Parasites in sympatric populations of native and invasive freshwater bivalves

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Abstract An increasing threat to local, native freshwater mussels (Unionida)—an ecologically important but globally alarmingly declining group—is the invasion by exotic bivalves. The Enemy Release Hypothesis predicts that introduced species should benefit from enemy-mediated competition because they are less likely to be harmed by natural enemies, such as parasites, than their native competitors. We investigated within-site differences in parasitism between sympatric native (tot. five spp.) and invasive (tot. three spp.) bivalves in eight northern European waterbodies, which harboured totally 15 parasite taxa. In paired comparisons using within-site averages, the mean number of parasite species in the native bivalves was 2.3 times higher, and the sum of parasite prevalences 2.4 times higher, than in the invasive bivalves. This may lead to enemy-mediated competitive release of invaders and contribute to the success of invasive freshwater bivalves, in general. However, while the invasive clam *Corbicula fluminea* was completely free from parasites, parasite parameters of the other invader, *Sinanodonta woodiana*, were relatively high, indicating that the role of parasites can be invader-specific and urges further research. Understanding the factors affecting success of freshwater bivalve invasions, such as parasitism, can aid invasion

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control and conservation of local, native (endangered) bivalves.

Keywords Enemy release · Exotic species · Freshwater mussels · Introduced alien species · Non-indigenous species · Parasite benefit

Introduction

Biological invasions threaten biodiversity and cause drastic changes in the invaded ecosystems, leading to local extirpation of native species, biogenic homogenization and extensive economic costs (e.g. Olden et al., 2004; Pimentel et al., 2005; Keller et al., 2011; Lockwood et al., 2013). The most supported explanation (see e.g. Blakeslee et al., 2013) for the success of invasive species (when they have colonized the new, invaded area) is provided by the Enemy Release Hypothesis that invaders benefit from lower pressure of natural enemies when compared to native species (Elton, 1958). Rationale behind the Enemy Release Hypothesis is that (1) natural enemies are harmful and can control populations of their host/target species, and that (2) natural enemies, such as parasites, frequently are specialized to utilize only a small number of host/target species, or even genotypes that are available in their local environment. Therefore, as (3) invaders usually do not bring their own enemies with them to the new area during the colonization process, it (4) results in a situation where the pressure by the natural enemies in the invaded area can be remarkably lower for the invaders than for the local, native species (as well as when compared to the parasite pressure of the invader in its original range). Since parasites and disease are able to control and regulate host populations (Anderson and May, 1979; May and Anderson, 1979; Hudson et al., 1998) and can be highly specialized (i.e., host specific) (Price, 1980), they provide a promising 'enemy candidate'. Two extensive meta-analyses clearly show that the invaders (a) lose their own, natural parasites and pathogens when introduced to a new geographic area, and (b) that their colonization by new parasites in the introduced area does not make up that loss (Mitchell and Power, 2003; Torchin et al., 2003). The introduced animal populations were less heavily parasitized and had only half of the parasite species as compared to their

original, natural range (Torchin et al., 2003). In line with this, the invasive plant species which were more completely released from pathogens were more widely reported as harmful invaders (Mitchell and Power, 2003).

Many freshwater mussels (Unionoida) have declined dramatically, so that they are the most imperiled animal group in the world (Lydeard et al., 2004; Lopes-Lima et al., 2017). Invasive bivalves can remarkably harm the native mussels (Haag et al., 1993; Ferreira-Rodriguez et al., 2018), either directly—biofouling by e.g. zebra mussel *Dreissena polymorpha* (Pallas, 1771)—or indirectly via competition over food, space or host fish or by changing the bottom habitat (Sousa et al., 2014; Ożgo et al., 2020). Therefore, the introduction of invasive bivalves is a serious and increasing threat to local, native bivalves, as non-indigenous bivalve species expand their range at increasing pace (Sousa et al., 2014). In addition, when considering ecosystem functions, some freshwater bivalves can be ranked among the world's most problematic biological invaders. For example, recent invasions of the zebra mussel *D. polymorpha* and Asian clam *Corbicula fluminea* (Müller, 1774) have altered entire aquatic ecosystems by their filtration and burrowing activities, and they have severely affected native bivalve communities by altering bottom habitats and competing for resources (Karatayev et al., 1997; Strayer et al., 1998; Ward and Ricciardi, 2007; Sousa et al., 2009; Higgins and Vander Zanden, 2010; Ferreira-Rodriguez et al., 2018; Modesto et al., 2019).

