations is a critical step toward a comprehensive understanding of the population dynamics of these pest mussels.

Although the first paper on zebra mussel endosymbionts appeared almost 150 years ago (CLAPARÈDE and LACHMANN, 1858), little is still known about their biology, infection prevalence (i.e., percent of mussels with endosymbionts), and infection intensity (i.e., number of endosymbionts per infected mussel). Compared to the wide diversity of virulent parasites known from other bivalves, particularly commercially valuable marine species (LAUCKNER, 1983; SPARKS, 1985; SINDERMANN, 1990), zebra mussels appear to have relatively few

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serious diseases. Prior to their arrival in North America, however, relatively little attention was paid to their diseases (MOLLOY, 1992). In their review of the international literature on natural enemies of *Dreissena*, MOLLOY *et al.* (1997) cited 176 species involved in predation, 34 in parasitism, and 10 in competitive exclusion. All known species of endosymbionts associated with *Dreissena* spp. have been recorded from attached mussels.

The spread of zebra mussels to Belarus began over 200 years ago and was associated with shipping activities through newly constructed canals (OVCHINNIKOV, 1933; LYAKHNOVICH *et al.*, 1984; STAROBOGATOV and ANDREEVA, 1994). Three canals connecting the Dnieper and Zapadnyi Bug rivers (1775), the Dnieper and Neman rivers (1804), and Dnieper and Zapadnaya Dvina rivers (1805) were constructed in what is now Belarus to connect shipping routes from the Black Sea and Baltic Sea basins (Figure 1). Only the Dnieper-Bug Canal is still operational; as the other two were closed ca. 100 years ago. Although the Dnieper-Bug Canal and Dnieper-Neman Canal are considered to have been the routes for *D. polymorpha* invasion into Western Europe (KINZELBACH, 1992; STAROBOGATOV and ANDREEVA, 1994), the major part of Belarus was colonized through the Dnieper-Zapadnaya Dvina Canal (BURLAKOVA, 1998). Because different regions were colonized through different canals, the movement of zebra mussel endosymbionts across Belarus may not have been uniform. The

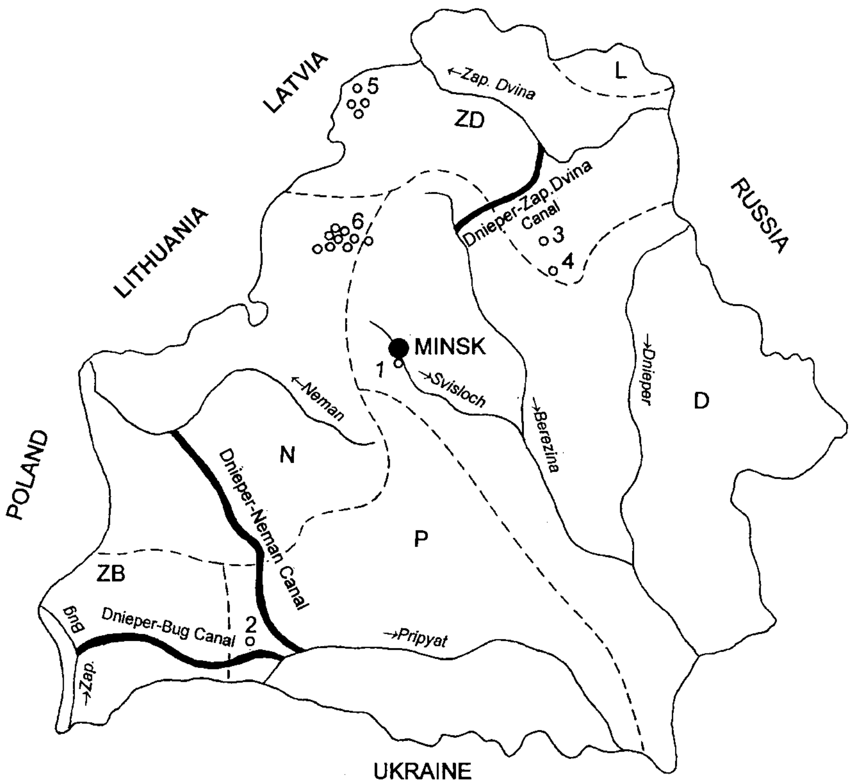

Figure 1. Map of the Republic of Belarus. The open circles indicate studied waterbodies: 1 – Svisloch River, 2 – Dnieper-Bug Canal, 3 – Lake Lepelskoe, 4 – Lake Lukomskoe, 5 – Braslavskie lakes, 6 – lakes in Naroch region. Dashed lines indicate borders of the following drainage river basins: Zapadnaya Dvina River drainage basin (ZD), Dnieper River basin (D), Neman River basin (N), Pripyat River basin (P), Zapadnyi Bug River basin (ZB), and Lovat River basin (L).

present study of the distribution of endosymbionts that are host specific to zebra mussel populations in Belarus is a first step in a long-term study to reveal the pathways by which zebra mussels have spread in the past. Thus, while an invader of new waterbodies itself, *D. polymorpha* has also been a vector for the spread of its endosymbionts. The impact of this vectoring activity on aquatic biodiversity is completely unknown.

