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First data on parasites of the invasive brown bullhead *Ameiurus nebulosus* (Siluriformes: Ictaluridae) in Ukraine

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Summary

This study describes the parasite community of non-native brown bullhead, *Ameiurus nebulosus* (Actinopterygii: Ictaluridae), collected at three sites in the river Vistula Basin (Lake Svitiaz, Lake Pisochne, and Lake on Plastova) and one site in the river Diester Basin (Lake Stryiska), in Ukraine. Our data represent the first comprehensive study of parasite community in this fish species in Europe. Sixteen parasite taxa were found, including species co-introduced from North America and species acquired in the European range. Maximum parasite richness (13 spp.) was recorded in Lake Svitiaz situated in a Natural Protected Area, while lowest species richness (3 spp.) was observed at Lake on Plastova, an artificial pond in the city of Lviv. Three co-introduced monogenean species, *Gyrodactylus nebulosus*, *Ligictaluridus pricei* and *Ligictaluridus monticellii*, are recorded in Ukraine for the first time, widening the knowledge of the European distribution of these North American parasites. Metric features for hard parts of invasive and native monogeneans showed overlap in ligictalurid parasites, but slightly smaller metrics in Ukrainian *G. nebulosus*, possibly reflecting water temperature during fish sampling. Though prevalence and abundance of acquired parasites was relatively low, infection parameters for metacercariae of *Diplostomum* spp. were relatively high at Lake Svitiaz and the natural Lake Stryiska in Lviv. In two lakes in the Vistula basin, we found high prevalence and abundance of *Anguillicola crassus*, an Asian nematode infecting eels, possibly supporting the invasional meltdown hypothesis. Our study confirms both further spread of non-native parasites in Europe and use of non-native fish as competent hosts for local native and introduced parasites.

Keywords: fish parasites; invasive species; monogeneans; parasite co-introduction; range expansion

Introduction

The issue of invasive fish species has come to the forefront of scientific interest in recent decades (Gozlan *et al.*, 2010; Catford *et al.*, 2012; Simberloff *et al.*, 2013; Zenni & Nuñez, 2013; Ricciardi, 2015). One of the reasons is the negative effects that such species may have on all trophic levels of aquatic communities, e.g. by reducing the abundance of native fish, zooplankton and/or macrophytes (Hermoso *et al.*, 2011; Gallardo *et al.*, 2016). A further important aspect of invasive fish introductions is the co-introduction of their natural parasites, which, in some cases, can have deleterious effects on native fish hosts, particularly those with which the parasite does not share evolutionary history (Taraschewski, 2006; Kmentová *et al.*, 2019; Sarabeev *et al.*, 2022). Among the most

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frequently co-introduced non-indigenous parasites are helminths, arthropods and protozoans, with fish being the most common non-indigenous hosts (Lymbery *et al*., 2014).
Over the last 50 years or so, our understanding of host-parasite interactions has increased considerably (e.g. see Anderson & May, 1978, 1979, 1982; Brooks & Hoberg, 2007; Gómez-Arreaza *et al*., 2017; Kennerley *et al*., 2022). Host specificity implies that co-introduced parasites will primarily infect their natural (i.e. introduced) hosts, rather than species native to the invaded area (Taraschewski, 2006; Lymbery *et al*., 2014; Goedknegt *et al*., 2016). Nevertheless, a range of host-parasite interactions have been observed in invaded waters, and several hypotheses have been formulated to explain these, e.g. the enemy release hypothesis, parasite spillback, dilution effect and parasite spillover (summarised in Goedknegt *et al*., 2016). With regards to the non-native fish introductions, current research is increasingly focused on the possible negative impacts of both non-native hosts and their parasites on local economically-important hosts (Galli *et al*., 2003; Goedknegt *et al*., 2016).
The brown bullhead catfish *Ameirus nebulosus* Lesueur, 1819 (Ictaluridae) is native to Canada and the USA (Schindler, 1957). It was first introduced into Europe as an ornamental pond species in Poland in 1885 (Nowak *et al*., 2008) and is now common in most European countries (Rutkayová *et al*., 2013; Rechulicz & Płaska, 2018). The species generally inhabits backwaters and pools of large lowland rivers, nutrient-rich lakes and ponds, reservoirs and irrigation canals (Page & Burr, 1991; Ulikowski *et al*., 2022). Due to its high tolerance of poor environmental conditions and high temperatures, along with a general lack of native predators, the distribution of brown bullhead (and its parasites) is highly likely to increase throughout Europe (Kutsokon *et al*., 2018; Bănăduc *et al*., 2022; Ulikowski *et al*., 2022).
Despite its present wide European distribution (Rutkayová *et al*., 2013; Rechulicz & Plaska, 2018), knowledge of brown bullhead parasites and pathogens remains relatively scarce. In 2012, a mass mortality event was reported for a Hungarian brown bullhead population, the deaths being linked to an outbreak of European sheatfish ranavirus (Fehér *et al*., 2016). Seven ciliate parasite species and the acanthocephalan *Acanthocephalus anguillae*, all likely of local origin, have been reported for brown bullhead caught in the Serbian River Danube (summarised in Điknović *et al*., 2018). There have been several reports of North-American monogeneans co-introduced with brown bullhead in Polish lakes (Prost, 1973), ponds and oxbows of the Czech Republic (Ondračková *et al*., 2020) and the River Tisza (Galli *et al*., 2010). The brown bullhead has also been reported to act as an intermediate or paratenic host

Fig. 1. Map illustrating the study area. Red spots = sampling localities: 1 – Lake Svitiaz, 2 – Lake Pisochne, 3 – Lake on Plastova, 4 – Lake on Stryiska.

of the cestode *Ophiotaenia europaea*, infecting colubrid snakes in Europe (Ondračková *et al*., 2021). To date, however, there has been no comprehensive study investigating the overall parasite fauna of brown bullhead in Europe.

