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EXOTIC MOLLUSCS IN THE GREAT LAKES HOST EPIZOOTICALLY IMPORTANT TREMATODES

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ABSTRACT One of the most significant ecological and economic impacts of exotic species is associated with their role as vectors for the introduction of parasites into invaded areas. Exotic parasites may have devastating impacts on invaded ecosystems; moreover, invaders may also become hosts for aboriginal parasites, promoting native diseases that otherwise would not have emerged. During 2009 and 2010, exotic molluscs were collected from 27 sites in the Lower Great Lakes and their tributaries, the Finger Lakes, and Lake Oneida. Seven species of exotic molluscs were examined for the presence of trematodes, including the zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena rostriformis bugensis*), faucet snail (*Bithynia tentaculata*), European stream valvata (*Valvata piscinalis*), Asian clam (*Corbicula fluminea*), Chinese mystery snail (*Cipangopaludina chinensis*), and the New Zealand mudsnail (*Potamopyrgus antipodarum*). Most of the examined molluscs were infected with trematode larvae that may be harmful to their subsequent vertebrate hosts, including fish, birds, and mammals. These included *Sphaeridiotrema* sp. cercariae and *Cyathocotyle bushiensis* metacercariae from *B. tentaculata*, *Echinostoma* sp. cercariae from *V. piscinalis*, and echinostomatid metacercariae from *Dreissena* spp. and *C. fluminea*. Many exotic molluscs that were believed to be free of parasites have already acquired trematodes native to North America. Hotspots of trematode infections were recorded in the western basin of Lake Erie and in Lake Oneida, where several species of exotic molluscs had a high prevalence of trematodes, and thus potentially pose risk of transmission to definitive hosts.

KEY WORDS: exotic species, parasites, trematodes, molluscs, Great Lakes

INTRODUCTION

Exotic species are considered to be one of the major threats to global biodiversity (Wilcove et al. 1998). Their introduction and proliferation also often result in significant economic damage to industries and livelihoods (Pimentel et al. 2005). One of the most significant ecological and economic impacts of exotic species is associated with their role as vectors for the introduction of parasites into invaded areas (Brooks & Hoberg 2006, Brooks & Hoberg 2007, Hoberg & Brooks 2008). Exotic parasites introduced along with the free-living invaders may have devastating impacts on invaded ecosystems, including a risk to public health (Taylor et al. 2001, Lv et al. 2009), risk of extinction of endangered species (Holmes 1996, Dobson & Foufopoulos 2001, Mitchell et al. 2005), and mass mortalities of native hosts (Burreson et al. 2000, Edgerton et al. 2002, Cole & Franson 2006, Taraschewski 2006). The impact of infections on host populations throughout the world is expected to increase during the next 50–100 y as a result, in part, of the introduction of new disease agents (Scott 1988, Harvell et al. 2002), and will likely be facilitated by global climate change (Harvell et al. 2002, Brooks & Hoberg 2006, Brooks et al. 2006a, Poulin 2006, Brooks & Hoberg 2007, Marcogliese 2008). Dobson and Foufopoulos (2001) found that most of the outbreaks (about 60%) of emerging infectious diseases (EIDs) recorded in the wildlife of North America from 1998 to 2000 were caused by pathogens of exotic or likely exotic origin. Exotic parasites introduced with their exotic hosts may switch to new naive hosts with which they have no previous history of associations via ecological fitting, facilitating EID (Brooks & Hoberg 2007, Agosta et al. 2010, Mastitsky et al. 2010). The geographical scale of these EIDs is extremely wide (Harvell et al. 2002, Cattadori et al. 2005, Kutz et al. 2005, Mouritsen et al. 2005, Hoberg & Brooks 2008).

Invaders may also become hosts for aboriginal parasites, promoting native diseases that otherwise would not have emerged in the invaded regions (Torchin et al. 2003, Hoberg & Brooks 2008, Kelly et al. 2009, Mastitsky & Veres 2010, Mastitsky et al. 2010). All this can render considerable economic costs, especially when commercially exploited populations are under threat (Nepszy et al. 1972, Burreson et al. 2000, Pimentel et al. 2005, Brooks & Hoberg 2006).

Since 1840, the number of aquatic exotic species in the Great Lakes Region has been growing exponentially (Ricciardi 2006), resulting in a parallel growth of the risk of introduction of pathogenic exotic diseases. Some exotic parasites have already been discovered as a result of their significant population effects, such as, for example, the European protozoan *Glugea hertwigi,* which caused high-rate die-offs of the rainbow smelt in Lake Erie and Lake Ontario during the 1960s and 1970s

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(Nepszy et al. 1972), or the European trematode *Leyogonimus polyoon,* which has recently caused mass mortalities of waterfowl in northwestern Wisconsin (Cole & Franson 2006). Less pathogenic exotic parasites may already be present in the Great Lakes Region but remain largely undiscovered because of the lack of attention from the scientific community. New parasites may arrive as a result of continuing introductions of new free-living exotic species or because of repeated introductions of infected exotic hosts that have already been introduced into the region but initially were free of their specific parasites. This article focuses on the occurrence, prevalence, and intensity of infection with trematodes of 7 of the most common exotic molluscs in the Great Lakes Region.

MATERIALS AND METHODS

Sampling Protocol

During 2009 and 2010, exotic molluscs were collected for parasitological examination from 27 sites located in 12 waterbodies, including the Lower Great Lakes and their tributaries, Finger Lakes, and Lake Oneida (Table 1). Most sites were sampled once, and 5 sites were sampled twice. Seven species of exotic molluscs were examined for the presence of parasites and commensals during this study, including zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena rostriformis bugensis*), faucet snail (*Bithynia tentaculata*), European stream valvata (*Valvata piscinalis*), Asian clam (*Corbicula fluminea*), Chinese mystery snail (*Cipangopaludina chinensis*), and New Zealand mud snail (*Potamopyrgus antipodarum*). Although we sampled all locations within the state of New York where the exotic snail *Lymnaea auricularia* was previously reported, we did not find this species. We suggest that the snail has either been extirpated or that it may be present in extremely low densities below detection level.

