

Field evidence for a parasite spillback caused by exotic mollusc *Dreissena polymorpha* in an invaded lake

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Abstract This study provides field evidence in support of the “parasite spillback hypothesis” that predicts a positive numerical response of native parasites to the presence of an exotic host that is competing for these parasites with native hosts. We examined the role that the exotic mollusc *Dreissena polymorpha* (zebra mussel) plays as the second intermediate host of the echinostomatid trematode *Echinoparyphium recurvatum* in Lake Naroch, Belarus. We found that due likely to the disproportionately high abundance of its novel exotic host, the metacercarial stage of this parasite has become substantially more abundant than that of other echinostomatid trematodes recorded in native molluscs. This finding suggests an increased load (the “spillback”) of *E. recurvatum* on native waterfowl that serve as its final hosts. The risk of aquatic birds becoming infected with this trematode via feeding on *D. polymorpha* was found to vary both spatially and seasonally. This risk was particularly high in the autumn at a depth of 2 m and at sites of bird gatherings.

Introduction

Over the last several decades, the number of studies on different aspects of biology and ecology of exotic species has grown exponentially. Yet, many of the effects caused by exotic species remain poorly understood and thus are hard to predict. The mechanisms of parasitological impacts that invaders cause in the recipient ecosystems have received especially inadequate attention. At the same time, parasites of exotic species may have devastating effects in invaded regions, including extinction risk for endangered species (Holmes 1996; Atkinson et al. 1995; Mitchell et al. 2005), mass mortalities of native hosts (Burrenson et al. 2000; Edgerton et al. 2002; Cole and Franson 2006; Taraschewski 2006), and public health issues (Taylor et al. 2001; Lv et al. 2009). Considerable economic damage has been documented when exotic parasites afflicted commercially exploited native populations (Burrenson et al. 2000; Wheelis et al. 2000; Pimentel et al. 2005).

The negative parasitological effects on biota native to a recipient ecosystem can occur due to the (1) introduction and subsequent switch of exotic parasites to the novel native hosts and/or (2) acquisition and amplification of the native parasites by an invader. Either way, invasion of an exotic species may result in promotion of diseases that otherwise would not have emerged. Whereas the impacts determined by the first of these mechanisms (“parasite spillover”) have been rather well documented (e.g., Daszak et al. 2000; Dobson and Foufopoulos 2001; Prenter et al. 2004), the second mechanism (“parasite spillback”) has previously been overlooked and, to become formalized in invasion ecology, requires accumulation of field and experimental data (Kelly et al. 2009).

The positive numerical response of native parasites to the presence of an exotic host is likely often driven by the

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behavioral and/or ecological traits of the latter (Kelly et al. 2009). The theory of epidemiology of parasitic diseases (Anderson and May 1981; Dobson 1990) suggests that exotic species with different abundances may play particularly different roles in the parasite systems of invaded areas. Successful invaders that form extremely abundant populations are usually represented by species that occupy novel or relatively unsaturated ecological niches (Karatayev et al. 2009). One of such highly competitive and gregarious invaders is the Ponto-Caspian bivalve mollusc *Dreissena polymorpha* (zebra mussel; Karatayev et al. 2002). This mollusc, now widely distributed in Europe and North America, is known to host over 40 commensal and parasite taxa (Molloy et al. 1997; Karatayev et al. 2000; Mastitsky 2004; Mastitsky and Gagarin 2004; Mastitsky and Samoilenko 2005) and thus may be used as a very suitable model species for testing the “parasite spillback hypothesis”. This hypothesis states that the parasite spillback occurs “...when a nonindigenous species is a competent host for a native parasite, with the presence of the additional host increasing disease impacts in native species” (Kelly et al. 2009). In the current paper, we provide evidence in support of this hypothesis by presenting the results of a field study on the role that exotic *D. polymorpha* plays as an intermediate host of a native echinostomatid trematode in an invaded lake. We found that, due likely to its dominant position in the molluscan community of this lake, *D. polymorpha* has also become a dominant species in terms of the hosted densities of echinostomatid metacercariae, a pattern implying an increased load of these parasites on the native waterfowl that serve as their final hosts.

