Research Paper

Author for correspondence:
P.A. Tierney,
E-mail: tiernep1@tcd.ie

Evidence for enemy release in invasive common dace *Leuciscus leuciscus* in Ireland: a helminth community survey and systematic review

P.A. Tierney[1] , J.M. Caffrey[2], S.M. Matthews[1], E. Costantini[1] and C.V. Holland[1]

[1]Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland and [2]INVAS Biosecurity Ltd., 82 Lakelands Close, Stillorgan, Co Dublin, Ireland

Abstract

Invasive species lose parasites in the process of invasion and tend to be less parasitized than conspecifics in the native range and sympatric native species in the invasive range (enemy release). We evaluated enemy release in an invasive freshwater fish in Ireland, common dace *Leuciscus leuciscus*, using helminth parasite community surveys at the core and front of the invasive range of common dace. Furthermore, we undertook a systematic literature review of helminth infection in common dace across its native range in Great Britain and Europe and invasive range in Ireland. The helminth parasite community survey revealed that invasive common dace were infected with fewer helminth species at the invasion front than at the core. Four helminth taxa – Acanthocephala, Monogenea, Digenea and Nematoda – were present in dace at the invasion core compared to only a single helminth species (*Pomphorhynchus tereticollis*) at the front. The systematic review revealed that invasive common dace in Ireland hosted fewer species of helminths than common dace in the native range. We report a total of three helminth species in common dace in Ireland compared to 24 in Great Britain and 84 in Continental Europe. Our results support the hypotheses that invasive populations are less parasitized than native populations and that more recently established populations host fewer parasites. However, we demonstrate that invasive species may continue to experience release from parasites long after initial invasion.

Introduction

Invasive species are recognized globally as one of the largest threats to biodiversity as well as to human health, the environment and the economy (IUCN, 2000; Pimentel *et al.*, 2001; Hulme, 2014; Lucy *et al.*, 2016). The success of invasive species may be partially explained by their capacity to escape natural enemies such as competitors, predators and parasites in the process of invasion, known as enemy release (Keane & Crawley, 2002; Colautti *et al.*, 2004; Liu & Stiling, 2006). Evidence is mixed as to whether and to what extent enemy release confers a competitive advantage to invasive species (Blossey & Notzold, 1995; Lacerda *et al.*, 2013; Heger & Jeschke, 2018). However, there is strong evidence that invasive species host fewer parasite species compared to conspecifics in their native range (Torchin *et al.*, 2003; Goedknegt *et al.*, 2016; Sarabeev *et al.*, 2017; Schoeman *et al.*, 2019).

Parasites are lost in the process of invasion due to a combination of failure to arrive with invading hosts and failure to persist in the new environment (Macleod *et al.*, 2010). Non-native species must overcome a number of barriers to invasion: geographic barriers in order to be introduced to a novel range, growth and reproduction barriers in order to establish new populations, and dispersal barriers in order to invade new ranges (Blackburn *et al.*, 2011). Parasites must overcome the same barriers to invasion as free-living organisms, often with the additional barrier of switching to native hosts in the introduced range, especially if introduced parasites have multi-host life cycles (Lymbery *et al.*, 2014). Moreover, small founding populations of non-native hosts are likely to harbour only a subset of the parasite fauna of the source population (Hatcher & Dunn, 2011; Lymbery *et al.*, 2014). Among invaders that co-introduce parasites, freshwater fish are the most common and account for over half of documented cases, probably reflecting the high incidence of invasive fish in freshwater ecosystems (Lymbery *et al.*, 2014). Parasites that are successfully co-introduced alongside their invasive hosts may go on to establish infections in native hosts, known as parasite spillover (Prenter *et al.*, 2004; Dunn & Hatcher, 2015; Sures *et al.*, 2019).

While parasites of invasive species are typically lost during the invasion process, invaders often acquire novel parasites as they are exposed to the local parasite community in their invasive range (Sheath *et al.*, 2015; Gendron & Marcogliese, 2016; Loxton *et al.*, 2016). Invasive species usually do not accumulate a sufficient number of local parasite species to replace the lost parasite diversity (Torchin & Mitchell, 2004; Loxton *et al.*, 2016; Schoeman *et al.*, 2019; Stuart *et al.*,

2020) (although see Gendron *et al.*, 2012; Lacerda *et al.*, 2013). This may be due to low competency of invasive hosts for native parasites (Paterson *et al.*, 2013; Tierney *et al.*, 2020) or the absence of host-specific parasites in the invaded range (Kennedy & Bush, 1994; Torchin & Mitchell, 2004). However, it has been suggested that invasive species are more likely to be infected with parasite species that are directly transmitted (e.g. Monogenea, Myxosporea, Crustacea) or generalist parasite species that can utilize many species of intermediate hosts (Dobson & May, 1986; Bauer, 1991; Torchin & Mitchell, 2004; Heger & Jeschke, 2018).

Parasite diversity of an invasive host varies across its invasive range and is expected to be lowest at the expanding edge of the range (the invasion front) (White & Perkins, 2012; David *et al.*, 2018; Stuart *et al.*, 2020). Host density at an invasion front is typically low, which inhibits parasite transmission, and parasites are likely to lag behind the establishment of their invasive hosts or be lost along the invasion corridor due to stochastic events or transience of hosts (Phillips *et al.*, 2010). Lags in parasite establishment along an invasion gradient have been observed in fish (Gaither *et al.*, 2013; David *et al.*, 2018), amphibian (Phillips *et al.*, 2010) and small mammal invasions (Stuart *et al.*, 2020). This decrease in parasite infection along an invasion corridor leads to enhanced enemy release at the invasion front compared to the core of the invasive range (site of first introduction and expansion) (White & Perkins, 2012).

The cyprinid fish, common dace *Leuciscus leuciscus* (Linnaeus 1758), is native to continental Europe with the exception of Ireland, Spain, Italy and Greece (Welcomme, 1988; Kottelat & Freyhof, 2007). Common dace was first introduced to Ireland from Great Britain in 1889 by the accidental release of bait fish into the Munster Blackwater River, County Cork (Went, 1950). Common dace invaded the lower River Barrow in 1992 (Caffrey *et al.*, 2007), and by 2015 their range had spread approximately 90 km upstream (Delanty *et al.*, 2017). Two helminth species (both native to Ireland) have previously been recorded in common dace in Ireland: the eel acanthocephalan *Acanthocephalus clavula* (Kane, 1966) and the generalist acanthocephalan *Pomphorhynchus tereticollis* (Tierney *et al.*, 2020). The current study is the first survey of the helminth community of invasive common dace to be conducted in Ireland.