Successful establishment and further population growth of introduced freshwater bivalves has been linked, for example to fouling (*D. polymorpha* prefers shells of unionids over conspecifics), induction of cross-resistance (infection with glochidia of the Chinese pond mussel *Sinanodonta woodiana* (Lea, 1834) early in the season creates acquired immunity against native unionids in host fishes), potentially longer breeding season, high fecundity and a wide spectrum of suitable fish hosts (*S. woodiana*), as well as free-living instead of parasitic larva (*D. polymorpha*, *C. fluminea*) (Douda et al., 2012; Sousa et al., 2014; Yanovych 2015; Donrovich et al., 2016; Dzierżyńska-Białończyk et al., 2018; Labecka and Domagała, 2018; Urbańska et al., 2018, 2019). However, the role of parasites in success of bivalve invasions has not been thoroughly explored. This is surprising, considering that freshwater bivalves harbor a rich community of

parasites (Molloy et al., 1997; Grizzle and Brunner, 2009; Carella et al., 2016; Brian and Aldridge, 2019). Indeed, parasitism was recently named as one of the priority research topics on freshwater mussel conservation assessment (Ferreira-Rodríguez et al., 2019). Some of these parasites are capable of markedly reducing the reproductive output, growth and survival of the bivalve host (Taskinen and Valtonen, 1995; Taskinen, 1998b; Jokela et al., 2005; Müller et al., 2014). In addition, parasites of freshwater bivalves can be host specific and adapted to their local host population (Taskinen et al., 1991; Saarinen and Taskinen, 2005), a prerequisite of the Enemy Release Hypothesis. Thus, if occurring at a higher rate in the native bivalves than in the invasive competitors, parasites could benefit the invaders. Parasitism of invasive bivalves has been studied in the invaded areas (e.g. Molloy et al., 1997; Burlakova et al., 2006; Mastitsky et al., 2010; Karatayev et al., 2012; Cichy et al., 2016), and there is evidence for parasite escape, i.e., fewer parasites in the invaded area as compared to the original range in the case of *D. polymorpha* (Molloy et al., 1997), but to our knowledge their parasite pressure has not been compared to sympatric native competitors at the same site.

One prediction of the Enemy Release Hypothesis is that introduced species should benefit from enemy-mediated competition because they are less likely to be affected by natural enemies than their native competitors (Elton, 1958; Keane and Crawley, 2002). The studies examining enemy-mediated competitive release, i.e., that invasive species benefit from competitive release as the native competitors are preferred by (native) enemies, compared enemy prevalence or enemy effects on invasive and native species in the introduced range (see Prior et al., 2015). In a recent review, studying parasites of sympatric native and invasive bivalve populations was pointed as one of the most important research needs with respect to invasion threats in conservation of endangered freshwater mussels conservation (Brian and Aldridge, 2019). Therefore, the aim of this study was to compare parasite pressure in sympatric populations of native and invasive bivalves, i.e. within-site differences in parasite species richness and summed prevalence of infection (see e.g., Torchin and Lafferty, 2009). This study can potentially contribute to the conservation of imperiled native mussels, as it should increase our knowledge and understanding of bivalve-parasite

relationships, explore the explanations for success of invasions and possibly increase our ability to manage invasions.

Our study included eight European waterbodies which were inhabited by at least one of the three invasive bivalves—*C. fluminea* (Corbiculidae), *D. polymorpha* (Dreissenidae) and *S. woodiana* (Unionidae)—and at least one of the five native Unionidae mussels [*Anodonta anatina* (Linnaeus, 1758), *A. cygnea* (Linnaeus, 1758), *Pseudanodonta complanata* (Rossmässler, 1835), *Unio pictorum* (Linnaeus, 1758) and/or *U. tumidus* Philipsson, 1788]. *D. polymorpha* is originally from Black Sea and Caspian Sea drainages and has invaded Europe gradually since 1700s (Karatayev et al., 2007). *C. fluminea* and *S. woodiana* are both native to Asia and have colonized Europe since 1970–1980s (Watters, 1997; Lucy et al., 2012). Our hypothesis was that the invasive bivalves would have, on average, fewer parasite species and lower prevalence of infection than the native ones.

