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Parasite acquisition by the invasive Chinese sleeper (*Perccottus glenii* Dybowski, 1877) (Gobiiformes: Odontobutidae) in Latvia and Ukraine

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Abstract

The *Perccottus glenii* is one of the most invasive of European fish species. During August-September 2019, we examined Chinese sleeper from six waterbodies in Latvia and Ukraine for parasites. Seventeen parasite species were registered, including two ciliate species, one coccidia, one monogenean, one cestode, six trematodes, three nematodes, one acanthocephalan, one parasitic copepod, and one bivalve glochidia. Maximum species richness was registered in Ukraine, with eight species at Vylkove and three species at Lake Kartal. Numbers in Latvia were generally lower with three species at Ilgas and just one at Gailezers. The parasite fauna registered in Latvia was poor overall, the richest site being the University pond. Two non-native parasite species were registered, the monogenean *Gyrodactylus perccotti* and the copepod *Neoergasilus japonicus*. *Gyrodactylus perccotti* was observed in Lake Kartal and the Danube delta in Ukraine, but not in Latvia, while *N. japonicus* only occurred in the University Pond in Latvia. This is the first record of this species in Latvia. Low parasite acquisition by the Chinese sleeper in Latvia may be caused by the release of this fish from aquaria, which is commonly registered in the region. It is likely that such low parasite loads have contributed to the formation of stable populations and the subsequent increase in expansion.

KEYWORDS

Danube delta, Daugava basin, enemy release hypothesis, non-native species, parasite communities, Prypiat basin

1 | INTRODUCTION

The Chinese sleeper, *Perccottus glenii* Dybowski, 1877 (Gobiiformes: Odontobutidae), is a bottom-dwelling freshwater fish with a native range stretching from the River Uda in Far-Eastern Asia (Sea of Okhotsk drainage, Russia) southward to the River Yangtze in the Fujian Province of China (Bogutskaya, Naseka, Shedko, Vasil'eva, & Chereshnev, 2008; Kottelat & Freyhof, 2007). The species was introduced to Ukraine in 1972, when it was found in the Velykyi Lubin fish farm in the Dniester river basin (see Kutsokon, 2017). The first records of Chinese sleeper in Latvia come from small natural ponds in the Daugava floodplain on the outskirts of Daugavpils (Pupina, Pupins, Skute, Pupina, & Karklins, 2015). While they appear to have been introduced as 'hitchhikers' with commercially important fishes (i.e. silver carp *Hypophthalmichthys molitrix* [Valenciennes, 1844] and bighead carp *Hypophthalmichthys nobilis* [Richardson, 1845]) in Ukraine, introductions in Latvia are most likely the result of release by the local aquarists or fishermen (Kutsokon, 2017; Plikšs & Aleksejevs, 1998). Since their introduction, they have become highly invasive in both countries.

The Chinese sleeper competes with local fishes for food, habitat and spawning sires and preys on small-sized fish (Copp, Garthwaite, & Gozlan, 2005; Koščo, Manko, Miklisová, & Košuthová, 2008). In some cases, Chinese sleeper populations have increased to such a level that waterbodies become overloaded, causing overconsumption of local juvenile fish (Hoch & Kvasha, 2003). Presence of invasive Chinese sleeper can also affect amphibian populations, causing significant impacts on the biodiversity of the invaded ecosystem. Juvenile Chinese sleepers, for example, compete with the fire-belly toad *Bombina bombina* Linnaeus, 1761 for food, while adults prey on the tadpoles (Pupina et al., 2018). In a number of invaded waterbodies, Chinese sleeper predation on amphibian larvae has resulted in population declines of smooth newt *Lissotriton vulgaris* (Linnaeus, 1758) and great crested newt *Triturus cristatus* (Laurenti, 1768) as well as some frog and toad species (Reshetnikov, 2001).

