Parasite-mediated predation between native and invasive amphipods

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Parasites can structure biological communities directly through population regulation and indirectly by processes such as apparent competition. However, the role of parasites in the process of biological invasion is less well understood and mechanisms of parasite mediation of predation among hosts are unclear. Mutual predation between native and invading species is an important factor in determining the outcome of invasions in freshwater amphipod communities. Here, we show that parasites mediate mutual intraguild predation among native and invading species and may thereby facilitate the invasion process. We find that the native amphipod *Gammarus duebeni celticus* is host to a microsporidian parasite, *Pleistophora* sp. (new species), with a frequency of infection of 0–90%. However, the parasite does not infect three invading species, *G. tigrinus*, *G. pulex* and *Crangonyx pseudogracilis*. In field and laboratory manipulations, we show that the parasite exhibits cryptic virulence: the parasite does not affect host fitness in single-species populations, but virulence becomes apparent when the native and invading species interact. That is, infection has no direct effect on *G. d. celticus* survivorship, size or fecundity; however, in mixed-species experiments, parasitized natives show a reduced capacity to prey on the smaller invading species and are more likely to be preyed upon by the largest invading species. Thus, by altering dominance relationships and hierarchies of mutual predation, parasitism strongly influences, and has the potential to change, the outcome of biological invasions.

Keywords: parasites; invasions; amphipod; intraguild predation; microsporidian

1. INTRODUCTION

Parasites can reverse the outcome of competitive interactions (Hanley *et al.* 1995; Yan *et al.* 1998) and parasite-mediated apparent competition has been implicated in species invasions (Settle & Wilson 1990; Rushton *et al.* 2000). However, predation has arguably been shown to generate the most dramatic outcomes in interactions between invaders and natives (Zaret & Paine 1973; Schoener & Spiller 1996; Fritts & Rodda 1998). Thus, we must understand the factors that mediate predation if we are to explain and predict the success of biological invasions.

Exotic amphipod crustaceans have invaded many native communities throughout the world, through both coincidental transport with humans and deliberate introductions for fish farming, angling or ecological experiments (Pinkster *et al.* 1992; Dick *et al.* 1997; Van der Velde *et al.* 2000). Since the early 1900s, fresh waters in Ireland have been invaded by three amphipod species: the European *Gammarus pulex* and the North American *G. tigrinus* and *Crangonyx pseudogracilis* (Strange & Glass 1979; Costello 1993). The invaders have excluded the native *G. duebeni celticus* from some sites, but in others the native species maintains long-term populations, even though these sites are connected to sites invaded many years previously. Sometimes, two or more species are present in

apparent coexistence, or in the process of invasion and replacement. Mutual intraguild predation (IGP), that is predation between potentially competing species (Polis *et al.* 1989), is a powerful force underlying exclusions among these four species (Dick 1996). The native *G. d. celticus* is larger than the three invading species (*G. d. celticus* is larger than *G. pulex*, which is larger than *G. tigrinus*, which in turn is larger than *C. pseudogracilis*; ranges of body lengths of 12–17 mm, 10–14 mm, 10–12 mm and 4–7 mm, respectively), but sits midway in a hierarchy of mutual IGP, preying more upon the smaller invaders *G. tigrinus* and *C. pseudogracilis* than they prey on it, while the largest invader, *G. pulex*, shows greater predation on *G. d. celticus* than vice versa (Dick 1996).

These natives and invaders are host to a range of acanthocephalan, protozoan and microsporidian parasites, some shared, some not, at different levels of prevalence (Dunn & Dick 1998). In this study, we investigate how parasitism influences predatory interactions and the outcome of biological invasions by surveying amphipod parasitism in the field and manipulating amphipod parasitism and native and invader assemblage composition in both field and laboratory experiments.

2. MATERIAL AND METHODS

(a) Field survey

We surveyed 95 sites in Northern Ireland between July and September 2000 (figure 1). All uninvaded sites had connections

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Figure 1. The occurrence of native and invading amphipod species and the infection status of the native species with *Pleistophora* sp. in 95 assemblages sampled in Northern Ireland. Open circles, native only; black circles, invader(s) only; grey circles, co-occurring native and invader(s); crosses, parasitized native; thin black line, indirect catchment connections.

with invaded sites, with no physical barriers present to prevent invaders reaching them. Further, *G. tigrinus* and *G. pulex* have had *ca.* 80 and 50 years, respectively, to invade these rivers and lakes since their introduction and *C. pseudogracilis* has had *ca.* 20 years (Costello 1993). Kick sampling collected at least 150 individual amphipods from each site. We screened *G. d. celticus* from 83 populations, *G. tigrinus* from 13 populations, *G. pulex* from 26 populations and *C. pseudogracilis* from six populations for a microsporidian parasite that necrotizes amphipod abdominal musculature, forming an opaque mass of degenerated tissue clearly visible using light microscopy (C. MacNeil, personal observation). At two sites (Articlave and Macosquin Rivers, UK grid references C784336 and C827285, respectively), which contained only *G. d. celticus*, 50 Surber samples (each covering 0.05 m² and collecting a minimum of 30 individuals) were taken at random within a 50 m reach and each was assessed for parasite prevalence at this patch level. During June 2001, these two sites were revisited and the *G. d. celticus* populations were sampled to examine the effects of parasitism on size and fecundity.