Materials and methods

Collection and examination of bivalves

The study was performed by collecting bivalves from sites where at least one native and one invasive bivalve species are living in sympatry, in the same particular site, to ensure that they are exposed to same parasites when they live in the same environment. Bivalve samples were collected from eight waterbodies, of which one was in Estonia and seven in Poland, between May and July during 2017–2018 (Table 1, Supplementary Tables 1–8). Collection was performed by hand picking (visual detection; with or without an aquascope), and—in Lake Gosławskie and Lake Siecino, Poland—also by snorkelling and scuba diving. The target sample size was 30 bivalve individuals per species per site. Characteristics of the study sites, with e.g., fish community and introduction of the invasive bivalves, are given in Supplementary Table 9.

Bivalves were stored on ice and examined fresh, except for samples from Lake Võrtsjärv, which were stored frozen. Parasite examination was performed by dissecting the bivalve, counting adult watermites (crawling on gills and mantle cavity), separating different tissues and examining the tissues, piece by piece, by pressing between two large glass plates and

Table 1 Occurrence (X) of the 15 observed parasite taxa in each native (*Anodonta anatina*, *Anodonta cygnea*, *Pseudanodonta complanata*, *Unio pictorum* and *Unio tumidus*) and invasive (*Sinanodonta woodiana*, *Dreissena polymorpha* and *Corbicula fluminea*), all eight waterbodies combined

Bivalve	N_{sites}	$N_{bivalves}$	Trematoda sporocysts					Ac	Cl	N1	N2	Gly	Con	M1	M2	M3	Ra	Tot.
			Rf	Rc	Bp	Cd	Pm											
Native																		
A.ana	6	218	X	X	–	X	–	X	X	–	X	X	X	X	X	X	–	11
A.cyg	2	67	–	–	–	–	–	X	X	–	–	–	X	X	X	X	X	7
P.com	3	89	–	–	–	–	–	–	X	–	–	X	X	X	X	X	–	6
U.pic	4	136	–	–	–	–	–	X	X	–	–	X	X	X	X	X	X	8
U.tum	6	173	–	X	–	–	–	X	X	–	–	X	X	X	X	X	X	9
N of host species			1	2	0	1	0	4	5	0	1	4	5	5	5	5	3	
Mean±s.e.	5.0±0.8	136±27																8.2±0.9
Invasive																		
S.woo	4	121	–	X	–	–	–	–	X	–	–	X	—	X	X	X	–	6
D.pol	6	170	–	–	X	–	X	–	–	X	–	X	X	–	–	–	–	5
C.flu	2	85	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
Mean±s.e.	4.0±1.2	125±25																3.7±1.9
N of host species			0	1	1	0	1	0	1	1	0	2	1	1	1	1	0	
Tot. *N* of hosts			1	3	1	1	1	4	6	1	1	6	6	6	6	6	6	
t-test *p*-value	0.501	0.792																0.043

Numbers of waterbodies per bivalve species, the total number of individuals studied and the total number of observed parasite taxa per bivalve species are given in columns N_{sites}, $N_{bivalves}$ and Tot., respectively, and for these parameters the average values (Mean ± s.e.) are given, as well as the *t* test result (2-sided *p*-value) comparing the means of native and invasive bivalve species. Number of host species observed per parasite taxa is given separately for the native and the invasive bivalves. In addition, the total number of host species for each parasite taxon (combining the invasive and native bivalves)—a measure of host specificity of the parasite— is given on the row Tot. *N* of hosts

Trematoda sporocysts = Tissue-dwelling, larval, (castrating) trematodes, Rf, *Rhipidocotyle fennica*; Rc, *Rhipidocotyle campanula*; Bp, *Bucephalus polymorphus*; Cd, *Cercaria duplicata* and Pm, *Phyllodistomum macrocotyle*; Ac, *Aspidogaster conchicola* (adult trematode), Cl, *Chaetogaster limnaei* (Oligochaeta), *N1*, unknown larval nematode in gonad, *N2*, unknown larval nematode in gills; Gly, *Glyptotendipes* sp. (Chironomidae); Con, *Conchophthirus* sp. (Ciliata)