Material and methods

Study area

The study was conducted in 2005 in Lake Naroch, a waterbody where echinostomatid infection was found to be common in *D. polymorpha* (Mastitsky 2003). Lake Naroch is a large mesotrophic waterbody situated in the northwestern part of Belarus (54°50'N, 26°45'E; surface area, 79.6 km²; mean depth, 8.9 m; maximal depth, 24.8 m). Together with two other interconnected lakes (Myastro and Batorino), these form the so-called “Narochanskaya Lake System”. Lake Naroch is divided by a peninsula into small (northwestern) and large (southeastern) stretches (Fig. 1). A considerable part of this waterbody is shallow, e.g., a depth of 2 m constitutes about 14% of the entire bottom area (Ostapenya 1985). The large littoral zone and high water transparency (6.7±0.6 m in 2005, mean±standard deviation; Zhukova et al. 2007) determine ample development of semisubmerged and submerged macrophytes (Gigevich

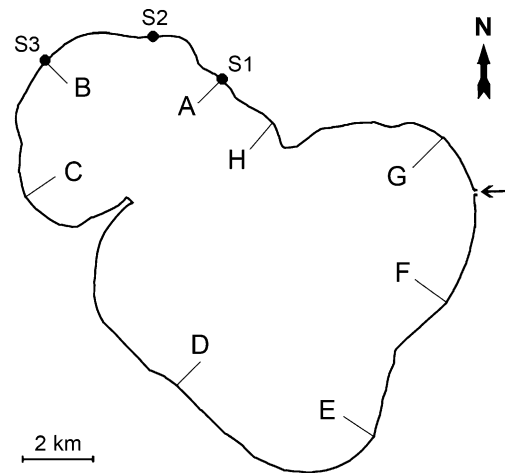


Fig. 1 Map of Lake Naroch. Population density of *D. polymorpha* and native molluscs was estimated in May and October 2005 along the transects A through H. In July 2005, *D. polymorpha* and native molluscs were collected for comparative parasitological examination at the three sites (filled circles) denoted as S1 to S3. These sites represented the following typical littoral Lake Naroch biotopes: S1 sandy bottom covered with rare stands of *Chara* spp.; S2 sandy bottom with rather abundant cobbles; S3 sandy bottom covered with dense stands of *Chara* spp.

1985; Zhukova et al. 2005). The main substrate in the littoral zone is sand; however, cobble and gravel are also present in the northeastern littoral part of the lake. Bottom areas deeper than 7 m are completely covered with silt.

D. polymorpha was first found in Lake Naroch in 1989 (Ostapenya et al. 1993). Supposedly, the source waterbody for this invasion was the abovementioned Lake Myastro, where zebra mussels were recorded somewhat earlier, in 1984 (Ostapenya et al. 1993). Juvenile or adult zebra mussels might have been introduced into Lake Myastro from fishing gear from commercial fisheries (Burlakova et al. 2006). Over the first 5 years since introduction, the size of *D. polymorpha* population has grown exponentially and then stabilized (Burlakova et al. 2006).

Distribution and abundance of *D. polymorpha* and other molluscs

In order to estimate and compare the densities of *D. polymorpha* and other molluscs that could potentially serve as intermediate hosts for echinostomatids in Lake Naroch, we conducted lake-wide surveys in May and October 2005. The molluscs were collected with a Petersen grab sampler (0.025 m²) from depths of 0.8, 2, 4, 6, and, occasionally, from 8 m along eight transects that included all typical habitats within the lake and embraced all its parts (Fig. 1). Similar transects were used by Burlakova et al. (2006) to estimate the abundance of *D. polymorpha* in 1990–1997. We took three replicate grabs at most of the sampling sites;

however, up to eight replicates were taken at some sites with low molluscan densities. All molluscs found in a sample were identified to the lowest taxonomic level possible and counted. Additional samples of up to 50 zebra mussels were collected at each site and preserved in 10% buffered formalin for subsequent parasitological examination.

Dissection protocol

We used the abovementioned formalin-preserved samples to reveal the lake-wide patterns of distribution and abundance of echinostomatid metacercariae in *D. polymorpha*. Depending on their availability, ten to 40 randomly selected zebra mussels were dissected from each sampling site to estimate the prevalence and intensity of echinostomatid infection (all parasitological terms used in the paper are in accordance with Bush et al. 1997). Molluscs were cut open with a scalpel, and their soft tissues were repeatedly flushed with tap water from a pipette into a zooplankton counting chamber. Soft tissues were also transferred into a counting chamber, inspected for major signs of infection, and then homogenized with forceps. All dissections were conducted under the stereomicroscope at $\times 20$ – 70 .