The brown bullhead was first observed in Ukraine in the Shatsk Lakes (Vistula River drainage) around 1937, having been introduced from the River Prypyat in Belarus (Ivlev & Protasov, 1948). In 2017, the species was found in the city of Lviv (Upper Dniester basin; Kutsokon *et al*., 2018). The main aim of this study was to provide a comprehensive description of the parasite community of non-native brown bullhead in Ukraine. We also provide a comparison of the metric features of North American monogeneans in their invasive and native areas.

Material and Methods

Brown bullhead were sampled with a 80×73×72 cm (10 mm mesh size) dipnet from four localities in Ukraine, three situated in the Vistula basin (Lake Svitiaz, Lake Pisochne, Lake on Plastova) and one in the Dniester basin (Lake on Stryiska) between April and November 2021 (Fig. 1). Two of the lakes, Svitiaz (51.483444, 23.793333) and Pisochne (51.567722, 23.901417), lie adjacent to the Shatsk glacial lakes, a Natural Protected Area. The others, Lake on Stryiska (49.800658, 24.016692), is a natural lake in the southern part of the city (Zubria river drainage), and Lake on Plastova (49.859328, 24.079917), a pond in the north (Poltva river drainage), lie within the city of Lviv itself. The fish were transported live to the laboratory, where they were kept in aerated tanks until dissection. All fish were dissected within three days of sampling to ensure maximum parasite recovery (Kvach *et al*., 2016, 2018).

A total of 102 fish were studied for parasites (Table 1). Prior to dissection, each fish was measured to the nearest 1 mm for standard (SL) and total (TL) length, after which the fins, skin, gills, muscles and internal organs were examined for presence of parasites. Living unicellular and myxozoan microparasites were examined under light microscopy, while monogeneans and mites were preserved in Glycerin-ammonium-picrate (GAP) and prepared as semi-permanent slides (Malmberg, 1970). Digeneans, cestodes and nematodes were preserved in hot 4 % formaldehyde (Cribb & Bray, 2010). Encysted and capsuled parasites were isolated from the cyst/capsule before fixation. Cestodes and digeneans were stained with iron acetic carmine, dehydrated in ethanol of increasing concentration and mounted in Canada balsam as permanent slides (Georgiev *et al*., 1986). Glochidia and crustaceans were preserved in 4 % formaldehyde and identified under light microscopy. All parasites were identified to species level or, where not possible, to the lowest taxonomic level possible.

The morphology of non-native monogenean parasites was examined using an Olympus BX53F2 light microscope equipped with phase contrast optics (Olympus, Japan). Drawings of the hard structures of the haptor and copulatory organs were produced with the aid of a drawing attachment. Measurements (in micrometers) were obtained using cellSens standard digital image analysis software v.3.2 (Olympus, Japan). Bray-Curtis index based on presence/absence data was used for calculation of a qualitative similarity between parasite communities in Ukrainian localities, and between Ukraine (this study), the native American and Canadian range, and Puerto-Rico (non-native range), using published data (see Supplementary material for details). All statistical analyses were performed using Primer v.5.0 and Statistica v.12.0 (StatSoft, Inc.).

Ethical Approval

This research was undertaken in line with the ethical requirements of the Czech Republic and has been approved by the appropriate ethics committee.

Results

Brown bullhead parasite community in Ukraine

A total of 16 parasite taxa were found on Ukrainian brown bullhead (Table 2), with maximum parasite richness (13 spp.) found at Lake Svitiaz and minimum (3 spp.) at Lake on Plastova. The majority of parasite species were acquired in the bullhead's European range (up to 13 spp.), though just four species reached a prevalence of > 20 %. Of these, larvae of the Asian (i.e. non-indigenous) nematode *Anguillicola crassus* were most prevalent and abundant at Lakes Svitiaz and Pisochne, while metacercariae of *Diplostomum* eye flukes were abundant at Lake Svitiaz and Lake on Stryiska. Metacercariae of *Hysteromorpha trilloba* and larvae of *Streptocara crassicauda* were found at a single site, Lake Svitiaz, with prevalence of 45 % and 30 %, respectively (Table 1).

Three monogenean species were co-introduced to Europe with

Table 1. Number and size (mean ± standard deviation, minimum and maximum in parentheses) of brown bullhead (*Ameiurus nebulosus*) examined from different Ukrainian localities.

Parameters	Lake Svitiaz	Lake Pisochne	Lake on Plastova	Lake on Stryiska
Number	20	10	20	52
Standard length (mm)	128.6±9.7 (112–150)	138.2±23.8 (95–176)	73.9±9.7 (55–95)	61.5±7.8 (43–80)
Total length (mm)	153.6±10.8 (131–177)	157.2±31.6 (109–199)	90.8±9.9 (78–115)	75.3±9.1 (56–95)

Table 2. Parasites of invasive brown bullhead (*Ameiurus nebulosus*) from different Ukrainian localities.
P, % – prevalence, MI – mean intensity, IR – intensity range, A – abundance; sd – standard deviation.

