A co-invasive microsporidian parasite that reduces the predatory behaviour of its host *Dikerogammarus villosus* (Crustacea, Amphipoda)

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SUMMARY

Parasites are known to affect the predatory behaviour or diet of their hosts. In relation to biological invasions, parasites may significantly influence the invasiveness of the host population and/or mediate the relationships between the invader and the invaded community. *Dikerogammarus villosus*, a recently introduced species, has had a major impact in European rivers. Notably, its high position in trophic web and high predatory behaviour, have both facilitated its invasive success, and affected other macroinvertebrate taxa in colonized habitats. The intracellular parasite *Cucumispora dikerogammari*, specific to *D. villosus*, has successfully dispersed together with this amphipod. Data presented here have shown that *D. villosus* infected by this parasite have a reduced predatory behaviour compared with healthy individuals, and are much more active suggesting that the co-invasive parasite may diminish the predatory pressure of *D. villosus* on newly colonized communities.

Key words: activity, biological invasion, parasite-induced behavioural changes, predation, microsporidia.

INTRODUCTION

Parasites are known to directly decrease their host fitness. In addition they may also influence community structures through the regulation of keystone species, or modify competitive interactions and biodiversity patterns (e.g. Poulin, 1999; Preston and Johnson, 2012). Considering that more than 50% of living organisms are estimated to be parasites (Price, 1980), their impact on food webs within an ecosystem are considerable. Thus there is a growing interest in the role of parasites in modulating biological invasions (e.g. Dunn and Perkins, 2012). Populations of exotic species may either escape their typical parasites during the translocation process because of sampling bottlenecks, or be less sensitive to parasites present in colonized areas, i.e. the parasite release hypothesis (PRH). This phenomenon may result in an increase of the invasion success (e.g. review in Torchin and Mitchell, 2004).

Although many reports of PRH have been documented (MacLeod *et al*. 2010) the co-introduction of a host and parasite are also common (Dunn, 2009). Co-introduced parasites can affect the new community. They may be a potential threat to the local fauna as an emerging disease (Tompkins *et al*. 2003; Bacela-Spychalska *et al*. 2012), or the 'invasive' parasite may control the population size of its invasive host and limit its negative impact on the newly colonized community (Goddard *et al*. 2005). In addition there are indirect moderations of the relationships among species composing the community and from parasites affecting a host's behaviour, especially when the host is a key species in the food-web (Prenter *et al*. 2004; Hatcher *et al*. 2006). Parasites infecting predators are of particular interest in ecosystems since they may indirectly affect prey populations through host behaviour moderations. Assemblages including amphipod crustaceans are well described (e.g. Dick *et al*. 2010; Médoc *et al*. 2011). In these amphipods, phylogenetically diverse parasites such as microsporidia and acanthocephalans alter predation rates of infected individuals in different ways, a phenomenon that will also depend on the native or invasive nature of their hosts. Médoc *et al*. (2011) showed that the acanthocephalan *Polymorphus minutus* affects the diet and therefore the trophic ecology of its invasive host *Gammarus roeseli*. Another acanthocephalan, *Pomphorhynchus laevis* may either decrease (Fielding *et al*. 2003) or increase (Dick *et al*. 2010) the predatory impact of the infected individuals of the invasive species *Gammarus pulex*. Studies of MacNeil *et al*. (2003) demonstrated that when infected by a microsporidian, *Gammarus duebeni celticus*, that is native to Ireland, it will not only reduce this species predation on two small gammarid invaders, but will also facilitate its own predation by another invasive species *G. pulex*. The coexistence of different gammarid species is therefore mediated by the parasite's ability to modulate intraguild

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predation (Hatcher *et al.* 2008; MacNeil and Dick, 2011).