This paper documents zebra mussel endosymbionts from 15 lakes, the Svisloch River, and the Dnieper-Bug Canal and examines if zebra mussel infection correlated with water quality parameters. Waterbodies studied differed considerably in a number of limnological conditions and in their *D. polymorpha* densities. Although Belarussian waterbodies were colonized with zebra mussels almost 200 years ago, this is the first comprehensive report of the species composition of zebra mussel endosymbionts and their infection prevalence and intensity. It is also the first study ever conducted on the prevalence and intensity of *Dreissena* infection with the commensal ciliate *Ancistrumina limnica* and parasitic ciliate *Ophryoglena* sp. The results presented herein are part of a more extensive study that we, as members of the International Research Consortium on Molluscan Symbionts (www.nysm.nysed.gov/biology/ircoms/bio_ircoms.html), are conducting to examine the role that endosymbionts play in the population dynamics of *Dreissena* spp. in the former Soviet Union, Western Europe, and North America.

2. Study Area

In Belarus there are 1,072 lakes with surface areas greater than 0.1 km^2 (Kurlovich and Serafimovich, 1981). Most of these lakes were formed during the last glaciation and are found in northern Belarus (Belarussian Lakeland), especially in the drainage basin of the Zapadnaya Dvina River. Lake colonization by zebra mussels was not equally likely among drainage basins. Zebra mussels were much more common in the Zapadnaya Dvina River basin and were disproportionately abundant in the Dnieper River basin. Zebra mussels have yet to be recorded from the glacial lakes in the Pripyat or Lovat drainage basins (authors, unpublished data). Although zebra mussels first colonized Belarus at the beginning of the 19th century, the dispersal process is still continuing, with *D. polymorpha* now recorded from 107 lakes, including 93 lakes in the Zapadnaya Dvina River basin, 10 lakes in Neman River basin, 3 lakes in the Dnieper River basin, and one lake in Zapadnyi Bug River basin.

We studied *D. polymorpha* populations in the Svisloch River (within the city of Minsk), the Dnieper-Bug Canal (250 km southwest of Minsk), Lake Lukomskoe (120 km northeast of Minsk), and Lake Lepelskoe (120 km northeast of Minsk), four lakes from the Braslavskaya lake system (200 km north of Minsk), and nine lakes from the Naroch region (110 km northwest of Minsk) (Table 1, Figure 1). Trophic status and morphometry of the lakes varied from shallow eutrophic to deep meso-oligotrophic (Table 1). The density of zebra mussels in the waterbodies varied from very low in Lake Lotviny and Lake Malye Svakshty to high in the Svisloch River. Waterbodies studied also differed in the year of initial zebra mussel colonization. The oldest zebra mussel populations were in Dnieper-Bug Canal and Lake Lepelskoe. The Dnieper-Bug Canal was built in 1775 to connect the Dnieper River (Black Sea basin) and Zapadnyi Bug River (Baltic Sea basin) and is considered as the route for zebra mussel invasion into Central and Western Europa (Kinzelbach, 1992). For almost a century following 1805, Lake Lepelskoe was a part of Dnieper-Zapadnaya Dvina Canal. This canal was another route connecting the Dnieper River (Black Sea basin) and the Zapadnaya Dvina River (Baltic Sea basin), and the one through which zebra mussels colonized northern Belarus (Burlakova, 1998). Zebra mussels were first reported from Lake Lepelskoe in 1929 (Ovchinnikov, 1933), but probably colonized this lake much earlier, i.e., in the beginning of nineteenth century after construction of the Dnieper-Zapadnaya Dvina canal. Zebra mussels colonized the Svisloch River in the mid-1980s (Burlakova, 1998). The

Table 1. Abiotic and biotic parameters for waterbodies studied.

Waterbodies studied	Surface (km^2)	Volume (millions m^3)	Maximum depth (m)	Secchi depth (m)	pH	Color, (Pt-Co Degree)	Permanganate oxidizability (mg O/L)	Hydrocar-bonate (mg/L)	Trophic Status	*Dreissena* density (m^2)
Svisloch River	n.r.	n.r.	2.0	0.2	8.1	40	8.6	195	n.r.	1,797
Dnieper-Bug Canal	n.r.	n.r.	4.0	1.0	n.r.	n.r.	n.r.	n.r.	n.r.	n.r.
Lake Lepelskoe	9.2	41.2	26.8	2.0	8.6	30	6.8	162	mesotrophic	n.r.
Lake Lukomskoe	36.7	243.0	11.5	3.0	8.2	20	7.7	180	eutrophic	500
Braslavskie lakes:										
Drivyaty	36.2	223.5	12.0	2.4	8.5	25	7.8	128	eutrophic	n.r.
Severnyi Voloso	4.2	30.5	29.2	10.0	8.3	10	5.2	125	meso-oligotrophic	n.r.
Strusto	13.0	94.2	23.0	4.8	8.2	15	5.2	146	mesotrophic	n.r.
Voiso	3.3	14.2	9.1	2.0	7.9	15	6.4	137	eutrophic	n.r.
Naroch region lakes:										
Bolduk	0.8	11.9	39.7	4.5	8.5	25	8.7	159	meso-oligotrophic	274
Dolzha	1.0	5.4	13.7	2.6	8.4	25	13.3	168	eutrophic	183
Lotviny	0.4	2.8	15.1	1.9	8.4	25	9.4	201	eutrophic	< 1
Myadel	16.4	102.0	24.6	4.8	8.7	25	6.7	163	mesotrophic	762
Malye Shvakshty	1.9	2.9	3.2	2.5	8.0	60	11.8	137	eutrophic	< 1
Bolshiye Shvakshty	9.6	22.3	5.3	3.1	8.6	30	8.9	167	eutrophic	112
Spory	0.7	3.3	20.8	2.6	8.8	25	7.9	213	eutrophic	25
Svir	22.3	104.3	8.7	1.8	8.7	40	9.2	171	eutrophic	388
Volchin	0.5	7.9	32.9	3.8	8.5	20	7.2	167	mesotrophic	195

Braslavskaya lake system and Lake Lukomskoe were colonized in the late 1960s (LYAKHNOVICH *et al.*, 1984), lakes in the Naroch region were colonized in the late 1980s, and the process of *D. polymorpha* spread is still continuing (BURLAKOVA, 1998). Lakes in the Naroch region do not form a single lake system and belong to two different rivers basins (Figure 1).