In shallow littoral sites (<2 m) molluscs were collected by hand, whereas Ekman and boxcore grabs were used in deeper sites. To standardize our sampling procedure, at each sampling time and at each location, we planned to examine 50 exotic molluscs. However, because of various limitations (e.g., lack of molluscs), this wasn't always possible. For all infected molluscs, the prevalence (percent of infected molluscs) and intensity of infection (number of parasites in the infected individuals) were estimated using the following protocol. Before dissection, we cleaned and dried the shell surface and measured the shell length to the nearest 0.1 mm with calipers. Molluscs were then cut open with a scalpel and dissected in unchlorinated tap water within a plankton-counting chamber or a Petri dish under a stereomicroscope (20–70×). In most cases, the entire soft body of each mollusc was dissected, with special attention given to the gills and digestive gland, each piece of which was carefully checked for the presence of parasites. The number of parasites was counted and identified whenever possible, and photographs were taken using a compound microscope to facilitate further identification. All molluscs were dissected within 72 h of collection. Cercariae and metacercariae were identified to the level of morphotype (e.g., xiphidiocercaria) or family according to the diagnostic keys of Schell (1985), and further to genus or species using primary literature specific to the respective taxa (Burns 1961, McLaughlin et al. 1993, Sudarikov et al. 2002).

RESULTS

Dreissena polymorpha *and* Dreissena rostriformis bugensis

This is the first report of several taxa of trematodes from the North American populations of zebra and quagga mussels (Table 2). Metacercariae of Echinostomatidae, large metacercariae (unidentified), and small metacercariae (unidentified) were found in both dreissenid species. In addition, the metacercariae of Psilostomatidae, tentatively identified as *Sphaeridiotrema* sp., were found in *D. r. bugensis* from Lake Oneida.

Prevalence of dreissenid infection with trematodes varied from none to virtually 100% within and among the sampled waterbodies. High prevalence of infection of both zebra and quagga mussels was found in the western basin of Lake Erie, whereas no or very low infection was recorded in the central and eastern basins. Similarly high variations were found in Lake Oneida (Table 2). No trematode infection was found in dreissenids from Eighteen Mile Creek or in the Finger Lakes, with the exception of 2 echinostomatid metacercariae found in zebra mussels in Lake Owasco and 2 unidentified metacercariae found in quagga mussels from Lake Cayuga: one in July 2009 and another in July 2010.

Infection intensity of zebra and quagga mussels in Lake Erie was always lower for large metacercariae than for small metacercariae (Table 2). The highest infection intensity of *D. polymorpha* with large metacercariae (7 cysts per mussel) and small metacercariae (25 cysts per mussel) was found in the same 10.0-mm mussels from the western basin of Lake Erie. At the same exact location, we found the highest infection intensity for *D. r. bugensis*. In a 14.2-mm-long quagga mussel, we recorded 15 cysts of large metacercariae and 51 cysts of small metacercariae.

Bithynia tentaculata

Five populations of the faucet snail were examined for the prevalence and intensity of infection with trematodes (Table 3). The 4 species of trematodes found were *Cyathocotyle bushiensis* and Echinostomatidae spp. (metacercariae), *Sphaeridiotrema* sp. (cercariae and rediae), and Xiphidiocercariae (cercariae), tentatively identified as *L. polyoon*. The prevalence of infection of *B. tentaculata* populations infected with *C. bushiensis* was generally higher compared with the infection of this snail with other trematodes. There was a strong variation of the prevalence of *B. tentaculata* infection with *C. bushiensis* within and among the studied waterbodies (Table 3).

Intensity of *B. tentaculata* infection with Xiphidiocercaria sp. and Echinostomatidae sp. cysts was low, and low to moderate with *C. bushiensis* (Table 3). The highest number of *C. bushiensis* metacercariae (45 cysts per snail) was found in *B. tentaculata* collected from the concrete wall of the Cornell biological station boat ramp on Lake Oneida. In Golden Hill Creek in May 2010, we found a high level of intensity of *B. tentaculata* infection with rediae and cercariae of *Sphaeridiotrema* sp. The highest number of cercariae of this parasite (6,850) was found in a 13.1-mm *B. tentaculata* collected from the mouth of the Golden Hill Creek in Golden Hill State Park.

Other Molluscs

Echinostomatid metacercariae were found in *C. fluminea*, with 4 of the 33 molluscs dissected from Lake Owasco being infected with echinostomatid cysts. The prevalence of infection

TABLE 1.

Occurrence of exotic molluscs examined for trematodes in the Great Lakes Region in 2009 and 2010.

Sampled Sites and Coordinates	*Bithynia tentaculata*	*Cipangopaludina chinensis*	*Corbicula fluminea*	*Dreissena polymorpha*	*D. r. bugensis*	*Potamopyrgus antipodarum*	*Valvata piscinalis*
Lake Erie, western basin, June 2009							
Station ER60, 41°53.470 N, 083°11.700 W	nf	nf	nf	30	3	nf	nf
Lake Erie, eastern basin, July 2009							
Station E1, 42°06.310 N, 080°18.070 W	nf	nf	nf	5	15	nf	nf
Station E2, 42°10.080 N, 080°09.760 W	nf	nf	nf	20	15	nf	nf
Station E3, 42°12.200 N, 080°02.600 W	nf	nf	nf	nf	15	nf	nf
Station E7, 42°25.010 N, 079°29.260 W	nf	nf	nf	nf	15	nf	nf
Lake Erie, central basin, July 2009							
Station C3, 41°32.200 N, 081°57.870 W	nf	nf	nf	nf	4	nf	nf
Station C6, 41°46.860 N, 081°19.570 W	nf	nf	nf	nf	3	nf	nf
Station C9, 41°58.870 N, 080°40.170 W	nf	nf	nf	4	11	nf	nf
Lake Erie, western basin, July 2009							
Station W1, 41°53.050 N, 083°05.010 W	nf	nf	nf	18	15	nf	nf
Station W3, 41°50.220 N, 083°07.600 W	nf	nf	nf	10	13	nf	nf
Station W5, 41°46.200 N, 083°05.440 W	nf	nf	nf	nf	15	nf	nf
Station W7, 41°44.980 N, 082°56.060 W	nf	nf	nf	4	10	nf	nf
Station W10, 41°45.200 N, 082°45.310 W	nf	nf	nf	nf	15	nf	nf
18 Mile Creek (Lake Ontario tributary)							
July 2009, 43°20.116 N, 078°42.899 W	nf	nf	nf	20	nf	nf	nf
Golden Hill Creek, Golden Hill State Park, NY							
July 2009, 43°22.266 N, 078°28.540 W	15	nf	nf	nf	nf	nf	nf
May 2010, 43°22.281 N, 078°28.611 W	57	nf	nf	nf	nf	nf	nf
Unnamed Creek (Lake Ontario tributary), NY							
May–July 2009, 43°16.230 N, 079°01.271 W	nf	nf	nf	nf	nf	270	nf
Lake Cayuga, NY							
July 2009, 42°53.901 N, 076°44.969 W	nf	nf	nf	20	20	nf	nf
July 2010, 42°28.266 N, 076°30.211 W	nf	nf	nf	33	33	nf	nf
July 2010, 42°27.754 N, 076°30.289 W	50	nf	nf	nf	nf	nf	nf
Lake Seneca, Geneva, NY, July 2009, 42°52.341 N, 076°57.315 W	nf	nf	nf	nf	20	nf	nf
Lake Canandaigua, NY, July 2009 42°52.448 N, 077°16.337 W	nf	nf	nf	2	20	nf	nf
Lake Otisco, NY, July 2009 42°50.670 N, 076°15.909 W	nf	nf	nf	20	nf	nf	nf

continued on next page

TABLE 1.