One hypothesis for the initial success of the Chinese sleeper is its temporary release from parasites and pathogens in its new territory, often termed the "enemy release hypothesis" (Keane & Crawley, 2002; Torchin, Lafferty, Dobson, McKenzie, & Kuris, 2003). At the same time, non-native species can act as new distribution vectors for local parasitic species, which then go on to infest local host species (Mack et al., 2000). At least four parasite species have been co-introduced with Chinese sleeper from Asia to Europe, including the coccidian *Goussia obstinata* Sokolov & Moshu, 2014 (Sokolov & Moshu, 2014), the myxozoan *Henneguya alexeevi* Schulman, 1962 (Sokolov, Shedko, Protasova, & Reshetnikov, 2012), the monogenean *Gyrodactylus perccotti* Ergens & Yukhimenko, 1973 (Ondračková, Matějusová, & Grabowska, 2012) and the cestode *Nippotaenia perccotti* (Akhmerov, 1941) (Košuthová, Letková, Koščo, & Košuth, 2004), all of which are related to the stenoxenous parasite group, specific to a narrow group of hosts, especially the shovel-snouts (family Odontobutidae). As such, these parasites can be used as biological markers for the analysis of vectors and expansion routes in ecosystems invaded by Chinese sleeper (Reshetnikov, Sokolov, & Protasova, 2011). Indeed, presence of *G. perccotti* and *N. perccotti* formed the basis for a hypothesized single origin of Chinese sleeper in the "Carpathian Population", comprising sites along the Dnieper, Dniester, Danube and the Vistula basin (Kvach, Kutsokon, Stepien, & Markovych, 2016). This hypothesis was later confirmed by molecular studies, which showed three different haplotype groups in Central and Eastern Europe (Grabowska et al., 2020). Latvian Chinese sleeper populations are characterized by the presence of specific haplotypes that are absent from anywhere else in Europe and have not been confirmed in China (Grabowska et al., 2020; Xu et al., 2014). The present study aims to assess whether there is any relationship between the parasite fauna of Chinese sleeper populations in Ukraine (Carpathian population) and Latvia (a specific group of unknown origin).

2 | MATERIALS AND METHODS

Fish were sampled between August and September 2019 from six waterbodies, three in Latvia and three in Ukraine (Figure 1). In Latvia, fish were sampled from two localities in the Middle Daugava floodplain, the Ilgas Natura 2000 Microreserve (55.691217N, 26.771125E) and the 'University Pond' in Daugavpils (55.871375N, 26.507927E), and from Lake Gailezers (56.969952N, 24.241505E) in the Daugava delta at Riga. In Ukraine, fish were taken from two sampling sites on the Danube delta, Lake Kartal (45.287011N, 28.518269E) and the Vylkove canals (45.408632N, 29.583742E), and from Lake Krysyne (51.590806N, 27.086361E) in the Prypyat basin of the Dnieper drainage area.

A total of 105 Chinese sleeper were sampled (Latvia = 60, Ukraine = 45; Table 1) using either a 10-m beach seine (6-mm mesh) or a 0.5-m long dipnet (0.5-cm mesh) in the vegetation zone (depth 1-m). All fish were placed into canisters filled with the aerated local water and immediately transported to the laboratory, where they were examined for parasites within 48 hr of catching (see Kvach, Ondračková, Janáč, & Jurajda, 2016). Both standard (SL) and total (TL) length of each fish was measured before section, following which the fins, skin, gills, eyes, muscles, viscera and internal organs (gut, liver, gall bladder, spleen, swimming bladder, kidneys, uterine bladder, gonads, mesentery and brain) were examined for parasites. Microparasites (unicellular and myxosporidians) were examined alive under a light microscope. Monogeneans were removed from the host tissue and preserved in a mixture of ammonium picrate and glycerin as semi-permanent slides (Malmberg, 1970), while acanthocephalans were pressed between two slides and fixed in 70% ethanol. Cestodes, trematodes and nematodes were preserved in hot 4% formalin (Cribb & Bray, 2010), while copepods and glochidia were preserved in 4% formalin at room temperature. For species identification, cestodes and the trematodes were stained in iron acetocarmine, dehydrated in ethanol and mounted in Canada balsam as permanent slides (Georgiev, Biserkov, & Genov, 1986), while acanthocephalans, nematodes and copepods were mounted in glycerol as temporary slides.

