Research Paper

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Limited parasite acquisition by non-native *Lepomis gibbosus* (Actinopterygii: Centrarchidae) at two ponds in the Upper Rhine basin, Germany

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Abstract

Metazoan parasite communities of *Lepomis gibbosus* (Centrarchidae), one of the most successfully introduced fish species in Europe, were studied at two isolated ponds (Knielingen, Tropfen) along the Upper Rhine in Germany. Nine parasite taxa were observed, including North American species co-introduced to Europe (ancyrocephalid monogeneans, diplostomid trematodes), circumpolar species infecting *L. gibbosus* in both their native and non-native ranges (bothriocephalid cestodes) and locally acquired parasitic nematodes. Both parasite communities consisted predominantly of North American species. Acquisition of local parasites was not observed at Tropfen, where the fish community comprised just two species, with *L. gibbosus* dominant. Low prevalence and abundance of acquired parasites was found at Knielingen, which supported a diverse fish community. At Tropfen, a high abundance of the North American parasite *Posthodiplostomum centrarchi* probably contributed to the lower condition index, hepatomegaly and splenomegaly observed. Due to low local parasite competency, *L. gibbosus* appears to have no significant impact on parasite dynamics in affected habitats.

Introduction

Parasite communities in species translocated to new areas usually comprise a reduced number of naturally co-introduced and locally acquired parasites (e.g. Torchin *et al.*, 2003; Prenter *et al.*, 2004). The number of co-introduced parasites depends on both their presence and density in the founder population and their ability to persist in the new environment (MacLeod *et al.*, 2010). Factors affecting the host's ability to acquire local parasites are less clear, but include both host competence and environmental conditions (Paterson *et al.*, 2012). Introduction of a novel host species can also affect local parasite communities through the introduction of non-native parasite species that may be adopted by local hosts, and through any effects the invading host has on local parasite dynamics (e.g. Telfer & Bown, 2012; Lagrue, 2017).

One of the most successful introduced fish species in Europe is the pumpkinseed sunfish *Lepomis gibbosus* (L., 1758) (Actinopterygii: Centrarchidae). *Lepomis gibbosus* is native to freshwaters of eastern North America, ranging from New Brunswick in Canada to northeastern Georgia in the USA (Scott & Crossman, 1973). At the end of 19th century, the species was imported together with five other centrarchid species to sites in (mainly) western Europe for recreational angling and as an aquarium and garden pond fish (Holčík, 1991). Of the three *Lepomis* species introduced, only *L. gibbosus* dispersed successfully over the following century. The species is now established in most European countries following subsequent introductions and natural spreading into adjacent waterbodies (Copp & Fox, 2007). Several European populations have attained high densities, with subsequent impacts on local fish (Ribeiro & Leunda, 2012) and macroinvertebrate fauna (van Kleef *et al.*, 2008).

Lepomis gibbosus was first introduced to Germany as a sport fish between 1881 and 1887 (Nehring *et al.*, 2010). An established population was later observed in the wild in the River Neckar (a Rhine tributary). The first record of *L. gibbosus* in the River Rhine was in 1903, from where it spread further into a number of tributaries. Since 1980, the species has established numerous populations in the Rhine, Main and Danube basins (summarized in Wiesner *et al.*, 2010). In the Rhine basin, the species commonly occurs in water bodies adjacent to the main river, attaining high local population densities (Lelek & Buhse, 1992).

In contrast to the increasing number of studies on life-history traits (e.g. Cucherousset *et al.*, 2009), behaviour (e.g. Almeida *et al.*, 2014) and dispersal (e.g. Fobert *et al.*, 2013) throughout Europe in recent decades, knowledge regarding parasite communities in this

widely established non-native species remains scarce (but see Hockley *et al.*, 2011 or Stoyanov *et al.*, 2018). The majority of parasite studies to date have focused on a single parasite species, either acquired (Stavrescu-Bedivan *et al.*, 2014; Masson *et al.*, 2015) or co-introduced (Rubtsova, 2015; Kvach *et al.*, 2017), or a select group of parasites such as endoparasites (Košuthová *et al.*, 2009), nematodes (Pilecka-Rapacz & Sobecka, 2008) or monogeneans (Sterud & Jørgensen, 2006; Havlátová *et al.*, 2015). In their native range, centrarchid fishes exhibit high parasite diversity, summarized in Hoffman (1999). Native *L. gibbosus* is known to host over 100 parasite species, with monogenean and digenean parasites being the most common in terms of species richness (Hoffman, 1999) and abundance (e.g. Chapman *et al.*, 2015).