The distribution of invasive common dace in Ireland provides an opportunity to study helminth parasite community dynamics of an invasive species at the core and front of its invasive range. By sampling from the invasion core on the Munster Blackwater (over 120 years post-introduction) and from the invasion front on the upper River Barrow (less than five years post-colonization), we can utilize a 'space for time' substitution (e.g. Kołodziej-Sobocińska *et al.*, 2018) to study how the helminth parasite community of invasive common dace has changed over time since introduction. In the absence of longitudinal data across the invasion history of an invasive species, a 'space for time' substitution method allows us to infer the timing of events in an invasion by studying spatially separate populations at different stages of invasion. We then supplement our own data with information on the helminth species of common dace across their European range to assess the helminth parasite community between the native and invasive range of common dace.

We aim to answer three main research questions: (1) Is there evidence for enemy release – that is, is the parasite diversity of common dace in Ireland reduced compared to common dace in its native range? (2) Have common dace replaced lost diversity by acquiring local parasites in its invasive range? (3) Do we find enhanced enemy release at the invasion front?

At the macroscale, the recorded parasite diversity of a species is likely to vary across its native range due to variation in the diversity of other hosts and heterogeneity in research effort (Poulin *et al.*, 2020). Host diversity is known to drive parasite diversity (Hechinger & Lafferty, 2005; Thieltges *et al.*, 2011; Kamiya *et al.*, 2014; Johnson *et al.*, 2016). Due to species extirpations caused by glaciation events, northern and western Europe have a lower native biodiversity of freshwater fish than central and Mediterranean European regions (Reyjol *et al.*, 2007). As islands, Great Britain and Ireland have yet lower native freshwater fish biodiversity than continental Europe (Wheeler, 1977). Combining the effect of enemy release and low host biodiversity, we expect helminth parasite diversity in invasive common dace to be lowest in Ireland, at an intermediate level in Great Britain and highest in Continental Europe.

Materials and methods

Invasive common dace were caught by electrofishing in July and August 2015 and 2017, from the core of the common dace invasive range on the Munster Blackwater and at the invasion front on the upper River Barrow (see Tierney *et al.*, 2020). Recent fish community surveys have recorded 11 species of fish in the Munster Blackwater comprising six native fish (brown trout *Salmo trutta*, Atlantic salmon *Salmo salar*, European eel *Anguilla anguilla*, lamprey *Lampetra* sp., three-spined stickleback *Gasterosteus aculeatus* and European flounder *Platichthys flesus*) and five non-native species (common dace, Eurasian minnow *Phoxinus phoxinus*, roach *Rutilus rutilus*, stoneloach *Barbatula barbatula* and gudgeon *Gobio gobio*) (Kelly *et al.*, 2014). In the River Barrow, recent large-scale surveys recorded 12 species comprising five native (brown trout, Atlantic salmon, European eel, lamprey and three-spined stickleback) and seven non-native species (common dace, Eurasian minnow, roach, stoneloach, gudgeon, European perch *Perca fluviatilis* and Northern pike *Esox lucius*), along with one non-native hybrid (bream × roach) (Delanty *et al.*, 2017). Native twaite shad *Alosa fallax* and non-native freshwater bream *Abramis brama*, rudd *Scardinius erythrophthalmus* and tench *Tinca tinca* are also likely be present in the River Barrow (Delanty *et al.*, 2017). Over the two sampling years, a total of 168 common dace were collected from the River Barrow and 119 common dace from the Munster Blackwater (table 1). Subsite sample size varied between years due to the distribution and availability of common dace in these rivers. The size range of the sampled dace were similar between regions (Gaussian Generalized Linear Model: df = 285, coefficient ± standard error (SE) = −0.02 ± 0.03, $t = -0.6$, $P = 0.55$) (table 1).

Fish were euthanized on site using anaesthesia by eugenol oil or percussive stunning and decerebration. Fish were bagged and transported on ice to the laboratory where they were frozen and stored at −20°C until dissection. The eyes, gills, alimentary tract, swim bladder and body cavity were examined for helminth parasites. Keys by Brown *et al.* (1986), Moravec (1994), Gibson *et al.* (2002), Jones *et al.* (2005), Bray *et al.* (2008) and Yamaguti (1963) and the paper by Špakulová *et al.* (2011) were used for parasite identification. The identification of *P. tereticollis* was additionally confirmed with molecular analysis (see Tierney *et al.*, 2020). Five digenean trematode specimens and three nematode specimens found in common dace were unidentifiable beyond class (Digenea) and phylum (Nematoda), respectively, because the characteristic features in these specimens were not sufficiently clear to allow for morphological identification.

Table 1. Sample size and size range (standard length) of common dace *Leuciscus leuciscus* sampled (n = 287).

Location	Site	2015			2017			Both years		
		N	Length range (mm)	Mean length (mm) ± SD	n	Length range (mm)	Mean length (mm) ± SD	n	Length range (mm)	Mean length (mm) ± SD
River Barrow (invasion front)	Monasterevin	40	67–130	110±16	5	89–125	106±17	45	67–130	109±16
	Portarlington	33	100–241	163±45	82	89–206	144±18	115	89–241	150±29
	River Slate	8	115–235	148±42	–	–	–	8	115–235	148±42
	Total	**81**	**67–241**	**135±41**	**87**	**89–206**	**142±20**	**168**	**67–241**	**138±32**
Munster Blackwater (invasion core)	Fermoy	33	98–150	117±13	48	72–194	137±36	81	72–194	129±31
	Glanworth	38	107–210	152±32	–	–	–	38	107–210	152±32
	Total	**71**	**98–210**	**136±31**	**48**	**72–194**	**137±36**	**119**	**72–210**	**136±33**

SD, standard deviation.

Statistics were conducted using R (R Core Team, 2018). Helminth community structure was analysed at the component and infracommunity levels (Bush *et al.*, 1997) following Kennedy & Hartvigsen (2000). We described component community structure using total number of taxa and Simpson's Index of Diversity, calculated as:

$$D = 1 - \frac{\sum \mathrm{in}\,(n-1)}{N(N-1)}$$

where *n* is the total number of individuals of taxon *i* and *N* is the total number of individuals of all taxa, using the R package vegan (Oksanen *et al.*, 2019). The value of D ranges from zero to one and increases with increased diversity and evenness (Pielou, 1966; DeJong, 1975).

To describe infracommunity structure, we calculated mean taxonomic richness, maximum taxonomic richness, prevalence, mean intensity (Bush *et al.*, 1997), aggregation (mean-to-variance ratio, $\sigma^2/\bar{x}$; Wilson *et al.*, 2002) and mean and maximum Brillouin's Index of Diversity (Pielou, 1966). Brillouin's Index was calculated in R using the formula:

$$HB = \frac{\ln(N!) - \sum \ln(ni!)}{N}$$

where *N* is the total number of parasite individuals in a host and *ni* is the number of individuals of taxon *i*. Brillouin's index measures the diversity of a fully censused collection where HB increases with increased diversity (Pielou, 1966).