M1 = larval/egg stages of watermites in the mantle, M2 = larval/egg stages of watermites in the gills, M3 = adult watermites, Ra = *Rhodeus amarus* (bitterling)

inspecting with a preparation microscope using transmitted light (Taskinen et al., 1991). The tissues examined included mantle, gills, digestive gland and gonad, which are the typical sites of parasites in freshwater bivalves (e.g., Edwards and Vidrine, 2013; Taskinen et al., 1997). Bivalve sex was determined microscopically (presence and abundance of oocytes in gonad), and larval production as percentage of gill marsupia filled with glochidia was evaluated. In addition, shell measurements (length, width, height) and age determination (from annual growth rings on shell) were performed, but these aspects are not included in the present study. Numbers of parasites were counted or their abundance was estimated. If the mantle and gills were examined only from one side of the bivalves, the numbers were doubled. However, in the present analyses, only presence-absence data were used (prevalence of infection, i.e. the proportion of infected individuals), because summed prevalences have been previously used as a measure of parasite load in studies of Enemy Release Hypothesis (Lafferty et al., 2010; Torchin et al., 2003). Ciliates cannot be

reliably observed from frozen samples. Therefore, ciliate parasites were not recorded for Lake Võrtsjärv since the bivalves from this lake were stored frozen.

Statistical analyses

We used parasite taxa richness (number of parasite taxa) and sum of prevalences (sum of the prevalence of all parasite taxa for each host species) as the response variables as they have generally been used as the measures of parasite pressure in studies exploring 'enemy release' (Lafferty et al., 2010; Torchin et al., 2003). First, a site-specific analysis was performed to get an idea of the bivalve and parasite community in a given waterbody. This was done by comparing prevalences of infection of every possible parasite taxa for each pair of native vs. invasive bivalve species using χ^2-test. If the number of cells with an expected count value lower than five was greater than one, a Yates continuity correction (Sokal and Rohlf, 1981) was applied.

In addition, if there was at least three native and invasive bivalve species in a given site, difference in the mean prevalence of a given parasite taxon between native and invasive bivalves was analysed using t-test (for example, see Gosławskie Lake, Supplementary Table 3). This approach did not differentiate the bivalve species. For instance, mean value for the invasive species *S. woodiana*, *D. polymorpha* and *C. fluminea* against the mean value of the native species *A. anatina*, *U. pictorum* and *U. tumidus* was used in the case of Gosławskie Lake, without taking into consideration possible differences between the three invasive or between the three native bivalve species. However, this approach was in line with our hypothesis, that "invasive bivalves would have, on average, fewer parasite species and lower prevalence of infection than the native ones", which does not separate bivalve species within the native or invasive group. Detailed reports of these site-specific analyses, where all possible native vs. invasive bivalve combinations are analysed for each parasite taxon, are given in "Site-specific results" of the Supplementary materials and in Supplementary Tables 1–8.

Second, to get a comprehensive picture over the all studied waterbodies, the average number of parasite taxa and the average sum of prevalences pooled for all invasive *vs*. native bivalves per site were used as the response variables in comparisons performed over all

sites between invasive and native bivalves (for example, see Fig. 1). If only one native or invasive bivalve species was present, its values represented the average for native/invasive group in that lake. Then these averages were used in a *t*-test to analyse within-site differences in the mean average parasite taxa richness and summed prevalences between the native and invasive bivalves. In this approach, for each site, only those bivalve species were included in the statistical analyses for which the number of individuals was at least 15. This was done to avoid biases due to different sample size, because even though the aim was to collect and study 30 individuals per bivalve species per site, this was not always possible (see Table 1 and Supplementary Tables 1–8).