3. Methods

3.1. Species Composition, Prevalence of Infection, and Water Quality

To determine species composition and prevalence of infection of *D. polymorpha* with endosymbionts, 71 samples were taken. In the Svisloch River monthly samples were taken from May through October 1996, December 1996, January 1997, and March through December 1997. In the Dnieper-Bug Canal, samples were taken monthly from June through November 1997. Braslavskie lakes were sampled in June 1996, Lake Lukomskoe and Lake Lepelskoe in June 1997, and lakes in the Naroch region in July 1998.

All mussels were collected at ca. 1.5–2.5 m depth, kept at 5–10 °C in a refrigerator, and dissected within 72 hr. All samples were processed in the laboratory using the following standardized protocol. Mussels from each sample were first sorted into seven 5-mm size classes based on shell length: 1.0 mm $\leq$ L $\leq$ 4.9 mm; 5.0 $\leq$ L $\leq$ 9.9 mm; 10.0 mm $\leq$ L $\leq$ 14.9 mm; 15.0 mm $\leq$ L $\leq$ 19.9 mm; 20.0 mm $\leq$ L $\leq$ 24.9 mm; 25.0 mm $\leq$ L $\leq$ 29.9 mm, and 30.0 mm $\leq$ L $\leq$ 34.9 mm. In each size class, 50 mussels were examined for prevalence whenever possible. Before dissection, we cleaned and dried shell surfaces and measured mussel length to the nearest millimeter with calipers. Mussels were then cut open with a scalpel, and their mantle cavities and tissues checked using a stereomicroscope (20–70X), and symbionts taxonomically identified.

Water quality parameters were determined from water samples collected from 4–7 sites systematically distributed across each waterbody (sample number directly correlated with waterbody width). At each sampling site, we determined transparency (by Secchi disc), pH, water color (comparing with Pt-Co scale), permanganate oxidizability, and hydrocarbonate content. The correlations between endosymbiont infection intensity and zebra mussel density and water quality parameters (e.g., oxidizability, Secchi depth, water color, and hydrocarbonates) were tested using Person correlation coefficients (STATISTICA for Windows Release 5.0 B, StatSoft, Inc., 1996).

3.2. Intensity of Infection

To study intensity of infection we used 60 samples collected from the Svisloch River, Dnieper-Bug Canal, Lake Lukomskoe, Lake Lepelskoe, and the nine lakes in the Naroch region. This involved using some of the same mussels examined to determine infection prevalence (see above). To study infection by the ciliate *Conchophthirus acuminatus* (Scuticociliatida: Conchophthiridae), however, 20 mussels in each size class were examined whenever possible. All mussels were cut open with a scalpel, and their mantle cavities were repeatedly flushed with unchlorinated tap water from a pipette to remove all symbionts from exposed epithelial surfaces. Because some symbionts, especially *C. acuminatus* and *A. limnica*, are also present within gill water tubes and suprabranchial cavities (LARUELLE *et al.*, 1999), gill tissues were also cut up and flushed by pipette. The number of symbionts in all rinse water was counted in a plankton counting chamber. In addition, all other *D. polymorpha* tissues were also thoroughly examined using a stereomicroscope (20–70X).

4. Results

We found 14 types of parasites and other symbionts within the mantle cavity and/or associated with zebra mussel tissues, including ciliates (*C. acuminatus*, *A. limnica*, and *Ophryoglena* sp.), trematodes (*Bucephalus polymorphus* and at least one species of Echinostomatidae, *Phyllodistomum*, and *Aspidogaster*), nematodes, oligochaetes, mites, chironomids, and

Table 2. Prevalence (%) of *Dreissena polymorpha* endosymbionts in the waterbodies studied.

Endosymbionts	Type of symbiont	Svisloch River		Dnieper-Bug Canal	Lakes (June 1997)		Braslavskie lakes (June 1996)			
		average 1996 (n = 1201)	average 1997 (n = 2200)	average 1997 (n = 1620)	Lepelskoe (n = 304)	Lukomskoe (n = 256)	Drivyaty (n = 215)	Strusto (n = 218)	Severnyi Voloso (n = 204)	Voiso (n = 254)
CILIOPHORA										
Conchophthirus acuminatus	C	85.8	87.4	95.6	97.7	88.7	81.9	99.1	98.0	95.7
Ancistrumina limnica	C	0.7	21.6	21.5	0.3	0.4	n.r.	n.r.	n.r.	n.r.
Ophryoglena sp.	P	–	–	42.7	–	–	–	–	–	
TREMATODA										
Echinostomatidae	P	–	0.5	0.3	–	28.5	4.2	10.6	–	0.8
Phyllodistomum	P	–	–	–	0.3	2.0	–	–	–	0.8
Bucephalus polymorphus	P	–	0.6	0.4	3.3	–	–	–	–	–
Aspidogaster	P	–	–	0.2	–	–	–	–	–	–
NEMATODA	C	5.5	23.4	16.3	10.2	10.2	3.3	2.8	2.0	5.9
HIRUDINEA										
Helobdella stagnalis	C	–	–	0.5	–	0.4	–	–	–	–
Erpobdella octoculata	C	–	0.05	–	–	–	–	–	–	–
OLIGOCHAETA										
Oligochaeta	C	–	0.3	0.6	–	–	–	–	0.5	–
Chaetogaster limnaei	C	–	3.3	2.1	9.2	3.1	–	–	–	–
Hydracarina	C	–	–	0.5	–	0.4	0.5	–	0.5	–
Chironomidae	C	–	0.1	0.3	–	–	–	–	–	–