Prevalence of the acanthocephalan *P. tereticollis* was modelled with a binomial generalized linear mixed model (GLMM) and intensity of *P. tereticollis* was modelled with a negative binomial GLMM using the R package glmmTMB (Brooks *et al.*, 2017). Data on *P. tereticollis* combined intra-intestinal adult and extra-intestinal subadult parasite individuals (see Tierney *et al.*, 2020). Models incorporated invasion region (front or core) and host standard length as fixed effects, and subsite and year as random effects. Model fit was validated using the R package DHARMa (Hartig, 2019). All other helminth taxa detected in common dace occurred at too low prevalence and intensity to be fitted to a model.

A systematic literature search of helminth parasites of common dace across their European range was conducted in Web of Science using the search string (dace OR 'Leuciscus leuciscus') AND (parasit* OR helminth) and in Google Scholar using the search terms 'Leuciscus leuciscus', 'dace', 'parasite', 'helminth'. Additional searches were conducted by replacing 'Leuciscus leuciscus' with 'freshwater fish'. Records of non-helminth parasites, experimental infections and records of the subspecies Siberian dace, *Leuciscus leuciscus baicalensis*, were excluded. The Natural History Museum Host-Parasite database (Gibson *et al.*, 2005) and references in the collected literature were also checked for additional relevant material that had not been captured in the literature search.

Results

Helminth community survey

Four helminth taxa were recorded in common dace across their invasive range in Ireland: one acanthocephalan species, one monogenean species and a number of nematode and digenean trematode individuals, which were unidentifiable to species level. All four taxa were present in common dace at the invasion core (although during different years) and one species was recorded at the invasion

Table 2. Parameters of component and infracommunity structure in invasive common dace *Leuciscus leuciscus* from the front (Upper River Barrow) and core (Munster Blackwater) of its invasive range in Ireland.

	Front			Core			
	2015	2017	Both years	2015	2017	Both years	All sites
n	81	87	168	71	48	119	287
Mean taxonomic richness ± SD	0.04 ± 0.19	0	0.02 ± 0.13	0.35 ± 0.54	0.54 ± 0.54	0.43 ± 0.55	0.19 ± 0.42
Max. taxonomic richness	1	0	1	2	2	0	2
Total number of taxa	1	0	1	3	2	4	4
Mean Brillouin Index ± SD	0	0	0	0.01 ± 0.07	0.001 ± 0.01	0.01 ± 0.05	0.003 ± 0.03
Max. Brillouin Index	0	0	0	0.46	0.07	0.46	0.46
Simpson's Index	0	0	0	0.14	0.01	0.04	0.03

SD, standard deviation.

front. At the invasion core, we recorded three and two helminth taxa in 2015 and 2017, respectively (table 2). At the invasion front, we recorded one helminth species in 2015 but did not detect any helminths in 2017. Helminth community diversity in dace was greater at the invasion core than the invasion front, as measured by taxonomic richness, total number of taxa, Brillouin's Index and Simpson's Index (table 2). The maximum taxonomic richness per fish was two, which was recorded in both years at the invasion core. Here, Brillouin's and Simpson's diversity indices were lower in 2017 than 2015, but mean taxonomic richness increased from 2015 to 2017.

The majority of common dace (82%) were uninfected. Among the four helminth taxa recorded in common dace, the acanthocephalan *P. tereticollis* was the most prevalent (table 3). The prevalence of *P. tereticollis* ranged from zero at the front in 2017 to 52% (95% confidence interval: 37–67) at the core in 2017. At the invasion core, prevalence of *P. tereticollis* was significantly higher than at the front (binomial GLMM: df = 282, coefficient ± SE = 6.02 ± 1.49, $Z = 4.05$, $P < 0.001$). Intensity of *P. tereticollis* infection did not differ significantly between the invasion core and front (negative binomial GLMM: df = 41, coefficient ± SE = 0.83 ± 1.30, $Z = 0.63$, $P = 0.53$). Both prevalence (binomial GLMM: df = 282, coefficient ± SE = 0.07 ± 0.01, $Z = 5.71$, $P < 0.001$) and intensity (negative binomial GLMM: df = 41, coefficient ± SE = 1.05 ± 0.17, $Z = 6.35$, $P < 0.001$) of *P. tereticollis* increased with host size (see also Tierney *et al.*, 2020). *Pomphorhynchus tereticollis* infection at the front was highly aggregated with a small number of infected fish (3.7%) hosting high worm burdens (mean intensity ± standard deviation (SD) = 48 ± 35) (table 3). *Pomphorhynchus tereticollis* was the only helminth that infected common dace populations at the invasion front. The other three helminth taxa all occurred in few hosts and in low numbers (prevalence less than 6% and intensity less than 2; table 3). The monogenean *Discocotyle sagittata* was represented by only a single individual, recorded in the core in 2017. The three nematode individuals and five digenean trematode individuals found in common dace were all recorded from the invasion core in 2015.

Systematic review

The literature search yielded 443 records of 109 helminth species from 20 European countries (see supplementary material for the full dataset). For the purposes of this study, locations were categorized into four broad biogeographical ranges: Ireland, Great Britain,

Nordics and Continental Europe (excluding Nordics) (adapted from Reyjol *et al.*, 2007). We combined our own survey data for helminth species present with the previous record for *A. clavula* in common dace in Ireland to give a total of three helminth species recorded in invasive common dace in Ireland, representing two acanthocephalan species and one monogenean species. This number was low compared to the number of helminth species in the native range of common dace in Great Britain, the Nordics and Continental Europe (fig. 1). Digenean trematodes are the most commonly recorded helminth parasite species of common dace in Great Britain, the Nordics and Continental Europe (fig. 1). In the Nordics and Continental Europe, monogeneans are the next most common, while, in Great Britain, similar numbers of acanthocephalan, cestode and monogenean species are recorded.

Although every effort was made to be comprehensive, it was not possible to gather information relating to specific site and sample size for every record due to some data being drawn from checklists that did not report such details. In total, we obtained site data for 163 records. The number of papers that recorded helminth species in common dace (as a rough proxy for sample effort) varied between countries and sites (supplementary table S1). We note that this approach is likely to underestimate sample efforts where records came from existing checklists, which were coded as one paper. Additionally, some papers included in the systematic review specifically studied only a single parasite species or taxon, including Thomas & Ollevier (1992) on *Anguillicola crassus* (Belgium), Zrnčić *et al.* (2009) on *Posthodiplostomum cuticula* in Croatia, Kirk & Lewis (1994) on *Sanguicola* spp. in Great Britain (Anglian and Thames regions) and Perrot-Minnot *et al.* (2019) on *Pomphorhynchus laevis* and *P. tereticollis* in France. Where relatively comprehensive surveys of the helminth community have been conducted in common dace, the number of helminth species in the component community is similar across the native range. For example, in England, a total of ten species of helminth have been recorded in common dace in the River Avon (Kennedy, 1974), 14 species in the River Kivijoki system in Finland (Ieshko *et al.*, 1997), nine species in the River Morava in the Czech Republic (Gelnar *et al.*, 1994) and ten species in the Tamis River region in Serbia (Djikanovic *et al.*, 2012) (supplementary table S1).