The second procedure (above) was also applied to the number of bivalve individuals collected to estimate the possible difference in sample sizes for the native and invasive bivalves. Mean ($\pm$ s.e.) average number of bivalves studied was 32 ± 4 and 30 ± 3 for the native and invasive bivalves, respectively. The difference was statistically not significant indicating that sample sizes for the native and invasive bivalves over the eight study sites did not differ from each other (paired *t*-test, $n = 8$, $t = 0.506$, df = 7, $p = 0.629$) (see Supplementary Tables 1–8 for details).
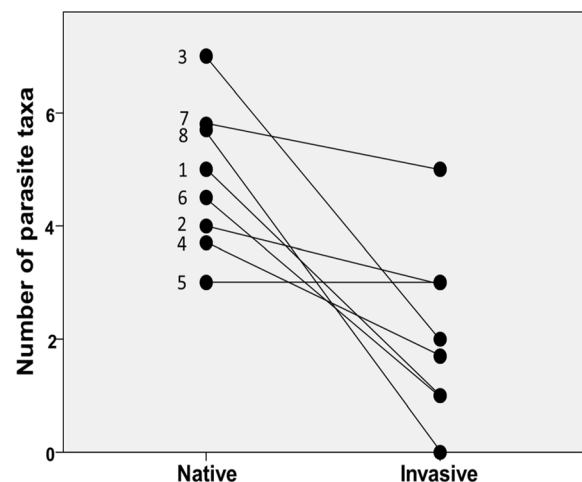

Fig. 1 Mean parasite taxa richness for native and invasive freshwater bivalves in eight northern European waterbodies. 1—Lake Võrtsjärv, 2—Czarny Młyn Pond, 3—Warta-Gopło Canal, 4—Gosławskie Lake, 5—Nowy Lipsk Pond, 6—Siecino Lake, 7—Szeszupa River, 8—Rospuda River. Values connected by a line belong to the same study site. Mean number of parasite taxa was significantly higher in native bivalves as compared to invasive bivalves (paired *t*-test, $p = 0.008$)

Differences were regarded as statistically significant, when $p < 0.050$. When $0.050 \leq p \leq 0.099$, the difference was interpreted as marginally significant, indicating that there is a trend, but the risk of wrong conclusion is increased.

Results

Five native (*A. anatina*, *A cygnea*, *P. complanata*, *U. pictorum* and *U. tumidus*) and three invasive (*S. woodiana*, *D. polymorpha* and *C. fluminea*) freshwater bivalve species and a total of 15 parasite taxa (*Rhipidocotyle fennica* Gibson et al., 1992, *R. campanula* (Dujardin, 1845), *Bucephalus polymorphus* von Baer, 1827, *Cercaria duplicata* von Baer, 1827, *Phyllodistomum macrocotyle* (Lühe, 1909), *Aspidogaster conchicola* von Baer, 1827, *Chaetogaster limnaei* von Baer, 1827, unknown larval nematode from gonad, unknown larval nematode from gills, *Glyptotendipes* sp. (Lenz), *Conchophthirus* sp. (Claparéde and Lachmann), larval/egg stages of watermites in the mantle, larval/egg stages of watermites in the gills, adult watermites and larvae of bitterling *Rhodeus amarus* (Bloch, 1872) were discovered from the eight waterbodies (Table 1).

Mean (± s.e.) average parasite taxa richness over the eight study sites was 2.3 times higher for the native than for the invasive bivalves (4.8 ± 0.5 vs. 2.1 ± 0.6 taxa; range 3–7 and 0–5 taxa, respectively), the difference being statistically significant (paired *t* test, $n = 8$, $t = 3.703$, df = 7, $p = 0.008$) (Fig. 1). Furthermore, the mean (± s.e.) average summed prevalence of infections of different parasites over the eight study sites was 2.4 times higher for the native than for the invasive bivalves (151 ± 27 vs. 64 ± 24 %, range 43-264 and 0-170 %, respectively), the difference being statistically significant (paired *t* test, $n = 8$, $t = 2.378$, df = t, $p = 0.049$) (Fig. 2).