Parasite prevalence, intensity and abundance were calculated for each parasite species (Bush, Lafferty, Lotz, & Shostak, 1997). Prevalence (P) was estimated as 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). Intensity was estimated as (a) the number of individuals of a particular parasite species in a single infected host (presented as the intensity range [IR], i.e. minimum-maximum), and (b) the mean intensity (MI), estimated as the average intensity of a particular parasite species among the infected members of a particular host species. Abundance (A) represents the number of individuals of a particular parasite in/on a single host, regardless of whether or not the host is infected. In each case, the standard deviation (sd) was calculated for the mean parameters. To assess similarity, parasite communities were evaluated using the Czekanowski-Sørensen index (ICS, %; Sørensen, 1948), where

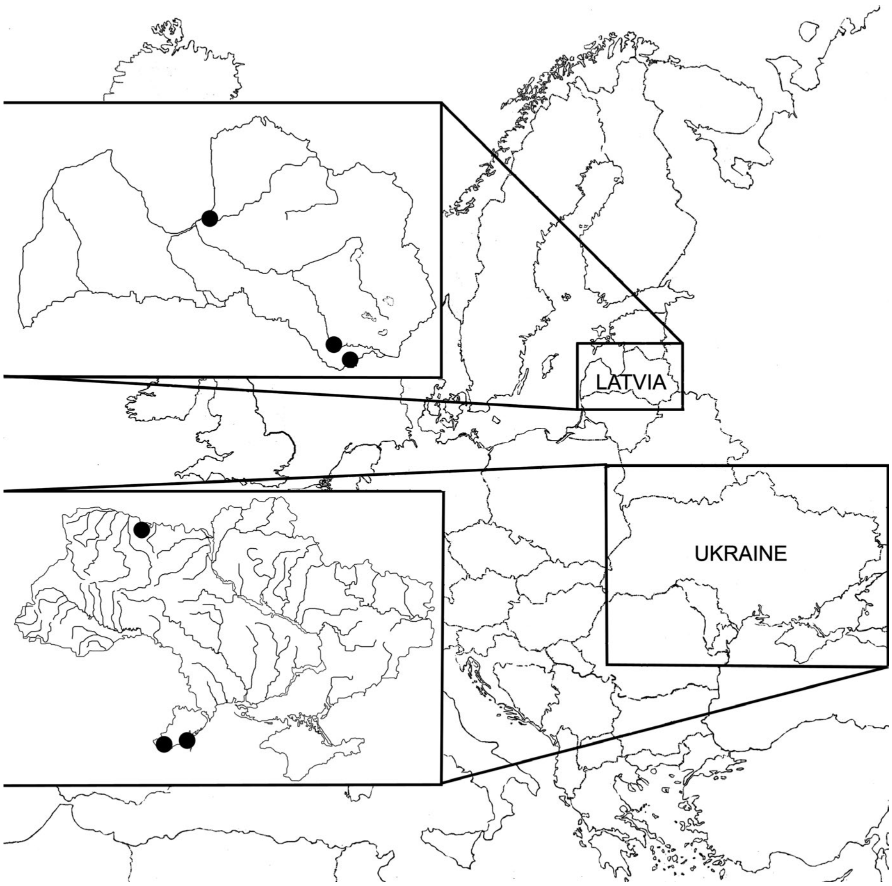

FIGURE 1 Map indicating the sampling sites in Latvia and Ukraine. Black dots = sampling localities: 1) Ilgas Marsh, 2) Lake Gailezers, 3) University Pond, 4) Lake Kartal, 5) Danube delta, 6) Lake Krysyne

TABLE 1 The number (N) and size (SL, standard length in mm, TL, total length in mm, m ± sd, mean ± standard deviation) of Chinese sleeper sampled in Latvia and Ukraine

Parameters		Latvia			Ukraine		
		Ilgas	Gailezers	University Pond	Kartal	Vylkove	Krysyne
N		20	20	20	15	20	10
SL	m ± sd	64.7 ± 12.7	59.2 ± 15.3	55.7 ± 18.5	49.9 ± 6.9	60.2 ± 19.7	36.5 ± 5.2
	min–max	52–100	35–82	43–130	40–51	28–107	27–44
TL	m ± M	79.6 ± 17.1	71.5 ± 18.3	67.3 ± 20.5	61.2 ± 7.4	72.2 ± 23.0	45.9 ± 6.0
	min–max	65–134	42–97	53–150	62–74	35–124	35–55

ICS = $2c/a+b \times 100\%$, with a being the number of parasite species found in Host A, b the number of parasite species found in Host B, and c the number of parasite species common to both hosts. An ICS ≥50% is considered as showing high similarity.