Parasite species (site)	Index	Lake Svitiaz	Lake Pisochne	Lake on Plastova	Lake on Stryiska
CILIOPHORA					
Trichodina spp. (gills)	P, %			15.0	3.8
	MI±sd			4.0±5.2	14.5±14.8
	IR			1–10	4–25
	A			0.6	0.6
CNIDARIA					
Myxozoa gen. sp. (gall bladder)	P, %	5.0	10.0		
	MI±sd	1.0	1.0		
	IR	1	1		
	A	0.1	0.1		
MONOGENEA					
Gyrodactylus nebulosus (fins)	P, %	10.0	10.0		9.6
	MI±sd	1.5±0.7	1.0		1.6±1.3
	IR	1–2	1		1–4
	A	0.2	0.1		0.2
Ligictaluridus pricei (gills)	P, %	45.0	80.0	60.0	82.7
	MI±sd	7.0±4.1	11.5±4.9	10±13.7	8.4±6.8
	IR	2–16	5–19	1–46	1–30
	A	3.2	9.2	5.95	6.9
Ligictaluridus monticellii (nasal cavity)	P, %	25.0	10.0		73.1
	MI±sd	2.6±1.5	7.0		4.1±4.1
	IR	1–5	7		1–16
	A	0.7	0.7		3.0
Ligictaluridae larvae (fins)	P, %				3.8
	MI±sd				1.0±0.0
	IR				1
	A				0.04
CESTODA					
Paradilepis scolecina (heart, kidney)	P, %	10.0			1.9
	MI±sd	1.0±0.0			1.0
	IR	1			1
	A	0.1			0.02
DIGENEA					
Diplostomum spp. met (eyes)	P, %	85.0		5	51.9
	MI±sd	21.6±11.1		2.0	4.2±3.9
	IR	6–43		2	1–16
	A	18.4		0.1	2.2

Hysteromorpha triloba met (muscles)	P, %	45.0	20.0		
	MI±sd	2.6±1.0	4.0±0.0		
	IR	1–4	4		
	A	1.2	0.8		
NEMATODA					
Anguillicola crassus L3 (mesentery, liver)	P, %	70.0	80.0		
	MI±sd	7.0±6.2	3.9±2.2		
	IR	1–22	1–8		
	A	4.9	3.1		
Goezia ascaroides (gut)	P, %	10.0			
	MI±sd	3.5±3.5			
	IR	1–6			
	A	0.4			
Streptocara crassicauda L3 (mesentery, liver)	P, %	30.0			
	MI±sd	5.7±4.0			
	IR	1–11			
	A	1.7			
Agamonema sp. (mesentery)	P, %				1.9
	MI±sd				1.0
	IR				1
	A				0.02
CRUSTACEA					
Argulus foliaceus (gills)	P, %	5.0	10.0		
	MI±sd	1.0	2.0		
	IR	1	2		
	A	0.1	0.2		
Ergasilus sieboldi (gills)	P, %	10.0			
	MI±sd	1.0±0.0			
	IR	1			
	A	0.1			
ARACHNIDA					
Unionicolidae gen. sp. (gills, gut wall, swim bladder)	P, %	20.0	10.0		
	MI±sd	1.3±0.5	3.0		
	IR	1–2	3		
	A	0.3	0.3		
Species richness		13	8	3	7

the fish host. Of these, *Ligictaluridus pricei*, located on the gills, were the only parasite species observed at all four sampling sites, with highest prevalence at Lake on Stryiska (83 %) and highest abundance at Lake Pisochne (9.2). *Ligictaluridus monticellii*, located in the nasal cavity, were found at three sites, with maximum prevalence at Lake of Stryiska (73 %). The fins of bullhead from Lakes Svitiaz, Pisochne and Stryiska were infected with *Gyrodactylus nebulosus*, with a prevalence of 10 % at all sites (Table 1).

As all three monogenean species are reported from Ukraine for the first time, we provide a detailed morphometric analysis of the parasites below.

Platyhelminthes: Monogenea: Gyrodactylidae
***Gyrodactylus nebulosus* Kritsky & Mizelle, 1968**
Host: *Ameiurus nebulosus*
Site of infection: fins