(b) *Parasite identification, transmission and host specificity*

The small subunit rRNA gene of the parasite was PCR amplified for sequencing from three infected individuals using microsporidian-specific primers (PCR and sequencing primers are listed in table 1). PCR products were purified and submitted for direct sequencing in both directions. We generated 1483 base pairs of sequence representing full small subunit rDNA, internal transcribed spacer and partial large subunit rDNA genes from this parasite. We measured transmission efficiency and host specificity by feeding parasitized tissue (from Articlave River natives) to 30 unparasitized adults of each species (natives from an unparasitized population: Six Mile Water, grid reference J200849) and screening for infection after 50 days by light microscopy and by PCR amplification. Controls ($n = 30$ in each case) were natives and invaders (all three species) fed with unparasitized tissue. In addition, visibly unparasitized natives ($n = 30$) from a parasitized population (Articlave River) were screened by PCR amplification to ascertain whether the visible presence or absence of the parasite was a robust indicator of infection status.

Table 1. Microsporidian-specific small subunit rRNA and large subunit rRNA primers used for PCR amplification and sequencing of the parasite *Pleistophora* sp.

primer	sequence 5'–3'	reference
V1f	CACCAGGTTGATTCTGCCTGAC	Weiss <i>et al.</i> (1994)
18sf	GTTGATTCTGCCTGACGT	Baker <i>et al.</i> (1995)
350sf	CCAAGGACGGCAGCAGGCGCGAAA	
530f	GTGCCAGCAGCCGCGG	Vossbrinck <i>et al.</i> (1993)
HG2f	ACGTAAGCTGGAGGATCGAAGA	Gatehouse & Malone (1998)
964r	CGCGTTGAGTCAAATTAAGCCGCACA	
981r	TGGTAAGCTGTCCCGCGTTGAGTC	
HG2r	ATCCTAGTTAGTTTCTTCTCCTCCTT	Gatehouse & Malone (1998)
HG4r	TCTCCTTGGTCCGTGTTTCAA	Gatehouse & Malone (1998)

(c) Field manipulations

The impact of parasitism on native–invader interactions was investigated in artificial field populations in which we manipulated species composition and parasitism under natural physico-chemical conditions. We focused on *G. d. celticus*–*G. tigrinus* native–invader interactions at a mixed-species site in Lough Neagh (a lake of 383 km² area, site grid reference H957873) over 14 days. This represents the system where the native has co-occurred with an invader for the longest period of time (H. B. N. Hynes, personal communication). We used ‘bioassay’ tubes (PVC pipe, length of 20 cm, diameter of 5 cm, with 1 mm pore size nylon mesh covering both ends) with food and shelter (MacNeil *et al.* 2000). There were five treatments (six replicates per treatment) each containing 10 animals: single species (parasitized *G. d. celticus*, unparasitized *G. d. celticus*, *G. tigrinus*) and mixed species (unparasitized *G. d. celticus* + *G. tigrinus*, parasitized *G. d. celticus* + *G. tigrinus*). Survival data were arcsine transformed and compared using analysis of variance (ANOVA) and post hoc Fisher protected least significant difference tests (SUPERANOVA statistical package; Abacus Concepts 1989).

(d) Laboratory interactions

In laboratory microcosms, we investigated the effect of parasitism on predation by *G. d. celticus* of each of the three invading species. Interactions were observed in aerated 1.5 l tanks of field source water at 12 °C in a 12 L : 12 D cycle. Glass pebbles provided habitat structure while permitting observation. Food (catfish food pellets and leaf material) was provided in excess. Each replicate contained a single *G. d. celticus* (predator), which was either parasitized or unparasitized, male or female, plus three male and three female invaders (eight replicates per treatment). Single-species controls of native (single male or female) and invaders (three males and three females) were run concurrently (eight replicates per treatment). Survival was examined daily, and arcsine-transformed data for survival of invaders at 14 days were analysed using repeated measures ANOVA. As the largest most aggressive invader, *G. pulex*, has been shown to prey on all three other species and has successfully excluded the native species over short periods (1–2 years) at many sites (Dick *et al.* 1993), we carried out a reciprocal experiment of the *G. d. celticus*–*G. pulex* mixed treatment with one male or female invader plus six parasitized natives (three male and three female) or six unparasitized natives (eight replicates per treatment). Single-species controls of invader (single male or female) and natives (three males and three females) were run concurrently (eight replicates per treatment).