All statistical analyses was undertaken using Statistica for Windows 10, with the discriminant function and the Fischer criterium calculated separately.

3 | RESULTS

The standard length of Chinese sleepers from the six sites ranged from 28 to 130 mm, with total length ranging from 35 to 150 mm (Table 1). We registered 17 parasite species in the six water bodies, comprising two ciliate species, one coccidia, one monogenean, one cestode, six trematodes, three nematodes, one acanthocephalan, one parasitic copepod and one bivalve glochidia (Table 2). Maximum species richness was recorded in Ukraine, with eight species at Vylkove and six species at Lake Kartal. In Latvia, species richness was lower with three species at Ilgas and one at Gailezers.

Microparasites were represented by three parasite taxa, two ciliates (*Trichodina* sp., *Ichthyophthirius multifiliis* Fouquet, 1876) and an unidentified coccidian (Table 2). Among the metazoans, only three species were represented by adult stages, the monogenean *G. perccotti*, the acanthocephalan *Acanthocephalus lucii* (Müller, 1776) and the parasitic copepod *Neoergasilus japonicus* (Harada, 1930); all others were in the larval stage. *Gyrodactylus perccotti* and *N. japonicus* are registered as non-native parasites species, first one in Ukraine

TABLE 2 Parasites of Chinese sleeper from six localities in Latvia and Ukraine

Parasite species (location)		Latvia			Ukraine		
		Ilgas	Gailezers	University Pond	Kartal	Vylkove	Krysyne
CILIATA							
Ichthyophthirius multifiliis (fins)	P, %						10.0
	MI ± sd						1.0
	IR						1
	A						0.1
Trichodina sp. (fins, gills)	P, %				20.0	20.0	40.0
	MI ± sd				83.5 ± 55.0	1.3 ± 0.6	5.8 ± 5.5
	IR				1–111	1–2	1–11
	A				16.7	0.3	2.3
COCCIDIA							
Coccidia gen. sp. (rectum)	P, %	10.0	5.0				
	MI ± sd	3.0 ± 2.8	2.0				
	IR	1–5	2				
	A	0.3	0.1				
MONOGENEA							
Gyrodactylus perccotti (fins)	P, %				5.0	6.7	
	MI ± sd				1.0	1.0	
	IR				1	1	
	A				0.1	0.1	
CESTODA							
Ophiotaenia europaea pl. (mesentery)	P, %				5.0	40.0	
	MI ± sd				1.0	1.7 ± 0.8	
	IR				1	1–3	
	A				0.1	0.7	
TREMATODA							
Apophallus sp. mtc. (fins)	P, %			15.0			
	MI ± sd			7.7 ± 9.1			
	IR			1–18			
	A			1.2			
Cotylurus sp. mtc. (gut walls)	P, %			5.0			
	MI ± sd			11.0			
	IR			11			
	A			0.6			
Isthmiophora melis mtc. (head muscles)	P, %						30.0
	MI ± sd						7.3 ± 8.5
	IR						1–17
	A						2.2
Holostephanus luhei mtc. (gills, mesentery)	P, %				35.0		
	MI ± sd				3.6 ± 2.1		
	IR				1–8		
	A				1.3		

(Continues)

TABLE 2 (Continued)

Parasite species (location)		Latvia: Ilgas	Latvia: Gailezers	Latvia: University Pond	Ukraine: Kartal	Ukraine: Vylkove	Ukraine: Krysyne
Metorchis xanthosomus mtc. (muscles, mesentery)	P, %	10.0				6.7	
	MI ± sd	1.0 ± 0.0				1.0	
	IR	1				1	
	A	0,1				0.1	
Strigeidae gen. sp. mtc. (gills)	P, %	5.0					
	MI ± sd	1.0					
	IR	1					
	A	0.1					
NEMATODA							
Cosmocephalus obvelatus L3 (mesentery, liver)	P, %				5.0	6.7	
	MI ± sd				1.0	1.0	
	IR				1	1	
	A				0.1	0.1	
Eustrongylides tubifex L3 (viscera)	P, %				5.0		
	MI ± sd				1.0		
	IR				1		
	A				0.1		
Spiroxys contortus L3 (mesentery, liver, muscles)	P, %				15.0	66.7	10.0
	MI ± sd				3.3 ± 4.0	1.9 ± 1.2	1.0
	IR				1–8	1–5	1
	A				0.5	1.3	0.1
ACANTHOCEPHALA							
Acanthocephalus lucii (gut)	P, %			5.0			
	MI ± sd			2.0			
	IR			2			
	A			0.1			
CRUSTACEA							
Neoergasilus japonicus (fins)	P, %			5.0			
	MI ± sd			1.0			
	IR			1			
	A			0.1			
BIVALVIA							
Unionidae gen. sp. gl. (fins)	P, %				20.0		
	MI ± sd				3.8 ± 4.2		
	IR				1–10		
	A				0.8		