continued

Sampled Sites and Coordinates	*Bithynia tentaculata*	*Cipangopaludina chinensis*	*Corbicula fluminea*	*Dreissena polymorpha*	*D. r. bugensis*	*Potamopyrgus antipodarum*	*Valvata piscinalis*
Lake Oneida, NY, Cornell biological station boat ramp, 43°17.334 N, 075°93.066 W							
June 2010	30	nf	nf	nf	nf	nf	53
July 28, 2010	20	nf	nf	nf	nf	nf	nf
July 23, 2010	nf	nf	nf	33	34	nf	nf
Dump place, 43°22.377 N, 076°01.186 W							
June 2010	25	nf	nf	nf	nf	nf	nf
July 2010	nf	nf	nf	33	33	nf	nf
Lake Owasco, Auburn, NY, August 2010							
Melrose Park, 42°90.257 N, 076°54.063 W	nf	nf	33	33	nf	nf	nf
Boat channel, 42°92.331 N, 076°53.910 W	nf	10	nf	nf	nf	nf	nf
Niagara River, Beaver Island, NY, July 2010							
42°96.897 N, 078°94.334 W	49	nf	nf	nf	nf	nf	nf
Woods Creek, Niagara River tributary, NY							
June 2010, 43 3.603 N, 078°58.694 W	nf	20	nf	nf	nf	nf	nf

Cell values are numbers of molluscs dissected. nf, host mollusc not found and/or not examined at the station.

was 12.1%, and the intensity of infection did not exceed 1 metacercaria per mussel. The cercariae of *Echinostoma* sp. (3.8% prevalence, 178.5 ± 163.5 cercariae per snail infection intensity, mean ± SE) and the metacercariae of unidentified digenean trematodes (9.4% prevalence, 1 metacercariae per snail infection intensity) were revealed in *V. piscinalis* collected at the boat ramp site in Lake Oneida. No trematodes were found in *P. antipodarum* (270 snails dissected) or in *C. chinensis* (30 snails dissected).

DISCUSSION

Dreissena polymorpha *and* Dreissena rostriformis bugensis

In Europe, 7 genera of trematodes have been reported as parasites of *Dreissena* (Molloy et al. 1997, Stunžėnas et al. 2004). For these parasites, dreissenids may serve as the first intermediate host (*Bucephalus polymorphus, Phyllodistomum* spp.), second intermediate host (*Echinoparyphium recurvatum, Echinoparyphium paraulum,* and *Echinoparyphium echinatoides*) or the only host (*Aspidogaster* spp.). The parasites *B. polymorphus, Phyllodistomum* spp., and *E. recurvatum* were reported in *Dreissena* exclusively from Europe (Molloy et al. 1997, Stunžėnas et al. 2004). Although North American populations of zebra mussels were examined repeatedly for the presence of parasites since the introduction of dreissenids during the 1980s (Mills et al. 1996, Carlton 2008), no natural infections of *D. polymorpha* with echinostomatid and psilostomatid trematodes were found before the beginning of our study (Conn & Conn 1993, Toews et al. 1993, Conn & Conn 1995, Laruelle et al. 2002). Thus far, reports of trematodes in North American *Dreissena* were limited to *Aspidogaster limacoides* and unidentified Plagiorchiidae (Toews et al. 1993). The trematode *A. limacoides* requires only a single host to complete its life cycle; *Aspidogaster* is not specific to dreissenids and uses a wide variety of freshwater molluscs as hosts (Molloy et al. 1997).

Because metacercariae of many Echinostomatidae species are known from North American freshwater molluscs (Conn & Conn 1995), it was not surprising to find echinostomatid trematodes in dreissenids during our study. The prevalence of infection of dreissenid species with these trematodes in the Great Lakes Region was higher than that generally reported from Europe (Table 2). In contrast, low to moderate prevalence of infection was usually found in European zebra mussel populations. Ginezinskaja (1959) reported less than 1% infection of *D. polymorpha* with *E. recurvatum*, Chernogorenko and Boshko (1992) reported less than 1% infection with *E. echinatoides*, and Kochnev (1977) reported less than or equal to 8.5% of mixed infection with *E. recurvatum* and *E. paraulum*. In their study in Belarus, Karatayev et al. (2000) found echinostomatid metacercariae in zebra mussels in 10 of the 17 waterbodies studied, with the prevalence ranging from 0.3–28.5%. In only 2 waterbodies in Belarus was the prevalence of the zebra mussel infection with echinostomatids as high as 100% (Mastitsky 2005, Mastitsky & Veres 2010). The effect of echinostomatids on *Dreissena* and other intermediate hosts is usually benign (Molloy et al. 1997, Laruelle et al. 2002); however, infection of amphibian kidneys by metacercariae can result in severe pathology (Martin & Conn 1990), and definitive hosts can be affected negatively. The parasite *E. recurvatum* is common and, at times, fatal in North American waterfowl (McDonald 1969, Roscoe & Huffman 1982). Other echinostomatids could also be moderately to highly pathogenic to their definitive hosts (McDonald 1981). In Lake Oneida, high prevalence of echinostomatid infection coupled with the high density of dreissenids may result in

TABLE 2.

Prevalence and intensity of infection of *Dreissena polymorpha* and *Dreissena rostriformis bugensis* with trematodes in the Great Lakes Region.