Studies conducted here were used to determine if a co-invasive parasite will modulate the behaviour of its host: i.e. in the predatory behaviour of the amphipod *Dikerogammarus villosus* (Sowinsky 1894). This invader, of Ponto-Caspian origin, has dispersed successfully to the main waterways of Western and Central Europe within two decades (Bollache *et al.* 2004; Grabowski *et al.* 2007) and was found recently in England (MacNeil *et al.* 2010). Its arrival has led to drastic changes in macroinvertebrate communities, outnumbering other taxa in these newly colonized ecosystems (Dick and Platvoet, 2000; Bollache *et al.* 2004). This was facilitated by its high fecundity, short maturation time, and above all, by its extremely effective predatory behaviour (Bollache *et al.* 2008; Pöckl, 2009; Van der Velde *et al.* 2009). The microsporidian parasite *Cucumispora dikerogammari* (Ovcharenko and Kurandina 1987) infects *D. villosus* in its native habitats but also spread successfully with this host throughout Europe (Wattier *et al.* 2007; Ovcharenko *et al.* 2010). This muscle-infecting parasite is virulent to its host and is mainly trophically transmitted, with *D. villosus* being easily infected after consumption of parasitized conspecific (Bacela-Spychalska *et al.* 2012). After infection, the parasite will eventually kill its host along with intense within-host multiplication, but as compensatory response, infected females of *D. villosus* will reproduce earlier (Bacela-Spychalska *et al.* 2012). A recent theoretical model suggests that an infectious pathogen infecting a predator will strongly stabilize the dynamics of a predator–prey system, provided that the fitness of infected predators is not zero and that infected individuals are less effective predators than uninfected individuals (Kooi *et al.* 2011). We tested if *C. dikerogammari* influences the predatory behaviour of *D. villosus*, as a proxy for parasite-modulation of the invader's impact on prey communities. Since parasite-induced feeding rate may be a by-product of the pathogenic effect of the parasite, we also tested if the host locomotory activity is reduced by the infection.

METHODS

Sampling, acclimatization and infected status

Dikerogammarus villosus were sampled in 2008 in a Reservoir on the Bug River in Zegrze, Poland (52°23′1.52″N; 20°11′7.03″E). Before the experiments began, specimens were kept in the laboratory for acclimatization for 48 h under stable conditions (15 ± 1 °C, light:dark cycle 12:12 h) in a tank filled with de-chlorinated, UV-treated and aerated tap water. Animals were fed *ad libitum* with a mixture of frozen commercial chironomid larvae (Katrinex, Poland), decaying oak leaves and commercial fish food pellets (SERA, Germany). For the experiments, three categories of animals were determined: I_{WS} – infected with phenotypic signs of infection, I_{NS} – infected with no phenotypic signs of infection and U – Uninfected. The first group consisted of 30 adult animals showing visible signs of the disease (as described by Ovcharenko *et al.* 2010) associated with late stages of infection. However early-stage infected animals cannot be distinguished phenotypically from uninfected animals. Therefore, to ensure comparable sample sizes with I_{WS} animals, given that the prevalence in the natural population was around 50% (Bacela-Spychalska *et al.* 2012), 60 non I_{WS} animals were taken. Infection status of all animals was checked after the experiments, using a PCR–RFLP diagnostic method as described by Ovcharenko *et al.* (2010). All 90 individuals were isolated in small individual chambers (6 cm diameter) filled with aerated water. Light and temperature were the same as during acclimatization.

Experiment 1: activity

To measure activity level, animals were placed individually in horizontal transparent glass tubes (length 23 cm and diameter 3 cm) filled with aerated water.

After a 5 min acclimatization period, the activity of each specimen was measured as the number of crosses of a line partitioning the tube in two equal volume areas over 3 bouts of 2 min, each separated by 2 min without recording (adapted from Fielding *et al.* 2005). Animals were then relocated to their individual chamber and left without food for 12 h.

Experiment 2: predation

Each *D. villosus* individual was given eight live chironomid larvae, a prey species known for *D. villosus*. Krisp and Maier (2005) have shown that *D. villosus* can consume up to eight prey items under typical temperatures (as used in this study) over a 24 h period. The number of larvae eaten was noted after 1, 6 and 24 h. Individuals which moulted during the experiment were excluded from the analysis.

After this second experiment was completed, the sex of each individual was determined (using setosity of antennae 2). Specimens were then measured (linear dimension of the fourth coxal plate, see Bollache *et al.* 2000) using a stereoscopic microscope (Nikon SMZ 1500) and Lucia G 4.81 software. Individuals were then anaesthetized with CO_2-saturated water, and placed individually in 1·5 mL tubes filled with pure ethanol for subsequent infection status and parasite species diagnostic PCR-RFLP analysis, as described in Ovcharenko *et al.* (2010).

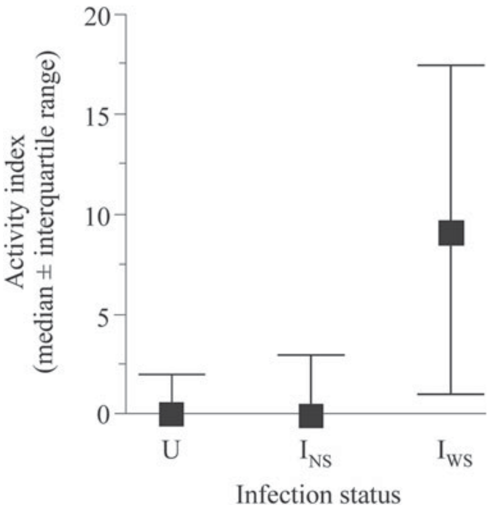

Fig. 1. Activity of *Dikerogammarus villosus* according to their infection status by *Cucumisprora dikerogammari*. U: uninfected; I_{NS}: infected but with no phenotypic signs of infection; I_{WS}: infected with phenotypic signs of infection.