Therefore, in the present study we aimed to characterize all metazoan parasites of *L. gibbosus* from two isolated artificial ponds in Germany at the component and infracommunity levels. We also evaluate the potential impact of both acquired and natural North American parasite species on the health of *L. gibbosus* by assessing the relationship between parasite abundance and host condition indices.

Materials and methods

Study area

Fish were collected from two isolated ponds near the cities of Rheinstetten (Tropfen pond; 48°58′09.55″N, 8°17′43.98″E) and Karlsruhe (Knielingen pond; 49°02′19.29″N, 8°20′12.02″E) on 11 July 2017. Tropfen is a small temporary pond of *c.* 1100 m², modified in 2008 to promote threatened amphibian species. *Lepomis gibbosus* first appeared in the pond in 2010/2011, although the source is unknown. The fish community currently consists of just two species, *L. gibbosus* and the three-spined stickleback *Gasterosteus aculeatus* L., 1758, while the reduced invertebrate community consists of one mollusc, the acute bladder snail *Physella acuta* (Draparnaud, 1805), one ephemeropteran, the pond olive *Cloeon dipterum* (L., 1761), and a very low abundance of odonata larvae; the most common species are highly mobile aquatic beetles and Heteroptera (Keller, 2015; Herzog, 2016). Knielingen, a former gravel pit created in 1940, covers approximately 15,000 m², with maximum depth of 8 m and mean depth of 4–5 m. It is inhabited by a range of fish species, either stocked by anglers (e.g. common carp *Cyprinus carpio* (L., 1758), tench *Tinca tinca* (L., 1758), eel *Anguilla anguilla* (L., 1758)) or naturally reproducing (*L. gibbosus*, perch *Perca fluviatilis* (L., 1758), sunbleak *Leucaspius delineatus* (Heckel, 1843), roach *Rutilus rutilus* (L., 1758) and common bream *Abramis brama* (L., 1758)). The littoral zone supports a range of habitats, with vegetation, woody debris and steep banks. It is not known when *L. gibbosus* were first introduced to the pond.

Fish and parasite sampling

Twenty individuals of *L. gibbosus* were collected from each pond in July 2017 using either seine netting (7 m long, 4 mm mesh size; Tropfen) or hook-and-line angling (Knielingen). The fish were transported live in aerated river water to the laboratory and dissected within 48 h of transport to ensure minimum loss of parasites (Kvach *et al.*, 2016). Prior to dissection, the standard length (SL, mm) and total and eviscerated body weight (W_T and W_E, g) were measured for each fish (table 1). The wet weight of the

Table 1. Fish length (SL), age, condition index (CI), hepatosomatic index (HSI), splenosomatic index (SSI), gonadosomatic index (GSI) and parasite community descriptors for *Lepomis gibbosus* in the Knielingen and Tropfen ponds (Upper Rhine near Karlsruhe, Germany). Knielingen: established population; Tropfen pond: founder population.

	Knielingen	Tropfen
n	20	20
Mean SL (range)	59 (50–67)	56 (52–63)
Age	2+; 3+	2+
Mean CI (range)	1.74 (1.44–2.01)	1.50 (1.28–1.68)
Mean HSI (range)	1.08 (0.42–1.97)	2.69 (1.57–5.63)
Mean SSI (range)	0.51 (0.09–1.28)	1.67 (0.42–2.65)
Mean GSI (range); male	1.9 (1.3–3.2), n = 17	2.2 (1.5–3.2), n = 10
Mean GSI (range); female	8.0 (7.2–8.6), n = 3	5.4 (2.5–8.3), n = 9
Mean (±SD) parasite abundance (range)	103.5 ± 59.1 (4–272)	491.9 ± 157.6 (284–882)
Parasite prevalence (%)	100	100
Total species richness	10	5
Infracommunity (IC) richness	3–7	4–5

gonads, liver and spleen (excluding weight of parasites) were measured for each fish to the nearest 0.001 g using an EG 620-3NM laboratory scale (Kern, Balingen, Germany), and sex was determined by inspection of gonads. A sample of scales was also taken to estimate fish age through mean spacing of scale annuli.