* C = Commensal; P = Parasite; n.r. – not recorded; n – number of mussels dissected.

Table 3. Prevalence (%) of *Dreissena polymorpha* symbionts in the lakes in Naroch region.

Endosymbiont	Type of symbiont*	Bolduk (n = 74)	Dolzha (n = 89)	Lotviny (n = 44)	Myadel (n = 118)	Malye Shvakshty (n = 55)	Bolshiye Shvakshty (n = 61)	Spory (n = 70)	Svir (n = 221)	Volchin (n = 134)
CILIOPHORA										
Conchophthirus acuminatus	C	99	100	100	99	35	93	86	98	81
Ancistrumina limnica	C	–	–	2.3	0.9	1.8	1.6	2.9	2.3	4.5
TREMATODA										
Echinostomatidae	P	–	–	–	2.5	–	–	25.7	0.5	3.7
NEMATODA	C	4.1	10.1	52.0	24.0	20.0	37.7	17.1	13.1	15.8
HIRUDINEA										
Helobdella stagnalis	C	–	1.1	–	–	–	–	–	–	–
OLIGOCHAETA										
Oligochaeta	C	–	1.1	2.3	0.9	–	3.3	–	0.9	3.0
Chaetogaster limnaei	C	–	6.7	6.8	11.9	–	3.3	2.9	1.4	3.0
Hydracarina	C	–	–	–	–	1.8	–	–	0.5	–
Chironomidae	C	–	–	–	–	–	–	–	–	0.8

* C = Commensal; P = Parasite; n – number of mussels dissected.

Table 4. Infection intensity* of *Dreissena polymorpha* endosymbionts from the waterbodies studied.

Endosymbiont	Svisloch River	Dnieper-Bug Canal	Lakes		Lakes in Naroch region								
			Lepelskoe	Lukomskoe	Bolduk	Dolzha	Lotviny	Myadel	Malye Shvakshty	Bolshiye Shvakshty	Spory	Svir	Volchin
CILIOPHORA													
Conchophthirus acuminatus	142 ± 8 (1950)	553 ± 54 (6276)	113 ± 12 (838)	383 ± 58 (3705)	632 ± 86 (3218)	2979 ± 258 (10663)	3224 ± 556 (14035)	1003 ± 85 (4000)	266 ± 168 (2533)	432 ± 102 (4556)	482 ± 76 (3330)	705 ± 79 (7456)	67 ± 7 (1238)
Ancistrumina limnica	8.6 ± 1.1 (299)	3.7 ± 0.5 (165)	1 (1)	1 (1)	–	–	1 (1)	1 (1)	7 (7)	1 (1)	1 (1)	1.4 ± 0.2 (2)	1.3 ± 0.3 (3)
Ophryoglena sp.	–	8.4 ± 1.1 (299)	–	–	–	–	–	–	–	–	–	–	–
TREMATODA													
Echino-stomatidae	1.4 ± 0.2 (3)	2.6 ± 1.4 (8)	–	4.1 ± 0.6 (23)	–	–	–	1 (1)	–	–	1.6 ± 0.3 (6)	1 (1)	1 (1)
NEMATODA	2.3 ± 0.1 (41)	1.5 ± 0.1 (11)	1.4 ± 0.2 (3)	1.6 ± 0.2 (3)	1 (1)	1 (1)	1.9 ± 0.4 (8)	1.3 ± 0.1 (3)	1.6 ± 0.2 (3)	1.9 ± 0.2 (5)	1.3 ± 0.2 (3)	1.2 ± 0.1 (2)	1.8 ± 0.2 (4)
HIRUDINEA													
Helobdella stagnalis	–	1.3 ± 0.2 (2)	–	1 (1)	–	1 (1)	–	–	–	–	–	–	–
Erpobdella octoculata	1 (1)	–	–	–	–	–	–	–	–	–	–	–	–
OLIGOCHAETA													
Oligochaeta	1 (1)	1 (1)	–	–	–	1 (1)	1 (1)	1 (1)	–	1 (1)	–	1 (1)	1 (1)
Chaetogaster limnaei	1.3 ± 0.1 (5)	1.2 ± 0.1 (3)	1.1 ± 0.1 (4)	1.5 ± 0.4 (4)	–	1 (1)	1 (1)	1.4 ± 0.2 (3)	–	1 (1)	1 (1)	1.3 ± 0.3 (2)	1.3 ± 0.3 (2)
Hydracarina	–	1.1 ± 0.1 (2)	–	1 (1)	–	–	–	–	1 (1)	–	–	1 (1)	–
Chironomidae	1 (1)	1 (1)	–	–	–	–	–	–	–	–	–	–	1 (1)

* Cell values are mean intensity (± standard errors). Maximums are in parentheses.