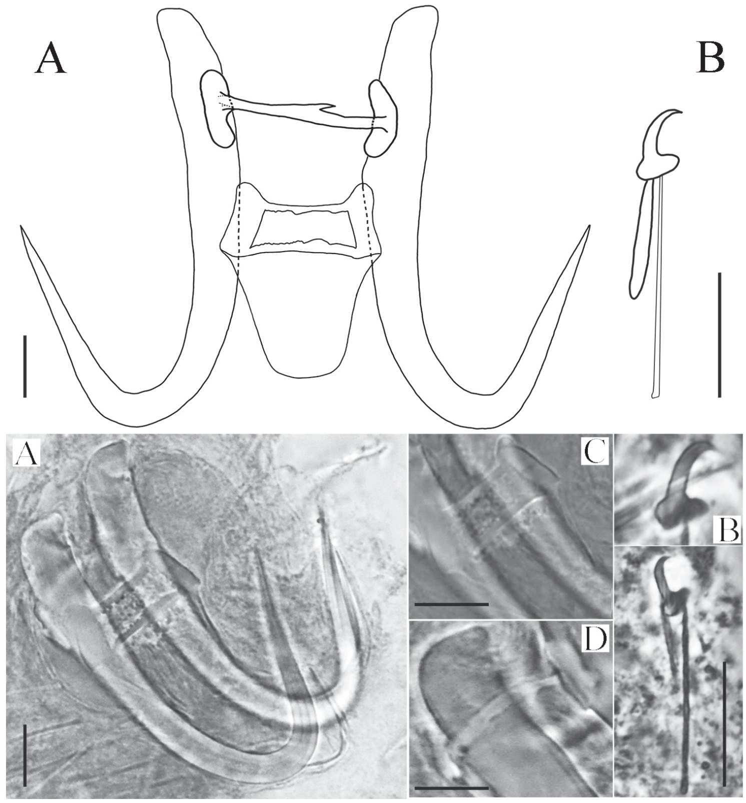

Fig. 2. *Gyrodactylus nebulosus* ex *Ameiurus nebulosus*, Lake Svitiaz, Ukraine. A – drawing (upper) and photograph (lower) of opisthaptoral central hook complex; B – drawing (upper) and photograph (lower) of a marginal hook; C – ventral bar; D – dorsal bar (scale bar 10 μm).

Geographical range: USA, Canada, Czech Republic, Bulgaria, Poland (reported as *G. fairporti*).

Description. Haptor length 51.4±3.8 (44.6–55.9; n=6) (Fig. 2), relatively wide along its length with short straight roots 16.5±1.9 (13.4–18.8). Shaft length 36.8±2.6 (33.6–41.1), hamulus point length 27.2±0.7 (26.8–28.3), hamulus aperture distance 22.6±1.1 (20.7–23.6) (Fig. 2, A). Ventral bar 23.5±1.2 (21.3–24.6) long, median portion length 6.2±0.9 (5.3–7.3), trapezoidal shaped, with a membrane narrowed to the bottom – 14.7±1.0 (13.3–15.6), total length of the ventral bar 23.6±2.0 (21.2–26.5) (Fig. 2, C). Dorsal bar (Fig. 2, D) width 4.1±0.5 (3.3–4.8). Marginal hooks total length 27.1±1.1 (25.9–29.2), shaft length, 21.5±1.1 (20.4–23.5). Marginal hook sickle slender, 5.6±0.4 (5.3–6.4) long, toe short – 1.9±0.5 (1.4–2.7); angling acutely from the blade base – 3.1±0.9 (2.2–4.5). Comparative measurement data of *G. nebulosus* from its native and non-native range is shown in Supplementary Table S1.

Platyhelminthes: Monogenea: Dactylogyridae
***Ligictaluridus pricei* (Müller, 1936)**
Synonym: *Ancyrocephalus pricei*, *Cleidodiscus pricei*
Host: *Ameiurus nebulosus*
Other hosts: *A. melas, Ictalurus punctatus, Noturus flavus, N. gyrinus*
Site of infection: gills

Geographical range: USA, Mexico, Czech Republic, Poland, Bulgaria, Hungary, Japan.

Description. Haptor length (Fig. 3) 69.1±10.6 (55.8–86.4; n=12), width 70.7±8.7 (54.9–86.4; n=12). Dorsal hamuli (Fig. 3, A) smaller than ventral, hamulus total length 40.7±3.2 (34.6–49.4; n=10), length to notch 39.7±1.9 (36.3–47.0; n=10), superficial root length 10.5±2.0 (6.9–13.7; n=9), blade length 13.7±2.7 (10.5–16.8; n=10). Ventral hamuli (Fig. 3, B) total length 42.7±4.1 (34.8–49.5; n=10), length to notch 41.3±3.7 (34.2–47.4; n=10), superficial root length 11.2±2.1 (7.5–15.0; n=11), blade length 13.8±1.1 (11.7–15.6; n=10). Dorsal bar (Fig. 3, C) length 40.4±3.5 (36.4–46.9; n=12), bar median width 8.2±2.05 (5.4–12.0; n=12). Ventral bar (Fig. 3, D) length 42.6±5.4 (34.4–50.1; n=12), bar median width 9.8±1.9 (6.8–13.0; n=12). Marginal hooks (Fig. 3, E) of larval type, 7 hooks. I pair 12.6±1.7 (9.5–14.0; n=7), II pair 14.8±1.9 (10.3–18.3; n=139), III pair 15.2±1.8 (11.1–17.6; n=13), IV pair 15.5±2.1 (11.3–18.4; n=11), V pair 15.6±2.1 (11.1–17.5; n=7), VI pair 15.0±2.5 (11.5–17.4; n=4), VII pair 14.5±0.6 (13.6–15.0; n=4). Penis (Fig. 3, F) is a curved tube, length 32.0±3.5 (28.0–39.1; n=10), diameter 1.8±0.2 (1.6–2.4; n=10), diameter to length ratio 1:0.06. Accessory piece 27.1±3.6 (21.2–33.0; n=10). Comparative measurement data of *L. pricei* from its native and non-native range is shown in Supplementary Table S2.