Anodonta anatina ($n_{tot} = 218$ individuals) was found from six out of eight sites and harboured in total 11 different parasite taxa, while *A. cygnea* ($n_{tot} = 67$) was found from two waterbodies and harboured altogether seven parasite taxa (Table 1). Corresponding figures for *P. complanata* ($n_{tot} = 89$) were three lakes/rivers and six parasite taxa, for *U. pictorum* ($n_{tot} = 136$) four sites and eight parasite taxa and for *U. tumidus* ($n_{tot} = 173$) six waterbodies and nine parasite taxa (Table 1). Of the invasive mussels, *S. woodiana*
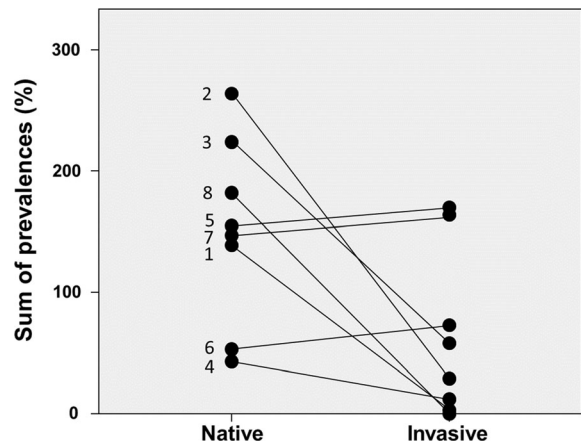

Fig. 2 Mean sum of prevalences of infection of different parasites for native and invasive freshwater bivalves in eight northern European waterbodies. 1—Lake Võrtsjärv, 2—Czarny Młyn Pond, 3—Warta-Gopło Canal, 4—Gosławskie Lake, 5—Nowy Lipsk Pond, 6—Siecino Lake, 7—Szeszupa River, 8—Rospuda River. Values connected by a line belong to the same study site. Mean sum of infection prevalences of parasites was significantly higher in native bivalves than in the invasive ones (paired *t*-test, $p = 0.049$)

($n_{tot} = 121$ individuals) was found from four lakes/rivers and harboured six different parasite taxa, and *D. polymorpha* ($n_{tot} = 170$) was found from six waterbodies and harboured five parasite taxa, while *C. fluminea* ($n_{tot} = 85$) was found from two sites and did not harbour any parasites (Table 1). The total parasite pool infecting native mussels consisted of 12 taxa while that of invasive bivalves included 10 parasite taxa (Table 1). When combiner over the eight waterbodies, the total number of parasite taxa infecting each native and invasive mussel species varied from six to 11 and from zero to six per bivalve species, respectively (Table 1). The mean (± s.e.) total number of observed parasite taxa for native and invasive bivalves (per bivalve species, combined over all sites) was 8.2 ± 0.9 and 3.7 ± 1.9, respectively, the difference being statistically significant (*t*-test, $t = 2.553$, df = 6, $p = 0.043$) (Table 1).

Site-specific results with parasite taxon-specific comparisons between all possible combinations of native and invasive mussels revealed statistically significant differences with respect to all parasite taxa other than *B. polymorphus*, *C. duplicata* and the unknown nematodes from gonad and gills (Supplementary Tables 1–8).

Discussion

Detailed discussion on results of each of the eight sites is provided in Supplementary Materials. In addition, parasite-specific discussion with respect to life cycles, hosts, host specificity and earlier findings of geographic distributions (Dimock and LaRochelle, 1980; Davids et al., 1988; Taskinen et al., 1991; Gibson et al., 1992; Conn et al., 1996; Vidrine, 1996; Fried and Graczyk, 1997; Molloy et al., 1997; Taskinen, 1998a; Jokela et al., 2005; Edwards and Vidrine, 2006; Ibrahim, 2007; Reichard et al., 2007; Mastitsky et al., 2010; Mastitsky and Veres, 2010; Edwards and Vidrine, 2013; Cichy et al., 2016; Rouchet et al., 2017) is also give in Supplementary Materials.