Individual fish were examined under a binocular microscope (Olympus SZX 10; Olympus Optical Co., Okaya, Japan) for the presence of metazoan parasites, using standard methodology (Ergens & Lom, 1970). Fish skin, fins, gills and opercula were examined for ectoparasitic species, and eyes, heart, liver, spleen, kidney, peritoneal cavity, intestinal tract and muscle tissue were examined for endoparasitic species. Trematoda and Cestoda were removed from the particular tissues, preserved in 4% formaldehyde, stained with iron acetic carmine, dehydrated in ethanol of increasing concentration, and mounted in Canada balsam as permanent slides (Georgiev *et al.*, 1986). Monogenea were gently removed from the gills, preserved in a 1:1 mixture of ammonium picrate and glycerine (Monogenea) as semi-permanent slides (Malmberg, 1970), and nematodes were preserved in hot 4% formaldehyde and then identified in glycerol temporary slides (Moravec, 2013). Parasites were identified under an Olympus BX50 light microscope equipped with phase contrast, differential interference contrast and Olympus MicroImage™ Digital Image Analysis software (Olympus Optical Co., Okaya, Japan) with corresponding keys. Monogenean parasites were identified according to the shape of sclerotized parts of the haptor and copulatory organs, using the key in Gusev *et al.* (1985). Scolex morphology was used for identification of *Triaenophorus* species according to Kuperman (1973) and *Bothriocephalus* species according to Kuchta *et al.* (2008). Moravec (2013) was used for identification of nematode species, based on the morphology of anterior section, tail and caeca, and the total length of larva (*Contracaecum*) and length and position of tridents (*Camallanus*). The methods used for identification of the trematode metacercariae (*Posthodiplostomum*) followed Kvach *et al.* (2017), using both morphological and molecular characteristics. All parasites have been

deposited at the Invertebrate Collection of the Faculty of Science, Masaryk University Brno, Czech Republic.

Data analysis

Prevalence was expressed as the percentage of infected fish in a sample and mean abundance was expressed as the mean number of parasites for all hosts in a sample. Metazoan parasite community structure was analysed at the infracommunity (including all parasites on a single host) and component community (all parasites in a host population) levels (Bush et al., 1997). Somatic condition (CI) was calculated for eviscerated body weight (W_E) using the formula $CI = 10^5 \times W_E/SL^b$, where b represents the slope of the weight–length relationship. The weight–length relationship, weight = a × length^b (Cone, 1989), was calculated using all individuals from both sites. Hepatosomatic index (HSI) was calculated as HSI = W(liver minus weight of parasites) $\times 10^2/W_E$; splenosomatic index: SSI = W(spleen) $\times 10^3/W_E$; and gonadosomatic index: GSI = W(gonads) $\times 10^2/W_E$. Mean and range values for condition indices are shown in table 1.

Between-site variability in fish SL and condition index was tested using the t-test (equal variance [CI] or unequal variance [SL, HSI, SSI]) on a sample of fish of the same age (2+) (Knielingen N = 18, Tropfen N = 20). GSI was not analysed because of the low sample size. Data were checked for normality prior to performing parametric tests. Differences in infracommunity species richness and abundance of all and individual parasite species were analysed using the non-parametric Mann–Whitney U test. Because comparisons were conducted for five parasite species, α level was Bonferroni corrected to 0.05/5 = 0.001. Relationships between (1) parasite abundance and fish SL, and (2) parasite abundance and condition index were tested for using Spearman's rank correlation. All statistical analyses were performed using PAST software (PAlaeontologicalSTatistics, v.1.77, http://folk.uio.no/ohammer/past/; Hammer et al., 2001).