Discussion

Invasive common dace in Ireland had a lower diversity of helminth parasites compared to common dace in their native

Table 3. Population biology parameters of helminth taxa recorded in common dace *Leuciscus leuciscus* at the front (Upper River Barrow) and core (Munster Blackwater) of their invasive range.
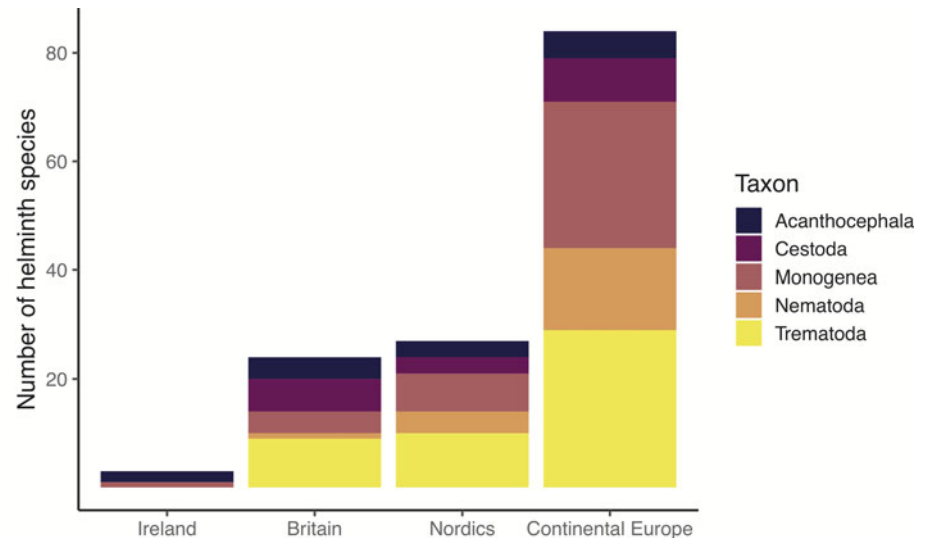
Helminth	Taxon	Host tissue(s)	Year	Front					Core				
				n	N	Prevalence (95% CI)	Intensity ± SE	σ²/x̄	n	N	Prevalence (95% CI)	Intensity ± SE	σ²/x̄
Pomphorhynchus tereticollis	Acanthocephala	Intestine, mesenteries	2015	3	144	3.7 (1–10)	48.0 ± 35.2	99.2	19	100	26.8 (16–39)	1.1 ± 1.3	8.4
			2017	0	0	0	–	–	25	314	52.1 (37–67)	12.6 ± 3.3	27.5
Discocotyle sagittata	Monogenea	Gills	2015	0	0	0	–	–	0	0	0	–	–
			2017	0	0	0	–	–	1	1	2.1 (0–11)	1	1
Unidentified nematodes	Nematoda	Intestine	2015	0	0	0	–	–	2	3	2.8 (0–10)	1.5 ± 0.5	1.6
			2017	0	0	0	–	–	0	0	0	–	–
Unidentified digenean trematodes	Digenea	Intestine	2015	0	0	0	–	–	4	5	5.6 (2–13)	1.3 ± 0.3	1.4
			2017	0	0	0	–	–	0	0	0	–	–

n, number of infected hosts; *N*, number of helminth individuals; CI, confidence interval; SE, standard error.

range and a lower diversity of helminth taxa at the invasion front compared to the invasion core. The total number of species recorded in dace was markedly lower in Ireland compared to Great Britain, the Nordics and Continental Europe where common dace are native. These findings support the hypothesis that common dace have lost parasites in the process of invasion and have experienced release from helminth parasites. Populations of common dace at the long-established invasion core had higher component and infracommunity diversity than those at the recently colonized invasion front. This supports the hypotheses that enemy release is enhanced at the invasion front and more recently established populations host less diverse parasite communities.

The lower number of total helminth species in common dace in Ireland compared to Great Britain is as expected. Holland & Kennedy (1997) found a reduced parasite fauna in most freshwater fish in Ireland compared to Great Britain and demonstrated that the helminth parasites found in Ireland are a subset of the British parasite fauna. In the literature review, we found fewer helminth parasites in Britain compared to Continental Europe, but the difference in scale and in sample effort between these areas must be noted. It would be expected that a geographically smaller area would have lower biodiversity (Rosenzweig, 1995). Moreover, there are fewer papers reporting helminths in common dace in Great Britain than in Continental Europe, probably by virtue of fewer researchers specializing in fish parasitology. Nonetheless, when we compare Great Britain and Europe at a similar scale, the parasite community of common dace at the population level has similar richness across the native range. For example, the River Avon in England and the River Morava in the Czech Republic have both been well studied (see Kennedy, 1974; Moravec, 2001) and have similar numbers of recorded helminth species. Our finding of enemy release in invasive common dace compared to Great Britain remains valid when examined at the scale of river/host population. Esch *et al.* (1988) studied three English rivers and found between eight and nine helminth species infecting common dace populations. This is in contrast to our findings of zero to four helminth taxa in total at the population level in Irish rivers. These considerations highlight the limitations of producing checklists of species: that biases are likely to exist in sampling effort, geographic coverage and possible inclusion of accidental infections (Holland & Kennedy, 1997; Poulin *et al.*, 2015, 2020; Poulin, 2019). Helminth parasite species richness is likely to have been underestimated in some regions due to lack of study and, in some cases (e.g. France, Perrot-Minnot *et al.*, 2019; and Croatia, Zrnčić *et al.*, 2009), the available records focussing on a given helminth species or taxon rather than the complete helminth community.

We did not find evidence that common dace co-introduced novel helminth species to Ireland when introduced from Great Britain. *Pomphorhynchus tereticollis* is considered native to Europe, including the British Isles (Perrot-Minnot *et al.*, 2018). It is hypothetically possible that genetically distinct strains of *P. tereticollis* could have been introduced from Great Britain with the introduction of common dace (O'Mahony *et al.*, 2004a, b). However, given that the Irish strain of the parasite is considered to be widespread and any founder population of genetically distinct strains co-introduced with dace would have been small, such an introduction would have been unlikely to impact the native *P. tereticollis* strain. *Discocotyle sagittata* is similarly widespread throughout Ireland and Great Britain (Kennedy, 1974; Molloy *et al.*, 1993; Holland & Kennedy, 1997; Byrne *et al.*,

Fig. 1. Total number of helminth species recorded in common dace *Leuciscus leuciscus* in its invasive range in Ireland and its native range in Great Britain, the Nordics and Continental Europe.

2002). As the nematode and digenean trematode specimens recovered from common dace were unidentifiable, we cannot state whether they represent novel species to Ireland. However, considering that the prevalence and intensity of these taxa were so low, it is unlikely that these would represent co-introduced species maintained by the invasive population of common dace. *Discocotyle sagittata*, nematodes and digeneans were rare in common dace and each taxon was present only in one locality in one year, respectively. This could be an indication that these were accidental infections of parasites maintained by other hosts and not regular components of the dace parasite community (e.g. as with *Crepidostomum* sp. in eel in Thomas, 1958).