Table 5. Pearson correlation matrix for nine lakes studied in Naroch region in 1998. Significance of correlation coefficients are given in parenthesis.

	C. acuminatus intensity (ciliates/mussel)	*Dreissena* density (ind/m^2)	Transparency (m)	pH	Hydrocarbonates (mg/L)	Color (Pt-Co Degree)	Permanganate oxidizability (mg O/L)
C. acuminatus intensity, ciliates/mussel	1.00						
Dreissena density, ind/m^2	−0.12 (P = 0,76)	1.00					
Transparency, m	−0.37 (P = 0,33)	0.61 (P = 0.08)	1.00				
pH	−0.15 (P = 0,70)	0.45 (P = 0,22)	0.20 (P = 0.61)	1.00			
Hydrocarbonates, mg/L	0.35 (P = 0,36)	−0.27 (P = 0,49)	−0.35 (P = 0,36)	0.58 (P = 0,10)	1.00		
Color, Pt-Co Degree	−0.28 (P = 0,46)	−0.22 (P = 0,56)	−0.40 (P = 0,29)	−0.62 (P = 0,07)	−0.55 (P = 0,12)	1.00	
Permanganate oxidizability, mg O/L	0.48 (P = 0,19)	−0.44 (P = 0,24)	−0.52 (P = 0,15)	−0.66 (P = 0,052)	−0.30 (P = 0,43)	0.47 (P = 0,21)	1.00

leeches (Tables 2, 3). In this paper we have included only species that could be found during dissection and have not considered species which generally require special histological techniques for their observation (e.g., the ciliates *Hypocomagalma dreissenae*, *Sphenophrya dreissenae*).

4.1. Ciliates

Conchophthirus acuminatus was the only endosymbiont found in all zebra mussel populations sampled. The prevalence of *C. acuminatus* infection was always much higher than that of all others symbionts and ranged from 35% to 100% (Tables 2, 3). Mean infection intensity (± SE) varied from 67 ± 6 ciliates/mussel in the Lake Volchin to 3,324 ± 556 in Lake Lotviny (Table 4). Whereas the maximum intensity of 14,035 ciliates/mussel was observed in a 26.4 mm long mussel from Lake Lotviny, the smallest infected mussel was 1.1 mm long, had one *C. acuminatus*, and was found in the Svisloch River. We did not find a significant correlation between infection intensity and zebra mussel density, oxidizability, Secchi depth, water color, or hydrocarbonates (significance of the Pearson correlation coefficients were $0.19 < P < 0.76$) (Table 5). Although the highest intensity of infection was found in Lake Lotviny, this lake had the lowest *D. polymorpha* density (Tables 1, 4) (e.g., it took more than an hour for a diver to collect only 97 *D. polymorpha*). Almost the same low zebra mussel density was found in Lake Bolshye Shvakshty; however, infection intensity was also low. In Lake Dolzha both zebra mussel density and infection intensity were high.

Our study indicated that the commensal *A. limnica* was widely distributed in Belarussian *D. polymorpha* populations. This ciliate is a nonspecific invader of freshwater lamellibranchs and gastropods (MOLLOY *et al.*, 1997). We found this species in the mantle cavities of zebra mussels in 11 of the 17 waterbodies studied. The prevalence in infected *D. polymorpha* populations ranged from 0.3% to 21.6% and was much higher in the Dnieper-Bug Canal and Svisloch River than in all the lakes studied. Both the highest mean (± SE) intensity of infection observed in the monthly samples, i.e., 8.6 (± 1.1) *A. limnica*/mussel, and the highest intensity of infection observed in a single mussel, 299 *A. limnica*/mussel (mussel 25 mm long), were recorded from the Svisloch River.

The Dnieper-Bug Canal was the only waterbody in which we found parasitic ciliates identified as *Ophryoglena* sp. (D. H. LYNN, personal communication) inside the digestive gland of zebra mussels. The prevalence of infection varied from 11% in August to 80% in November. During the sampling period, the infection intensity varied from 1 to 291 ciliates/mussel. We found a significant ($P < 0.001$ *t*-test) increase in mean (± SE) intensity of infection with this *Ophryoglena* sp. from 3.3 ± 0.2 ciliates/mussel on June 30 to 24.8 ± 5.7 on July 26 and then a decrease to 1.5 ± 0.2 on September 23.

4.2. Trematodes

The most common trematodes observed in Belarussian zebra mussels were in the family Echinostomatidae. We found echinostomatid metacercarial cysts within zebra mussels in 10 of the 17 waterbodies, and infection prevalence varied from 0.3% to 28.5% (Tables 2, 3). The maximum was recorded in Lake Lukomskoe. *Bucephalus polymorphus* (Bucephalidae) was observed parasitizing *D. polymorpha* in 4 of the 17 waterbodies, and the prevalence of infection was low, ranging from 0.4% to 3.3%. The highest prevalence of infection was recorded in the Lake Lepelskoe (one of the oldest zebra mussel populations in Belarus). Sporocysts of *Phyllodistomum* were recorded from zebra mussels in 3 of the 17 populations sampled. A maximum prevalence of 2.0% was found in Lake Lukomskoe. *Aspidogaster* was the rarest trematode genus observed in *D. polymorpha*. We found this genus only in the Dnieper-Bug Canal, and the infection prevalence was very low (0.2%).

