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Metazoan Parasites of Introduced Round and Tubenose Gobies in the Great Lakes: Support for the "Enemy Release Hypothesis"

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ABSTRACT. *Recent invasion theory has hypothesized that newly established exotic species may initially be free of their native parasites, augmenting their population success. Others have hypothesized that invaders may introduce exotic parasites to native species and/or may become hosts to native parasites in their new habitats. Our study analyzed the parasites of two exotic Eurasian gobies that were detected in the Great Lakes in 1990: the round goby* Apollonia melanostoma *and the tubenose goby* Proterorhinus semilunaris*. We compared our results from the central region of their introduced ranges in Lakes Huron, St. Clair, and Erie with other studies in the Great Lakes over the past decade, as well as Eurasian native and nonindigenous habitats. Results showed that goby-specific metazoan parasites were absent in the Great Lakes, and all but one species were represented only as larvae, suggesting that adult parasites presently are poorly-adapted to the new gobies as hosts. Seven parasitic species are known to infest the tubenose goby in the Great Lakes, including our new finding of the acanthocephalan* Southwellina hispida*, and all are rare. We provide the first findings of four parasite species in the round goby and clarified two others, totaling 22 in the Great Lakes—with most being rare. In contrast, 72 round goby parasites occur in the Black Sea region. Trematodes are the most common parasitic group of the round goby in the Great Lakes, as in their native Black Sea range and Baltic Sea introduction. Holarctic trematode* Diplostomum spathaceum *larvae, which are one of two widely distributed species shared with Eurasia, were found in round goby eyes from all Great Lakes localities except Lake Huron proper. Our study and others reveal no overall increases in parasitism of the invasive gobies over the past decade after their establishment in the Great Lakes. In conclusion, the parasite "load" on the invasive gobies appears relatively low in comparison with their native habitats, lending support to the "enemy release hypothesis."*

INDEX WORDS: Apollonia*, enemy release hypothesis, exotic species, parasitism,* Proterorhinus*, round goby, tubenose goby.*

INTRODUCTION

Two species of Eurasian gobies, the round goby *Apollonia melanostoma* (formerly known as *Neogobius melanostomus*) and the tubenose goby *Proterorhinus semilunaris* (formerly included with *P. marmoratus*; see Stepien and Tumeo 2006 for recent name changes) were discovered in Lake St. Clair of the North American Great Lakes in 1990, where they were introduced by ballast water exchange (Jude *et al.* 1992, Charlebois *et al.* 1997). Both species originated from the Ponto-Caspian basin (Miller 1986, Smirnov 1986) and now are well-established in the Great Lakes, with the round goby becoming one of the most common benthic nearshore fishes (Corkum *et al.* 2004, Carman *et al.*

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2006). These gobies also have successfully invaded new habitats in Eurasia, including the Baltic and Aegean seas (Skóra and Stolarski 1993, Eryilmaz 2002), the Danube River, and basins of the North Sea (Bíró 1971, Harka 1990, van Beek 2006).

Invasion theory suggests that some of a species' initial colonization success may be due to temporary release from parasites and pathogens, with fewer in the new environment than in native habitats (Torchin *et al.* 2003). Release from parasites and pathogens, which is predicted to be greatest early in the invasion, forms part of the "enemy release hypothesis" (Keane and Crawley 2002). Exotic species also may serve as sources for new parasite species to invade native host populations (Mack *et al.* 2000). Following a successful introduction, one would expect exotic species to become increasingly parasitized by the parasites harbored by ecologically similar native species. It thus appears likely that sampling the parasite load of an exotic population over the time course following an introduction would yield increasing numbers of parasites, until the new hosts reach a parasite load similar to that of native species.

Parasites of the round and tubenose gobies have been relatively well-studied in their native habitats (e.g., Naidenova 1974, Gaevskaya *et al.* 1975, Kvach 2005, Özer 2007). Several studies have additionally focused on their parasites in invasive habitats, including the upper Danube River basin (Koubková and Baruš 2000, Moravec 2001, Ondračková *et al.* 2005) and the Baltic Sea (Rokicki and Rolbiecki 2002, Rolbiecki 2006, Kvach and Skóra 2007). Previous studies of goby parasites in the Great Lakes included Muzzall *et al.* (1995), Pronin *et al.* (1997), and Camp *et al.* (1999), and ours is the first to analyze their parasites in Lake Erie.

The aim of this study was to evaluate parasitism of nonindigenous gobies in the Great Lakes, in comparison with other studies in native and exotic areas. We analyzed specimens from the central region of their exotic Great Lakes range and proximate to the point of their original discovery, including Lakes Erie, St. Clair, and Huron. We compared our results with other studies, dating to 1994, in order to preliminarily examine whether parasite load may have increased over the invasion's time course, whether species composition differed among investigations, and whether overall number and types of parasitic species differ between their exotic and native habitats.