In July 2005, we conducted similar dissections of *D. polymorpha* and other molluscs from the littoral zone of Lake Narocho to reveal if, and to what extent, they share the infection by echinostomatid metacercariae. The molluscs were collected in a small stretch of the lake from a depth of 0.5–1 m at three sites representing typical littoral habitats (Fig. 1). We chose this depth range for our comparative parasitological analysis as the waterfowl feeding on *D. polymorpha* are known to prefer littoral sites shallower than 2 m (Molloy et al. 1997). At each site, we estimated the density of molluscan populations using ten replicate quadrat samples of 0.25 m² each. Wherever possible, from each site, we dissected 20 randomly selected nondreissenid molluscs and 40 randomly selected zebra mussels.

Statistical analysis

The data on the density of molluscs and intensity of echinostomatid infection appeared to have right-skewed non-normal distributions. Although median values and quartiles would be more proper descriptors of such distributions (Rózsa et al. 2000), we used arithmetic mean and standard error as this allowed for comparing of our results with the previously published data. Yet, we used non-parametric Kruskal–Wallis ANOVA by ranks with help of STATISTICA 6.0 software (StatSoft, Inc. 2001) to test for differences among non-normally distributed samples. The *G*-test for independence (Sokal and Rohlf 2001) was employed with the help of an MS Excel template available

online (<http://udel.edu/~mcdonald/statgtestind.html>) to compare the prevalences of infection.

We used the density of echinostomatid metacercariae (per square meter) as a measure of infection risk posed by an infected molluscan species to waterfowl. To estimate the density of echinostomatids hosted by a certain molluscan species at a sampling site, we multiplied the mean density of this species by the mean abundance of echinostomatid metacercariae. The latter was calculated by multiplying the mean intensity by prevalence of infection (Bush et al. 1997).

The significance level $\alpha=0.05$ was accepted as an initial level in all statistical tests. However, we applied a sequential Bonferroni correction to this initial level when multiple tests were simultaneously run on the same datasets (Rice 1989).

Results

Diversity, distribution, and abundance of molluscs

Eleven molluscan taxa were identified during the survey in May 2005, though the actual species richness in the collected samples was somewhat higher. More precise identifications were impeded particularly by the presence of juvenile Lymnaeidae, whose species-specific morphological features were underdeveloped. In contrast, in October 2005, we were able to identify 24 taxa. On both survey dates and at nearly all depths sampled, *D. polymorpha* appeared to be the dominant species among all molluscs found. The average fraction of zebra mussels in total molluscan density varied among depths from 56.5 ± 8.2 to $70.4 \pm 6.6\%$ in May and from 23.5 ± 8.3 to $69.2 \pm 3.8\%$ in October. The subdominant taxa were represented by native *Bithynia tentaculata* and Pisidiidae gen. spp. (Fig. 2). The specific fractions of other molluscan taxa never exceeded an average of 10%.

D. polymorpha was found in all parts of Lake Narocho and at all depths sampled. The density of zebra mussels varied significantly among depths and transects but not between survey dates (depth, $P < 0.001$; transect, $P = 0.004$; date, $P = 0.345$; Kruskal–Wallis ANOVA with Bonferroni-corrected $\alpha = 0.017$). On both dates, the mean density of *D. polymorpha* population demonstrated similar bell-shaped bathymetric distributions with peaks at 2–4 m (Fig. 3). No zebra mussels were found deeper than 8 m. On a lake-wide scale, the highest numbers of *D. polymorpha* were recorded in the small stretch along the transects B (up to $4,963 \pm 1,027$ ind./m²) and C (up to $2,340 \pm 642$ ind./m²; Fig. 1). Having pooled together the data from both sampling dates, we estimated that the mean density of zebra mussel within the surveyed range of depths was