4.3. Other Symbionts

Among other endosymbionts, nematodes were the most frequently observed and were present in all populations sampled, with prevalences ranging from 2% to 52% (Tables 2, 3). A mean (± SE) maximum intensity of 2.3 ± 0.1 nematodes/mussel and a maximum of 41 nematodes/mussel were observed in the Svisloch River (Table 4). Among oligochaetes, the most common species in zebra mussel populations was *Chaetogaster limnaei* which was observed in 11 of the 17 waterbodies studied, with infection prevalence and intensity ranging from 1.4% to 11.9% and 1 to 1.5 ± 0.4 oligochaetes/mussel.

In addition, two species of leeches (*Helobdella stagnalis* and *Erpobdella octoculata*), unidentified chironomid larvae, and unidentified mites were recorded from the mantle cavity. The prevalence and infection intensity of all these symbionts were always low, and *E. octoculata* was found only once (an 11 mm specimen from a 17.2 mm long mussel in the Svisloch River).

5. Discussion

5.1. Ciliates

The ciliate *C. acuminatus* is known to be the most common symbiont of *D. polymorpha*, and its relationship with zebra mussels, although obligate, is far more likely to be commensal than parasitic (Molloy *et al.*, 1997). According to Kidder (1934), all *Conchophthirus* spp. have an obligate association with bivalves and likely can tolerate only brief periods in open waters, as during their transfer to new hosts. *C. acuminatus*, in particular, is known to be extremely host specific, having been recorded only from *D. polymorpha* (Molloy *et al.*, 1997). This species has been found in zebra mussels in many European waterbodies (Raabe, 1934, 1950, 1966; Dobrzanska, 1958; Fenchel, 1965; Burlakova, 1998), and we found this ciliate in all 17 zebra mussel populations sampled. It should be noted that, in contrast, *C. acuminatus* has never been found in North American *D. polymorpha* (authors, unpublished data). Because *C. acuminatus* infects only attached zebra mussels, these data support two hypotheses: (1) that zebra mussels invaded North America in their planktonic veliger stage, and (2) that all European waterbodies populated by *C. acuminatus*-infested *D. polymorpha* were more likely to be colonized by attached mussels than by veligers, or if the waterbody was colonized by veligers, the water current that was a source of veligers was also a source of *C. acuminatus*.

There are several reports of the prevalence of *C. acuminatus* in *D. polymorpha* (Raabe, 1956, 1966, 1971; Fenchel, 1965; Burlakova *et al.*, 1998), but only one paper to date has examined the intensity of infection (Burlakova *et al.*, 1998). *C. acuminatus* has the highest prevalence of infection among all 34 symbionts found in *D. polymorpha* (Molloy *et al.*, 1997), and very often all specimens in a zebra mussel population are infected. For example, Fenchel (1965) observed 100% infection with *C. acuminatus* in two Danish lakes.

Within our study, the prevalence of *C. acuminatus* infection was always much higher than that of all others symbionts and ranged from 35% to 100%. These data are consistent with our previous study in which high prevalences of zebra mussel infection with *C. acuminatus* were recorded (Burlakova *et al.*, 1998).

Zebra mussels, while relatively small bivalves, have one of the highest intensities of infection ever reported for ciliates in the order Scuticociliatida (Burlakova *et al.*, 1998). The factors affecting *C. acuminatus* infection prevalence and intensity in zebra mussel populations had not been comprehensively investigated prior to Burlakova *et al.* (1998). In this latter study, we provided evidence that intensity and/or prevalence can be affected by hostdependent factors, such as mussel size and the presence of highly infected mussels in a microhabitat (especially when these latter mussels die). Abiotic factors, such as salinity (RAABE, 1956), depth (RAABE, 1966, 1971; BURLAKOVA *et al.*, 1998), and water current (authors, unpublished data) may also affect prevalence.

We did not find a significant correlation between infection intensity and the abiotic or biotic parameters recorded in this study, including mussel density (Table 5). In Lake Bolshye Shvakshty both zebra mussel density and infection intensity were very low, whereas in Lake Lotviny with a similarly low *D. polymorpha* density we found the highest infection intensity recorded in the entire study (Tables 1, 4). In contrast, both zebra mussels density and infection intensity were high in Lake Dolzha.

Protozoans have occasionally been observed from the digestive gland of zebra mussels. Ciliates in the family Ophryoglenidae (suborder Ophryoglenina) were reported living inside the digestive gland (ZDUN *et al.*, 1994). The ciliates recorded from the digestive gland of *D. polymorpha* in 8 of 13 Russian waterbodies (MOLLOY *et al.*, 1996) were later determined to be ophryoglenines (D. H. LYNN, personal communication). KAZUBSKI (personal communication in STANCZYKOWSKA, 1977) reported „dangerous" infections by small and large ciliates in zebra mussels. The larger form occurred in the digestive gland and was considered to be in the family Ophryoglenidae. Likewise, ZDUN *et al.* (1994) indicated that ophryoglenine ciliates may have a pathogenic effect on *Dreissena*.

In our study, the *Ophryoglena* sp. was only found in Dnieper-Bug Canal (Figure 1, Table 2). In contrast, we have observed this parasite commonly in Western European *D. polymorpha* populations (authors, unpublished data). This suggests that the Dnieper-Bug Canal was the main route for *D. polymorpha* invasion into Western Europe, but not to Central and Northern Belarus.