	D. polymorpha			*D. r. bugensis*		
Sampled Sites	Large Metacercariae	Small Metacercariae	Other Metacercariae	Large Metacercariae	Small Metacercariae	Other Metacercariae
Lake Erie, western basin, June 2009	53.3 1.81 ± 0.34 (6)	4.5 4.00 (4)	0	100.0 1.33 ± 0.33 (2)	0	0
Lake Erie, eastern basin, June 2009						
Station E1	0	0	0	6.7 4.0	0	0
Station E2	0	75.0 3.27 ± 0.69 (9)	0	0	0	0
Lake Erie, western basin, July 2009						
Station W1	27.8 1.20 ± 0.20 (2)	5.6 2.00 (2)	0	73.3 1.18 ± 0.18 (3)	0	0
Station W3	70.0 3.71 ± 0.75 (7)	80.0 11.75 ± 2.86 (25)	0	92.3 4.67 ± 1.12 (15)	84.6 10.64 ± 4.22 (51)	0
Station W5	nf	nf	0	13.3 1.00 (1)	60.0 2.11 ± 0.42 (4)	0
Station W7	25.0 1.00 (1)	50.0 9.00 ± 8.00 (17)	0	10.0 2.00 (2)	90.0 5.00 ± 1.44 (16)	0
Lake Cayuga, July 2009	0	0	0	0	0	5.0 1.00 (1)†
July 2010	0	0	0	0	0	3.0 1.00 (1)†
Lake Oneida, boat ramp, July 2010	0	0	63.6 2.57 ± 0.50 (11)*	0	0	24.2 1.13 ± 0.13 (2)* 3.0 2.00 (2)‡
Lake Owasco, August 2010	0	0	6.1 1.00 (1)*	nf	nf	0

* Echinostomatidae.
† Unidentified digenean metacercaria.
‡ Psilostomatidae (*Sphaeridiotrema* sp.?).
Cell values are prevalence (above the line) and intensity (below the line, mean ± SE); maximum values are in parenthesis. Only sites where infected mussels were found are included. nf, host dreissenid not found at the station.

a substantial increase of waterfowl infection, as they prey heavily on zebra mussels (Molloy et al. 1997).

Bithynia tentaculata

From the standpoint of diversity and adverse impacts on their vertebrate hosts, the trematode fauna of *B. tentaculata* in their native range far exceeds all other exotic molluscs examined in this study. At least 73 trematode taxa are known from the native range of *B. tentaculata*, and 4 of them have been documented to cause pathogenic effects in their definitive hosts, such as aquatic birds and mammals (Mastitsky et al. 2010). The faucet snail trematode *B. tentaculata* was first recorded in North America in Lake Michigan in 1871, but was probably introduced in 1870 (Mills et al. 1993). Three host-specific trematode species nonnative to North America have already been reported in the Great Lakes Region from populations of *B. tentaculata*, including *C. bushiensis, Sphaeridiotrema* sp., and *L. polyoon* (Cole & Friend 1999). In contrast to their native range in Europe, in North America—and especially in the Great Lakes Region—*C. bushiensis* and *Sphaeridiotrema globulus* infections have periodically caused mass mortalities in waterfowl since 1928 (reviewed in Herrmann and Sorensen (2009)). During the 2006 migration, an estimated 22,000–26,000 birds died in the Upper Mississippi River National Wildlife and Fish Refuge (Sauer et al. 2007). High levels of *B. tentaculata* infection with *C. bushiensis* found in 2 of the 5 populations sampled in this study, coupled with a high level of the faucet snail density, suggest that there is a serious risk for epizootics among waterfowl in the examined Lower Great Lakes Region.

Corbicula fluminea

In their native range, *C. fluminea* has been reported to host *Phyllodistomum mingensis* (Tang 1985), 5 species of *Echinostoma* (*Echinostoma cinetorchis, Echinostoma lindoensis, Echinostoma*

TABLE 3.

Prevalence and intensity of infection of *Bithynia tentaculata* with trematodes in the Great Lakes Region.

Sampled Sites	*Sphaeridiotrema* sp., Cercariae and Rediae	*Cyathocotyle bushiensis*, Metacercariae	Xiphidiocercariae (*Leyogonimus polyoon*?), Cercariae	Echinostomatidae gen. spp., Metacercariae
Golden Hill Creek				
July 2009	0	33.3 1.8 ± 3.7 (3)	0	0
May 2010	12.3 2,499 ± 877 (6,850)	7.0 7.0 ± 3.3 (15)	3.5 4.0 ± 1.0 (5)	0
Lake Cayuga, July 2010	0	0	0	4.0 1.0 (1)
Lake Oneida, 2010				
Boat ramp, June	0	13.3 13.5 ± 10.5 (45)		0
Boat ramp, July	0	60.0 4.9 ± 1.7 (17)		0
Niagara River, July 2010	0	6.1 4.0 ± 1.5 (6)		4.1 5.5 ± 0.5 (6)

Cell values are prevalence (above the line) and intensity (below the line, mean ± SE), with maximum values in parentheses. Only sites where infected snails were found are included.

macrorchis, Echinostoma melis, and *Echinostoma revolutum*) (Keeler & Huffman 2009), and 7 species of Aspidogastrea (Tang 1992). The definitive host of *P. mingensis* is the fish *Lateolabrax japonicus* (Tang 1992), and vertebrate hosts of the *Echinostoma* species may include fish, amphibians, turtles, and humans (Chai 2009, Keeler & Huffman 2009). Despite a long history of *C. fluminea* research since their introduction into North America in 1938 (reviewed in McMahon (1999)), only aspidogastrid trematodes *Aspidogaster conchicola* and *Cotylapsis insignis* have been reported so far from North America (Danford & Joy 1984). Fried et al. (1987) infected North American *C. fluminea* experimentally with *Echinostoma* metacercariae in the laboratory, but noted no natural infections. Our discovery of the echinostomatid metacercariae naturally occurring in a single sampled population of *C. fluminea* indicate that these trematodes already use the Asian clam as their intermediate host in the Great Lakes Region. Additional studies are necessary to estimate how widely these trematodes are distributed across North American populations of *C. fluminea*, and further taxonomic identifications of the metacercariae are required to evaluate potential pathogenic impacts on their vertebrate hosts.

Valvata piscinalis

At least 12 trematode taxa have been reported from the European stream valvata in its native range (Ginetzinskaja 1959, Sudarikov et al. 2002), including *C. bushiensis*, *E. recurvatum* (Sudarikov et al. 2002), and a sanguinicolid species (Ginetzinskaja 1959). Thus far, none of these trematodes has been reported for North American populations since the initial introduction of the snail in Lake Ontario in 1897 (reviewed in Grigorovich et al. (2005)). However, as *V. piscinalis* is known to host *C. bushiensis* and *E. recurvatum* in its native range (Sudarikov et al. 2002), and because these 2 parasites are present in the Great Lakes Region, we suggest that their finding in North American populations of the snail is only a matter of time. The ability of the European valvata to host *C. bushiensis* is especially alarming because, in addition to *B. tentaculata*, *V. piscinalis* can contribute to the circulation of this highly pathogenic trematode in the Great Lakes Region. Our discovery of *Echinostoma* sp. cercariae along with unidentified digenean metacercariae indicates that *V. piscinalis* in the Great Lakes Region already hosts at least 2 species of trematodes that may pose a risk to their vertebrate hosts.