We found notably few monogeneans and digenean trematodes in common dace in Ireland, although they are among the most frequently reported taxa in the native range. The generalist digenean eye flukes of the family *Diplostomidae* are frequently acquired parasites of invasive fish species (Ondračková *et al.*, 2009; Francová *et al.*, 2011; Lacerda *et al.*, 2013; Tyutin *et al.*, 2013; Gendron & Marcogliese, 2017). In Ireland, there was a notable absence of eye flukes in dace, despite eight species of the family *Diplostomidae* having been previously recorded in introduced cyprinids in Ireland (Holland & Kennedy, 1997). Given that diplostomids are known to detrimentally impact the foraging ability and anti-predator response of their fish host (Crowden & Broom, 1980; Seppälä *et al.*, 2011; Lacerda *et al.*, 2013; Gopko *et al.*, 2017), the release from eye flukes in Ireland may be advantageous for invasive common dace. Monogeneans, being directly transmitted, theoretically should be less likely to be lost during invasion since additional intermediate hosts are not required for their persistence. Host-specific monogenean parasites have been found to have been successfully co-introduced in a number of invasions and capable of host switching to native fish (Galli *et al.*, 2007; Sarabeev *et al.*, 2018; Šimková *et al.*, 2019). Conversely, several studies have refuted that directly transmitted parasites make especially successful invaders. Lymbery *et al.* (2014) found no association between parasite life cycle and host switching, and Lyndon & Kennedy (2001) found that the indirectly transmitted acanthocephalans are the most successful parasite colonizers of the British Isles. Holland & Kennedy (1997) also noted that monogeneans and digeneans are both poorly represented in the Irish helminth parasite fauna compared to that of Great Britain. The success of acanthocephalans as colonizers was mirrored in our study; two of the three species recorded in

common dace in Ireland were acanthocephalans. In contrast, the Acanthocephala make up 19% of total parasite species in common dace in Great Britain and 6% of total parasite species in common dace in Continental Europe. Moreover, the acanthocephalan *P. tereticollis* was the only helminth to infect common dace at the invasion front.

Helminth diversity in common dace was particularly low at the invasion front. This population of common dace had effectively no parasite diversity, being infected with only one species, the generalist acanthocephalan *P. tereticollis* (see Tierney *et al.*, 2020). Moreover, that species was present in only one year at low prevalence and intensity, raising the possibility that stochastic events may have caused it to disappear from the front population in the latter of the two sampling years. Additionally, given that parasites tend to be spatially aggregated in their environment (Sherrard-Smith *et al.*, 2015), it is possible that differences in subsite sample sizes between 2015 and 2017 resulted in differences in detection between years. Nonetheless, our findings of low helminth diversity at the invasion front support theoretical predictions (Phillips *et al.*, 2010; White & Perkins, 2012) and other empirical studies (Gendron *et al.*, 2012; Loxton *et al.*, 2016; David *et al.*, 2018; Stuart *et al.*, 2020) that demonstrate that parasite diversity is lowest in most recently invaded parts of the range. These findings also fit the colonization time hypothesis that areas recently colonized by host species have the lowest diversity of parasites (Guégan and Kennedy, 1993).

We expected that invasive species acquire local parasites over time (Kvach & Winkler, 2011; Emde *et al.*, 2012; White & Perkins, 2012). However, parasite diversity in common dace was low even in the invasion core where common dace have been established for over 120 years, especially considering the possibility that dace may be merely an accidental host for some of the recorded taxa. The acquisition of local parasite species by invasive common dace seems markedly slow compared to other fish invaders – for example, Ponto–Caspian gobies. Gendron *et al.* (2012) found that, following an initial period of parasite release, invasive round goby *Neogobius melanostomus* in the Great Lakes accumulated native parasites and had similar parasite diversity to native species by 15 years post-colonization. Francová *et al.* (2011) found that round goby acquired native parasites and reported no difference between the parasite species richness of native and invasive round goby populations in the River Danube. In contrast, Kvach & Stepien (2008), studying invasive round goby

and tubenose goby, *Proterorhinus semilunaris*, in the Great Lakes, found lower parasite species richness compared to the native Ponto–Caspian range and that most parasite species were rare, but observed no increase in parasite richness over ten years. Both Kvach & Stepien (2008) and Gendron *et al.* (2012) recorded that the helminth parasite communities of invasive gobies were composed entirely of acquired native parasites with no evidence of goby specialists or helminths co-introduced by gobies.

The low helminth diversity of common dace in Ireland may be similarly due to a lack of co-introduced cyprinid-specific parasites and an absence of suitable parasites in the invaded range. Ireland has a depauperate freshwater fish fauna, dominated by salmonids and other anadromous fish (Wheeler, 1977; Fahy, 1989). Furthermore, Ireland has no native cyprinids, although a number of cyprinid species such as bream, rudd and roach have been introduced prior to the 20th century (Fitzmaurice, 1984; Fitzsimons and Igoe, 2004). The River Barrow has a relatively rich community of other non-native cyprinid species (Delanty *et al.*, 2017), which one might expect would promote greater parasite diversity in common dace. However, we observed markedly low parasite diversity in this river. Given that Ireland's cyprinid fauna are the result of introductions and presumably underwent parasite loss over the course of their invasions, there may be few cyprinid-specific helminth parasite species present in the local parasite community adapted to infect common dace. If cyprinid-specialist parasites are present, their transmission may be diluted by the presence of dominant native hosts such as salmonids. Adaptation of local parasites to introduced common dace may take some time. For example, the parasite community of introduced bream in Ireland comprises 16 species, similar to the total number of helminth species in its native British range (Holland & Kennedy, 1997). However, this may be explained by the length of time since colonization; unlike common dace, bream are thought to have been present in Ireland since around the 5th century (Hayden *et al.*, 2010). Furthermore, in the ecological context of Ireland where biodiversity is known to be low, it may not be possible for an invasive species to regain similar parasite richness to its native parasite diversity without the occurrence of subsequent invasion and co-introduction events to introduce suitable and/or specific parasites.

Conclusions

Invasive common dace in Ireland are infected with a considerably less diverse parasite community than common dace in their native ranges in Britain and Continental Europe, supporting the hypothesis that this invasive species has undergone enemy release. The generalist acanthocephalan *P. tereticollis* was the only helminth parasite species detected in the common dace populations at the invasion front, and all helminth taxa found at the invasion core, other than *P. tereticollis*, were rare, despite this population being established for over 120 years. Our findings provide evidence that not only do recently established populations host less diverse parasite communities, but that enemy release may persist in invasive populations long after establishment. This apparent slow acquisition of local parasites by common dace may be explained by the biogeographical and ecological context of Ireland, where biodiversity is low and native cyprinids are absent.

