Parasitism may enhance rather than reduce the predatory impact of an invader

Jaimie T. A. Dick[1,*], Michael Armstrong[1], Hazel C. Clarke[1], Keith D. Farnsworth[1], Melanie J. Hatcher[2], Marilyn Ennis[1], Andrew Kelly[1] and Alison M. Dunn[3]

[1]*School of Biological Sciences, Queen's University Belfast, Belfast BT9 7BL, UK*
[2]*School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK*
[3]*Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK*
Author for correspondence (j.dick@qub.ac.uk).

Invasive species can have profound impacts on communities and it is increasingly recognized that such effects may be mediated by parasitism. The 'enemy release' hypothesis posits that invaders may be successful and have high impacts owing to escape from parasitism. Alternatively, we hypothesize that parasites may increase host feeding rates and hence parasitized invaders may have increased community impacts. Here, we investigate the influence of parasitism on the predatory impact of the invasive freshwater amphipod *Gammarus pulex*. Up to 70 per cent of individuals are infected with the acanthocephalan parasite *Echinorhynchus truttae*, but parasitized individuals were no different in body condition to those unparasitized. Parasitized individuals consumed significantly more prey (*Asellus aquaticus*; Isopoda) than did unparasitized individuals. Both parasitized and unparasitized individuals displayed Type-II functional responses (FRs), with the FR for parasitized individuals rising more steeply, with a higher asymptote, compared with unparasitized individuals. While the parasite reduced the fitness of individual females, we predict a minor effect on population recruitment because of low parasite prevalence in the peak reproductive period. The parasite thus has a large *per capita* effect on predatory rate but a low population fitness effect, and thus may enhance rather than reduce the impact of this invader.

Keywords: enemy release; functional-response; invasive-species; parasites; predation; trait-mediated-indirect-effects

1. INTRODUCTION

Parasitism is recognized as a powerful force in shaping biological communities (Hatcher *et al.* 2006; Hudson *et al.* 2006) and parasites may play critical roles in the success and impacts of invasive species (Dunn 2009). Invaders often show lower parasite diversity and load in their new ranges and it has been proposed that such 'enemy release', and consequent increase in competitive ability, can aid the invasion process and

impacts (Keane & Crawley 2002; Torchin *et al.* 2003). A reduction in food intake by parasitized animals is well documented, but parasites may also increase host feeding and growth (e.g. Arnott *et al.* 2000; Wright *et al.* 2006). Thus, counter to perceived wisdom, parasites might increase the competitive and/or predatory impacts of invading individuals. Further, if the negative fitness consequences of such a parasite are low, the net population effect of the parasite might be to enhance the impact of the invader.

The amphipod crustacean *Gammarus pulex* is native to Europe but invasive in Ireland and elsewhere (Dick 2008). *Gammarus pulex* often actively replaces native amphipods and significantly alters community structure, for example, decreasing macro-invertebrate species diversity (Kelly *et al.* 2006). In Ireland, the fish acanthocephalan parasite *Echinorhynchus truttae* uses either the native *G. duebeni celticus* or the invasive *G. pulex* as its intermediate host. Prevalence is low in the native (0–1%), but high in the invader (up to 70% in stream patches; MacNeil *et al.* 2003) and thus any impact of the parasite on invader host predatory strength is likely to have substantial community ramifications.

The 'functional response' (FR) of predators is the relationship between prey density and prey consumption. Derivation of FRs illuminates predator behaviour and their impacts on prey populations (Holling 1959). Furthermore, comparative FRs can explain and predict higher invader versus native species community impacts (Bollache *et al.* 2008). Here, in the invasive *G. pulex*, we take the novel approach of examining the FRs of parasitized and unparasitized individuals to illuminate their relative population and community impacts. First, we measured parasite prevalence in the field and examined parasite : host mass ratio and the body condition of *G. pulex* with and without *E. truttae*. Second, we examined if there are major negative fitness consequences of the parasite by measuring its potential effect on host population recruitment, that is female reproductive output. Third, we investigate the impact of parasitism on predatory strength by deriving FRs for individuals with and without the parasite.

2. MATERIAL AND METHODS

From January–September 2008, we collected adult male and female (more than 8 mm) *G. pulex* from the River Lagan, N. Ireland (J308646) and juvenile (3–5 mm) *Asellus aquaticus* from Kiltonga Lake (J334716). Experimental animals were maintained as described in Bollache *et al.* (2008).