MATERIALS AND METHODS

Round and tubenose gobies (hereafter referred to as gobies) were sampled from October-November 2006 using seines in four localities: 1) Maumee Bay, Lake Erie (near Oregon, Ohio), 2) Lake St. Clair (near the Clinton River's mouth, Michigan), 3) Lake Huron (near Port Sanilac, Michigan), and 4) Saginaw River (in Saginaw, Michigan) (Fig. 1), under Ohio and Michigan scientific collecting permits to C. Stepien. In total, 75 specimens (33 males, 38 females, and 4 juveniles) of the round goby and 10 specimens (4 males and 6 females) of the tubenose goby were collected, transported in aerated buckets, and then kept alive in aquaria until they were examined (within 24 hours). Sex and standard lengths (mm) of the fish were recorded. Protocols were analogous to those followed in studies of their parasites in Eurasia by Kvach (2002), thereby facilitating comparison of our results with investigations conducted in their native and other invasive habitats. The fish thus were anesthetized via double-pithing (in order to not dislodge the parasites) and immediately studied under the light dissecting microscope according to standard parasitological procedures (Kvach 2005). Following examination, the fish were further anesthetized and sacrificed under the University of Toledo

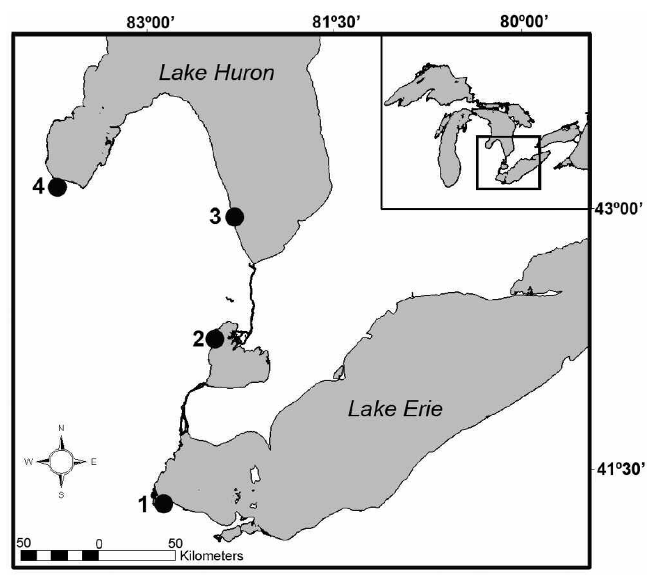

FIG. 1. Map of the investigation area. Sampling localities: 1. Maumee Bay, Lake Erie in Oregon, Ohio; 2. Lake St. Clair near the Clinton River mouth, Michigan; 3. Lake Huron near Port Sanilac, Michigan; 4. Saginaw River, a Lake Huron tributary, at Saginaw, Michigan.

IACUC (Institutional Animal Care and Use Committee) procedure.

The mucus from skin, fins, and gills were scraped off by scalpel from the physiologically live, anesthetized fish to microscope slides and examined for endoparasites using dissecting and compound microscopes (Kvach 2005). The skin, fins, gills, muscles, brain, eyes, gut, liver, spleen, kidneys, body cavity, and mesentery were examined for metazoan parasites. The encysted larvae were first isolated from cysts and the parasites were fixed in 70% ethanol. Trematodes and cestodes then were stained in acetic carmine and mounted in Canada balsam. Nematodes and acanthocephalans were mounted in glycerin-gelatin gel in semi-permanent mounts, or studied in gelatin gel temporary mounts. Identification of parasites followed Petrochenko (1958), Gaevskaya *et al.* (1975), Bauer (1987), Moravec (1994), and Hoffman (1999), and additionally used original species descriptions for various taxa (see Results).

The Index of Czekanowski-Sørensen (ICS, Czekanowski 1909, Sørensen 1948) was used to compare the parasite fauna:

$$ICS = \frac{2c}{a+b} \times 100\%, \quad (1)$$

where *a* was the number of parasite species found in host A, *b* was the number of parasite species found in host B, and *c* was the number of parasitic species common for both hosts. Comparisons were made to studies of Great Lakes goby parasites by Muzzall *et al.* (1995), Pronin *et al.* (1997), and Camp *et al.* (1999), as well as to the parasite fauna described for the round and tubenose gobies from Eurasian localities.

The following parasitological indices were calculated according to Bush *et al.* (1997):

1. Prevalence (P) was the number of hosts infected with one or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined for that parasite species (expressed as a percentage).
2. Intensity was the number of individuals of a particular parasite species in a single infected host (presented as intensity range, IR, i.e., minimum-maximum).
3. Mean intensity (MI) was the average intensity of a particular species of parasite among the infected members of a particular host species.
4. Abundance (A) is the number of individuals of a particular parasite in/on a single host regardless of whether or not the host is infected.

The abundance of parasite species was classified using the index of Zander *et al.* (1999), with: > 2 = core species, 0.6–2 = secondary species; 0.2–0.6 = satellite species; and < 0.2 = rare species. Standard deviations (SD) of the parameter means (M) were calculated.