Abbreviations: A, abundance; gl., glochidia; IR, intensity range; L3, 3rd stage larvae of nematodes; MI ± sd, mean intensity ± standard deviation; mtc., metacercariae; P, prevalence; pl., plerocercoids.

and second one in Latvia, with both being found sporadically on Chinese sleeper (Table 2).

According to the Czekanowski-Sørensen Index, Lake Kartal and the Vylkove canals in Ukraine showed high similarity (71.4%), as did Ilgas and Lake Gailezers in Latvia (50%); in all other cases, common species were not found (Table 3). Lake Kartal and Vylkove differed significantly from all other water bodies based on Mahalanobis distance and the Fischer criterium (Table 3; Figure 2). Differentiation between the waterbodies was primarily due to the abundance of the ciliate *Trichodina* sp., the cestode *Ophiotaenia europaea* Odening, 1963, the trematodes *Isthmiophora melis* (Schrank, 1788) and *Holostephanus luhei* Szidat, 1936, and the nematodes *Spiroxys*

TABLE 3 Czekanowski-Sørensen index (ICS), squared Mahalanobis distance (MD) and Fischer criterium (F; *df* = 17.81) matrix for parasite communities in six different waterbodies in Latvia and Ukraine

	Latvia			Ukraine		
	Ilgas	Gailezers	University Pond	Kartal	Vylkove	Krysyne
Ilgas						
ICS	100	50.0	0.0	0.0	22.2	0.0
MD	0.0	0.9	2.2	**7.1**	**8.5**	4.4
F	0.4	1.0	3.4	**1.4**	**3.3**	0.4
Gailezers						
ICS		100	0.0	0.0	0.0	0.0
MD		0.0	1.3	**6.2**	**7.9**	3.5
F			0.6	**3.0**	**3.3**	1.1
University Pond						
ICS			100	0.0	0.0	0.0
MD			0.0	**7.4**	**9.0**	4.6
F				**3.6**	**3.8**	1.5
Kartal						
ICS				100	71.4	33.3
MD				0.0	**12.6**	**9.0**
F					**5.3**	**2.9**
Vylkove						
ICS					100	40.0
MD					0.0	**10.7**
F						**3.2**
Krysyne						
ICS						100
MD						0.0
F						-

Note: Significant differences ($p < .05$) are in bold.

contortus (Rudolphi, 1819) and *Eustrongylides tubifex* Nitzsch, 1819 (Table 4).

4 | DISCUSSION

In this study, the parasite fauna of Chinese sleeper in the Latvian sites was surprisingly low. Our data compares favourably to previously published data at four other Latvian waterbodies (Birkineļi, Lake Gubišče, the Līksna pond and the Jersika pond) where five parasite taxa were registered: *Trichodina* spp., the monogenea *Ancyrocephalus cruciatus* Wedl, 1857 and *G. perccotti*, the trematode *Ichtyocotylurus platycephalus* Creplin, 1825 and an unidentified glochidia (Kirjušina, Lazdāne, & Zolovs, 2014). Unlike the study of Kirjušina et al. (2014), however, we recorded no ciliates, monogeneans or glochidia. On the other hand, we did register the metacercariae *Apophallus* sp., *Cotylurus* sp. and *Metorchis xanthosomus* Creplin, 1846, as well as an unidentified coccidian located in a fish's rectum (see Table 2). The heterophyid metacercariae *Apophallus* sp., located on the fins, was registered for the first time on the Chinese sleeper. Further, we registered two species, the trematode *M. xanthosomus* and the parasitic copepod *N. japonicus* which have never been found before in Latvia (Kirjušina & Vismanis, 2007). Metacercariae of *M. xanthosomus* were recorded at low abundance in the Ilgas marsh in Latvia, and a single specimen of *N. japonicus* was found in the University pond in Daugavpils (see Table 2). This latter waterbody was used as an aquacultural pond in the past; hence, we can assume that this species was present in Daugavpils before Chinese sleeper introduction, having being introduced to Latvia through aquacultural stocking.