Cipangopaludina chinensis

At least 9 species of trematodes use *C. chinensis* as their host in the native range of the Chinese mystery snail, including three species of *Echinochasmus* (*Echinochasmus elongatus*, *Echinochasmus redioduplicatus*, and *Echinochasmus rugosus*), 2 species of *Echinoparyphium* (*E. recurvatum* and *Echinoparyphium ilocanum*), and 4 species of *Echinostoma* (*E. cinetorchis*, *E. macrorchis*, *E. melis*, and *E. revolutum*) (Pace 1973, Keeler & Huffman 2009). Vertebrate hosts of these trematodes may include fish, amphibians, turtles, waterfowl, and humans (Chai 2009, Keeler & Huffman 2009). Although first records of *C. chinensis* in the North America date back to 1892, and sometime between 1931 and 1942 in the Great Lakes Region (reviewed in Mills et al. (1993)), none of these trematodes has ever been reported from the North American population of *C. chinensis*. Even the cosmopolitan *E. recurvatum*, commonly reported from freshwater molluscs of North America, has never been found in Chinese mystery snails in the New World. Thus far, only 1 trematode, *A. conchicola*, has been reported in *C. chinensis* in North America (Michelson 1970). The trematode *A. conchicola* is a cosmopolitan species, commonly occurring in freshwater molluscs of this region (Hendrix & Short 1965, Michelson 1970, Huehner & Etges 1977). We did not find any trematodes in *C. chinensis* during our survey. However, low sample size (only 30 snails were dissected) prevents us from a definite conclusion. Additional populations of the Chinese mystery snail should be examined for the presence of trematodes.

Potamopyrgus antipodarum

Fourteen species and higher taxa of trematodes were reported from native populations of the New Zealand mud snail (Macfarlane 1939, Winterbourn 1973, MacArthur & Featherston 1976, Jokela & Lively 1995, Dybdahl & Lively 1998). None of these species was associated with pathogenic impacts on their definitive hosts in the *P. antipodarum* native range. At the same time, in its invaded range in Europe, *P. antipodarum* acquired several parasites that are potentially pathogenic to their definitive hosts, including parasites from the family Sanguinicolidae (Gerard & Le Lannic 2003, Pointier et al. 2005, Morley 2008, Żbikowski & Żbikowska 2009) and *E. recurvatum* (Evans et al. 1981). Thus far, no parasites have been reported from North American populations of *P. antipodarum* since its initial introduction in 1987 (Bowler 1991). We also failed to find any parasites in 270 New Zealand mud snails dissected from Unnamed Creek in the Lake Ontario watershed. However, because *P. antipodarum* is known to host *E. recurvatum*, which is native to North America, we suggest that in the future this trematode may be discovered in the New Zealand mud snail.

General Findings

The average richness of trematode taxa per exotic mollusc found in this study (2.29 ± 0.29) was 8.5 times lower than in their native range (19.43 ± 3.40; $P = 0.018$, Wilcoxon's matched pairs test). The substantial reduction in parasite diversity associated with exotic species in introduced regions is a well-known phenomenon (Torchin et al. 2002, Torchin et al. 2003, Colautti et al. 2004, Prenter et al. 2004, Kelly et al. 2009, Mastitsky et al. 2010). However, it has also been shown that the reduction of parasite diversity in invaded areas occurred mainly as a result of the loss of low-impact species, whereas the number of high-impact parasite species (those documented as causing a distinct pathological effect in a large proportion of an infected host's population (e.g., livestock and wildlife), but not the exotic host of the parasite) did not differ significantly between the native and recipient areas (Mastitsky et al. 2010). Three mechanisms acting either individually or in combination can explain the similar numbers of high-impact parasites associated with freshwater exotic invertebrates in their native and invaded areas: (1) acquisition by the invaders of new high-impact parasites in the invaded regions, (2) high abundance of the invaders in their new ranges, and (3) high susceptibility of novel hosts to exotic parasites because of the "naive host syndrome" (Hoberg & Brooks 2008, Mastitsky et al. 2010). Our data provide evidence that all 3 of these mechanisms are taking place in the Great Lakes Region.

Mastitsky et al. (2010) found that 19 of the 22 examined freshwater invertebrates acquired parasites in the invaded regions, including those previously documented to cause epizootics. We found that at least 6 of the 7 examined species of exotic molluscs have already acquired novel trematode parasites in North America. The process of acquisition of aboriginal trematodes by exotic hosts, however, may be quite long. The Asian clam *C. fluminea* was first recorded in North America in 1938 (Burch 1944), but before our study, no trematodes with complex life cycles were reported from this species (Danford & Joy 1984). Similarly, early examinations of both *Dreissena* species in North America failed to reveal echinostomatid and psilostomatid trematodes (Conn & Conn 1993, Conn & Conn 1995, Laruelle et al. 2002). However, our discovery of high levels of infection by echinostomatid and other trematodes in both zebra and quagga mussels prove that they have also acquired trematodes that may be detrimental to their vertebrate hosts. We suggest that other exotic molluscs that are not yet known to host trematodes may acquire them in the future, or may already host such trematodes but remain largely undiscovered because of the lack of attention from the scientific community. This is especially probable for exotic molluscs, which are known in their native range to host cosmopolitan parasites like *E. recurvatum* and *E. revolutum* (Sorensen et al. 1997, Chai 2009).

The host population density is one of the major biotic factors promoting the transmission and persistence of parasitic diseases (Anderson & May 1981). As a result, outbreaks of native diseases can be facilitated by the high abundance of their novel exotic hosts (Kelly et al. 2009, Mastitsky & Veres 2010). In our study, most of the examined exotic molluscs were found to form high population densities. We also found that, at least in some cases, the prevalence of infection of exotic molluscs in the Great Lakes Region may exceed that usually reported from their native range. High host density coupled with the high level of infection can result in the high risk of parasite transmission to the subsequent vertebrate hosts.

In the native range, hosts and their parasites are usually coadapted as a result of the long history of coevolution, so that parasites are rarely highly virulent to their hosts (May & Anderson 1983, Taraschewski 2006). In contrast, exotic parasites in invaded areas can infect "naive hosts" that lack historically evolved resistance, and therefore can severely affect these novel hosts, often in the form of mass mortalities (Alderman et al. 1987, Burreson et al. 2000, Taraschewski 2006). The faucet snail *B. tentaculata* is suspected to be responsible for the introduction of 3 species of parasites new to the Great Lakes: *Sphaeridiotrema* sp., *C. bushiensis*, and *L. polyoon* (Cole & Franson 2006, Sauer et al. 2007). The transmission of *L. polyoon* from *B. tentaculata* to its vertebrate host caused mass mortalities of American coot in north-central Wisconsin (Cole & Franson 2006). In its native range, however, this parasite has never been reported to cause such mortalities. Host switching of exotic parasites to naive hosts via ecological fitting in invaded areas is very common across many taxa, including phytophagous insects and their host plants (reviewed in Brooks et al. (2006b), Agosta (2006), Agosta and Klemens (2008), Janz and Nylin (2008), and Brooks and Hoberg (2008)), and occurs on wide temporal and spatial scales (Hoberg & Brooks 2008, Agosta et al. 2010). This process is thought to be facilitated by global climate change, and is predicted to cause a sharp increase in EID in the future (Brooks & Hoberg 2007, Brooks & Hoberg 2008, Agosta et al. 2010).