Results

A total of 11,907 metazoan parasites were collected, with a mean abundance (±SD) of 298 ± 228. Nine parasite taxa were identified, and one larval nematode was impossible to identify because of the low quality of the preserved material. All fish examined were infected by three to seven parasite species. Three monogeneans, Onchocleidus similis Müller, 1936, Actinocleidus oculatus (Müller, 1934) and Actinocleidus recurvatus Mizelle & Donahue, 1944, were found on gills at both sites with 100% prevalence. In addition, the gill monogenean Onchocleidus dispar Müller, 1936 and trematode metacercariae of Posthodiplostomum centrarchi (Hoffman, 1958) were observed at both sites. Two cestodes (Bothriocephalus claviceps (Goeze, 1782) and Triaenophorus nodulosus (Pallas, 1781) larvae) and three nematodes (Camallanus lacustris (Zoega, 1776), Contracaecum ovale (von Linstow, 1907) and one unidentified larva) were collected at low abundance and prevalence at Knielingen (table 2).

Mean parasite abundance (table 1) was significantly higher at Tropfen compared to Knielingen (Mann–Whitney U test; Z = 5.4, P < 0.001), reflecting a higher mean abundance of the trematode P. centrarchi (371 found at Tropfen and 0.2 at Knielingen; Z = 5.7, P < 0.001; table 2). Mean abundance of monogenean species was similar between sites. Infracommunity richness ranged from 3–7 at Knielingen and 4–5 at Tropfen and did not differ significantly between the sites (Z = 0.7, P = 0.48).

Aside from two individuals from Knielingen, most of the fish examined were 2+ years old. At Knielingen, the 2+ fish were significantly larger (t = 2.3, P = 0.030) and exhibited higher CI (t = 5.5, P < 0.001) than those from Tropfen. On the other hand, HSI (t = 5.6, P < 0.001) and SSI (t = 7.2, P < 0.001) were significantly higher at Tropfen (table 1). Overall parasite abundance tended to increase with fish SL at Knielingen only ($r_s = 0.46$, P = 0.042), although there was no relationship with any of the condition indices. Likewise, neither site showed any relationship between fish condition and parasite species. At Tropfen, there was a positive relationship between HSI and abundance of P. centrarchi metacercariae and consequently overall abundance ($r_s = 0.79$, P < 0.001 and $r_s = 0.72$, P < 0.001, respectively).

Discussion

The parasite community of L. gibbosus in two isolated ponds in the Rhine river basin mainly consisted of natural centrarchid-specific North American parasites, i.e. four ancyrocephalid monogenean species and the diplostomid trematode P. centrarchi. All five parasites are reported in Germany and in the Rhine river basin for the first time. In addition, two circumpolar cestode species that also infect L. gibbosus in its native range were found at Knielingen, B. claviceps and T. nodulosus. At the same site, three nematode species were acquired by L. gibbosus, with C. lacustris representing a new host record.

Ancyrocephalid monogeneans, which have a direct life cycle and display high host specificity, were co-introduced with their fish hosts to Germany and appear to have persisted and established stable populations at both ponds. Comparable North American ancyrocephalid diversity to ours has also been found in Italian (River Po; Galli et al., 2005) and French (River Durance; Havlátová et al., 2015) non-native populations of L. gibbosus. In comparison, the monogenean community in Black Sea drainage populations in Ukraine, Bulgaria, Romania, Croatia, and the Czech and Slovak Republics, assessed between the 1950s and 1970s (Roman, 1953; Margaritov, 1968; Pashkevichute, 1971; references in Moravec, 2001) and more recently (Ondračková et al., 2011; Rubtsova, 2015; Kvach et al., 2018; Stoyanov et al., 2018), and in isolated ponds in Norway (Sterud & Jørgensen, 2006) and England (Hockley et al., 2011), was less diverse than in the present study. The first European introductions of L. gibbosus occurred in France and Germany over a hundred years ago (Welcomme, 1981), with donor populations consisting of hundreds of individuals originating from multiple sources (Wiesner et al., 2010). Release to open waters and population establishment was documented within a very short period, with the first records in France occurring in 1887 (Copp et al., 2002) and 1896 in Germany (Sieglin, 1902). Current French and German populations, therefore, are likely to represent the progeny of the original source fish. In this case, the high diversity of natural parasites is likely to be the result of co-introduction, survival and establishment from a large and diverse founder population.