5.2. Trematodes

Seven genera of trematodes have been reported in the literature as parasites of *Dreissena* spp. In their life cycles, zebra mussels can serve as the first intermediate host (e.g. *B. polymorphus* and *Phyllodistomum* spp.), second intermediate host (e.g., *Echinoparyphium recurvatum*), or the only host (*Aspidogaster* spp.) (MOLLOY *et al.*, 1997).

B. polymorphus requires three hosts to complete its life cycle. Infection commences in a zebra mussel when the earliest larval stage, the miracidium, hatches from an egg, enters a mussel's visceral mass, and gives rise to the sporocyst stage. Located primilarly in the gonads, *B. polymorphus* typically induces *Dreissena* sterility. Cercariae released into the surrounding waters attach to fish fry, encyst in their tissues, and transform into metacercariae. The final hosts of *B. polymorphus* are predatory fish that have consumed fish infected with metacercariae. Although there are numerous reports of *Anodonta* and *Unio* (Unionidae) infected with *B. polymorphus*, the accuracy of these host data is doubtful due to the similarity in appearance between the sporocysts and cercariae of *B. polymorphus* and species in another genus in the Bucephalidae, *Rhipidocotyle* (MOLLOY *et al.*, 1997). Based on careful examination of cercarial morphology, BATURO (1977) recorded *B. polymorphus* only in *D. polymorpha* and found *Rhipidocotyle campanula* (= *R. illense*) only in unionids. *B. polymorphus* appears to be widely distributed in Eurasian *Dreissena* populations (MOLLOY *et al.*, 1997).

The prevalence of *B. polymorphus* infection varied from 0.4% to 3.3% in our samples. Although very high prevalence rates (up to 73%) have been reported in *D. polymorpha* in southern France (WALLET and LAMBERT, 1986), low to moderate rates of prevalence are more typical: 1% (KUPERMAN *et al.*, 1994); 2% (CHERNOGORENKO and BOSHKO, 1992); 1 to 4% (BATURO, 1977); 2% to 5% (SMIRNOVA and IBRASHEVA, 1967); 9% (MOLLOY *et al.*, 1996); 14% to 20% (ARISTANOV, 1986); and 13% to 28% (DE KINKELIN *et al.*, 1968a).

Phyllodistomum spp. that parasitize zebra mussels require only one other host, a fish, to complete their life cycles. In choosing an intermediate host, the two most documented *Phyllodistomum* species recorded from zebra mussels, *P. folium* and *P. dogieli*, appear quite specific as they have been reported only from *D. polymorpha* (MOLLOY *et al.*, 1997). *Phyllodistomum* spp. are widely distributed in European *D. polymorpha* populations. Records of either *P. folium*, *P. dogieli*, or *P. angulatum* exist from the Netherlands (KRAAK and DAVIDS, 1991), Poland (KULCZYCKA, 1939; WISNIEWSKI, 1957), Belarus (KARATAYEV, 1983; LYAKHNOVICH *et al.*, 1983), Russia (KUPERMAN *et al.*, 1994; MOLLOY *et al.*, 1996), Ukraine (ZDUN, 1965), and Kazakhstan (SMIRNOVA and IBRASHEVA, 1967).

We observed *Phyllodistomum* in 3 of the 17 waterbodies studied, with the maximum prevalence of 2.0% observed in Lake Lukomskoe. According to the literature, the prevalence of zebra mussel infection in most infected populations also tends to be low: <1% (MOLLOY *et al.*, 1996); <3.7% (KUPERMAN *et al.*, 1994); 4.5% (SMIRNOVA and IBRASHEVA, 1967); <10% (KRAAK and DAVIDS, 1991); and <12.3% (LYAKHNOVICH *et al.*, 1983). ZDUN (1965) reported an exceptionally high prevalence of infection of 33%.

Echinoparyphium recurvatum (Echinostomatidae) is a cosmopolitan trematode species that has been reported from *D. polymorpha*, and three hosts are required for completion of its life cycle. In contrast to other trematodes, *Dreissena* is not the first host, but rather one of several possible second intermediate hosts. Adult echinostomatids, such as *E. recurvatum*, are parasites of the small intestines of waterfowl (e.g., anatid ducks) and occasionally mammals (MOLLOY *et al.*, 1997).

Echinostomatid metacercarial cysts were found in zebra mussels in 10 of the 17 waterbodies studied, with infection prevalence ranging from 0.3% to 28.5% (the latter being the highest prevalence of *Dreissena* infection ever reported). Literature reports of echinostomatids in *D. polymorpha* include <1% infection with *E. recurvatum* (GINEZINSKAJA, 1959), <1% infection with *E. echinatoides* (CHERNOGORENKO and BOSHKO, 1992), and ≤8.5% mixed infection with *E. recurvatum* and *Echinostoma paraulum* (KOCHNEV, 1977).

Aspidogaster spp. need only a single host to complete their life cycle, as eggs containing larvae infect molluscs and give rise to adult trematodes (ROHDE, 1994). *Dreissena* is the only one of several molluscan hosts of *Aspidogaster* spp. Vertebrates, such as fish, may also become hosts by ingesting infected molluscs (MOLLOY *et al.*, 1997). *Aspidogaster* was the trematode least encountered in our zebra mussel samples.