To estimate parasite prevalence, at least 150 adult *G. pulex* were screened each month for infection (presence of an orange/red cystacanth confirmed on dissection as *E. truttae*). For a subset of unparasitized and *E. truttae* parasitized males ($n = 63$ each group) and all females in the peak reproductive period (more than 85% females with bristled oostegites) of June–September ($n = 570$ unparasitized and 21 parasitized), we measured the body length, body mass (blotted wet weight with the mass of the parasite subtracted) and parasite mass. We used these data to calculate: (i) parasite : host mass ratio; and (ii) mass/length as an index of body condition of individuals with and without the parasite. Numbers of embryos carried by females capable of reproduction (setae present on oostegites) in June–September were compared between those unparasitized and parasitized (ANCOVA, length as covariate).

For the FR experiment, we selected similar sized male *G. pulex* (mean body length 14.2 mm) both unparasitized and parasitized (status confirmed by later dissection). We presented single males (starved for 24 h) with *A. aquaticus* at seven prey densities (4, 6, 8, 10, 16, 20, 30; $n = 3$ per density) in glass dishes (7.5 cm dia.) with
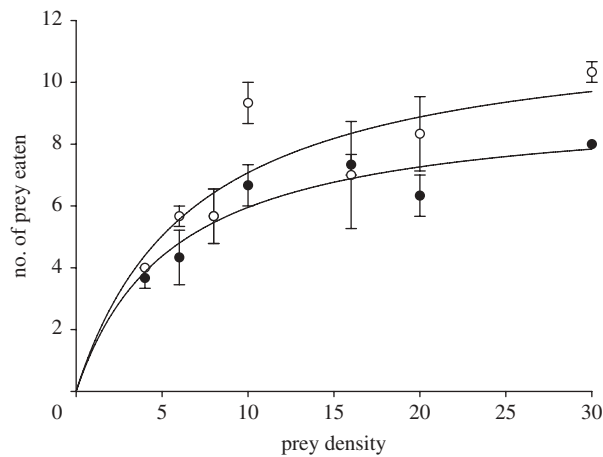
Figure 1. Relationship between the number of prey eaten and prey density, the 'functional response' (FR), at 40 h, for unparasitized *Gammarus pulex* (black circles) and those parasitized with *Echinorhynchus truttae* (white circles).

250 ml of continuously aerated water (mixed 50 : 50 amphipod/isopod source). Controls were three replicates of each prey density without predators. Replicates were initiated at 18.00 h and examined after 40 h. Mean prey eaten was examined with respect to 'parasite status' and 'prey density' (2-factor ANOVA). FRs were modelled (SIGMAPLOT 8) using a Monod function ($y = ax/(1 + bx)$), providing estimates of a (the scale parameter) and b (saturation parameter), maximum feeding rate (the asymptote $a/(bh)$, where h is experimental time) and adjusted R^2 values for the fitted curves (see Bollache *et al.* 2008).

3. RESULTS

Hosts always harboured a single parasite and prevalence ranged from 1.2–30.4% (mean 10.3%) for males and 2.7–22.4% (mean 10.0%) for females (paired $t_8 = 0.2$, n.s.). However, during the peak reproductive period, only 2.7–3.7% of females were parasitized. *Echinorhynchus truttae* weighed up to 17 per cent (for males) and 24 per cent (for females) of the (corrected) body mass of hosts. There was no significant difference in 'body condition' (corrected mass/length) of unparasitized and parasitized *G. pulex* males ($t_{124} = 1.5$, n.s.) or females ($t_{589} = 1.8$, n.s.). Unparasitized males and females were significantly smaller than those parasitized (mean $\pm$ s.e. males: 10.7 mm $\pm$ 0.05 versus 12.0 mm $\pm$ 0.17, $t_{1445} = 7.1$, $p < 0.001$; females 9.11 $\pm$ 0.03 versus 9.99 $\pm$ 0.16, $t_{589} = 5.1$, $p < 0.001$). Mean numbers of embryos carried by females was significantly higher in unparasitized compared with parasitized females (12.5 $\pm$ 0.3 versus 8.4 $\pm$ 1.6, ANCOVA $F_{1,588} = 33.9$, $p < 0.001$).