Presence of North American P. centrarchi has only recently been confirmed in several widely spaced European L. gibbosus populations (Kvach et al., 2017; Stoyanov et al., 2017), despite a long history of L. gibbosus occurrence in Europe. A number of studies over recent decades failed to detect this parasite (e.g. Piasecki & Falandysz, 1994; references in Moravec, 2001), suggesting its recent introduction and rapid spread, potentially related to the spread of its first intermediate host, physid snails (Kvach et al., 2017). The mollusc P. acuta sensu lato has been recorded in the

Table 2. Stage, infection site, prevalence, mean abundance with 95% confidence intervals (CI) and mean intensity of infection (with range in parentheses) of parasite species found on *Lepomis gibbosus* in the Knielingen and Tropfen ponds (Upper Rhine, near Karlsruhe, Germany). Knielingen pond: established population; Tropfen pond: founder population.

			Knielingen (n = 20)			Tropfen (n = 20)		
	Stage	Site	Prevalence	Mean abundance (95% CI)	Mean intensity (range)	Prevalence	Mean abundance (95% CI)	Mean intensity (range)
Monogenea								
Actinocleidus oculatus	Adult	Gills	100%	23.4 (16.8–30)	23.4 (2–56)	100%	33.3 (21.2–45.3)	33.3 (4–88)
Actinocleidus recurvatus	Adult	Gills	100%	31.5 (22.6–40.4)	31.5 (1–65)	100%	38.8 (24.1–53.5)	38.8 (6–130)
Actinocleidus spp.	Larva	Gills	70%	2.9 (1.4–4.4)	4.1 (1–12)	50%	2.3 (0.7–3.8)	4.3 (2–13)
Onchocleidus dispar	Adult	Gills	50%	2.4 (0.6–4.1)	5.2 (1–12)	90%	5.2 (3.4–6.9)	5.7 (1–12)
Onchocleidus similis	Adult	Gills	100%	39.3 (24.3–54.4)	39.4 (1–148)	100%	40.6 (8–130)	40.6 (8–130)
Onchocleidus spp.	Larva	Gills	45%	2.0 (0.2–3.8)	4.4 (1–15)	35%	0.9 (0.2–1.6)	2.6 (1–4)
Trematoda								
Posthodiplostomum centrarchi	Metacercaria	Internal organs	15%	0.2 (−0.1–0.4)	1.5 (1–15)	100%	371.0 (311.9–430.1)	371.1 (198–670)
Cestoda								
Bothriocephalus claviceps	Adult	Intestine	20%	0.3 (−0.01–0.5)	1.3 (1–2)			
Triaenophorus nodulosus	Plerocercoid	Liver	55%	1.0 (0.3–0.6)	1.9 (1–6)			
Nematoda								
Camallanus lacustris	Adult	Intestine	20%	0.5 (−0.1–0.5)	1.7 (1–2)			
Contracaecum ovale	Larva	Mesentery	30%	0.3 (0.03–0.6)	1.2 (1–2)			
Nematoda sp.	Larva	Liver	10%	0.1 (−0.1–0.2)	1			

Table 3. List of parasite species of *Lepomis gibbosus* documented in literature from five European countries, with % prevalence (and abundance in parentheses) where available; n.a., not available.