In conclusion, our study demonstrates that most of the examined exotic molluscs in the Great Lakes Region host trematodes that may be harmful for their vertebrate hosts, including fish and waterfowl. Many exotic molluscs that were believed to be free of parasites have already acquired trematodes native to North America, and other exotics may acquire them in the future. Hotspots of trematode infections were recorded in the western basin of Lake Erie and Lake Oneida, where several species of exotic molluscs had a high prevalence of trematodes, and thus posed high risks of transmission of the parasites to definitive hosts. Nevertheless, our study doesn't represent a complete assessment of the role of exotic molluscs as hosts for pathogenic parasites, and additional surveys are urgently necessary, as is a thorough identification of trematodes using molecular techniques. Risk assessment of the parasitological consequences of the introduction of exotic species requires more attention from aquatic ecologists and parasitologists. We suggest that parasitological assessment be an integral part in assessing the ecological and economic risks these species pose.

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LITERATURE CITED

Agosta, S. J. 2006. On ecological fitting, plant–insect associations, herbivore host shifts, and host plant selection. *Oikos* 114:556–565.

Agosta, S. J., N. Janz & D. R. Brooks. 2010. How specialists can be generalists: resolving the ''parasite paradox'' and implications for emerging infectious disease. *Zoologia* 27:151–162.

Agosta, S. J. & J. A. Klemens. 2008. Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecol. Lett.* 11:1123–1134.

Alderman, D. J., J. L. Polglase & M. Frayling. 1987. *Aphanomyces astaci* pathogenicity under laboratory and field conditions. *J. Fish Dis.* 10:385–393.

Anderson, R. M. & R. M. May. 1981. The population dynamics of microparasites and their invertebrate hosts. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 291:451–524.

Bowler, P. A. 1991. The rapid spread of the freshwater hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the middle Snake River, southern Idaho. *Proc. Desert Fishes Counc.* 21:173–182.

Brooks, D. R. & E. P. Hoberg. 2006. Systematics and emerging infectious diseases: from management to solution. *J. Parasitol.* 92: 426–429.

Brooks, D. R. & E. P. Hoberg. 2007. How will global climate change affect parasites–host assemblages? *Trends Parasitol.* 23:571–574.

Brooks, D. R. & E. P. Hoberg. 2008. Darwin's necessary misfit and the sloshing bucket: the evolutionary biology of emerging infectious diseases. *Evol. Edu. Outreach* 1:2–9.

Brooks, D. R., V. León-Règagnon, D. A. McLennan & D. Zelmer. 2006a. Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology* 87(Suppl.): S76–S85.

Brooks, D. R., D. A. McLennan, V. León-Règagnon & E. P. Hoberg. 2006b. Phylogeny, ecological fitting and lung flukes: helping solve the problem of emerging infectious diseases. *Rev. Mex. Biod.* 77: 225–234.

Burch, J. W. 1944. Checklist of West American mollusks, family Corbiculidae. *Minutes Conch. Club S. Calif.* 36:1–18.

Burns, W. C. 1961. The life history of *Sphaeridiotrema spinoacetabulum* sp. n. (Trematoda: Psilostomidae) from the ceca of ducks. *J. Parasitol.* 47:933–938.

Burreson, E. M., N. A. Stokes & C. S. Friedman. 2000. Increased virulence in an introduced range: *Haplosporidium nelsoni* (MSX) in the Eastern oyster *Crassostrea virginica*. *J. Aquat. Anim. Health* 12: 1–8.

Carlton, J. T. 2008. The zebra mussel *Dreissena polymorpha* found in North America in 1986 and 1987. *J. Great Lakes Res.* 34:770–773.

Cattadori, I. M., D. T. Haydon & P. J. Hudson. 2005. Parasites and climate synchronize red grouse populations. *Nature* 433:737–741.

Chai, J. Y. 2009. Echinostomes in humans. In: R. Toledo & B. Fried, editors. The biology of echinostomes: from the molecule to the community. New York: Springer. pp. 147–183.

Chernogorenko, M. I. & E. G. Boshko. 1992. Parasite fauna of aquatic organisms of the Dnestr and Dnestr Liman. In: V. E. Nesluzhenko, editor. Hydrobiological condition of the Dnestr and its reservoirs. Kiev: Naukova Dunka Publishers. pp. 321–329. (in Russian).

Colautti, R. I., A. Ricciardi, I. A. Grigorovich & H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.* 7:721–733.

Cole, R. A. & J. C. Franson. 2006. Recurring waterbird mortalities of unusual etiologies. In: G. C. Boere, C. A. Galbraith & D. A. Stroud, editors. Waterbirds around the world. Edinburgh: The Stationery Office. pp. 439–440.

Cole, R. A. & M. Friend. 1999. Miscellaneous parasitic diseases. Field manual of wildlife diseases: general field procedures and diseases of birds. Biological Resources Division information and technology report 1999–001. Madison, WI: USGS Biological Resources Division National Wildlife Health Center. pp. 249–258.

Conn, D. B. & D. A. Conn. 1993. Parasitism, predation, and other biotic associations between dreissenid mussels and native animals in the St. Lawrence River. In: J. L. Tsou, editor. Proceedings: Third International Zebra Mussel Conference. Palo Alto, CA: Electric Power Research Institute. pp. 223–234.

Conn, D. B. & D. A. Conn. 1995. Experimental infection of zebra mussels *Dreissena polymorpha* (Mollusca: Bivalvia) by metacercariae of *Echinoparyphium* sp. (Platyhelminthes: Trematoda). *J. Parasitol.* 81:304–305.

Danford, D. W. & J. E. Joy. 1984. Aspidogastrid (Trematoda) parasites of bivalve molluscs in western West Virginia. *Proc. Helm. Soc. Wash.* 51:301–305.

Dobson, A. & J. Foufopoulos. 2001. Emerging infectious pathogens of wildlife. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 356:1001–1012.