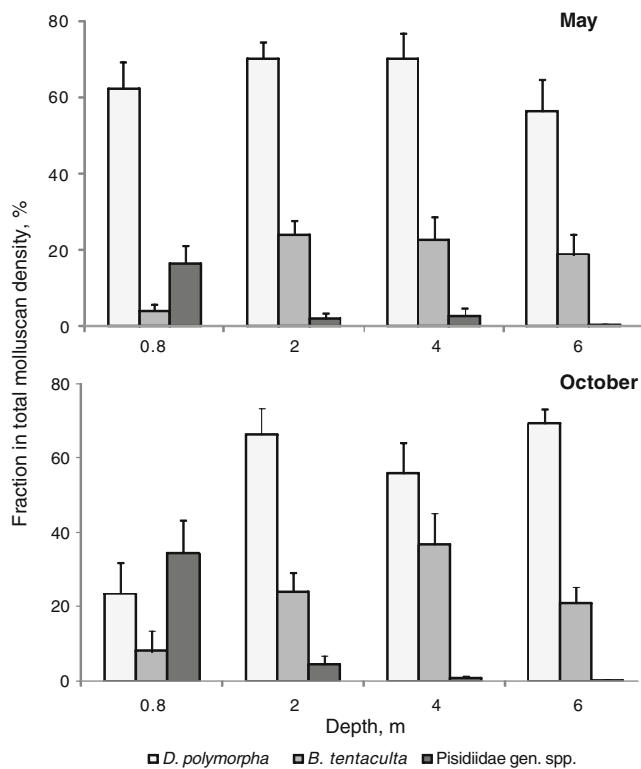


Fig. 2 Bathymetric distribution of the fraction of *D. polymorpha* and two subdominant native taxa (the snail *B. tentaculata* and fingernail clams Pisidiidae gen. spp.) in total molluscan density in May and October 2005

1,508±221 ind./m² ($n=177$). The occurrence of *D. polymorpha* in this pooled dataset (i.e., the percentage of samples containing zebra mussels) was 85%, which is higher than that of any other molluscan species encountered during the study. For example, the pooled occurrences of subdominant *B. tentaculata* and Pisidiidae gen. spp. were 74% and 29%, respectively.

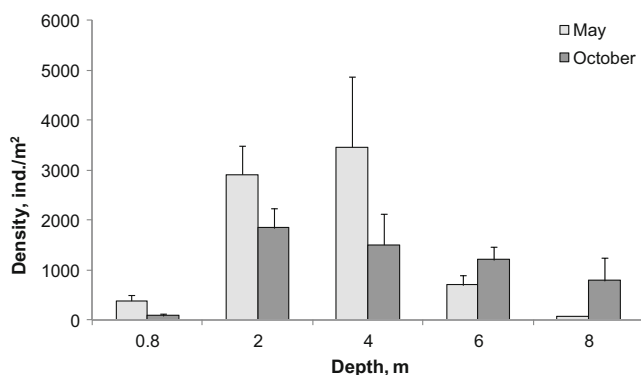


Fig. 3 Bathymetric distribution of *D. polymorpha* population density in May and October 2005

Distribution and abundance of echinostomatids in *D. polymorpha* population

Echinostomatid metacercariae were present in formalin-preserved samples of *D. polymorpha* collected in both May and October. All infected zebra mussels contained metacercariae of the species identified as *Echinoparyphium recurvatum* (Sudarikov et al. 2002).

The prevalence of *D. polymorpha* infection with *E. recurvatum* varied among samples from 0% to 100%. The percentage of infected mussels significantly differed between both the survey dates and among depths sampled (date, $P<0.001$; depth, $P<0.001$; G -tests for independence with Bonferroni-corrected $\alpha=0.025$). The overall prevalence of infection was much higher in October (36.5%, $n=619$) than in May (10.3%, $n=518$). On both dates, the maximal prevalence of echinostomatid infection in *D. polymorpha* was observed at depth of 2 m (Fig. 4a).