	Germany[1]	Bulgaria[2]	Poland[3,4]	Slovakia[5]	England[6]
Co-introduced parasites					
Onchocleidus similis Mueller, 1936	100 (40)	32 (1.4)			
Onchocleidus dispar Mueller, 1936	70 (3.8)	4 (0.04)			100 (20)
Actinocleidus oculatus (Mueller, 1934)	100 (28)				
Actinocleidus recurvatus Mizelle and Donahue, 1944	100 (35)				
Posthodiplostomum centrarchi (Hoffman, 1958)	58 (186)	8 (0.2)			
Acquired parasites					
Diplostomum sp. mtc.			39 (0.6)		
Tylodelphys clavata (Nordmann, 1832), mtc.			8 (0.1)		
Ichthyocotylurus platycephalus (Creplin, 1825), mtc.			2 (0.03)		
Bothriocephalus claviceps	10 (0.1)				
Triaenophorus nodulosus (Pallas, 1781)	28 (0.5)			12 (n.a.)	
Proteocephalus percae (Müller, 1780)				4 (n.a.)	
Schulmanela petruschewskii (Shulman, 1948)		4 (0.7)	15; 40 (n.a.; 1.1)		
Spiroxis contortus (Rudolphi, 1819)		10 (0.3)			
Raphidascaris acus (Bloch, 1779)			3 (<0.05)		
Camallanus lacustris (Zoega, 1776)	10 (0.2)				
Contracaecum ovale (Linstow, 1907)	15 (0.2)				
Contracaecum sp.		1 (0.02)	1 (0.001)		2 (0.02)
Nematoda sp. 1			1 (0.01)		
Nematoda sp. 2			1 (0.01)		
Nematoda sp. 3			1 (0.01)		
Nematoda sp. 4	5 (0.03)				
Nematoda sp. 5					2 (0.02)
Acanthocephalus lucii (Müller, 1776)			3 (0.1)		
Paracanthocephalus sp.			2 (0.04)		
Echinorhynchidae				2 (n.a.)	
Acanthocephala gen. sp.			1 (0.01)		2 (0.02)
Unio sp.			44 (11.2)		
Glochidia spp.					53 (1)
Ergasilus sieboldi (Nordmann, 1832)			6 (0.1)		
Caligus lacustris Steenstrup et Lütken, 1861			2 (0.02)		

[1] This study; [2] Lake Anasovsko Wetlands, Bulgaria (Stoyanov *et al.*, 2018); [3,4] Warm-water power plant discharge canal near Szczecin (Piasecki & Falandysz, 1994, Pilecka-Rapacz & Sobecka, 2008); [5] Coarse fishing lake in south-west England (Hockley *et al.*, 2011); [6] Rivers Bodrog, Tisa, Latorica, Ondava, Laborec in eastern Slovakia (Košuthová *et al.*, 2009)

Rhine since 1870, and was widely distributed in the upper Rhine at the beginning of the 20th century (Bernauer & Jansen, 2006; Leuven *et al.*, 2009), being the only mollusc species found in Tropfen (Keller, 2015; Herzog, 2016). *Posthodiplostomum centrarchi* was found at both our localities, but at markedly different intensities. The sporadic occurrence of *P. centrarchi* at Knielingen may result from the low density of mollusc intermediate hosts as a result of high predation pressure and/or the encounter-dilution effect, which predicts that the number of parasites per host will be negatively correlated with host density, as the total number of transmission stages is divided between all hosts in the area, reducing the probability of host–parasite contact (Buck & Lutterschmidt, 2017). A related alternative hypothesis, encounter-dilution via non-compatible hosts, predicts that frequent encounters with non-competent fish species can decrease a parasite's capability of infecting competent hosts through energy depletion or damage (Gendron & Marcogliese, 2017). At Knielingen, the fish community comprised a wide range of local species, presumed to be non-compatible for North American *Posthodiplostomum* cercariae. As Knielingen is ten times larger than Tropfen and *L. gibbosus* are less dominant, this decreases the parasite's chances of encountering a compatible host.

Generalist parasites (only endoparasitic helminths in this case) were found only at Knielingen, where native fish species such as percids and cyprinids co-occur. Although some of these parasites have a circumpolar distribution encompassing the centrarchid native range, it is assumed that they were acquired in the host's non-native range. Use of *L. gibbosus* as an intermediate host by the cestode *T. nodulosus*, and as a paratenic host by *B. claviceps*, has previously been documented in both its native (Hoffman, 1999) and introduced range (Košuthová *et al.*, 2009; Masson *et al.*, 2015 for *T. nodulosus*; Aisa & Gattaponi, 1981 for *B. claviceps*). The life cycle of *T. nodulosus* includes both cyclopoid copepods and a range of fish species as intermediate hosts, with esocid fish as definitive hosts (Kuperman, 1973). Although *L. gibbosus* appears to be a competent host for this species, low infection intensities indicate potential resistance to this parasite, as also noted by Masson *et al.* (2015). The cosmopolitan species *B. claviceps* is a specific parasite of eels, although other fish species may serve as paratenic hosts, thereby representing a possible additional source of eel infection (Scholz, 1997). While *B. claviceps* can use *L. gibbosus* as a paratenic host, it occurs only rarely as the cestode larvae survive only for a short period (Dupont & Gabrion, 1986). The low infection rates recorded in our data, therefore, suggest that *L. gibbosus* plays a relatively unimportant role in the population dynamics of both these cestode parasites.