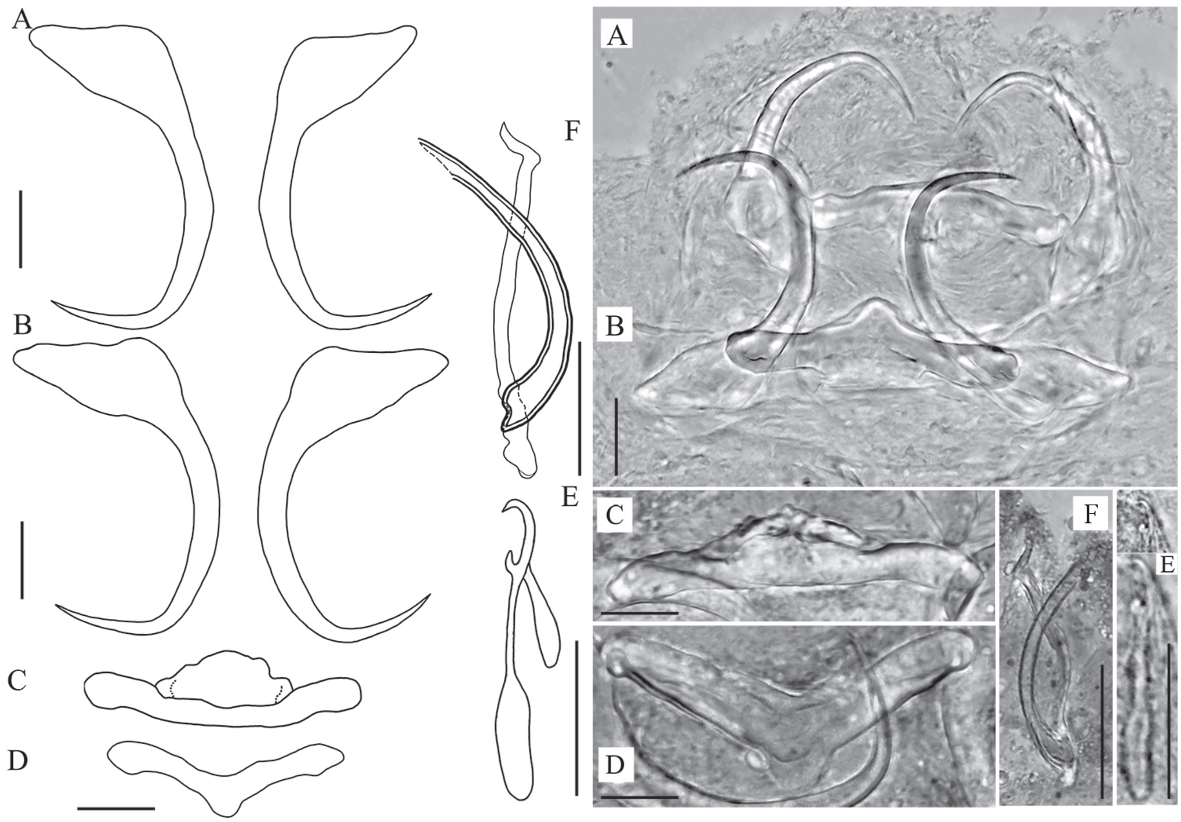

Fig. 3. *Ligictaluridus pricei* ex *Ameiurus nebulosus*, Lake Pisochne, Ukraine. Haptoral and genital hard structures A-E – drawing (left) and photograph (right); A – dorsal hamuli; B – ventral hamuli; of a marginal hook; C – ventral bar; D – dorsal bar; F – male copulatory complex: penis and accessory piece; E – marginal hook (scale bar 10 μm).

***Ligictaluridus monticellii* (Cognetti de Martis, 1924)**

Synonym: *Ancyrocephalus monticellii, Cleidodiscus monticellii, Haplocleidus monticellii*

Host: *Ameiurus nebulosus*

Other host species: *A. catus* (type host)

Site of infection: nasal cavity

Geographic range: USA, Czech Republic, Poland, Italy, Tisza River (Hungary).

Description. Haptor length (Fig. 4) 92.9±14.5 (72.4–127.2; n=12), width 113.6±11.7 (96.1–132.1; n=12). Dorsal hamuli (Fig. 4, A) smaller than ventral, hamulus total length 54.9±3.6 (49.8–61.6; n=11), length to notch 46.5±4.3 (40.9–55.9; n=11), superficial root length 25.6±4.2 (20.3–33.8; n=9), blade length 18.7±2.7 (13.2–24.1; n=12). Ventral hamuli (Fig. 4, B) total length 66.7±4.6 (56.1–74.5; n=11), length to notch 58.1±4.5 (49.9–68.1; n=11), superficial root length 25.1±6.2 (19.0–28.9; n=11), blade length 21.7±1.9 (17.7–26.7; n=11). Dorsal bar (Fig. 4, C) length 61.1±5.3 (53.7–71.2; n=12), bar median width 17.3±3.5 (10.5–21.8; n=12). Ventral bar (Fig. 4, D) length 57.1±8.9 (39.7–69.6; n=12), bar median width 11.3±1.4 (13.4–17.3; n=12). Marginal hooks (Fig. 4, E) of larval type, 7 hooks. I pair 16.8±0.8 (15.5–17.6; n=9), II pair 20.1±1.6 (18.4–24.2; n=9), III pair 19.4±1.0 (17.9–21.3; n=9), IV pair 19.4±0.8 (18.4–21.0; n=9), V pair 19.4±0.9 (17.9–20.8; n=9), VI pair 19.1±1.0 (17.6–20.1; n=8), VII pair 17.3±1.0 (16.2–19.1; n=8). Penis (Fig. 4, F) is a curved tube, length 43.2±5.3 (30.1–48.8; n=10), diameter 2.2±0.3 (1.8–2.7; n=10), diameter to length ratio 1:0.05. Accessory piece 42.1±6.6 (32.3–53.2; n=10). Comparative measurement data of *L. monticellii* from its native and non-native range is shown in Supplementary Table S3.