3. RESULTS

(a) Field survey

There were 59 native-only sites, 24 sites where both natives and invaders occurred and 12 invader-only sites (figure 1). *Gammarus duebeni celticus* was infected by the microsporidian parasite in 22 out of 83 populations (5356 out of 66 100 individuals sampled). Parasitism had no significant effects on the sizes of males ($t_{229} = 1.01$, n.s.) or females ($t_{92} = 0.001$, n.s.) or on the fecundity of females (ANCOVA with female weight as a covariate: $F_{1,70} = 3.63$, n.s.) from subsamples taken from the Articlave and Macosquin Rivers. Average prevalence ranged from 0 to 47% at different field sites, with the two sites that we examined intensively containing patches where prevalence was as high as 90% (figure 2). Parasitism was significantly more frequent in invaded, mixed-species, sites (parasite present at 50% of sites), compared with sites containing only the native *G. d. celticus* (parasite present at 17% of sites; $\chi^2_1 = 9.6$, $p < 0.01$). We found no evidence of parasitism in 16 250 invaders sampled (11 490 *G. pulex*, 3900 *G. tigrinus* and 860 *C. pseudogracilis*).

(b) Parasite identification, transmission and host specificity

Sequence analysis revealed 98% homology at the nucleotide level (WU-BLASTn) to *Pleistophora* sp. 2 on GenBank (AF044389). This novel sequence was submitted to GenBank and we provisionally designate this species *Pleistophora* sp. (GenBank AJ438985). Laboratory transmission experiments indicated host specificity by this parasite. No individuals of the invading species acquired the infection orally after 50 days, whereas transmission was 23% efficient to *G. d. celticus* ($p < 0.0001$, Fisher's exact probability test). Controls yielded no infection and PCR confirmed that visible absence of the parasite reflected no infection (even in individuals collected from the Articlave, where parasite prevalence was 45%).

(c) Field manipulations

In single-species treatments, survival was greater than 95% and did not differ significantly between parasitized and unparasitized *G. d. celticus* and *G. tigrinus* ($F_{2,15} = 0.3$, n.s.; figure 3). Further, in mixed-species treatments, *G. d. celticus* survival was not significantly affected by the presence of *G. tigrinus* ($F_{1,20} = 0.16$, n.s.) or by parasitism ($F_{1,20} = 0.13$, n.s.; interaction

Figure 2. Frequency distributions of parasitized amphipods in the (a) Articlave and (b) Macosquin Rivers.

$F_{1,20} = 0.9$, n.s.; figure 3). By contrast, survival of the invader *G. tigrinus* was reduced in the presence of *G. d. celticus* ($F_{2,15} = 47.3$, $p < 0.001$). However, while there was a dramatic effect of unparasitized *G. d. celticus* on *G. tigrinus* survival (survival reduced from 95% to 10%, $p < 0.0001$), parasitized *G. d. celticus* had only a marginal effect on *G. tigrinus* survival (survival reduced from 95% to 83%, $p = 0.034$; figure 3). The reduced survival of *G. tigrinus* was ascribed to predation by the native, as we observed numerous *G. tigrinus* body parts and instances of ongoing predation of the invader by unparasitized *G. d. celticus*.

(d) Laboratory interactions

In single-species treatments, survival of all four species was high (greater than 98%) over 14 days. In mixed-species treatments, parasitized *G. d. celticus* killed significantly fewer *G. tigrinus* than did unparasitized individuals ($F_{1,28} = 15.8$, $p < 0.001$; figure 4a), in accordance with results from the field, and male *G. d. celticus* killed more *G. tigrinus* than did females ($F_{1,28} = 4.7$, $p < 0.05$). In particular, female *G. tigrinus* suffered greater predation than did males ($F_{1,28} = 14.7$, $p < 0.001$).

Gammarus duebeni celticus also preyed heavily upon the smallest invader, *C. pseudogracilis*, but there was no effect of parasitism on the predatory impact of the native species ($F_{1,28} = 0.3$, n.s., figure 4b). Male *G. d. celticus* again exhibited a greater predatory effect than females ($F_{1,28} = 4.6$, $p < 0.05$), although there was no difference in the level of predation on male and female *C. pseudogracilis* ($F_{1,28} = 3.9$, n.s.).