Most parasites found on Chinese sleeper in Ukraine have been registered previously (Davydov, Kurovskaya, Temnikhanov, & Neborachek, 2012; Kvach, Drobiniak, Kutsokon, & Hoch, 2013; Kvach, Kutsokon, et al., 2016; Kvach, Ondračková, Kutsokon, & Dzyziuk, 2018). However, we registered three species for the first time in Ukrainian Chinese sleeper, i.e. *E. tubifex* at Lake Kartal, *M. xanthosomus* at Vylkove and *I. melis* at Lake Krysyne (see Table 2). The larvae of *E. tubifex* have previously been registered in Chinese sleeper from the River Vistula in Poland (Mierzejewska, Kvach, Woźniak, Kosowska, & Dziekonska-Rynko, 2012), while *M. xanthosomus* has been registered from the Upper Danube basin in Germany (Kvach, Janáč, Nehring, Ondračková, & Jurajda, 2017) and *I. melis* at

FIGURE 2 Discriminant function plot of parasite component communities for Chinese sleeper from six different localities in Latvia and Ukraine

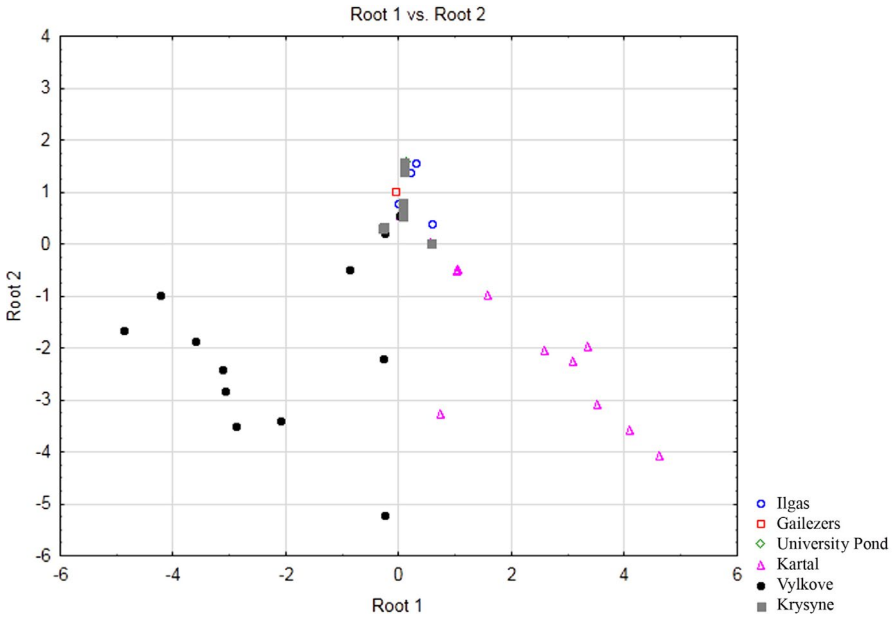

TABLE 4 Discriminant function analysis summary for parasite communities from six different waterbodies in Latvia and Ukraine