References

Bauer ON (1991) Spread of parasites and diseases of aquatic organisms by acclimatization: a short review. *Journal of Fish Biology* **39**, 679–686.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU and Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* **26**, 333–339.

Blossey B and Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* **83**, 887–889.

Bray RA, Gibson D and Jones A (2008) *Keys to the trematoda*, **Volume 3**. Wallingford, Oxfordshire, UK, CAB International Publishing and The Natural History Museum.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M and Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**, 378–400.

Brown AF, Chubb JC and Veltkamp CJ (1986) A key to the species of Acanthocephala parasitic in British freshwater fishes. *Journal of Fish Biology* **28**, 327–334.

Bush AO, Lafferty KD, Lotz JM and Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *The Journal of Parasitology* **83**, 575–583.

Byrne CJ, Holland CV, Poole R and Kennedy CR (2002) Comparison of the macroparasite communities of wild and stocked brown trout (*Salmo trutta* L.) in the west of Ireland. *Parasitology* **124**, 435–445.

Caffrey JM, Hayden B and Walsh T (2007) *Dace (Leuciscus leuciscus L.): an invasive fish species in Ireland. Irish Freshwater Fisheries, Ecology and Management* **5**. Dublin, Ireland, Central Fisheries Board.

Colautti RI, Ricciardi A, Grigorovich IA and MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* **7**, 721–733.

Crowden AE and Broom DM (1980) Effects of the eyefluke, *Diplostomum spathaceum*, on the behaviour of dace (*Leuciscus leuciscus*). *Animal Behaviour* **28**, 287–294.

David GM, Staentzel C, Schlumberger O, Perrot-Minnot MJ, Beisel JN and Hardion L (2018) A minimalist macroparasite diversity in the round goby of the Upper Rhine reduced to an exotic acanthocephalan lineage. *Parasitology* **145**, 1020–1026.

DeJong TM (1975) A comparison of three diversity indices based on their components of richness and evenness. *Oikos* **26**, 222.

Delanty K, Kelly FL, McLoone P, et al. (2017) *Fish stock assessment of the river barrow catchment 2015*. Dublin, Inland Fisheries Ireland.

Djikanovic V, Paunovic M, Nikolic V, Simonovic P and Cakic P (2012) Parasitofauna of freshwater fishes in the Serbian open waters: a checklist of parasites of freshwater fishes in Serbian open waters. *Reviews in Fish Biology and Fisheries* **22**, 297–324.

Dobson A and May R (1986) Patterns of invasions by pathogens and parasites. pp. 58–76 *in* Mooney H and Drake J (*Eds*) *Ecology and biological invasions of North America and Hawaii*. Berlin, Springer-Verlag.

Dunn AM and Hatcher MJ (2015) Parasites and biological invasions: parallels, interactions, and control. *Trends in Parasitology* **31**, 189–199.

Emde S, Rueckert S, Palm HW and Klimpel S (2012) Invasive Ponto-Caspian amphipods and fish increase the distribution range of the Acanthocephalan *Pomphorhynchus tereticollis* in the River Rhine. *PLoS ONE* **7**, e53218.

Esch GW, Kennedy CR, Bush AO and Aho JM (1988) Patterns in helminth communities in freshwater fish in Great Britain: alternative strategies for colonization. *Parasitology* **96**, 519–532.

Fahy E (1989) Conservation and management of brown trout, *Salmo trutta*, in Ireland. *Freshwater Biology* **21**, 99–109.

Fitzmaurice P (1984) The effects of freshwater fish introductions into Ireland. *EIFAC technical paper* **42** (Supplement 2), 448–457.

Fitzsimons M and Igoe F (2004) Freshwater fish conservation in the Irish republic: a review of pressures and legislation impacting on conservation efforts. *Biology and Environment* **104**, 17–32.

Francová K, Ondračková M, Polačik M and Jurajda P (2011) Parasite fauna of native and non-native populations of *Neogobius melanostomus* (Pallas, 1814) (Gobiidae) in the longitudinal profile of the Danube River. *Journal of Applied Ichthyology* **27**, 879–886.

Galli P, Strona G, Benzoni F, Crosa G and Stefani F (2007) Monogenoids from freshwater fish in Italy, with comments on alien species. *Comparative Parasitology* **74**, 264–272.

Gelnar M, Koubková B, Pláňková H and Jurajda P (1994) Report on metazoan parasites of fishes of the River Morava with remarks on the effects of water pollution. *Helminthologia* **31**, 47–56.

Gendron AD and Marcogliese DJ (2016) Reduced survival of a native parasite in the invasive round goby: Evidence for the dilution hypothesis? *Aquatic Invasions* **11**, 189–198.

Gendron AD and Marcogliese DJ (2017) Enigmatic decline of a common fish parasite (*Diplostomum* spp.) in the St. Lawrence River: evidence for a dilution effect induced by the invasive round goby. *International Journal for Parasitology: Parasites and Wildlife* **6**, 402–411.

Gendron AD, Marcogliese DJ and Thomas M (2012) Invasive species are less parasitized than native competitors, but for how long? The case of the round goby in the Great Lakes-St. Lawrence Basin. *Biological Invasions* **14**, 367–384.

Gibson D, Jones A and Bray RA (2002) *Keys to the trematoda*, Volume 1. Wallingford, Oxfordshire, UK, CAB International Publishing and The Natural History Museum.

Gibson D, Bray RA and Harris EA (2005) *The Natural History Museum host-parasite database*. London. Available at www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/index.html (accessed 1 February 2020).

Goedknegt MA, Feis ME, Wegner KM, Luttikhuizen PC, Buschbaum C, Camphuysen K, van der Meer J and Thieltges DW (2016) Parasites and marine invasions: ecological and evolutionary perspectives. *Journal of Sea Research* **113**, 11–27.

Gopko M, Mikheev VN and Taskinen J (2017) Deterioration of basic components of the anti-predator behavior in fish harboring eye fluke larvae. *Behavioral Ecology and Sociobiology* **71**, 68.

Guégan J-F and Kennedy C (1993) Maximum local helminth parasite community richness in British freshwater fish: a test of the colonization time hypothesis. *Parasitology* **106**, 91–100.

Hartig F (2019) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.6. Available at https://CRAN.R-project.org/, accessed 22 June 2020.

Hatcher MJ and Dunn AM (2011) Parasites and invasions. pp. 224–264 *in* Hatcher MJ and Dunn AM (*Eds*) *Parasites in ecological communities: from interactions to ecosystems*. Cambridge, Cambridge University Press.

Hayden B, Pulcini D, Kelly-Quinn M, O'Grady M, Caffrey J, McGrath A and Mariani S (2010) Hybridisation between two cyprinid fishes in a novel habitat: genetics, morphology and life-history traits. *BMC Evolutionary Biology* **10**, 1–11.

Hechinger RF and Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society B* **272**, 1059–1066.