Survival of *G. pulex* was over 95% and was not influenced by the presence of either unparasitized or parasitized *G. d. celticus* ($F_{1,28} = 0.5$, n.s.; figure 4c). Indeed, a third of the putative predators, *G. d. celticus*, were killed by

Figure 3. Survival (means and standard errors, untransformed data plotted for clarity) in the field of native *G. d. celticus* and invading *G. tigrinus* amphipods in single and mixed-species treatments in the presence and absence of *Pleistophora* sp.

the putative prey, *G. pulex*. In the reciprocal experiment, survival of the native *G. d. celticus* was reduced in the presence of *G. pulex* and survival was lower for parasitized than for unparasitized *G. d. celticus* ($F_{1,28} = 11.9$, $p < 0.01$; figure 5). In addition, survival of female *G. d. celticus* was lower than that of males ($F_{1,28} = 7.6$, $p < 0.01$) and male *G. pulex* exhibited a greater predatory effect than females ($F_{1,28} = 15.5$, $p < 0.001$).

4. DISCUSSION

In our study, parasite virulence can be thought of as cryptic, as the effect is not detectable in single-species treatments, but becomes evident only through interspecific interactions. These results highlight the need to consider host-parasite interactions in the context of the community to obtain a complete measurement of virulence (Herre 1993; Ebert & Herre 1996; Fritts & Rodda 1998). We have also provided an example of a parasite specific to the native and unable to transmit to invaders (see also Schmidt 1985; Settle & Wilson 1990). Invading species may lose parasites during translocations (Dobson & May 1986) and/or selection may favour parasite resistance during invasion (Bauer *et al.* 2000). For whatever reason, lack of the microsporidian parasite in the invaders imparted an advantage in IGP interactions with the native.

Parasitism reduced the predatory impact of *G. d. celticus* on *G. tigrinus*. Previous studies of predation by the native on the invader suggest that *G. d. celticus* should drive invading *G. tigrinus* extinct in the field (MacNeil & Prenter 2000). Nonetheless, we found evidence for (at least transient) coexistence of these two species at six field sites, and indeed these species often coexist at a variety of spatial scales (Dick 1996). Our results from both field and lab-

Figure 4. The effect of parasitism on predation by *G. d. celticus* on the three invading species. Bars show survival (means and standard errors) of the invaders when kept with parasitized (filled bars) or unparasitized (open bars) *G. d. celticus*. (a) Survival of *G. tigrinus*; (b) survival of *C. pseudogracilis*; and (c) survival of *G. pulex*.

oratory manipulations suggest that high prevalences of native parasitism may permit the spread of *G. tigrinus* into new habitats and the coexistence of native and invader. The sex-biased predation that we observed on *G. tigrinus* females might be expected to limit population growth more severely than predation directed towards males. Thus, parasitism of the native species may have disproportionate effects on the probability of coexistence as it results in a relaxation of the mortality pressures on females (usually regarded as the limiting sex) of the invading species.

There was no effect of parasitism on the predatory impact of the native species on *C. pseudogracilis*, possibly reflecting the large size difference between the species involved (Dick 1996). By contrast, parasitism increased the vulnerability of the native species to predation by the larger invading species *G. pulex*. *Gammarus pulex* continues to replace the native species in Ireland's fresh waters, with differential mutual IGP in favour of the invader cited as the 'driving force' in this replacement (Dick *et al.* 1993). *Gammarus pulex* has superior abilities to the native species, both to resist predatory attacks and

Figure 5. The effect of parasitism on predation of the native *G. d. celticus* by *G. pulex*. Bars show survival (means and standard errors) of the parasitized (filled bars) and unparasitized (open bars) *G. d. celticus* when kept with *G. pulex*.

to prey on moulted congeners (Dick *et al.* 1993; Dick 1996). Presence of the parasite would further disadvantage the native species in such IGP interactions with unparasitized invaders and thereby accelerate its replacement.

Invasions have serious consequences for the structure of biological communities (Vitousek *et al.* 1996; Lovel 1997; Ricciardi & Rasmussen 1998; Carius *et al.* 2001) and are a major cause of biodiversity loss (Groombridge 1992; Vitousek *et al.* 1996; Enserink 1999; Mooney & Cleland 2001). Here, we have shown that parasitism may mediate the outcome of invasions through its effect on predation hierarchies, which are key to the outcome of interactions between native and invading amphipods (Dick 1996). We have shown that parasitism alters the strength of these dominance relationships, weakening the predatory impact of the native species on the smaller invading species, thereby facilitating coexistence. Conversely, we have also shown that, by weakening the ability of the native species to withstand invasions, parasitism also has the potential to facilitate exclusion of the native.

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