RESULTS

We examined parasites from 75 round goby samples that averaged 54 ± 14 mm in standard length (SL), ranging from 26–105 mm. Tubenose goby samples ranged from 35–70 mm SL (mean 50 ± 10 mm) and were rare, found only at the Lake St. Clair locality, where we analyzed 10 specimens.

Monogeneans were absent in the parasite fauna of both gobies in the Great Lakes. Only a single parasite species—the nematode *Spiroxys contortus*—was found in both goby species. Most of the parasites were represented by larval stages alone, including plerocercoids (cestode larvae; designated by pl), metacercariae (trematode larvae; met), third stage nematode larvae (L3), cystacanths (acanthocephalan larvae; ca), and mite larva (l). Only a single species—the nematode *Rhabdochona* sp.—was present as an adult and was found in a single round goby specimen in Lake Erie (Table 1).

Our study found that the metazoan parasite fauna of the round goby in the central Great Lakes region included a single species of Cestoda, three Trematoda species, four Nematoda species, one Acanthocephala species, and a single species of Arachnida (Table 1). All 15 round gobies caught in Lake Huron proper were parasite-free. Five species of round goby parasites were found in Lake Erie and Lake St. Clair respectively, whereas six species were identified in the Saginaw River (a tributary of Lake Huron).

Only the trematode *Diplostomum spathaceum* parasitized round gobies at all three localities and it was the most abundant core species overall. The cestode *Proteocephalus* sp. pl (Saginaw River) and the trematode *Neochasmus umbellus* (Lake Erie) were each ranked as secondary species in relative abundances. The acanthocephalan *Neoechinorhynchus tumidus* (Lake St. Clair) was a satellite species, and other parasites were rare in all sample localities. The round goby parasite fauna of the

TABLE 1. The metazoan parasite community of round and tubenose gobies in the middle Great Lakes (Lakes Erie, St. Clair, and Huron). Samples were collected from October-November 2006. Fifteen round gobies (SL = 4.9±1.1) were sampled from Lake Huron, however all were parasite free. Abbreviations: pl = plerocercoid, met = metacercaria, ca = cystacanth, L3 – 3rd stage larva, l. = larva, SL = standard length (m), N = number of fish examined, P = prevalence (%), MI = mean intensity, IR = intensity range, A = abundance, ns = not sampled.

Host species	Parasite location	Indices	*Apollonia melanostoma* Round goby			*Proterorhinus semilunaris* Tubenose goby
Sampling site			Lake Erie	Lake St. Clair	Saginaw River	Lake St. Clair
N			30	15	15	10
SL (mm, M±sd)			61±15	51±11	56±6	50±10
CESTODA						
Proteocephalus sp. pl	Mesentery	P	ns	ns	20.0	ns
		MI(IR)	ns	ns	4.0±5.2 (1–10)	ns
		A	ns	ns	0.8	ns
TREMATODA						
Diplostomum spathaceum met	Eyes	P	17.6	20.0	60.0	ns
		MI(IR)	4.5±3.1 (1–9)	3.7±3.1 (1–7)	8.4±7.8 (2–22)	ns
		A	0.8	0.7	5.1	ns
Digenea gen. sp. met	Mesentery	P	ns	13.3	6.7	ns
		MI(IR)	ns	1.0±0.0(1)	2.0(2)	ns
		A	ns	0.1	0.1	ns
Neochasmus umbellus met	Muscles, eyes, brain	P	25.0	6.7	ns	ns
		MI(IR)	7.1±5.7 (1–19)	2.0(2)	ns	ns
		A	1.8	0.1	ns	ns
NEMATODA						
Anisakidae gen. sp. L3	Mesentery	P	1.5	ns	ns	ns
		MI(IR)	1.0(1)	ns	ns	ns
		A	0.01	ns	ns	ns
Philometra sp. L3	Mesentery	P	ns	6.7	6.7	ns
		MI(IR)	ns	1.0(1)	1.0(1)	ns
		A	ns	0.1	0.1	ns
Rhabdochona sp.	Intestine	P	1.5	ns	ns	ns
		MI(IR)	1.0(1)	ns	ns	ns
		A	0.01	ns	ns	ns
Spiroxys contortus L3	Mesentery	P	ns	ns	13.3	10.0
		MI(IR)	ns	ns	1.0±0.0(1)	1.0(1)
		A	ns	ns	0.1	0.1

TABLE 1. Continued.