Comparison with native range

Qualitative (Bray-Curtis) similarity of parasite communities between Ukrainian localities was highest between Lakes Svitiaz and Pisochne (66.2), followed by Lake on Stryiska and Lake on Plastova (49.2) (Fig. 5, see Supplementary Table S4). A comparison of brown bullhead parasite communities published from native North American (USA and Canada) and non-native European (Ukraine), however, indicated substantial differences, with relatively low Bray-Curtis values for the USA (12.1) and Canada (19.0) (see Supplementary Table S5). Using literature data, parasite diversity in brown bullhead native range measured by Shannon–Wiener index ranged between 3.8 and 4.6 in the Canada and USA, respectively. In contrast, the index values in non-native range were 2.8 in Ukrainian water bodies and 1.8 in Puerto Rico (Supplementary Table S6).

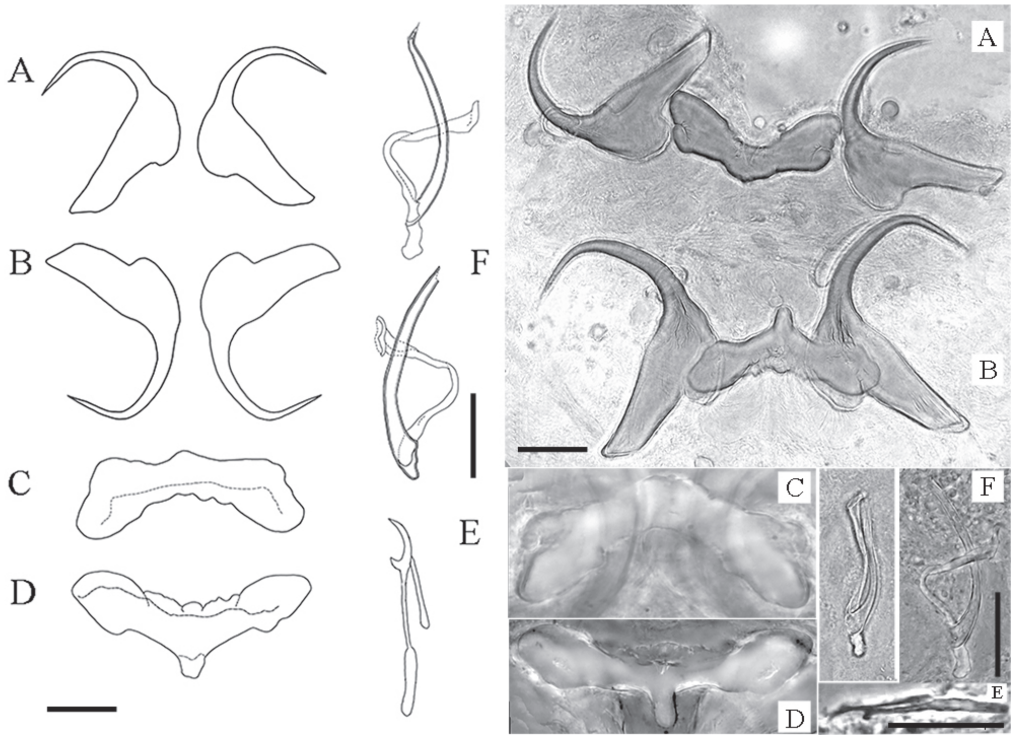

Fig. 4. *Ligictaluridus monticellii* ex *Ameiurus nebulosus*, Lake Stryiska, Ukraine. Haptoral and genital hard structures A-E – drawing (left) and photograph (right); A – dorsal hamuli; B – ventral hamuli; of a marginal hook; C – ventral bar; D – dorsal bar; F – male copulatory complex: penis and accessory piece; E – marginal hook (scale bar 10 μm).

Discussion

In this study, we provide the first data for parasites of the invasive brown bullhead in Ukraine. Our data also represent the first comprehensive study of the parasite communities of this non-indigenous fish species in Europe. Furthermore, the three monogenean species recorded, *G. nebulosus*, *L. pricei* and *L. monticellii*, are recorded in Ukraine for the first time, widening the European distribution of these North American parasites.