Parasite species	Wilks' Lambda	Partial Lambda	F-remove (5.81)	*p*-value	Tolerance	1-Tolerance (R-Squared.)
Ichthyophthirius multifiliis	0.16	0.89	1.94	.10	0.98	0.02
Trichodina sp.	**0.18**	**0.77**	**4.78**	**.00**	**0.86**	**0.14**
Coccidia gen. sp.	0.15	0.98	0.29	.92	0.73	0.27
Gyrodactylus perccotti	0.15	0.93	1.21	.31	0.95	0.05
Ophiotaenia europaea	**0.21**	**0.68**	**7.50**	**.00**	**0.91**	**0.09**
Apophallus sp.	0.15	0.95	0.78	.57	0.05	0.95
Cotylurus sp.	0.15	0.98	0.41	.84	0.96	0.04
Isthmiophora melis	**0.17**	**0.84**	**3.05**	**.01**	**0.98**	**0.02**
Holostephanus luhei	**0.21**	**0.68**	**7.78**	**.00**	**0.30**	**0.70**
Metorchis xanthosomus	0.15	0.96	0.59	.70	0.68	0.32
Strigeidae gen. sp.	0.15	0.95	0.82	.54	0.99	0.01
Cosmocephalus obvelatus	0.16	0.91	1.69	.15	0.81	0.19
Eustrongylides tubifex	**0.17**	**0.86**	**2.61**	**.03**	**0.36**	**0.64**
Spiroxys contortus	**0.18**	**0.81**	**3.85**	**.00**	**0.78**	**0.22**
Acanthocephalus lucii	0.15	0.97	0.45	.81	0.05	0.95
Neoergasilus japonicus	0.15	0.95	0.78	.57	0.99	0.01
Unionidae gen. sp.	0.16	0.90	1.84	.12	0.94	0.06

Note: Significant differences ($p < .05$) are in bold.

many localities in the European part of Russia (Sokolov, Reshetnikov, & Protasova, 2014).

In our study, the Chinese sleeper hosted two adult stage helminth species, the monogenean *G. perccotti* and the acanthocephalan *A. lucii*. While monogeneans are characterized by a direct life cycle, acanthocephalans infect fish via consumption of the isopod *Asellus aquaticus* Linnaeus, 1758 (Brown, Chubb, & Veltkamp, 1986). Hence, the finding of two specimens of this parasite on a fish from the University pond confirms its predatory behaviour on isopods. *Acanthocephalus lucii* has previously been recorded on Chinese sleeper from the Danube basin (Kvach et al., 2017; Kvach, Ondračková, Kutsokon, et al., 2018).

For a number of parasites, the Chinese sleeper plays the role of second intermediate host (e.g. the cestode *O. europaea* and the trematodes *Apophallus* sp., *Cotylurus* sp., *H. luhei*, *I. melis*, *M. xanthosomus*, Strigeidae gen. sp.) or paratenic host (e.g. the nematodes *Cosmocephalus obvelatus* Creplin, 1825, *S. contortus*, *E. tubifex*). With the adult stages of the trematodes *Apophallus* sp., *Cotylurus* sp., *H. luhei*, *M. xanthosomus* and Strigeidae gen. sp. and nematodes *C. obvelatus* and *E. tubifex* going on to parasitize fish-eating birds

(Moravec, 2013; Sudarikov, Lomakin, Atajev, & Semenova, 2006). Infestation with nematodes occurs primarily through consumption of invertebrates, with the nematode *C. obvelatus*, for example, parasitizing fish that prey on amphipods while *E. tubifex* is passed on through consumption of oligochaetes (Moravec, 2013). Nematode infestation may also occur through predation on infected fish, however, and this is likely to be a common route for the Chinese sleeper (Grabowska, Grabowski, Pietraszewski, & Gmur, 2009; Koščo et al., 2008; Rau et al., 2017).

Three parasites that include amphibians and reptiles in their life cycles were only found in Ukraine, the cestode *O. europaea*, the trematode *I. melis* and the nematode *S. contortus*. The definitive hosts of *O. europaea* are grass snakes *Natrix* sp., though they also have a second intermediate host in anuran amphibians (Biserkov & Kostadinova, 1997). Adults of *S. contortus* parasitize the stomachs of terrapins such as the European pond turtle *Emys orbicularis* Linnaeus, 1758, while the larvae develop in planktonic cyclopids but also commonly infect freshwater fish and frogs (Hedrick, 1935; Moravec, 2013). In Ukraine, therefore, the Chinese sleeper now plays a role in the life cycles of reptile parasites. Their infection with these parasites is likely to result from feeding on planktonic crustaceans at the fry stage or cannibalism of infected fry (Grabowska et al., 2009). While semi-aquatic reptiles are common components of the Ukrainian fauna (Marushchak, Nekrasova, Pupins, Tytar, & Ceirans, 2019) they tend to be rare and protected in Latvia (Pupins, Pupina, & Pupina, 2017), probably contributing to the absence of this group of parasites in the parasite community of Latvian Chinese sleeper. The definitive hosts of the trematode *I. melis* are predatory mammals and the list presently includes over 30 species, including dogs, foxes, rats, hedgehogs and even humans (Radev, Kanev, Hrusanov, & Fried, 2009). While this parasite was only found only in the Prypyat river basin, its infection parameters were relatively high (Table 2). Finally, anuran amphibians, mainly *B. bombina*, *Pelophylax esculentus* Linnaeus, 1758 and *Rana temporaria* Linnaeus, 1758, are the hosts of metacercariae (Radev et al., 2009; Sudarikov et al., 2006). As the host of *O. europaea*, *I. melis* and *S. contortus* larvae, the Chinese sleeper plays a similar role in their life cycles as do frogs and, as such, they play an important role in the discrimination of Chinese sleeper populations.