Host species	Parasite location	Indices	*Apollonia melanostoma* Round goby			*Proterorhinus semilunaris* Tubenose goby
Sampling site			Lake Erie	Lake St. Clair	Saginaw River	Lake St. Clair
N			30	15	15	10
SL (mm, M±sd)			61±15	51±11	56±6	50±10
ACANTHOCEPHALA						
Neoechinorhynchus tumidus ca	Mesentery, liver	P	ns	13.3	13.3	ns
		MI(IR)	ns	2.0±0.0(2)	1.0±0.0(1)	ns
		A	ns	0.3	0.1	ns
Southwellina hispida ca	Mesentery	P	ns	ns	ns	10.0
		MI(IR)	ns	ns	ns	1.0(1)
		A	ns	ns	ns	0.1
ARACHNIDA						
Unionicola sp. 1.	Mesentery	P	1.5	ns	ns	ns
		MI(IR)	1.0(1)	ns	ns	ns
		A	0.01	ns	ns	ns
Number of parasite species			5	5	6	2

Saginaw River and Lake St. Clair shared greater similarity (ICS = 72.7%; Table 1) than was found between samples from Lakes Erie and St. Clair (ICS = 40.0%) and between those from the Saginaw River and Lake Erie (ICS = 18.2%).

Four of the parasitic species we discerned in our round goby samples also were previously described from them in the Great Lakes (i.e., *Proteocephalus* sp. pl, *Diplostomum* spp. met, and the nematodes *Rhabdochona* sp. and *S. contortus* L3; Table 2). In addition, we discovered four species of parasites not previously known for the round goby (i.e., the trematode *N. umbellus*, nematode *Philometra* sp., acanthocephalan *N. tumidus*, and arachnid *Unionicola* sp.).

We found only two parasite species in our tubenose goby samples, including a third stage larva of *S. contortus* (newly identified to species in our study; Table 2) and a cystacanth of *Southwellina hispida* (which is a new finding by us), both of which were rare. The comparative similarity of our data to that of Muzzall *et al.* (1995) is relatively low, with an ICS = 40% (one common species) and there is no similarity between our data and the study by Pronin *et al.* (1997), noted by an ICS = 0.

DISCUSSION

Comparative Life Histories of Exotic Goby Parasites

Few adult parasites have been identified in the Great Lakes gobies, with most comprising early life history stages that are generally less host-specific. Our study identified the round goby as the definitive (final) host for only a single species, the nematode *Rhabdochona* sp. (in Lake Erie). In addition, an adult *Rabdochona decaturensis* was noted by Muzzall *et al.* (1995) in a single round goby specimen from Lake St. Clair. The intermediate hosts of *Rhabdochona* are mayflies (Ephimeroptera) (Moravec 1994, Hoffman 1999), which are eaten by both goby species in the Great Lakes (French and Jude 2001). In addition, the spiny-head worm *Acanthocephalus dirus* was found in a sole round goby specimen in Lake Michigan (Camp *et al.* 1999). Pronin *et al.* (1997) noted that the tubenose goby in Lake St. Clair is a host for the adult acanthocephalan *Leptorhynchoides tecatus*, which we did not find. The round goby is a second intermediate host (where the parasite passes its larval or nonsexual stages) for three species: the trematodes *Diplosto-*

TABLE 2. Comparative metazoan parasite fauna of round and tubenose gobies in the Great Lakes, found by studies to date. Abbreviations: pl = plerocercoid, met = metacercaria, ca = cystacanth, L3 – 3rd stage larva, l. = larva. Note: **D. spathaceum** ***found by us and*** **Diplostomum** ***sp. found by previous authors are likely the same species. Similarly,*** **Rhabdochona** ***sp. (our data) and*** **R. decaturensis** ***(Muzzall*** **et al.** ***1995) (noted as*** **Rhabdochona** ***spp. here); as well as*** **Spiroxys** ***sp. (Muzzall*** **et al.** ***1995) and*** **S. contortus** ***(our data) (noted as*** **Spiroxys** ***spp. L3) are respectively combined.***

Host species	*Apollonia melanostoma* Round goby				*Proterorhinus semilunaris* Tubenose goby		
Authors	Muzzall *et al.* 1995	Pronin *et al.* 1997	Camp *et al.* 1999	Present study	Muzzall *et al.* 1995	Pronin *et al.* 1997	Present study
Years of sampling	1994	1994	1995–1997	2006	1994	1994	2006
Locality	*	*	**	***	*	*	*
Number of fish examined	144	46	309	75	48	20	10
CESTODA							
Proteocephalus ambloplitis pl		+					
Proteocephalus sp. pl		+		+		+	
Scolex pleuronectis		+					
TREMATODA							
Clinostomum complanatum met		+					
Diplostomum spp. met	+	+	+	+			
Ichthyocotylurus pileatus met		+					
Digenea gen. sp. met				+			
Neochasmus umbellus met				+			
Rhipidocotyle sp. met		+					
NEMATODA							
Anisakida gen. sp. L3				+			
Contracaecum sp. L3					+		
Eustrongylides sp. L3			+				
Eustrongylides tubifix L3	+	+					
Philometra sp. L3				+			
Rhabdochona spp.	+			+			
Raphidascaris acus L3		+				+	
Spinitectus sp. L3	+						
Spiroxys spp. L3	+			+	+		+
ACANTHOCEPHALA							
Acanthocephalus dirus			+				
Leptorhynchoides tecatus						+	
L. tecatus ca	+						
Neoechinorhynchus tumidus ca				+			
Neoechinorhynchus sp. ca					+		
Southwellina hispida ca							+
MOLLUSCA							
Unionidae gen. sp. l.	+						
ARACHNIDA							
Unionicola sp. l.				+			
Total	7	9	3	10	3	3	2