The parasite fauna of brown bullhead in Europe is poorly described compared to its native range (Supplementary Table S7), with most studies focusing on monogenean parasites (Chechyna *et al*., 1953; Prost, 1973; Šimková *et al*., 2003; Ondračková *et al*., 2020). The three monogenean species recorded in this study, i.e. *G. nebulosus*, *L. pricei* and *L. monticellii*, are specific parasites of bullheads (Hanek & Fernando, 1971; de León *et al*., 2010, Leis *et al*., 2020) and have been co-introduced to Europe from North America. Though these parasites have already been recorded in other European countries, they are reported in Ukraine for the first time. *Gyrodactylus nebulosus* was first recorded in Europe in Poland (Prost, 1973; denoted as *G. fairporti*), with further records from the River Tisza (Galli *et al*., 2010), ponds, oxbows and side arms of the River Elbe in the Czech Republic (Ondračková *et al*., 2020) and lakes in Bulgaria, where it was reported to infect related black bullhead *Ameiurus melas* (Vancheva *et al*., 2020). In Ukrainian lakes, the species has a lower prevalence (10 %) and abundance (0.1–0.2) than similar localities in the Czech Republic (Elbe river basin), where up to 47 % of fish were infected, with some sites having mean abundances reaching 1.15 (Ondračková *et al*., 2020). Although the highest prevalence and abundance recorded to date has been reported from Bulgaria (Lake Srebarna, Danube river basin), where up to 72 % of fish were infected with abundances of 5.3±4.9 (Vancheva *et al*., 2020), the authors, in fact, referred to closely related *Gyrodactylus melas*. Further morphometrical and molecular study of *G. nebulosus* by Ondračková *et al*. (2020) showed that previous records of *G. nebulosus* include at least two species, i.e. *G. nebulosus* and *G. melas*, strictly host specific to brown and black bullhead, respectively. Morphological comparisons indicate that *G. nebulosus* collected in Ukraine have slightly shorter haptoral hard parts (see Supplementary Table S1); this may be related to different periods of material collection, since the associated changes in water temperature possibly affect the size of the haptoral hard parts (Mo, 1993).

As with *G. nebulosus*, both North American dactylogyrids *L. pricei* and *L. monticellii* were first reported to infect brown bullhead in Poland (Prost, 1973), though an earlier report is known from Italy on *Ameiurus catus* (Linnaeus, 1758) (Cognetti & Maktiis, 1924). Later European reports (summarised in Nitta & Nagasawa, 2015; Vancheva *et al*., 2020) are known from Bosnia and Herzegovina in 1988 (Nedić et al., 2021), Hungary (Adamczyk, 1973), Romania

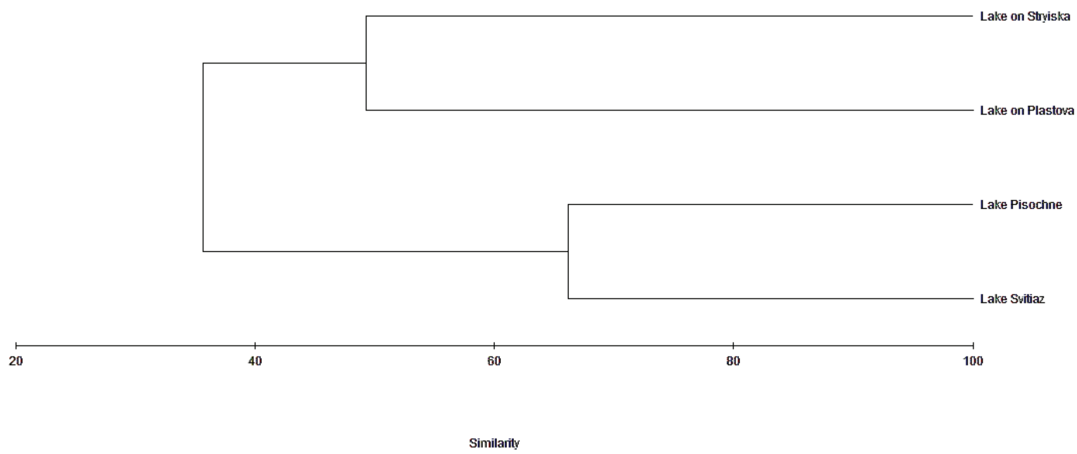

Fig. 5. Bray-Curtis similarity of brown bullhead (*Ameiurus nebulosus*) parasite communities from different Ukrainian localities.

(Roman-Chiriac, 1960) and the Czech Republic (Moravec, 2001; Šimková *et al*., 2003). In contrast, *L. monticellii* in brown bullhead has only the above-mentioned record from Poland (Prost, 1973). A related non-native species, *L. pricei*, had been recorded at high prevalence (100 %) and abundance (13.3) levels in Bulgaria (black bullhead, Vancheva *et al.*, 2020) and Ukraine (this study). Morphological comparisons between non-native regions indicate that Ukrainian *L. pricei* are either similarly sized or even slightly larger compared to other studies (Prost, 1973; Klassen & Beverley-Burton, 1985; Vancheva *et al*., 2020; Supplementary Table S2). While information on the distribution and infection rate of *L. monticellii* is scarce, morphological comparisons between specimens from Ukraine and the USA (Klassen & Beverley-Burton, 1985) show no significant difference. In comparison, the measurements of anchor features and copulatory organ provided by Prost (1973) were slightly larger than Ukrainian specimens (see Supplementary Table S3).