Enemy Release Hypothesis (Elton, 1958) suggests that invasive species should lose parasites during the invasion process, which should lead to a lower parasite load in the new, introduced range, benefitting the invaders in competition against the local, native competitors. Large body of empirical evidence indicates that the invaders, indeed, are frequently released from parasites when introduced to new area (Mitchell and Power, 2003; Torchin et al., 2003). One prediction of the Enemy Release Hypothesis is that introduced species should benefit from enemy-mediated competitive release because they are less likely to be affected by natural enemies than their native competitors (Elton, 1958; Keane and Crawley, 2002). Therefore, we compared parasite pressure of invasive and native freshwater bivalves living in sympatry. The overall mean site-specific average parasite taxon richness and sum of prevalences were, both, more than two times higher among the native bivalves than in the invasive bivalves. Site-specific comparisons between pairs of native and invasive bivalves at individual parasite taxon level frequently also indicated higher parasite prevalence in the native bivalve than in the invasive counterpart. Thus, the results support the Enemy Release Hypothesis and the view that the invasive bivalves benefit from a lower parasite pressure than the sympatric populations of native species.

A prerequisite of enemy-mediated competitive release is that parasitism is a cost, i.e., parasites must be harmful. Larval trematodes using bivalve as the 1st intermediate host (bucephalids, gorgoderids) are inevitably very harmful, causing partial or complete sterility, parasite-induced mortality and lowered growth (Davids and Kraak, 1993; Taskinen and Valtonen, 1995; Taskinen, 1998b; Jokela et al., 2005; Müller et al., 2014). Adult watermites ingest mucus and tissues of their bivalve host (Fisher et al., 2000). Results by Gangloff et al. (2008) suggest that ectoparasitic adult watermites (Unionicola spp.) and ectoparasitic adult trematodes (Aspidogaster spp.) are strongly negatively associated with both physiological condition (glycogen) and reproductive output of bivalve. Numbers of eggs/larval stages of watermites in the present study were very high—up to thousands of eggs/larval mites embedded in mantle tissue of a single mussel individual, for example, suggesting potential for high virulence. The effect of echinostomatid trematode metacercariae on mussel host is usually benign (Laruelle et al., 2002), but bitterling (R. amarus) embryos can be costly to a mussel (Reichard et al., 2006). Therefore, many of the parasites of the present study are potentially costly to host bivalve, and the higher parasite prevalences in native bivalves should benefit the invasive competitors.

Another prerequisite of enemy-mediated competitive release is that there must be competition between native and invasive bivalves. Freshwater bivalves can be assumed to compete with each other as they all are benthic filter feeders, thereby sharing the same ecological niche in terms of food and space. As mentioned earlier, invasive bivalves can remarkably harm native mussels either directly (biofouling by e.g. zebra mussel Dreissena polymorpha) or indirectly via competition over food, space or host fish or by changing the bottom habitat (reviewed by Sousa et al., 2014). Competition between native and invasive mussels is indicated by the negative correlation between their densities on local scale (Vaugh and Spooner, 2006) and illustrated, for example, by the rapid decline of native mussels after introduction of Dreissena to North American Great Lakes (Strayer and Malcom, 2007).

Invasive species can acquire parasites in the invaded area either by bringing them along themselves or by infection by parasites of the native species. If bivalves are introduced as larvae, probability that they transport their own parasites to the invaded area is close to zero. Introduction of D. polymorpha to North America and S. woodiana to Europe have happened presumably by veliger and glochidium larvae, respectively (Watters, 1997; Karatayev et al., 2007), though the introduction and spread of D. polymorpha in Europe might have also occurred at an adult stage

(Burlakova et al., 2006). Consequently, North American *D. polymorpha* populations have no records of original parasites of *D. polymorpha* while those in Europe have (Burlakova et al., 2006) and they were also observed in the present study (trematodes *B. polymorphus* and *P. macrocotyle*). Based on the few studies on invasive hosts and parasites, adaptation of novel hosts/parasites to those in the introduced region is, in general, a long process (Taraschewski, 2006), but Karatayev et al. (2012) observed that *D. polymorpha* has acquired echinostomatids from native hosts in North America 26 year after it was first time recorded. Thus, it is possible that some of the parasites of native mussels have jumped to *D. polymorpha* also in Europe during the up to 200 years of invasion. Results of Petkeviciute et al. (2014) support the view that the gorgoderid trematode *P. macrocotyle* is a specific parasite of *D. polymorpha*, while *C. duplicata* is specific to unionid mussels. Similarly, Taskinen et al. (1991) concluded that the bucephalid trematode *B. polymorphus* is a specific parasite of *D. polymorpha*, while *R. fennica* and *R. campanula* are specific to unionids. So, at least *B. polymorphus* and *P. macrocotyle* were brought to Europe by *D. polymorpha*—they did not jump to *D. polymorpha* from native mussels—meaning that *D. polymorpha* was not released from these two enemies during the invasion process. In spite of this, the prevalence of infection was always (when possible to analyse) higher in the native counterpart(s) than in *D. polymorpha*—except for *P. macrocotyle*, a *Dreissena*-specific trematode, and *Conchophthirus* ciliate—in Szeszupa River (Suppl. Table 7). There are at least five *Dreissena*-specific ciliate parasites including *Conchophthirus acuminatus* (Claparéde and Lachmann, 1858) and *C. klimentinus* (Molloy et al., 1997). Thus, it is possible that the high *Conchophthirus* infection of *D. polymorpha* in Szezszupa River was caused by a ciliate species specific to *D. polymorpha*.