* Lake St. Clair basin; ** Lake Michigan; ***Lake Erie, Lake St. Clair, and Saginaw River.

mum spathaceum and *Neochasmus umbellus*, as well as unidentified metacercariae (Digenea gen. sp. met). Piscivorous birds are the definitive hosts of *D. spathaceum*, which uses limnetic snails (Lymnaeidae) as its first intermediate host (Hoffman 1999). Our study found *D. spathaceum* larvae in the eyes of round gobies from all sampling localities except Lake Huron proper. All studies to date of Great Lakes round goby parasites found *Diplostomum* spp. metaceracaria (Muzzall *et al.* 1995, Pronin *et al.* 1997, Camp *et al.* 1999, our study; Table 2). The round goby also is a second intermediate host for the trematode *N. umbellus*, whose definitive hosts include a variety of North American predatory fishes (Hoffman 1999). These two trematodes are the most abundant round goby parasites in the Great Lakes (Table 1).

Unidentified metacercariae encysted in mesentery (designated as Digenea gen. sp. met) of the round goby were found in the Saginaw River and Lake St. Clair in our study (Table 1). Muzzall *et al.* (1995) and Pronin *et al.* (1997) found that the round goby in Lake St. Clair and the St. Clair River is a second intermediate host of the trematodes *Clinostomum complanatum*, *Ichthyocotylurus pileatus*, and *Rhipidocotyle* sp.

The round goby is a paratenic host for five species (the cestode *Proteocephalus* sp., the nematodes Anisakidae gen. sp., *Philometra* sp., and *Spiroxys contortus*, and the acanthocephalan *Neoechinorhynchus tumidus*), defined as an animal that acts as a substitute intermediate host for a species, usually having acquired the parasite through ingestion of the original host. The tubenose goby is a paratenic host for two parasitic species, the nematode *S. contortus* and the acanthocephalan *Southwellina hispida* (Table 1).

We found scolexes of unidentified *Proteocephalus* cestodes encysted in the mesentery of round gobies (Table 1). The endemic Ponto-Caspian cestode *Proteocephalus gobiorum* occurs exclusively in gobies, and has been found in round gobies from the northern Caspian Sea (adults in the gut; Dogiel and Bychowsky 1939) and the Black Sea basin, including the Southern Bug River (adults in the gut; Koval and Piryanyk 1957) and the Dniester Estuary (a plerocercoid in the body cavity; Kvach 2004b). This parasite has not been found in the Great Lakes. However, plerocercoids of the conspecific North American *Proteocephalus ambloplitis* and *Proteocephalus* sp. have been identified in the body cavities of round gobies from Lake St. Clair (Pronin *et al.* 1997) and the Saginaw River (this study). The second intermediate hosts of *Proteocephalus* spp. are planktonic crustaceans that are prey of juvenile round gobies (Smirnov 1986).

Our study found unidentified anisakid nematode larva encysted in the mesentery of a round goby from Lake Erie (Table 1). According to Pronin *et al.* (1997), *Raphidascaris acus* larvae have been found in round and tubenose gobies, and Muzzall *et al.* (1995) additionally noted larvae of the nematode *Contracaecum* sp. in the tubenose goby (Table 2).

Here we describe the first record of larvae of the nematode *Philometra* sp. in the round goby, occurring in samples from Lake St. Clair and the Saginaw River (Table 1). In Lakes Huron and Erie, *Philometra cylindracea* is common in the body cavities of many fishes, especially yellow perch *Perca flavescens* (see Dechtiar *et al.* 1988, Dechtiar and Nepszy 1988, Hoffman 1999). Fishes are the definitive and paratenic hosts of this parasite.

Turtles and amphibians are the definitive hosts of the nematode *S. contortus*, whose first intermediate host is the crustacean *Cyclops* (Hoffman 1999). In Lakes Huron and Erie, unidentified larval *Spiroxys* have been noted in the body cavities of many fishes (Dechtiar *et al.* 1988, Dechtiar and Nepszy 1988), and a single species in the genus – *S. contortus* – has been described from North America (Hoffman 1999). Sampling in the preferred habitats of turtles and amphibians, we found larval *S. contortus* in round and tubenose gobies from the Saginaw River and Lake St. Clair near the Clinton River's mouth (Table 1). Muzzall *et al.* (1995) also found this parasite species in round and tubenose gobies from Lake St. Clair. In addition, the Great Lakes gobies are paratenic hosts for the nematodes *Eustrongylides tubifex*, *Eustrongylides* sp., and *Spinitectus* sp. (Muzzall *et al.* 1995, Pronin *et al.* 1997, Camp *et al.* 1999).