Statistical analyses

Activity data were analysed using non-parametric tests since homoscedasticity conditions were not met, even after transformations (Wilcoxon signed-rank test for analysing repeated measurements, Kruskal–Wallis tests for comparison among groups and Spearman's correlation). Analysis of predation data was made using a linear model for repeated measures, with infection status and sex as factors and size as a co-variable. Statistical analyses were done using JMP 6.0 software (SAS Institute).

RESULTS

Among the animals with no phenotypic signs of infection, the diagnostic PCR–RFLP revealed that 29 individuals did not harbour parasite (U) while 31 were infected (I_{NS}). All infected individuals (including the 29 with visible signs) were only infected by *C. dikerogammari* microsporidia.

Repeated measures analyses on activity revealed no significant difference over time (Wilcoxon signed-rank test between the first two measures and between the second and the third, $T = 74{\cdot}5$, $N = 89$, $P = 0{\cdot}20$ and $T = 47{\cdot}5$, $N = 89$, $P = 0{\cdot}45$, respectively). The sums of the scores from the three replicates were therefore used as the activity index. The I_{WS} individuals were more active than U or I_{NS} individuals (Kruskal–Wallis test: $\chi^2_2 = 14{\cdot}72$, $P = 0{\cdot}0006$, $N = 29$, 29 and 31, respectively) (Fig. 1). Males were also slightly more active than females (median and interquartile range were 1 [0–14] and 0 [0–2·75], respectively, Wilcoxon test: $z = -2{\cdot}10$, $P = 0{\cdot}036$, $N = 45$ and 44, respectively), but we found no relationship between gammarid size and activity (Spearman's correlation: $rs = 0{\cdot}07$, $P = 0{\cdot}50$, $N = 89$).

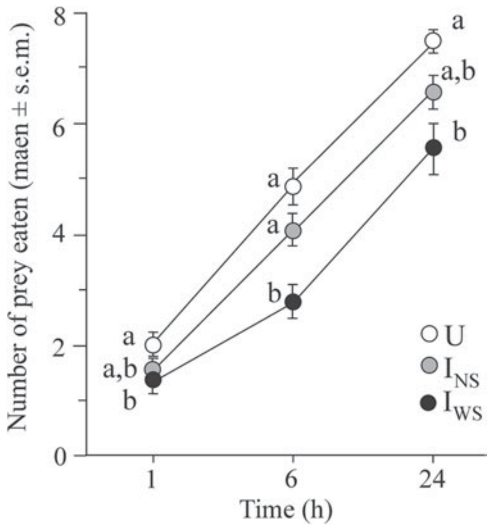

Fig. 2. Number of prey eaten by *Dikerogammarus villosus* according to time, and according to their infection status by *Cucumisprora dikerogammari*. U: uninfected; I_{NS}: infected but with no phenotypic signs of infection; I_{WS}: infected with phenotypic signs of infection. At each time, values followed by the same letters were not significantly different after a Tukey HSD post-hoc test at $\alpha = 0{\cdot}05$.

For the predation rate, the 'size' covariate and the 'sex' factor were not significant, nor were the interactions among variables. Thus they were removed from model. Predation rate was significantly different according to the infection status ($F_{2,\ 86} = 11{\cdot}98$, $P < 0{\cdot}0001$) and increased with time ($F_{2,\ 85} = 12{\cdot}81$, $P < 0{\cdot}0001$). The interaction between time and infection status was significant (Pilai's trace: $F_{4,\ 172} = 6{\cdot}98$, $P < 0{\cdot}0001$). It was demonstrated that the I_{WS} gammarids preyed significantly less on chironomids compared with the U ones, while the predation rate of I_{NS} individuals was intermediate between these two values (Fig. 2). In addition, while the predation pressure increased constantly with time for U individuals, I_{WS} animals preyed less in the first 6 h of the experiment.

Finally, we found no correlation between the level of activity and the intensity of feeding rate at 24 h, whatever the infection status was ($r\,s = -0{\cdot}29$, $P = 0{\cdot}12$ for U, $N = 29$; $r\,s = 0{\cdot}02$, $P = 0{\cdot}90$ for I_{NS}, $N = 31$; $r\,s = 0{\cdot}32$, $P = 0{\cdot}09$ for I_{WS}, $N = 29$).

DISCUSSION

We suggest that a parasite co-introduced with its invasive host will significantly modify its activity and predatory behaviour.