5.3. Others Symbionts

Among other zebra mussels symbionts, nematodes were frequently observed in the mantle cavities of *D. polymorpha*. Evidence to date suggests that they are likely free-living species without any obligate association with zebra mussels (MOLLOY *et al.*, 1997). We found nematodes in all zebra mussels populations studied, and the prevalence of infestation varied from 2% to 52%. The mean (± SE) maximum infestation intensity (i.e., highest among the monthly infection intensity means) was 2.3 ± 0.1 nematodes/mussel and the maximum intensity of 41 nematodes/mussel were found in the Svisloch River. In the St. Lawrence River (New York State), juvenile and adults of at least four species of nematodes were observed, including at least one *Mononchus* sp. and dorylamid; the highest prevalence and mean intensity were respectively, 40% and 2.8 nematodes/mussel (CONN *et al.*, 1994).

The oligochaete, *C. limnaei*, is a common commensal of snails (TIMM, 1987; MONAKOV, 1998). This species, however, has also been reported from *Dreissena* in the Dnestr River/Liman in Ukraine (CHERNOGORENKO and BOSHKO, 1992) and St. Lawrence River, New York State (CONN *et al.*, 1996). We observed *C. limnaei* in zebra mussels in 11 of 17 waterbodies studied, and the prevalence and intensity of infestation varied from 1.4% to 11.9% and 1 to 1.5 ± 0.4 oligochaetes/mussel. A much higher prevalence (mean 27% and maximum 80%) was reported from St. Lawrence River (CONN *et al.*, 1996). The mean and maximum intensities of infestation in this latter study were ca. 3 and 18 oligochaetes/mussel, respectively.

Two species of leeches, *Caspiobdella fadejewi* and *Helobdella stagnalis*, were reported as endosymbionts of *D. polymorpha* in the Volga Basin, Russia (KUPERMAN *et al.*, 1994). We found *H. stagnalis* in three of the zebra mussel populations studied. The prevalence and intensity of infestation were low (respectively, ≤ 1.1% and 1 leech/mussel). *Erpobdella octoculata* was found only once. Both *H. stagnalis* and *E. octoculata* are known as free-living predators (LUKIN, 1976) and are likely to have inadvertently entered *Dreissena*'s mantle cavity.

Chironomid larvae have been observed in the mantle cavities of *D. polymorpha* both in Europe and North America. *Chironomus bathophilus* was observed in *D. polymorpha* in the Volga Basin (KUPERMAN *et al.*, 1994) and *Paratanytarsus* sp. in the St. Lawrence River (New York State and Quebec Province) (CONN *et al.*, 1994; RICCIARDI, 1994). Because tissue damage was not apparent in infested mussel, RICCIARDI (1994) considered the chironomid-*Dreissena* association to be commensal.

Unidentified mites were found in the mantle cavities of *D. polymorpha* populations from 6 of the waterbodies. Both the prevalence and intensity of infection were low. The impact of mites on zebra mussels is unknown (MOLLOY *et al.*, 1997).

5.4. Ecological Impact

Among parasites and commensals associated with zebra mussels, at least five species of ciliates (*C. acuminatus*, *C. klimentinus*, *H. dreissenae*, *S. dreissenae*, *S. naumiana*) are known to be species specific (MOLLOY *et al.*, 1997). Because no ciliate in the suborder Ophryoglenina has ever been reported as a parasite within bivalve organs, it is likely that the *Ophryoglena* sp. is highly host specific to *Dreissena* also. Among the trematodes, there is also evidence that *B. polymorphus*, *P. folium*, and *P. dogieli* appear to be quite specific to *Dreissena* (MOLLOY *et al.*, 1997). Therefore *D. polymorpha*, when invading new habitats, potentially may introduce up to nine alien (i.e., nonindigenous) species.

In this study the maximum numbers of alien species associated with *D. polymorpha* were found in the oldest zebra mussel populations in Belarus: Dnieper-Bug Canal (*C. acuminatus*, *Ophryoglena* sp., *B. polymorphus*) and Lake Lepelskoe (*C. acuminatus*, *Phyllodistomum*, *B. polymorphus*). In contrast, in the most recently colonized lakes in the Naroch region only one alien species (*C. acuminatus*) was found. In the Svisloch River, Lake Lukomskoe, Lake Drivyaty, and Lake Voiso, we found two host-specific endosymbionts of *D. polymorpha*. Thus, the spread of *Dreissena* endosymbionts is not uniform and may depend on the time of initial colonization.

The trematode species that use *Dreissena* as an intermediate host usually subsequently develop to adults in either waterfowl or fish (MOLLOY *et al.*, 1997). *E. recurvatum* has been reported as occasionally fatal to its final hosts, anatid ducks (MCDONALD, 1969). Among the fish parasites, to date the only trematode recorded to have negative impact on their hosts is *B. polymorphus*. Twenty species in six families (Cyprinidae, Percidae, Esocidae, Centrarchidae, Cobitidae, and Gasterosteidae) were observed with *B. polymorphus* metacercariae in an epizootic in the Seine Basin, but serious pathologies and deaths were recorded only in cyprinids (DEKINKELIN *et al.*, 1968b). However, this report of adverse effect of *B. polymorphus* on fish populations is the exception (MOLLOY *et al.*, 1997). In the Lake Lepelskoe *B. polymorphus* cysts were found in gills of Cyprinidae and adult trematodes in all predatory fish that we dissected (authors, unpublished data). *P. folium* was found in pike (*Esox lucius*) in Lake Lukomskoe. There is no evidence that *B. polymorphus* and *P. folium* cause serious fish pathology in these lakes (KARATAYEV *et al.*, 1998).

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