Both the round and tubenose goby are paratenic hosts of acanthocephalans. *Neoechinorhynchus tumidus* cystacanths were found in round gobies from the Saginaw River and Lake St. Clair (Table 1). Adult *N. tumidus* are common fish parasites throughout much of North America and Siberia (Petrochenko 1958, Hoffman, 1999), and infest a variety of Great Lakes fishes, including *Coregonus hoyi*, *C. clupeaformis*, *Prosopium cylindraceum*, *Oncorhynchus nerka*, and *Salvelinus* sp. in Lake Huron (Dechtiar *et al.* 1988). Additionally, we found *S. hispida* cystacanths in tubenose gobies from Lake St. Clair (Table 1). Its adults parasitize water birds in Eastern Europe, the Asian Far East, and North America; and fishes are its paratenic hosts (the cystacanths are encysted in mesentery; Petrochenko and Smogorzhevskaya 1962, Scholz *et al.* 1992, Hoffman 1999). In the Black Sea, a cystacanth of this species is known from the Black Sea golden mullet *Liza aurata* (Belofastova 2005), but is not found in gobies. In Japan, this species parasitizes the goby *Rhinogobius* sp. (Petrochenko 1958). In North America, this species apparently has adapted to infest the introduced tubenose goby *P. semilunaris*. Muzzall *et al.* (1995) found cystacanths of *Leptorhynchoides tecatus* in the round goby from Lake St. Clair. Because an adult of this acanthocephalan was noted in the tubenose goby in same area (Pronin *et al.* 1997), it is possible that gobies could be both the paratenic and definitive hosts of this parasite. The first intermediate hosts of acanthocephalans are primarily amphipods, which constitute one of the main dietary items of gobies.

The presence of a mite larva (*Unionicola* sp.) encysted in mesentery is a possible case of pseudoparasitism. The larvae of aquatic mites usually infest aquatic insects and bivalves and are not obligate parasites (Bauer 1987). *Unionicola* sp. l. is usually observed in mollusks of Unionidae family. Ours was its first finding in Great Lakes gobies, and merits further investigation.

Most species comprising the central Great Lakes parasite fauna of nonindigenous gobiids (6 of the 11 species we found) use them as paratenic hosts, only three as a second intermediate host, one as a definitive host, and there was a single case of possible pseudoparasitism. In most cases (a cestode and most of nematodes), infestation occurred during the juvenile stage when gobies eat planktonic crustaceans. The low representation of adults (a sole specimen) in the parasite community of introduced gobies is attributable to the fact that their larval stages are usually less host-specific. Larval parasites are generally more adaptive and opportunistic in colonizing new hosts, in comparison with their adult stages.

Parasite Fauna of Exotic versus Native Gobies

The parasitic fauna of Great Lakes gobies has lower species richness and lower numbers of individuals per host than is characteristic of their native areas (Naidenova 1974, Kvach 2005, and Özer 2007), as well as their Eurasian expansion populations (Koubková and Baruš 2000, Ondračková *et al.* 2005, Rolbiecki 2006, Kvach and Skóra 2007). Those expansion populations may experience greater parasitism than found in the Great Lakes samples due to the greater proximity of the former to native adult goby populations. Higher transport frequency of gobies and their native parasites via canals, waterways, and shipping from native to non-native areas in Eurasia may regularly "seed" the parasite fauna of new goby populations. In contrast, the Great Lakes round goby population is believed to have been founded by young juveniles that rise into the water column at night to feed, coinciding with uptake of most ballast water (Hensler and Jude 2007). Colonizing populations of the Great Lakes gobies are likely to have been relatively parasite-free and/or may have lost their native parasites due to environmental stress.

Studies to date show that 22 metazoan species are known to parasitize round gobies in the Great Lakes (Muzzall *et al.* 1995, Pronin *et al.* 1997, Camp *et al.* 1999, our data; Table 2). Most of the species (15) were identified in round gobies from Lake St. Clair (Muzzall *et al.* 1995, Pronin *et al.* 1997; Table 2), and only three species were noted in Lake Michigan (Camp *et al.* 1999). Seven species of tubenose goby parasites in Lake St. Clair now have been described in three studies (Muzzall *et al.* 1995, Pronin *et al.*1997, this study), with each finding two or three different species; only a single species was found by more than one study (see Table 2). Thus, few species and low numbers of these parasites are known to infest the exotic gobies in the Great Lakes. Moreover, the level of parasitism detected by the different studies does not support an increase over the past decade.

The similarity between our round goby parasite data and other published studies is relatively low (Table 3). According to the ICS metric, our parasite data for the round goby more closely resemble findings by Muzzall *et al.* (1995) in Lake St. Clair and the St. Clair River taken a decade ago, and are less similar to those described by Camp *et al.* (1999) for southern Lake Michigan, where we did not sample. Camp *et al.* (1999) described a depauperate parasite fauna of only three species despite sampling a relatively large number of round gobies (Table 2). Greater similarity between our investigation and that of Muzzall *et al.* (1995) likely is due to our dual examination of Lake St. Clair, which is the Great Lakes site where the round goby was first detected and thus is likely an older population. In addition, greater similarity between the studies may be due to the geographic proximity of Lake St. Clair and our site in western Lake Erie (see Fig. 1), and the more similar overall environmental conditions among Lakes Huron, St. Clair, and Erie. Over-

TABLE 3. Comparisons of the Index of Czekanowski-Sørensen (ICS; % similarity) for metazoan parasite fauna of the round goby in the Great Lakes among four studies to date.