The process of becoming a host for a new parasite depends on a complex set of interactions involving aspects of host biology and particular spatial and temporal scales (Paterson *et al.*, 2012). At Knielingen, we recorded just five specimens of *C. lacustris*, six specimens of *C. ovale* nematodes and one unidentified larva. Moravec (1971) recorded *C. lacustris* as being able to develop in a range of fish families serving as paradefinitive or post-cyclic hosts, whereas predatory fishes such as Percidae (predominantly *P. fluviatilis*) and Esocidae serve as typical definitive hosts (Moravec, 2013). Likewise, *C. ovale* was recorded as a parasite of cyprinid and other fishes with an almost cosmopolitan distribution (Moravec, 2013). Although the records presented here represent new host records for these parasites, the findings are not surprising as *L. gibbosus* infection by other *Camallanus* or *Contracaecum* species has also been documented in North America (Hoffman, 1999). Both our own results and those from other non-native populations throughout Europe (e.g. Hockley *et al.*, 2011; Stoyanov *et al.*, 2018) suggest that *L. gibbosus* acquire local parasites only occasionally, and at relatively low prevalence and abundance (see table 3).

In accordance with Masson *et al.* (2015), who examined the effect of the cestode *T. nodulosus* on the health of *L. gibbosus* in France, there was no relationship between CI and overall or individual parasite abundance in this study. Indeed, a lack of parasitism impact on host condition has previously been documented in many fish host–metazoan parasite systems (e.g. Laffargue *et al.*, 2004; Ondračková *et al.*, 2010), this phenomenon usually being explained by low parasite load, host resistance or simply low sample size. However, significant differences in CI were observed between the two ponds, with fish from the larger Knielingen pond (low *L. gibbosus* density) showing significantly higher CI and SL than fish from the smaller Tropfen pond (abundant and highly parasitized population). The better performance of fish from Knielingen could potentially be the result of a lower fish density, with subsequent lower intraspecific competition and parasite burden. The hundred-times higher infection rate of *P. centrarchi* at Tropfen was probably reflected in a significantly higher HSI and SSI compared to fish from the less parasitized

Knielingen population (table 2). Liver mass is usually associated with energy reserves and metabolic activity in fishes (Wooton, 1984); hence, any variation in liver mass may reflect the cost of parasitization on the host's condition. Although parasites have been shown to reduce HSI in several host–parasite systems (Malek, 2001), liver parasites appeared to induce hepatomegaly in our study, as also indicated by the significant increase in liver mass (excluding parasite mass) with increasing number of metacercariae. SSI, which describes the relative size of the spleen, may serve as an indicator of immune activation (Seppänen *et al.*, 2009), with splenic enlargement in fish infected by *P. centrarchi* probably representing an adaptive immunological response to cope with the infection, as in the case of trematode infection in Arctic charr (Seppänen *et al.*, 2009).

Lepomis gibbosus is one of the most successful introduced fish species in Europe, and is currently described as 'potentially invasive' in Germany (Nehring *et al.*, 2010). Any improvement in our knowledge of its parasite fauna, including co-introduced non-native species, and competence to local parasite species will contribute to our better understanding of this species' invasion success. Our results confirm the presence of established co-introduced monogenean populations and a potential negative impact from high North American trematode intensities on host fish health, possibly limiting the host's performance and its overall invasiveness. Given its relatively low competence to local parasites, *L. gibbosus* is not expected to have any significant effect on local parasite species dynamics through amplification effects.

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