In addition to almost always lower parasite load in *D. polymorpha* (except for the *D. polymorpha*-specific trematodes), when compared to native bivalves the complete absence of parasites in *C. fluminea* was striking (Suppl. Table 3, 4) and strongly supports the view of parasite benefit for *C. fluminea* when competing with native bivalves. In its original range, *C. fluminea* has been reported to host *Phyllodistomum mingensis* (Tang, 1985), five species of *Echinostoma* (Keeler and Huffman 2009) and seven species of

Aspidogastrea (Tang, 1992). Parasite escape by introduced *C. fluminea* has been observed also in North America. Despite a long history of *C. fluminea* research since their introduction in 1930s, only the host-generalist aspidogastrid trematodes *A. conchicola* and *Cotylapsis insignis* Leidy, 1857, have been reported from North America (Danford and Joy, 1984). In addition, Karatayev et al. (2012) also did not find any parasites from *C. fluminea* from Great Lakes area except echinostomatid metacercqriae in one out of 27 sites. Thus, besides the European waterbodies studied here, *C. fluminea* seem to enjoy a remarkable reduction of parasite pressure also in other regions it has invaded globally.

A meta-analysis revealed that a significantly higher extent of parasite escape is evident in aquatic than in terrestrial environments, possibly due to less frequent introductions per invader and introduction as a larval form free of parasites (Lafferty et al., 2010). Results by Mastitsky et al. (2010) indicate that over one third of invasive freshwater invertebrates did not successfully introduce any of their coevolved parasites to the invaded areas. Our results suggest that in the introduced range, the invasive freshwater bivalves may enjoy lower parasite pressure, i.e., have lower number of parasite species and lower combined prevalence of infection, than their native counterparts, giving a 'parasite benefit' for the invasive bivalves in competition against the native ones. However, the within-site variation between the native species was also relatively high in our study—not all native species were always strongly infected. In addition, variation between the invasive species was also large, from not-a-single-parasite in the Asia clam *C. fluminea* to considerably high values of parasite parameters in the Chinese pond mussel *S. woodiana* in Warta-Gopło Canal and Nowy Lipsk Pond (Suppl. Table 3, 5). This will rise many questions, for example: Are the parasites of European unionids better able to infect another unionid, *S.woodiana*, than phylogenetically distinct dreissenids or corbiculids—even if *S. woodiana* is a recent invader compared to e.g. *Dreissena*? Therefore, to better understand the role of parasites in invasions of freshwater bivalves, the importance of parasitism should be studied in relation to the genetic (and geographic) distance between the introduced and native bivalves, and in relation to time since introduction and routes of invasions—from both the host bivalves' and parasites' perspectives.

Freshwater mussels Unionida are important in maintaining aquatic biodiversity and ecosystem functions (Vaughn, 2018). Invasive bivalves can have devastating effects on the native mussels and on the whole freshwater ecosystems (Higgins and Vander Zanden, 2010; Sousa et al., 2014). So, research on the interplay between parasites, bivalves and invasions will potentially increase our understanding how host-parasite relationships are shaping the outcomes of invasions. This may thereby possibly contribute to our ability to manage invasions and protect imperiled native bivalves and aquatic ecosystems.

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