The number of *E. recurvatum* metacercariae in individual infected zebra mussels ranged from 1 to 190. Similarly to prevalence, the overall mean intensity of infection was significantly higher in October than in May (6.1 ± 1.2 vs. 2.7 ± 0.6 metacercariae/mussel; $P<0.001$, Kruskal–Wallis ANOVA with Bonferroni-corrected $\alpha=0.025$). There was also a significant difference in the intensity of infection among depths ($P<0.001$, Kruskal–Wallis ANOVA with

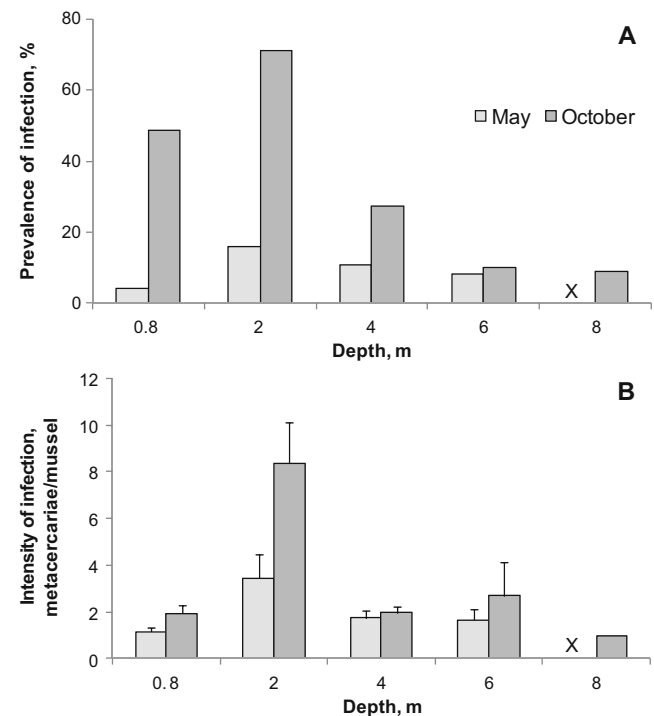


Fig. 4 Bathymetric distribution of the prevalence (a) and intensity (b) of infection of *D. polymorpha* with the trematode *E. recurvatum* in May and October 2005. In May, the mussels from depth of 8 m were not dissected, which is indicated with x

Bonferroni-corrected $\alpha=0.025$), with the highest numbers of metacercariae observed in the mussels from 2 m (Fig. 4b).

The density of *E. recurvatum* in *D. polymorpha* varied among sampling sites from 0 to 6,120 metacercariae/m² in May and from 0 to 38,610 metacercariae/m² in October. The density of metacercariae significantly differed among depths but not between sampling dates (depth, $P=0.004$; date, $P=0.156$; Kruskal–Wallis ANOVAs with Bonferroni-corrected $\alpha=0.025$). Reflecting the bathymetric distribution of *D. polymorpha* population density (Fig. 3), as well as that of the prevalence and intensity of infection (Fig. 4), the density of echinostomatid metacercariae in zebra mussels demonstrated bell-shaped distributions with the maxima recorded at 2 m (Fig. 5).

Comparative examination of molluscs for echinostomatid infection

We found ten molluscan taxa at the three littoral sites sampled in July 2005. As in May 2005 and October 2005, *D. polymorpha* dominated in these July samples in terms of the population density (Table 1). The other common species were *Gyraulus albus*, Pisidiidae gen. spp., *B. tentaculata*, and *Lymnaea auricularia*.

Five out of nine nondreissenid molluscan species were found to be infected with echinostomatid metacercariae (Table 1). All infected zebra mussels contained cysts of the trematode *E. recurvatum*. The metacercariae from the snail *Viviparus contectus* were tentatively identified as *Neoacanthoparyphium echinatoides*. At least one more morphologically different type of echinostomatid metacercariae was observed in the rest of the infected molluscs, but we were unable to identify the species of this trematode. Despite the high abundance of *D. polymorpha*, the density