Heger T and Jeschke JM (2018) Enemy release hypothesis. pp. 92–102 *in* Jeschke JM and Heger T (*Eds*) *Invasion biology: hypotheses and evidence*. Boston, Massachusetts, CABI.

Holland CV and Kennedy CR (1997) A checklist of parasitic helminth and crustacean species recorded in freshwater fish from Ireland. *Biology and Environment* **97**, 225–243.

Hulme PE (2014) Invasive species challenge the global response to emerging diseases. *Trends in Parasitology* **30**, 267–270.

Ieshko EP, Malakhova RP and Golitsyna NB (1997) Ecological characteristics of lake fish parasite fauna formation in the River Kivijoki system. pp. 311–318 *in* Lindholm T, Heikkilä R and Heikkilä M (*Eds*) *Ecosystems, fauna and flora of the Finnish-Russian Nature Reserve Friendship*. Helsinki, Finnish Environment Institute.

IUCN (2000) *IUCN guidelines for the prevention of biodiversity loss caused by invasive alien species*. Gland, Switzerland, IUCN.

Johnson PTJ, Wood CL, Joseph MB, Preston DL, Haas SE and Springer YP (2016) Habitat heterogeneity drives the host-diversity-begets-parasite-diversity relationship: evidence from experimental and field studies. *Ecology Letters* **19**, 752–761.

Jones A, Bray RA and Gibson D (2005) *Keys to the trematoda*. Volume 2. Wallingford, Oxfordshire, UK, CAB International Publishing and The Natural History Museum.

Kamiya T, O'Dwyer K, Nakagawa S and Poulin R (2014) Host diversity drives parasite diversity: meta-analytical insights into patterns and causal mechanisms. *Ecography* **37**, 689–697.

Kane MB (1966) Parasites of Irish fishes. *Scientific Proceedings of the Royal Dublin Society B* **1**, 205–220.

Keane RM and Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* **17**, 164–170.

Kelly FL, Connor L, Matson R, Feeney R, Morrissey E, Coyne J and Rocks K (2014) *Sampling fish for the water framework directive - summary report 2013*. Dublin, Inland Fisheries Ireland.

Kennedy CR (1974) A checklist of British and Irish freshwater fish parasites with notes on their distribution. *Journal of Fish Biology* **6**, 613–644.

Kennedy CR and Bush AO (1994) The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* **109**, 187–196.

Kennedy CR and Hartvigsen RA (2000) Richness and diversity of intestinal metazoan communities in brown trout *Salmo trutta* compared to those of eels *Anguilla anguilla* in their European heartlands. *Parasitology* **121**, 55–64.

Kirk RS and Lewis JW (1994) The distribution and host range of species of the blood fluke *Sanguinicola* in British freshwater fish. *Journal of Helminthology* **68**, 315–318.

Kołodziej-Sobocińska M, Brzeziński M, Niemczynowicz A and Zalewski A (2018) High parasite infection level in non-native invasive species: it is just a matter of time. *Ecography* **41**, 1283–1294.

Kottelat M and Freyhof J (2007) *Handbook of European freshwater fishes*. Berlin, Publications M. Kottelat, Cornol, Switzerland/J. Freyhof.

Kvach Y and Stepien CA (2008) Metazoan parasites of introduced round and tubenose gobies in the Great Lakes: support for the "enemy release hypothesis.". *Journal of Great Lakes Research* **34**, 23–35.

Kvach Y and Winkler HM (2011) The colonization of the invasive round goby *Neogobius melanostomus* by parasites in new localities in the southwestern Baltic Sea. *Parasitology Research* **109**, 769–780.

Lacerda ACF, Takemoto RM, Poulin R and Pavanelli GC (2013) Parasites of the fish *Cichla piquiti* (Cichlidae) in native and invaded Brazilian basins: release not from the enemy, but from its effects. *Parasitology Research* **112**, 279–288.

Liu H and Stiling P (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions* **8**, 1535–1545.

Loxton KC, Lawton C, Stafford P and Holland CV (2016) Reduced helminth parasitism in the introduced bank vole (*Myodes glareolus*): more parasites lost than gained. *International Journal for Parasitology: Parasites and Wildlife* **5**, 175–183.

Lucy FE, Roy H, Simpson A, et al. (2016) INVASIVESNET towards an international association for open knowledge on invasive alien species. *Management of Biological Invasions* **7**, 131–139.

Lymbery AJ, Morine M, Kanani HG, Beatty SJ and Morgan DL (2014) Co-invaders: the effects of alien parasites on native hosts. *International Journal for Parasitology: Parasites and Wildlife* **3**, 171–177.

Lyndon AR and Kennedy CR (2001) Colonisation and extinction in relation to competition and resource partitioning in acanthocephalans of freshwater fishes of the British Isles. *Folia Parasitologica* **48**, 37–46.

Macleod CJ, Paterson AM, Tompkins DM and Duncan RP (2010) Parasites lost - do invaders miss the boat or drown on arrival? *Ecology Letters* **13**, 516–527.

Molloy S, Holland C and Poole R (1993) Helminth parasites of brown and sea trout *Salmo trutta* L. from the west coast of Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **93B**, 137–142.

Moravec F (1994) *Parasitic nematodes of freshwater fishes of Europe.* Dordrecht, the Netherlands, Kluwer Academic Publishers.

Moravec F (2001) *Checklist of the metazoan parasites of fishes of the Czech Republic and the Slovak Republic (1873-2000).* Czech Republic, Academia, Praha.

Oksanen J, Blanchet FG and Friendly M, et al. (2019) *vegan: Community Ecology Package. R package version 2.5-6.* Available at https://CRAN.R-project.org/package=vegan.

O'Mahony EM, Bradley DG, Kennedy CR and Holland CV (2004a) Evidence for the hypothesis of strain formation in *Pomphorhynchus laevis* (Acanthocephala): an investigation using mitochondrial DNA sequences. *Parasitology* **129**, 341–347.

O'Mahony EM, Kennedy CR and Holland CV (2004b) Comparison of morphological characters in Irish and English populations of the acanthocephalan *Pomphorhynchus laevis* (Müller, 1776). *Systematic Parasitology* **59**, 147–157.

Ondračková M, Dávidová M, Blažek R, Gelnar M and Jurajda P (2009) The interaction between an introduced fish host and local parasite fauna: *Neogobius kessleri* in the middle Danube River. *Parasitology Research* **105**, 201–208.

Paterson RA, Lal A, Dale M, Townsend CR, Poulin R and Tompkins DM (2013) Relative competence of native and exotic fish hosts for two generalist native trematodes. *International Journal for Parasitology: Parasites and Wildlife* **2**, 136–143.

Perrot-Minnot MJ, Špakulová M, Wattier R, Kotlík P, Düşen S, Aydoğdu A and Tougard C (2018) Contrasting phylogeography of two Western Palaearctic fish parasites despite similar life cycles. *Journal of Biogeography* **45**, 101–115.