Dikerogammarus villosus, at a late stage of infection by *C. dikerogammari*, are much more active than early-stage infected and uninfected individuals. This pattern is opposite from what was observed by Fielding *et al.* (2005) in *G. duebeni celticus* that was infected with *Pleistophora mulleri*, a microsporidia that will necrotize the host's muscles. Although there are similarities in the description of infection signs (Terry *et al.* 2003; Ovcharenko *et al.* 2010) the differing results in infections are difficult to explain. It is possible however, that these parasites have a different location in host muscles, have a different impact on their functioning, or that the muscle tissue response for the infection varies (e.g. Bulnheim, 1975). However our results here, nor any other published study for that matter, cannot support these hypotheses. In the current study, an increase in activity after infection could have been associated with increased foraging, since microsporidia are known to impose a metabolic demand on their host (e.g. Naug and Gibbs, 2009). However, such an association between activity and foraging is not always shown after parasitic infection (e.g. larvae of freshwater mussels infecting the gills of rainbow darters, Crane *et al.* 2011), and we found no relationship between activity and predation behaviour in our study. Another possible explanation for this higher activity of infected *D. villosus* could be the parasite 'manipulation' of the host itself. Several parasite groups are known to increase their transmission rate by inducing various behavioural changes in their hosts (e.g. Thomas *et al.* 2005). Could it be the case for *C. dikerogammari*? This parasite is transmitted mainly trophically with the uninfected host becoming infected after consuming its dead infected conspecifics (Bacela-Spychalska *et al.* 2012). *Dikerogammarus villosus* are living mainly under stones and hunting from individual shelters (Platvoet *et al.* 2009). Therefore, parasites of *C. dikerogammari* could benefit by mediating the host's move from its shelter before dying, thus increasing the probability of consumption by conspecifics, which would in turn promote parasite transmission. In line with this hypothesis, higher activity was observed only when the body of the host is full of spores (the transmission stage). However, additional studies are needed to understand this behavioural change, which could, after all, just be a behavioural disorder with no translation in parasite transmission.

Heavily infected *D. villosus* exert a lower predation rate on chironomid larvae compared with healthy individuals. Animals at an early stage of infection show an intermediate behaviour between these extreme categories. While parasites may increase feeding activity in their hosts (Bernot and Lamberti, 2008; Naug and Gibbs, 2009; Dick *et al.* 2010), many other studies reported a decrease in food consumption (Kyriazakis *et al.* 1998), and notably in gammarids (Fielding *et al.* 2003, 2005; MacNeil *et al.* 2003). However in such studies this lower predation rate was explained by the decrease of activity, as muscles are damaged by the presence of parasite spores (Terry *et al.* 2003). In our case the situation is definitely different as these most infected individuals were also the most active.

Whatever the underlying causes for this change in predation rate, consequences can be important for resident macroinvertebrate communities affected by *D. villosus*. This predator is ranked high in the food web (Van Riel *et al.* 2006) and its introduction is usually associated with the displacement of other macroinvertebrates from the assemblages (e.g. Dick and Platvoet, 2000). Thus we may expect that a high prevalence of *C. dikerogammari* may significantly decrease *D. villosus*' impact on invaded ecosystems, as suggested by the model of Kooi *et al.* (2011). In another predatory–prey system involving amphipods, field studies were congruent with experimental data: the parasite-induced reduction of predation allowed the co-existence of predators and prey (MacNeil and Dick, 2011). *Cucumispora dikerogammari* is a parasite present in most *D. villosus* populations (Wattier *et al.* 2007). Its prevalence may exceed 50% locally (Bacela-Spychalska *et al.* 2012) and in those situations we may expect that the predatory pressure exerted by *D. villosus* is significantly reduced when compared with parasite-free populations. Furthermore this parasite in *D. villosus* will negatively impact its survival (Bacela-Spychalska *et al.* 2012). Nevertheless *D. villosus* is known to prey upon a wide range of invertebrate species (e.g. Boets *et al.* 2010). Our experiment, although limited to only one prey species, does not allow for too much generalization because the predatory behaviour as seen in *D. villosus* might not be the same towards all types of prey. However, our results are conservative since *D. villosus* preferentially prey upon on slow-moving animals, among which chironomids appear to be a preference (Boets *et al.* 2010). The host (*D. villosus*) – parasite (*C. dikerogammari*) relationship could therefore provide an example where a co-invasive parasite could limit the impact of its invasive host on native biodiversity. The co-occurrence of *D. villosus* with other macroinvertebrates at a local scale (and not only at a regional scale as shown by Piscart *et al.* 2010), in cases of high infection rate by *C. dikerogammari* (Bacela-Spychalska *et al.* 2012) supports our conclusions.

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