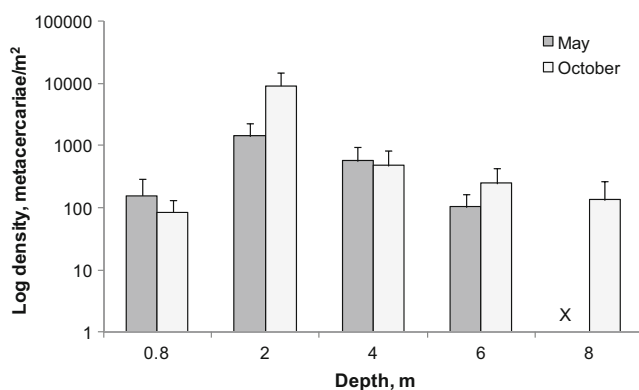


Fig. 5 Bathymetric distribution of the density of *E. recurvatum* metacercariae in May and October 2005. Because of the very high density of metacercariae in *D. polymorpha* at depth of 2 m in October, the data on this graph are presented on a log₁₀-scale. The data for a depth of 8 m in May are missing, which is denoted with x

of *E. recurvatum* metacercariae hosted by this bivalve was low, ranging among sites from 0 to 8.9 metacercariae/m² (Table 2). Yet, in other hosts, except for *V. contectus*, the density of echinostomatids was even lower and did not exceed an average of 1 metacercariae/m² (Table 2). The snail *V. contectus* was present at only one of the sampled localities (site 3, Table 1). Although this snail was very scarce at that site, the prevalence and intensity of its infection with *N. echinatoides* (?) appeared to be very high, i.e., 64.7% and 229±102 (range, 2 to 1,942) metacercariae/mussel, respectively. As a result, the average density of echinostomatid metacercariae in this snail was much higher than in all other molluscan hosts from any of the three sites sampled (Table 2).

Discussion

The “parasite spillback hypothesis” predicts a positive numerical response of native parasites to the presence of an exotic host that is competing for these parasites with native hosts. Our data on the host–parasite system represented by the exotic mollusc *D. polymorpha* and an echinostomatid trematode support this hypothesis.

Irrespective of sampling date, *D. polymorpha* was a dominant molluscan species at nearly all depths sampled (Fig. 2), with the average fraction in total molluscan density of up to 70.4±6.6%. Based on the results of two lake-wide surveys conducted in the beginning and in the end of growing season, the overall mean density and occurrence of zebra mussel were estimated to be 1,508±221 ind./m² and 85%, respectively. Both of these parameters were considerably higher than in any of the native molluscs encountered during the study. Hence, Lake Narocho represents an example of a typical invaded lentic waterbody, in which exotic *D. polymorpha* dominates its benthic community (Karatayev et al. 1998). Such a remarkable success of zebra mussel in European and North American waterbodies is determined by a unique combination of the life history traits absent in its ecological competitors, e.g., the sessile mode of life, the extremely high fecundity, presence of the free-living planktonic larva that can be easily dispersed by the water currents, and feeding on a wide spectrum of suspended particles (e.g., Karatayev et al. 2002). The dominant position of *D. polymorpha* in the molluscan community documented in Lake Narocho, as well as in many other invaded waterbodies, makes this bivalve capable of competing with native molluscs for aboriginal parasites and thus is an important prerequisite to a parasite spillback.

We found *D. polymorpha* to serve as the second intermediate host for the echinostomatid trematode *E. recurvatum*. Unfortunately, any published records on

Table 1 Mean population density (individuals per square meter) of molluscs collected at three littoral sites of Lake Naroch in July 2005 for comparative parasitological examination ($n=30$ at each site)

Species	Site 1	Site 2	Site 3	Presence of the parasites shared with <i>Dreissena</i>
<i>Anisus vortex</i>	0	0	0.8±0.5	–
<i>Anisus vorticulus</i>	0	1.3±1.3	0	–
<i>B. tentaculata</i>	0.4±0.4	12.7±8.0	2.8±1.2	+
<i>D. polymorpha</i>	287.6±163.3	118.0±69.7	112.8±40.6	Not applicable
<i>G. albus</i>	0	14.0±9.7	162.3±22.8	+
<i>Lymnaea auricularia</i>	1.1±0.5	6.0±3.1	4.8±1.9	+
<i>Lymnaea ovata</i>	0	2.0±1.4	0	–
<i>Lymnaea stagnalis</i>	0	0	0.4±0.4	+
Pisidiidae gen. spp.	39.1±7.4	25.3±5.7	5.6±5.8	–
<i>V. contectus</i>	0	0	4.8±1.8	+

Notations of the site names correspond to those in Fig. 1

Echinostomatidae from Lake Naroch for the period before invasion of *D. polymorpha* are lacking, and we cannot completely rule out that *E. recurvatum* might have been introduced into the lake along with the zebra mussel. However, the fact that this trematode is a cosmopolitan species (Yamaguti 1958; Sudarikov et al. 2002) allows us to consider it to be native to the Lake Naroch area.