Perrot-Minnot MJ, Guyonnet E, Bollache L and Lagrue C (2019) Differential patterns of definitive host use by two fish acanthocephalans occurring in sympatry: *Pomphorhynchus laevis* and *Pomphorhynchus tereticollis*. *International Journal for Parasitology: Parasites and Wildlife* **8**, 135–144.

Phillips BL, Kelehear C, Pizzatto L, Brown GP, Barton D and Shine R (2010) Parasites and pathogens lag behind their host during periods of host range advance. *Ecology* **91**, 872–881.

Pielou EC (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**, 131–144.

Pimentel D, McNair S, Janecka J, et al. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment* **84**, 1–20.

Poulin R (2019) Best practice guidelines for studies of parasite community ecology. *Journal of Helminthology* **93**, 8–11.

Poulin R, Besson AA, Morin MB and Randhawa HS (2015) Missing links: testing the completeness of host-parasite checklists. *Parasitology* **143**, 114–122.

Poulin R, Presswell B and Jorge F (2020) The state of fish parasite discovery and taxonomy: a critical assessment and a look forward. *International Journal for Parasitology.* https://doi.org/10.1016/j.ijpara.2019.12.009.

Prenter J, MacNeil C, Dick JTA and Dunn AM (2004) Roles of parasites in animal invasions. *Trends in Ecology and Evolution* **19**, 385–390.

R Core Team (2018) *R: a language and environment for statistical computing.* Vienna, Austria, R Foundation for Statistical Computing.

Reyjol Y, Hugueny B, Pont D, et al. (2007) Patterns in species richness and endemism of European freshwater fish. *Global Ecology and Biogeography* **16**, 65–75.

Rosenzweig ML (1995) *Species diversity in space and time.* Cambridge, Cambridge University Press.

Sarabeev V, Balbuena JA and Morand S (2017) Testing the enemy release hypothesis: abundance and distribution patterns of helminth communities in grey mullets (Teleostei: Mugilidae) reveal the success of invasive species. *International Journal for Parasitology* **47**, 687–696.

Sarabeev V, Balbuena JA and Morand S (2018) Invasive parasites are detectable by their abundance-occupancy relationships: the case of helminths from *Liza haematocheilus* (Teleostei: Mugilidae). *International Journal for Parasitology* **48**, 793–803.

Schoeman AL, Kruger N, Secondi J and du Preez LH (2019) Repeated reduction in parasite diversity in invasive populations of *Xenopus laevis*: a global experiment in enemy release. *Biological Invasions* **21**, 1323–1338.

Seppälä O, Karvonen A and Valtonen ET (2011) Eye fluke-induced cataracts in natural fish populations: is there potential for host manipulation? *Parasitology* **138**, 209–214.

Sheath DJ, Williams CF, Reading AJ and Robert Britton J (2015) Parasites of non-native freshwater fishes introduced into England and Wales suggest enemy release and parasite acquisition. *Biological Invasions* **17**, 2235–2246.

Sherrard-Smith E, Perkins SE, Chadwick EA and Cable J (2015) Spatial and seasonal factors are key determinants in the aggregation of helminths in their definitive hosts: *Pseudamphistomum truncatum* in otters (*Lutra lutra*). *International Journal for Parasitology* **45**, 75–83.

Šimková A, Řehulková E, Rasoloariniaina JR, Jorissen MWP, Scholz T, Faltýnková A, Mašová Š and Vanhove MPM (2019) Transmission of parasites from introduced tilapias: a new threat to endemic Malagasy ichthyofauna. *Biological Invasions* **21**, 803–819.

Špakulová M, Perrot-Minnot M-JJ and Neuhaus B (2011) Resurrection of *Pomphorhynchus tereticollis* (Rudolphi, 1809) (Acanthocephala: Pomphorhynchidae) based on new morphological and molecular data. *Helminthologia* **48**, 268–277.

Stuart P, Paredis L, Henttonen H, Lawton C, Ochoa Torres CA and Holland CV (2020) The hidden faces of a biological invasion: parasite dynamics of invaders and natives. *International Journal for Parasitology* **50**, 111–123.

Sures B, Nachev M and Grabner D (2019) The River Rhine as hotspot of parasite invasions. pp. 409–429 *in* Mehlhorn H and Klimpel S (*Eds*) *Parasite and disease spread by major rivers on earth. Parasitology research monographs, Vol 12.* Cham, Springer.

Thieltges DW, Hof C, Dehling DM, Brändle M, Brandl R and Poulin R (2011) Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna. *Global Ecology and Biogeography* **20**, 675–682.

Thomas JD (1958) Studies on *Crepidostomum metoecus* (Braun) and *C. farionis* (Müller), parasitic in *Salmo trutta* L. and *S. salar* L. in Britain. *Parasitology* **48**, 336–352.

Thomas K and Ollevier F (1992) Paratenic hosts of the swimbladder nematode *Anguillicola crassus*. *Diseases of Aquatic Organisms* **13**, 165–174.

Tierney PA, Caffrey JM, Vogel S, Matthews SM, Costantini E and Holland CV (2020) Invasive freshwater fish (*Leuciscus leuciscus*) acts as a sink for a parasite of native brown trout *Salmo trutta*. *Biological Invasions* **22**, 2235–2250.

Torchin ME and Mitchell CE (2004) Parasites, pathogens, and invasions by plants and animals. *Frontiers in Ecology and the Environment* **2**, 183–190.

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ and Kuris AM (2003) Introduced species and their missing parasites. *Nature* **421**, 628–630.

Tyutin AV, Verbitsky VB, Verbitskaya TI and Medyantseva EN (2013) Parasites of alien aquatic animals in the upper Volga basin. *Russian Journal of Biological Invasions* **4**, 54–59.

Welcomme RL (1988) *International introductions of inland aquatic species.* Technical paper, number 294. Rome, Italy, Food and Agriculture Organization of the United Nations.

Went AEJ (1950) Notes on the introduction of some freshwater fish into Ireland. *Journal of the Department of Agriculture* **47**, 3–8.

Wheeler A (1977) The origin and distribution of the freshwater fishes of the British Isles. *Journal of Biogeography* **4**, 1–24.

White TA and Perkins SE (2012) The ecoimmunology of invasive species. *Functional Ecology* **26**, 1313–1323.

Wilson K, Bjørnstad O, Dobson A, Merler S, Poglayen G, Randolph S, Read A and Skorping A (2002) Heterogeneities in macroparasite infections: patterns and processes. pp. 6–44 *in* Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H and Dobson AP (*Eds*) *The ecology of wildlife diseases.* Oxford, Oxford University Press.

Yamaguti S (1963) *Systema Helminthum. Volume IV. Monogenea and Aspidocotylea.* New York, Interscience Publishers Inc.

Zrnčić S, Oraić D, Mihaljević Ž, Ćaleta M, Zanella D, Jelić D and Jelić M (2009) First observation of *Posthodiplostomum cuticola* (Nordmann, 1832) metacercariae in cypriniformes from Croatia. *Helminthologia* **46**, 112–116.