	Muzzall *et al.* 1995	Pronin *et al.* 1997	Camp *et al.* 1999	Present study
Muzzall *et al.* 1995	100			
Pronin *et al.* 1997	25	100		
Camp *et al.* 1999	20	16.7	100	
Present study	35.3	21.1	15.4	100

all, no trend toward increasing round goby parasitism was evident, despite the decade separating the prior studies from ours.

Two species of widely-distributed fish parasites that are common in these gobies in Eurasia (see Özer 2007) also are their common parasites in the Great Lakes, including the Holarctic trematode *D. spathaceum* in the round goby and the nematode *S. contortus* in round and tubenose gobies. *Diplostomum spathaceum* was the most prevalent parasite in the Great Lakes round goby. The nematode *S. contortus* is a widespread parasite of North American and European freshwater fishes (Moravec 1994), as well as occuring in round gobies in brackish waters (Özer 2007). Both of these parasites are widely distributed and abundant throughout North America and Eurasia (see Prenter *et al.* 2004), and therefore were not introduced by the exotic gobies.

In contrast, 72 species of metazoan parasites have been described for the round goby from their native habitats in the Black Sea area, including 19 known from fresh water habitats and 59 in marine/brackish waters (compiled from references cited previously in this paper plus Ciurea 1931, Chernyshenko 1966, Gaevskaya and Dmitrieva 1997). The overall number of metazoan parasites occurring in the round goby in native Ponto-Caspian habitats thus is higher than in the Great Lakes. In the Sea of Azov, 16 species are known to parasitize the round goby, including 18 in Sevastopol Bay (Crimean Peninsula, Black Sea, Ukraine) (Naidenova 1974) and 16 in the northwestern Black Sea (near Odessa, Ukraine) (Kvach 2005). In the southern Black Sea (near Sinop, Turkey), there are only nine known species of round goby parasites (Özer 2007), similar to their species richness in Great Lakes habitats. The mean ICS metric for the round goby in the Black Sea region is 4.26%; with the most common parasite species found only in the Tyligul Estuary (*D. spathaceum*, ICS = 4.54%; Chernyshenko 1957, Kvach 2004a), and near Sinop, Turkey (*Spiroxys* sp., ICS = 6.4%, Özer 2007). It thus appears that there are fewer round goby parasites in freshwater habitats overall than in brackish or marine waters, a trend that characterizes their native and exotic habitats, including the Great Lakes.

In contrast to the seven parasite species known for the tubenose goby in the Great Lakes, 20 have been described from their native habitats in the Black Sea area, including two in fresh water (for *P. semilunaris* in the Romanian part of the Danube River and in the rivers of the northern coasts of the Sea of Azov; Chiriac and Udrescu 1957, Chaplina and Antsyshkina 1961) and 19 species in marine/brackish waters (for *P. marmoratus;* compiled from references cited previously in this paper plus Machkevsky *et al.* 1990, Gaevskaya and Dmirnieva 1997). In comparison to the round goby, the tubenose goby is much less common in native as well as invasive habitats and its parasites have been less intensively studied.

There are ~221 known species of fish parasites in Lake Huron (Dechtiar *et al.* 1988), and ~126 in Lake Erie (Dechtiar and Nepszy 1988). Therefore, the introduced gobies appear to have been colonized by only a small portion of the overall native parasite fauna. For example, 11 species are known to parasitize the spoonhead sculpin *Cottus ricei*, 15 species in mottled sculpin *C. bairdi*, and 13 species in slimy sculpin *C. cognatus* (Dechtiar *et al.* 1988, Muzzall and Bowen 2002). *Diplostomum* sp. was found in all three sculpin species and *Rabdochona* sp. also occurred in the slimy sculpin. The round goby parasite fauna in the Great Lakes (according to published records and our data) appears more similar to that of the slimy sculpin (ICS = 11.42%), and less like those of spoonhead sculpin (ICS = 6.1%) and mottled sculpin (ICS = 5.4%). No parasite species are shared between the tubenose goby and sculpins.

In other non-native water bodies, the metazoan parasite fauna of the round goby consists of 22 species in the Baltic Sea that was invaded in 1990 (Rokicki and Rolbiecki 2002, Rolbiecki 2006, Kvach and Skóra 2007), five species in the Slovak region of the Danube River (Ondračková *et al.* 2005), and nine species in the upper Volga River (Tyutin and Slynko 2006). Introduced round goby populations in Eurasia have low parasite faunal similarity with those in the Great Lakes, since only *Diplostomum* sp. is shared (ICS = 4.55% between the Great Lakes and the Baltic Sea, 7.40% with the upper Danube River, and 6.45% with the upper Volga River). The round goby parasite fauna is more similar between its native habitats and the introduced Baltic Sea location (ICS = 21.28%), and less like exotic populations in the upper Danube River (ICS = 10.39%) and the upper Volga River (ICS = 9.87%)—which are all greater than their respective similarities to the Great Lakes.