Most of the native molluscan species dissected during this study are known to be suitable hosts for *E. recurvatum* metacercariae (Sudarikov et al. 2002). Nevertheless, none of the five nondreissenid species from Lake Naroch that were positive for echinostomatid infection (Table 2) harbored this particular species. Although the metacercariae of *E. recurvatum* might be present in native molluscs from other, unexplored, parts of the lake, all of our data suggest *D. polymorpha* to be a very strong competitor for the metacercarial stage of this trematode against the native molluscs. We hypothesize that this successful competitive position of zebra mussel may be directly related to its high

abundance in Lake Naroch. Both theoretical models (Anderson and May 1981; Dobson 1990) and empirical data (Arneberg et al. 1998; Fichet-Calvet et al. 2003) suggest that the host density is one of the major biotic factors positively correlated with the transmission rate and persistence of parasites. It seems profitable for the trematode *E. recurvatum* to switch from native intermediate hosts to the disproportionately more abundant zebra mussels as this will ensure high likelihood of its further transmission to aquatic birds. The latter are known to readily change their common diets in favor of zebra mussel when it is available (Molloy et al. 1997). In addition, *E. recurvatum* may possess increased host specificity to *D. polymorpha* rather than to native molluscs. Thus far, this parasite has been the most common echinostomatid species ever reported to infect zebra mussel (Molloy et al. 1997). Experimental infections of *D. polymorpha* and native molluscs with the cercariae of *E. recurvatum* under different host density treatments could help test our field-based conclusions.

Table 2 Density of echinostomatid metacercariae (individuals per square meter) in their molluscan hosts at the three littoral sites of Lake Naroch sampled in July 2005

Molluscan host	Site 1	Site 2	Site 3	Average metacercarial density±SE
<i>B. tentaculata</i>	0 (2) ^a	0.7 (18)	0 (7)	0.2±0.2
<i>D. polymorpha</i>	0 (33)	3.2 (37)	8.9 (38)	4.0±2.6
<i>G. albus</i>	0 (–) ^b	0.9 (16)	0 (30)	0.3±0.3
<i>L. auricularia</i>	0 (20)	0 (9)	1.9 (18)	0.6±0.6
<i>L. stagnalis</i>	0 (–)	0 (–)	0.2 (22)	0.1±0.1
<i>V. contectus</i>	0 (–)	0 (–)	732 (17)	243.9±243.9

^a The numbers of dissected molluscs are presented in parentheses

^b The sign “dash” means that the host was not found

Comparative parasitological analysis of zebra mussel and native molluscs collected from the three shallow (0.5–1 m) sites of Lake Naroch in July 2005 revealed that, in terms of the hosted density of echinostomatid metacercariae, zebra mussel was second only to the snail *V. contectus* (Table 2). However, our May 2005 and October 2005 data suggest that the role of *D. polymorpha* as a source of echinostomatid infection for aquatic birds substantially increases at deeper sites. On one hand, this was due to remarkable dominance of *D. polymorpha* in total molluscan density at deeper sites (Fig. 2), making this bivalve a readily available food item for waterfowl. Aquatic birds feeding on *D. polymorpha* can dive as deep as 7 m (reviewed in Molloy et al. 1997), suggesting that, in Lake Naroch, they are at risk of getting infected with *E. recurvatum* within the whole range of depths inhabited by this bivalve. On the other hand, the prevalence, intensity, and density of *E. recurvatum* metacercariae in *D. polymorpha* also increased at deeper sites (Figs. 4 and 5). Irrespective of sampling date, the maximal average densities of *E. recurvatum* metacercariae were recorded at depth of 2 m (Fig. 5), indicating that the aquatic birds feeding on *D. polymorpha* at this depth are exposed to the highest risk of getting infected with the parasite. The average density of *E. recurvatum* in zebra mussel at 2 m was $1,423 \pm 844$ (range, 0 to 6,120) metacercariae/m² in May and $9,145 \pm 5,936$ (range, 932 to 38,611) metacercariae/m² in October. These average densities of *E. recurvatum* were disproportionately higher than those of other echinostomatids hosted by any of the native molluscs collected at shallows of Lake Naroch (Table 2). We suggest that *E. recurvatum* would not be able to reach such a high abundance without its novel exotic host, *D. polymorpha*. Although in this study we did not estimate the level of echinostomatid infection in native molluscs from deep areas of the lake, we think it is unlikely that their subdominant or minor positions in the molluscan community would result in as high densities of echinostomatid metacercariae as that of *E. recurvatum* hosted by *D. polymorpha*.