Dybdahl, M. F. & C. M. Lively. 1998. Host–parasite coevolution: evidence for rare advantage and time-lagged selection in a natural population. *Evolution* 52:1057–1066.

Edgerton, B. F., L. H. Evans, F. J. Stephens & R. M. Overstreet. 2002. Synopsis of freshwater crayfish diseases and commensal organisms. *Aquaculture* 206:57–135.

Evans, N. A., P. J. Whitfield & A. P. Dobson. 1981. Parasite utilization of a host community: the distribution and occurrence of metacercarial cysts of *Echinoparyphium recurvatum* (Digenea: Echinostomatidae) in seven species of molluscs at Harting Pond, Sussex. *Parasitology* 83:1–12.

Fried, B., S. Emili & W. S. Erringer. 1987. Experimental infections of *Corbicula fluminea* (Bivalvia: Corbiculidae) with *Echinostoma revolutum* cercariae. *J. Parasitol.* 73:655–656.

Gerard, C. & J. Le Lannic. 2003. Establishment of a new host–parasite association between the introduced invasive species *Potamopyrgus antipodarum* (Smith) (Gastropoda) and *Sanguinicola* sp. Plehn (Trematoda) in Europe. *J. Zool.* (*Lond.*) 261:213–216.

Ginezinskaja, T. A. 1959. On cercarial fauna of molluscs from Rybinskoye Dam Reservoir: II. Ecological factors influencing infection in molluscs by pathenogenic trematodes. *West. Leningr. Univ. Ser. Biol.* 4:62–77. (in Russian).

Grigorovich, I. A., E. L. Mills, C. B. Richards, D. Breneman & J. J. H. Ciborowski. 2005. European valve snail *Valvata piscinalis* (Muller) in the Laurentian Great Lakes basin. *Great Lakes Res.* 31:135–143.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld & M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158–2162.

Hendrix, S. S. & R. B. Short. 1965. Aspidogastrids from northeastern Gulf of Mexico river drainages. *J. Parasitol.* 51:561–569.

Herrmann, K. K. & R. E. Sorensen. 2009. Seasonal dynamics of two mortality-related trematodes using an introduced snail. *J. Parasitol.* 95:823–828.

Hoberg, E. P. & D. R. Brooks. 2008. A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. *J. Biogeogr.* 35:1533–1550.

Holmes, J. C. 1996. Parasites as threats to biodiversity in shrinking ecosystems. *Biodivers. Conserv.* 5:975–983.

Huehner, M. K. & F. J. Etges. 1977. The life cycle and development of *Aspidogaster conchicola* in the snails, *Viviparus malleatus* and *Goniobasis livescens*. *J. Parasitol.* 63:669–674.

Janz, N. & S. Nylin. 2008. The oscillation hypothesis of host–plant range and speciation. In: K. J. Tilmon, editor. Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects. Berkley: University of California Press. pp. 203–215.

Jokela, J. & C. M. Lively. 1995. Spatial variation in infection by digenetic trematodes in a population of freshwater snails (*Potamopyrgus antipodarum*). *Oecologia* 103:509–517.

Karatayev, A. Y., L. E. Burlakova, D. P. Molloy & L. K. Volkova. 2000. Endosymbionts of *Dreissena polymorpha* (Pallas) in Belarus. *Int. Rev. Hydrobiol.* 85:543–559.

Keeler, S. P. & J. E. Huffman. 2009. Echinostomes in the second intermediate host. In: R. Toledo & B. Fried, editors. The biology of echinostomes: from the molecule to the community. New York: Springer. pp. 61–87.

Kelly, D. W., R. A. Paterson, C. R. Townsend, R. Poulin & D. M. Tompkins. 2009. Parasite spillback: a neglected concept in invasion ecology? *Ecology* 90:2047–2056.

Kochnev, S. A. 1977. Infection with trematode metacercariae of *Dreissena polymorpha* in a reservoir warmed by waters of the thermo-electric station. Ekologiya Gelmintov. Yaroslavl, Russia: Yaroslavl State University Press. pp. 46–52. (in Russian).

Kutz, S. J., E. P. Hoberg, L. Polley & E. J. Jenkins. 2005. Global warming is changing the dynamics of Arctic host–parasite system. *Proc. Biol. Sci.* 272:2571–2576.

Laruelle, F., D. P. Molloy & V. Roitman. 2002. Histological analysis of trematodes in *Dreissena polymorpha*: their location, pathogenicity, and distinguishing morphological characteristics. *J. Parasitol.* 88: 856–863.

Lv, S., Y. Zhang, H.- X. Liu, L. Hu, K. Yang, P. Steinmann, Z. Chen, L.- Y. Wang, J. Utzinger & X.- N. Zhou. 2009. Invasive snails and an emerging infectious disease: results from the first national survey on *Angiostrongylus cantonensis* in China. *PLoS Negl. Trop. Dis.* 3:1–8.

MacArthur, C. P. & D. W. Featherston. 1976. Suppression of egg production in *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae) by larval trematodes. *N. Z. J. Zool.* 3:35–38.

Macfarlane, W. V. 1939. Life cycle of *Coitocaecum anaspidis* Hickman, a New Zealand digenetic trematode. *Parasitology* 31:172–184.

Marcogliese, D. 2008. The impact of climate change on the parasites and infectious diseases of aquatic animals. *Rev. Sci. Tech. Off. Int. Epizoot.* 27:467–484.

Martin, T. R. & D. B. Conn. 1990. The pathogenicity, localization and cyst structure of echinostomatid metacercariae (Trematoda) infecting the kidneys of the frogs *Rana clamitans* and *Rana pipiens*. *J. Parasitol.* 76:414–419.

Mastitsky, S. E. 2005. Role of the mollusc *Dreissena polymorpha* Pallas (Bivalvia: Dreissenidae) in transmission of trematode infections to vertebrate animals. *Vestnik Tyumenskogo Gosudarstvennogo Universiteta* 5:130–134. (in Russian with English summary).

Mastitsky, S. E., A. Y. Karatayev, L. E. Burlakova & D. P. Molloy. 2010. Parasites of exotic species in invaded areas: does lower diversity mean lower epizootic impact? *Divers. Distrib.* 16:798–803.

Mastitsky, S. E. & J. K. Veres. 2010. Field evidence for a parasites spillback caused by exotic mollusc *Dreissena polymorpha* in an invaded lake. *Parasitol. Res.* 106:667–675.

May, R. M. & R. M. Anderson. 1983. Epidemiology and genetics in the coevolution of parasites and hosts. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 219:281–313.

McDonald, M. E. 1969. Catalog of helminths of waterfowl (Anatidae). Bureau of Sport Fisheries and Wildlife special scientific report, wildlife no. 126. Washington, DC: U. S. Fish and Wildlife Service. 692 pp.