Regarding species composition, parasite communities at the four Ukrainian sites consisted mainly of acquired parasites, including the larval trematodes of *Diplostomum* spp., *Diplostomum spathaceum* and *Hysteromorpha triloba*, the larval nematodes *A. crassus* and *Agamonema* sp., and unidentified myxozoans (Table 1). In its native range, the brown bullhead is frequently infected with *Diplostomum* spp. eye flukes (both in the lens and vitreous humour), with high prevalence in some localities (Marcogliese & Compagna, 1999). In Ukraine, fish from Lake Svitiaz and the Lake on Stryiska also exhibited a high prevalence of *Diplostomum* metacercariae, probably reflecting the frequent occurrence of aquatic molluscs (intermediate hosts) and birds (definitive hosts) in the locality. Indeed, aquatic birds, the most numerous and diverse group of vertebrates in this wetland region (Tsaryk *et al*., 2002) provide excellent conditions for completion of the trematode life cycle and, particularly, of *Diplostomum* eye flukes.

Interestingly, brown bullhead in Lakes Svitiaz and Pisochne were infected with a high prevalence and abundance of the Asian nematode, *A. crassus*. This parasite infects the European eel (*Anguilla anguilla*) in its adult stage but uses various freshwater fishes as paratenic hosts (Moravec, 2013). Our data would suggest that brown bullhead is a susceptible host for this parasite. The larvae of *A. crassus* are able to act as 'immunological hitchhikers', avoiding the paratenic host's own immune response (Emde *et al*., 2014). Consequently, it has been suggested that distribution of larval *A. crassus* with an invasive paratenic host, e.g., round goby (*Neogobius melanostomus*), provides support for the 'invasional meltdown hypothesis' (Hohenadler *et al*., 2018; Kvach *et al*., 2019). In this case, the successful expansion of a non-native parasite is dependent on the spread of its invasive host, even when the parasites are introduced through other vectors (Taraschewski, 2006; Emde *et al.,* 2014). The two lakes in which the brown bullhead infected with *A. crassus* larvae were found form part of the Shatsk Lakes group, which lie within a Natural Protected Region with the country's highest abundance of European eel (Vasenko & Starko, 2022). As such, it is possible that brown bullhead could spread the invasive nematode, *A. crassus*, into other Ukrainian waters, providing further support for 'invasional meltdown'.

Non-indigenous species often lose some or all of their natural enemies, including parasites, during introduction to a new environment, giving them a potential advantage over local species (Torchin *et al*., 2003). A comparative analysis of our findings with those published previously showed that the brown bullhead has a wider parasite diversity in its native range than in its non-native areas (Supplementary Table S7). For example, specimens from the USA and Canada had Shannon–Wiener indices of 4.6 and 3.8, respectively, compared with 2.8 in non-native Ukrainian water bodies, while those introduced to Puerto Rico had an index value of 1.8 (Supplementary Table S6, S1). Note, however, that the indices for North America were calculated for a large area and, consequently, may be affected by a lack of publications for some regions. On the other hand, brown bullhead in their native range had a wide spectrum of parasite species through all higher taxonomic groups, while those in non-native areas had a much lower species richness, which may well support the 'parasite release or reduction hypothesis' (Goedknegt *et al*., 2016). At Ukrainian localities, the dominant species recorded in the brown bullhead parasite community were either specific species co-introduced directly from the native region, such as monogeneans, or species for which brown bullhead represent the intermediate or paratenic host, i.e. *A. crassus, H. triloba* and *D. spathaceum*. The poorest parasite community was recorded on fish from the Lake on Plastova, which comprised one introduced species (*L. pricei*) and sporadic occurrence of two local species (*Trichodina* spp., *Diplostomum* sp.). The Lake on Plastova is a small artificial pond that lies by the River Poltva (Vistula river basin) in the industrial part of Lviv with high disturbance factor and risk of organic pollution (municipal composting station), which potentially explains such a low parasite species richness. On the other hand, the parasite community of another invasive fish in this same pond, the Chinese sleeper (*Perccottus glenii*), was similar, or even higher, to that found at other localities in Ukraine (Kvach *et al*., 2022). Thus, the low infection parameters for brown bullhead at this site may be the result of some other factor, such as the young age of the fish population. In comparison, brown bullhead from the Lake of Stryiska (Dniester river basin) had the same infection parameters as those in the Shatsk Lakes, probably having been translocated from there due to human activity.

Our study confirms that the North American parasites *G. nebulosus, L. pricei* and *L. monticellii* were co-introduced into Europe and Ukraine with brown bullhead. However, as the three parasites are specific to North American catfish and have direct life-cycles we do not expect them to switch to local fish fauna. Co-introduced monogenean parasites have previously been used as a bio-indicator for assessing the relatedness of non-indigenous fish host populations (Ondračková *et al*., 2021). As all three parasite species in this case were previously recorded in brown bullhead from Poland (Prost, 1973), the only other European population for which all three parasites have been reported together, it is quite likely that the more recent Ukrainian populations are derived from fish previously introduced to Poland. A Polish origin is more probable considering that both bullhead populations occur in the same watershed, i.e. the Vistula river basin. The Lake on Stryiska (Dniester river basin) is located in Lviv, which lies within both the Black Sea (Dniester river watershed) and Baltic Sea (Vistula river watershed) river basins (Koinova & Chorna, 2019). Thus, the presence of bullhead at sites inside Lviv is most likely the result of translocation due to human activity (Kutsokon *et al*., 2018), while differences in fish parasite fauna in lakes inside Lviv most likely reflect temporary local conditions than any difference in river drainage (Kvach *et al*., 2022). This is also reflected in the brown bullhead's parasite fauna, which was similar across the entire western Ukrainian region.

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Conflicts of interest

The authors declare that they have no conflicts of interest.

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