Control *A. aquaticus* had high survival, with 98.2 per cent alive at 40 h. Thus, experimental deaths were owing to amphipod predation, which we also directly observed. Parasitized *G. pulex* consumed significantly more prey than did those unparasitized ($F_{1,28} = 8.12$, $p < 0.01$; figure 1), with more prey eaten at higher prey densities ($F_{6,28} = 11.2$, $p < 0.0001$), but the interaction was not significant ($F_{6,28} = 1.2$, n.s.). Monod models of FRs achieved high goodness of fit (table 1), reflecting Type-II FRs (see Bollache *et al.* 2008). The FR for parasitized

Table 1. Functional response parameters (a and b) with goodness of fit (adjusted R^2) for unparasitized and parasitized *G. pulex* (see figure 1) and predicted maximum intake rate $a/(bh)$.

parasite	a	b	adj. R^2	$a/(bh)$
absent	1.65	0.18	0.87	0.23
present	1.74	0.15	0.73	0.30

animals rose more steeply and with a higher asymptote compared with unparasitized individuals (figure 1 and table 1).

4. DISCUSSION

Parasites can mediate predator–prey interactions through long-term density effects (Anderson & May 1981; Wilmers *et al.* 2006). However, there is also growing interest in short-term effects ('trait-mediated indirect effects') of parasites on host–host interactions (Werner & Peacor 2003; Hatcher *et al.* 2006, 2008). There is also considerable evidence that behavioural manipulation by parasites can lead to increased vulnerability of the host to predation (Thomas *et al.* 2005). Here, we further demonstrate that parasitism of a predator can also modify predator/prey interactions by increasing the predatory impact of the host.

Parasitism with *E. truttae* significantly enhanced the predation rate of *G. pulex* on *A. aquaticus*, with a Type-II FR that rises more steeply and with a higher asymptote compared with unparasitized individuals. Considering that parasitized *G. pulex* preyed at a 30 per cent higher rate than those unparasitized, parasitism may effectively increase the pressure on prey populations by 3 per cent (at 10.3% mean prevalence) or up to nearly 10 per cent (at 30.4% prevalence). Further, in our study population, *E. truttae* can infect up to 70 per cent of individuals (MacNeil *et al.* 2003), increasing the impact of *G. pulex* on prey by over 20 per cent. Since we size matched males in the two experimental groups to remove any confounding effect of body size, and since parasitized males were significantly larger than unparasitized males in the field, our observed differences in FRs may be conservative and hence actual population level impacts of parasitism may be greater.

On the other hand, if the parasite has major fitness consequences for the invader, then any population level impacts owing to increased *per capita* effects on feeding rate might be negated. However, as parasite prevalence was low (maximum 3.7%) in the peak reproductive period, even with the parasite's effect of reducing fecundity by 32 per cent, we estimate a reduction of only 1.2 per cent in juvenile recruitment to the population. Hence, direct density effects of the parasite may be more than counterbalanced by behavioural changes, i.e. the *per capita* predatory impact. Another possible fitness effect, reduced longevity of hosts, seems unlikely as parasitized *G. pulex* were on average larger than those unparasitized.

Although a previous study reported decreased predation by *G. pulex* parasitized with *E. truttae*

(Fielding *et al.* 2003), only a single, low prey density was offered in that study, with intakes in accord with the low densities in the present study. The divergence in FRs we find here occurred at much higher densities, highlighting the utility of the FR approach over other experimental designs. The increase in FR of parasitized *G. pulex* probably results from direct metabolic demands of the parasite as well as from parasitic manipulation of the host. *Echinorhynchus truttae* cystacanths were large (up to 24% of corrected host weight), with parasitized *G. pulex* in a similar body condition as those unparasitized, suggesting that hosts compensate for the nutritional demands of the parasite. Furthermore, *E. truttae* induces increased activity and hence presumably the vulnerability of *G. pulex* to predation by the definitive host (MacNeil *et al.* 2003), which is likely to increase the nutritional demands of the host. For *G. pulex* with another acanthocephalan, *Pomphorynchus laevis*, elevated levels of glycogen (Plaistow *et al.* 2001) and respiratory pigment suggest higher oxygen consumption (Bentley & Hurd 1993).

Parasite-driven changes in host trophic interaction strengths have the potential to alter the wider community structure (Hatcher *et al.* 2006; Wood *et al.* 2007). Here, we find that the predatory impact of the invasive *G. pulex* is enhanced by parasitism. *Gammarus pulex* decreases the diversity and richness of communities it invades, particularly through predation on other macro-invertebrates (Kelly *et al.* 2002, 2006). The increase in predatory FR of parasitized hosts may enhance the impact of this invader. Clearly, there is a need to consider the effects of parasitism on trophic interactions between invasive and native species when investigating and predicting the impact of an invasion. Further, the 'enemy release' hypothesis must be critically evaluated in other invasion scenarios, since parasites may in fact increase the success and impacts of invasive species.

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