McDonald, M. E. 1981. Keys to trematodes reported in waterfowl. Resource publication 142. Washington, DC: U.S. Fish and Wildlife Service. 156 pp.

McLaughlin, J. D., M. E. Scott & J. E. Huffman. 1993. *Sphaeridiotrema globulus* (Rudolphi, 1814) (Digenea): evidence for two species known under a single name and a description of *Sphaeridiotrema pseudoglobulus* n.sp. *Can. J. Zool.* 71:700–707.

McMahon, R. F. 1999. Invasive characteristics of the freshwater bivalve, *Corbicula fluminea*. In: R. Claudi & J. H. Leach, editors. Nonindigenous freshwater organisms: vectors, biology, and impacts. Boca Raton, FL: Lewis Publishers. pp. 315–343.

Michelson, E. H. 1970. *Aspidogaster conchicola* from freshwater gastropods in the United States. *J. Parasitol.* 56:709–712.

Mills, E. L., J. H. Leach, J. T. Carlton & C. L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Great Lakes Res.* 19:1–54.

Mills, E. L., G. Rosenberg, A. P. Spidle, M. Ludyansky & Y. Pligin. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. *Am. Zool.* 36:271–286.

Mitchell, A. J., R. M. Overstreet, A. E. Goodwin & T. M. Brandt. 2005. Spread of an exotic fish–gill trematode: a far-reaching and complex problem. *Fisheries* (*Bethesda, Md.*) 30:11–16.

Molloy, D. P., A. Y. Karatayev, L. E. Burlakova, D. P. Kurandina & F. Laruelle. 1997. Natural enemies of zebra mussels: predators, parasites and ecological competitors. *Rev. Fish. Sci.* 5:27–97.

Morley, N. J. 2008. The role of the invasive snail *Potamopyrgus antipidarum* in the transmission of trematode parasites in Europe and its implications for ecotoxicological studies. *Aquat. Sci.* 70:107–114.

Mouritsen, K. N., D. M. Tompkins & R. Poulin. 2005. Climate warming may cause a parasite-induced collapse in coastal amphipod populations. *Oecologia* 146:476–483.

Nepszy, S. J., J. Budd & A. O. Dechtiar. 1972. Mortality of young-of-the-year rainbow smelt (*Osmerus mordax*) in Lake Erie associated with the occurrence of *Glugea hertwigi*. *J. Wildl. Dis.* 14:233–239.

Pace, G. L. 1973. The freshwater snails of Taiwan (Formosa). *Malacol. Rev.* (Suppl. 1):1–117.

Pimentel, D., R. Zuniga & D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52:273–288.

Pointier, J. P., P. David & P. Jarne. 2005. Biological invasions: the case of planorbid snails. *J. Helminthol.* 79:249–256.

Poulin, R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology* 132:143–151.

Prenter, J., C. MacNeil, J. T. A. Dick & A. M. Dunn. 2004. Roles of parasites in animal invasions. *Trends Ecol. Evol.* 19:385–390.

Ricciardi, A. 2006. Patterns of invasion of the Laurentian Great Lakes in relation to changes in vector activity. *Divers. Distrib.* 12:425–433.

Roscoe, D. E. & J. E. Huffman. 1982. Trematode (*Sphaeridiotrema globulus*)-induced ulcerative hemorrhagic enteritis in wild mute swans (*Cygnus olor*). *Avian Dis.* 26:214–224.

Sauer, J. S., R. A. Cole & J. M. Nissen. 2007. Finding the exotic faucet snail (*Bithynia tentaculata*): investigation of waterbird die-offs on the Upper Mississippi River National Wildlife and Fish Refuge, U.S. Geological Survey open-file report 2007–1065. http://pubs.usgs.gov/of/2007/1065/pdf/ofr_20071065.pdf. Accessed October 19, 2010.

Schell, S. C. 1985. Trematodes of North America north of Mexico. Moscow, ID: University Press of Idaho. 263 pp.

Scott, M. E. 1988. The impact of infection and disease on animal populations: implications for conservation biology. *Conserv. Biol.* 2:40–56.

Sorensen, R. E., I. Kanev, B. Fried & D. J. Minchella. 1997. The occurrence and identification of *Echinostoma revolutum* from North American *Lymnaea elodes* snails. *J. Parasitol.* 83:169–170.

Stunžėnas, V., J. R. Cryan & D. P. Molloy. 2004. Comparison of rDNA sequences from colchicine treated and untreated sporocysts of *Phyllodistomum folium* and *Bucephalus polymorphus* (Digenea). *Parasitol. Int.* 53:223–228.

Sudarikov, V. E., A. A. Shigin, Y. V. Kurochkin, V. V. Lomakin, R. P. Stenko & N. I. Yurlova. 2002. Metacercariae of trematodes: parasites of the freshwater molluscs of the Central Russia. Moscow: Nauka Press. 298 pp. (in Russian).

Tang, Z. 1985. Studies on the life history of *Phyllodistomum mingensis*. *Acta Zool. Sin.* 31:246–253.

Tang, C. 1992. Some larval trematodes from marine bivalves of Honk Kong and freshwater bivalves of costal China. In: B. Morton, editor. The marine flora and fauna of Honk Kong and southern China III, vol. 1. Hong Kong: Hong Kong University Press. pp. 17–29.

Taraschewski, H. 2006. Hosts and parasites as aliens. *J. Helminthol.* 80:99–128.

Taylor, L. H., S. M. Latham & M. E. J. Woolhouse. 2001. Risk factors for human disease emergence. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 356:983–989.

Toews, S., M. Beverly-Burton & T. Lawrimore. 1993. Helminth and protist parasites of zebra mussels, *Dreissena polymorpha* (Pallas, 1771), in the Great Lakes region of southwestern Ontario, with comments on associated bacteria. *Can. J. Zool.* 71:1763–1766.

Torchin, M. E., K. D. Lafferty, A. P. Dobson, V. J. McKenzie & A. M. Kuris. 2003. Introduced species and their missing parasites. *Nature* 421:628–630.

Torchin, M. E., K. D. Lafferty & A. M. Kuris. 2002. Parasites and marine invasions. *Parasitology* 124:137–151.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips & E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48:607–615.

Winterbourn, M. J. 1973. Larval Trematoda parasitising the New Zealand species of *Potamopyrgus* (Gastropoda: Hydrobiidae). *Mauri Ora.* 2:17–30.

Żbikowski, J. & E. Żbikowska. 2009. Invaders of an invader: trematodes in *Potamopyrgus antipodarum* in Poland. *J. Invertebr. Pathol.* 101:67–70.