The number of tubenose goby parasites in non-native Eurasian water bodies also is unlike that found the Great Lakes and includes 14 species in the upper Danube River basin (ICS with the Great Lakes = 9.52%; Ergens 1967, Koubková and Baruš 2000, Moravec 2001) and four species in the upper Volga River (ICS with the Great Lakes = 18.18%; Tyutin and Slynko 2006). The freshwater tubenose goby parasite fauna in its native habitats is more similar to that in the upper Volga River (which share one common species, the trematode *Plagioporus skrjabini*; ICS = 33.33%), than to the upper Danube River basin (which also shares a common species, the monogenean *Gyrodactylus proterorhini*; ICS = 12.5%).

The absence of monogeneans in Great Lakes gobies agrees with published data from other studies (Muzzall *et al.* 1995, Pronin *et al.* 1997, Camp *et al.* 1999). Monogenic parasites of gobies in the Black Sea basin include *G. proterorhini*, which is found both in their native habitat regions (Naidenova 1974, Gaevskaya *et al.* 1975), as well as introduced locations in the upper Danube River (Moravec 2001, Ondračková *et al.* 2005). In European waters, there are seven species of *Gyrodactylus* that specifically parasitize gobiids belonging to the genus *Pomatoschistus* (summarized by Huyse *et al.* 2003) and a single species (*Haliotrema cupensis*) that parasitizes the giant goby *Gobius cobitis* (Sasal *et al.* 1998). In conclusion, it appears that monogenean species parasitizing Great Lakes fishes are not yet well-adapted to parasitizing the invasive gobies. In addition, the exotic gobies have not introduced any goby-specific monogenean parasites from Eurasia to the Great Lakes fish fauna.

Overall, results of our study and others show that goby-specific metazoan parasites are absent in the Great Lakes. Trematode populations in the round goby are more abundant than are other parasites, as in their native Black Sea region and invasive populations in the Baltic Sea (Kvach 2005, Kvach and Skóra 2007).

SUMMARY AND CONCLUSIONS

Goby parasitism over the past decade in the Great Lakes appears unstable and opportunistic, and overall levels do not appear to have increased. A total of 22 parasite species have now been described in exotic round gobies from the Great Lakes and seven species are known for the tubenose goby, including our new finding of the acanthocephalan *S. hispida*. Trematodes are the most common parasites of round gobies in the Great Lakes, similar to their predominance in their native Black Sea habitats, as well as in their exotic range in the Baltic Sea. A single widely-distributed Holarctic trematode that parasitizes a variety of fish species in Europe and North America was the most common round goby parasite in both Europe and the Great Lakes.

In summary, we found that few species of goby parasites are shared between nonindigenous Great Lakes habitats versus native Ponto-Caspian localities, and those are widely-distributed species in other North American and Eurasian fishes. The round and tubenose gobies thus appear to have left their native parasites behind in the Ponto-Caspian region, which may have augmented their success in the Great Lakes (see Torchin *et al.* 2003). Nonindigenous gobies colonizing the Great Lakes apparently did not introduce new parasites to native fishes. Some generalized fish parasites have since colonized the exotic gobies in the Great Lakes, and we found only a single species whose adult stage lived in gobies. The current parasite “load” on nonindigenous gobies thus is relatively light, and our samples of round goby in Lake Huron proper were free of parasites. Moreover, our comparisons with other studies indicate that the species composition and degree of exotic goby parasitism varies extensively among locations and studies, but does not appear to have increased over the past decade. This should be further and more extensively studied with controlled quantitative experiments. Since many goby parasites have complex life cycles requiring more than one host, life history factors may augment the success of exotic species, rendering them (at least temporarily) relatively parasite-free. This period of low parasite load may extend for decades after an overseas colonization, as appears to be the case for Great Lakes gobies.

In native regions, gobies have more parasites in marine and brackish waters than in freshwater habitats. The round goby has been predicted to spread to North American coastal salt marshes in the future, due to its euryhalinity, the fact that genotypes common in their marine Eurasian waters are already in the Great Lakes, and the presence of its ready-made food source of *Mytilus* mussels in those habitats (see Stepien *et al.* 2005, Stepien and Tumeo 2006). Therefore, it would be interesting to examine their comparative parasitic fauna if and when they colonize those habitats.

In conclusion, the current parasite "load" of round and tubenose gobies in the Great Lakes appears light despite being in their second decade of establishment in the Great Lakes. Our findings lend support to the hypothesis of Torchin *et al.* (2003) that the success of introduced species may be facilitated by their "leaving their parasites behind", which merits further investigation.

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