As the definitive hosts of *I. melis* (predatory mammals) are mainly connected with forest habitats, they were not found in southern Ukrainian sites, which lie within the steppe zone. Instead, three other parasite species help discriminate the populations, *Trichodina* sp., *H. luhei* and *E. tubifex* (Table 4). *Trichodina* sp. occur at high abundance in warmer waters (Kvach, Ondračková, et al., 2016), thus they were only recorded in Ukraine and not Latvia, where they are likely to be rare due to the colder climate. Another possible reason of the absence of *Trichodina* sp. in our Latvian samples is that these ciliates tend occur in higher numbers in waters affected by organic pollution (Yeomans, Chubb, & Sweeting, 1997). The adult stages of two other listed species, *H. luhei* and *E. tubifex*, are parasites of cormorants (Sudarikov et al., 2006). Cormorant colonies are numerous on Lake Kartal but were not observed at any of the other sampling localities (unpublished personal observation).

We registered two non-native parasite species, *G. perccotti* and *N. japonicus*, in the Chinese sleeper (Table 2). The monogenean *G. perccotti* was only recorded in Ukraine at Lake Kartal and Vylkove on the Danube delta. While this species has previously been registered at Vylkove (Kvach, Ondračková, Kutsokon, et al., 2018), its occurrence at Lake Kartal indicates a wider range in the Lower Danube. In Latvia, the species was only previously been found at low abundance in Lake Gubišče (Kirjušina et al., 2014). The second non-native species, the copepod *N. japonicus*, is also of Far-Eastern Asian origin, though it has now spread worldwide through the vectors of aquaculture and the ornamental fish trade (Hudson & Bowen, 2002). This latter case probably represents an example of 'invasional meltdown', whereby several non-native species invade the same habitat and commonly facilitate the establishment of each other (Simberloff & von Holle, 1999). The co-introduction of *N. japonicus* with a non-native fish species has previously been recorded in Europe, when it was found on pumpkinseed *Lepomis gibbosus* Linnaeus, 1758 in the Czech Republic (Ondračková, Fojtů, Seifertová, Kvach, & Jurajda, 2019). As such, the Chinese sleeper appears to be another vector of *N. japonicus* range expansion in Europe.

While the Chinese sleeper parasite community in Ukraine was much richer than that in Latvia, it was still relatively poor compared with local taxonomically closely-related fish species such as gobiids. Infestation rates for the monkey goby *Neogobius fluviatilis* Pallas, 1814 along the Lower Danube and in Lake Kytay near the Danube delta for example, were relatively high (Kvach, Ondračková, Trichkova, et al., 2018). In Ukraine, a relatively high infestation rate was only recorded for *I. melis* from Lake Krysyne in the Dnieper river basin. Such low parasite loads are fairly typical for non-native species, however, and lends support to the "enemy release hypothesis" mentioned previously (Torchin et al., 2003). It is likely that a lowered parasite load helps the invasive Chinese sleeper establish stable populations and, subsequently, to actively expand into new areas. A similarly low parasite load to our own has also been registered in Hungarian Chinese sleeper populations, which are now known to form part of the same "Carpathian population" (Antal, Székely, & Molnár, 2015; Grabowska et al., 2020), first hypothesized in Kvach, Kutsokon, et al. (2016) and later confirmed through molecular genetics (Grabowska et al., 2020), centred on the Ukrainian Chinese sleeper population. Based on its parasite fauna, the Latvian Chinese sleeper population appears to originate from elsewhere, however, and is most likely the result of fish being released from aquaria. Such cases are commonly registered in Latvia (Pupina et al., 2015) and this may also help explain the low parasite acquisition of this fish.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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