Interestingly, the peaks of *E. recurvatum* density spatially overlapped with those of zebra mussel (Fig. 5). This could be determined by the mechanism of host finding used by the trematode. The cercariae of Echinostomatidae are known to positively react to the chemical cues released by their molluscan hosts (Haas et al. 1995; Körner and Haas 1998). It is likely that the numerous zebra mussels present at a depth of 2 m produce increased concentrations of such cues, thus attracting greater numbers of *E. recurvatum* cercariae. In turn, the bell-shaped pattern of *D. polymorpha* bathymetric distribution (Fig. 3) was apparently related to the availability of hard substrates for attachment. Lake Naroch has a large littoral zone with a sandy bottom and substantial wave activity where zebra

mussels can attach only to scarce rocks, shell fragments, wood debris, and the like. The main substrate for attachment of *D. polymorpha* in Lake Naroch is represented by submerged macrophytes (mainly *Chara* spp.), which are especially abundant at depths of 2 to 7 m (Gigevich 1985; Zhukova et al. 2005; this study). The presence of zebra mussels deeper than 8 m is limited by silt, on which they are unable to live (Karatayev et al. 1998).

The level of *E. recurvatum* infection in *D. polymorpha* was found to significantly vary not only with depth but also across the whole area of Lake Naroch. We suggest that this could be related to the pattern of lake-wide distribution of the aquatic birds that act as definitive hosts of echinostomatids. According to our observations (unpublished) and the results of a special ornithological study conducted in 2005–2006 (Ostrovskiy et al. 2008), the biggest flocks of waterfowl, mainly represented by common coot *Fulica atra* and mallard duck *Anas platyrhynchos*, were concentrated in the small stretch and in the southeastern part of big stretch of the lake near the mouth of the Narochanka River. The near-shore zones in these parts of Lake Naroch are covered by dense stands of the rooted semisubmerged macrophytes (*Phragmites* sp., and others) that serve as ideal nesting spots for waterfowl (Ostrovskiy et al. 2008). In correspondence with this distribution of waterfowl, the highest prevalence and intensity of echinostomatid infection in *D. polymorpha* were recorded along the transects A, C, H, and especially E (the Narochanka River mouth, up to 100% and 190 metacercariae/mussel, respectively; Fig. 1). A comparably high level of echinostomatid infection in zebra mussels has previously been documented only in the Komsomolskoe Reservoir, Belarus (prevalence of up to 100%, intensity of up to 182 metacercariae/mussel; Mastitsky et al. 2003), a waterbody which, similar to Lake Naroch, was characterized by uncommonly dense population of mallard ducks (Kozulin 1995).

In addition to variation in space, the level of *D. polymorpha* infection with *E. recurvatum* varied seasonally. Both the prevalence and mean intensity of infection were found to be significantly higher in October than in May. Similarly, the peak of *D. polymorpha* infection with echinostomatids in September has previously been recorded in the abovementioned Komsomolskoe Reservoir (Mastitsky et al. 2003). Being a large waterbody, Lake Naroch is used in the autumn by multiple migratory aquatic birds as a place for feeding and resting (Ostrovskiy et al. 2008). It is likely that the increased infection of *D. polymorpha* with *E. recurvatum* during this time of the year could facilitate the transmission of this parasite to its final hosts.

In conclusion, this study suggests that the introduction of *D. polymorpha* into Lake Naroch resulted in the amplification of the trematode *E. recurvatum* and likely increased the load of the parasite on native aquatic birds. This conclusion

requires further confirmation through the parasitological examination of aquatic birds. We predict that such an examination would reveal *E. recurvatum* to be the most common and abundant species among the echinostomatid trematodes that currently parasitize the molluscivorous birds of Lake Naroch.

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