

Research note

Differential influence of *Pomphorhynchus laevis* (Acanthocephala) on the behaviour of native and invader gammarid species

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Received 18 August 2000; received in revised form 13 September 2000; accepted 13 September 2000

Abstract

Although various species of acanthocephalan parasites can increase the vulnerability of their amphipod intermediate hosts to predation, particularly by altering their photophobic behaviour, their influence on the structure of amphipod communities and the success of invader species has so far received little attention. We compared the prevalence and behavioural influence of a fish acanthocephalan parasite, *Pomphorhynchus laevis*, in two species of amphipods, *Gammarus pulex* and *Gammarus roeseli* in sympatry in the river Ouche (Burgundy, eastern France). There, *G. pulex* is a resident species, whereas *G. roeseli* is a recent coloniser. Both uninfected *G. pulex* and *G. roeseli* were strongly photophobic, although less so in the invading species. However, there was no significant difference in reaction to light between infected and uninfected *G. roeseli*, whereas infected *G. pulex* were strongly photophilic. We discuss our results in relation to the parasite's ability to manipulate invading host species, the possibility that resistant individuals have been selected during the invasion process, and the role that acanthocephalan parasites can play in shaping the structure of amphipod communities. © 2000 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

Keywords: Host-parasite relationship; Behavioural modifications; Favouritisation; Biological invasions; Freshwater Crustacea; *Gammarus pulex*; *Gammarus roeseli*

In various freshwater systems in western Europe, populations of native amphipods are progressively displaced by introduced amphipods [1–3] that can show explosive range extension [4,5]. Several mechanisms, such as differential environmental tolerance [6], sterile interspecific mating [7], or differential aggression and mutual predation [3,8,9] can be involved in the regulation of the competitive interactions between native and introduced amphipod species. Additionally, both theoretical [10–12] and empirical evidence [13–15] have shown that parasites can play a major role in structuring animal communities. Recently, some studies have emphasized the importance of parasitism for the dynamics of amphipod populations and communities [16,17]. In particular, the outcome of biological invasions can depend to a large extent on the mediation of competition between invading and native species by parasites, i.e. 'apparent' competition [18]. On the one hand, the transmission of parasites from invading hosts to naive native hosts can mediate the displacement of the native species [19,20]. On the other hand, invasion can be facilitated if the invading

species is less susceptible than the native one to endemic parasites [21].

Various species of acanthocephalan parasites are exploiting amphipods as intermediate hosts. All acanthocephalan parasites rely on trophic transmission to complete their life cycle [22], and some species have evolved the ability to alter the behaviour of their intermediate host [23] to make it more vulnerable to predation by their definitive hosts, i.e. *favouritisation* [24]. Interactions between acanthocephalan parasites and their amphipod hosts have been widely studied [25–27], whereas the influence of acanthocephalan parasites on the structure of amphipod communities and the success of invader species has received little attention. Recently, however, Dunn and Dick [17] observed that the prevalence of a bird acanthocephalan, *Polymorphus minutus*, was higher in the native amphipod *Gammarus duebeni celticus* than in the invader species *Gammarus tigrinus* in a freshwater site in Ireland.

Here we compare the behavioural alteration due to a fish acanthocephalan parasite, *Pomphorhynchus laevis*, in two species of amphipods, *Gammarus pulex* and *Gammarus roeseli* in sympatry. *Gammarus pulex* is a resident species in France, whereas *G. roeseli* is a recent coloniser of Central European origin [1,28,29]. The spreading of *G. roeseli* from

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the Danube system to other rivers in western Europe seems to have been facilitated by the recent development of the canal network, especially in France [30]. The species has been reported to be infected with *P. laevis* in Czechoslovakia [31,32], while its susceptibility to the same parasite in other parts of its geographic range remains undocumented.

P. laevis is a non-specific parasite with larval stages (cystacanths) infecting various amphipod species (gammarids) whereas adults develop in several freshwater fishes [33]. The cystacanths of *P. laevis* are yellow-orange, and can be seen through the cuticle of infected gammarids that then show conspicuous yellow-orange dots. In addition to modified appearance, cystacanths of *P. laevis* are known to induce various changes in their intermediate host's phenotype. Infected gammarids show reduced O₂ consumption [34], increased haemocyanin concentration [35,36], and altered reaction towards light [26,27,37].

The study was conducted in the river Ouche at the Parc de la Colombière (Dijon, eastern France). In this site, *G. roeseli* lives in sympatry with infected *G. pulex*, with *G. pulex* being by large the more abundant species (approximately 90–95% *G. pulex* and 5–10% *G. roeseli*, A. Bauer, unpublished data). Gammarids were collected using the 'random-kick sampling' method [38], with a net retaining all size classes. We estimated the prevalence of *P. laevis* in *G. pulex* and *G. roeseli* from a large sample ($N = 1087$ from which there was 1036 *G. pulex* and 51 *G. roeseli*) collected in April 1999.

Several samples were collected in the same site (Ouche river) to obtain enough infected gammarids for behavioural experiments. In the laboratory, amphipods were maintained in aquaria filled with a mixture of water from the river and tap water (in a 50% proportion), maintained at 16°C, oxygenated and filtered. They were used in experiments within 72 h after collection.

A total of 459 gammarids were tested individually, to study the influence of species, sex, size and infection status on behaviour; amphipods harboring immature parasites were not retained in the analysis. At the end of the experiment, each amphipod was killed in 70% alcohol and sexed from the shape and size of segment 6 (propodus) of gnathopods 1 and 2, and the presence of eggs or embryos in the brood pouch. Individuals were measured by linear dimensions (body height at the level of the fourth coxal plate basis, see [39]). All gammarids were dissected for parasites. Parasite identity was determined following criteria of Brauer [40] and Brown et al. [41].

The experimental design and procedure used to quantify reaction to light is the same as described in Cézilly et al. [27]. Each individual was used only once in this setup. At the beginning of each trial, a single individual was placed at the bottom in the middle of the tank. After an acclimation period of 5 min, its position was recorded at 30 s intervals during 5 min. At the end of each trial, the behaviour of the individual was scored from the number of times that it was recorded in the light half of the aquarium. Thus, the score could range from 0 (strongly photophobic) to 10 (highly

photophilic). A score of 5 indicated no preference in relation to light. Because the distribution of scores did not conform to a normal distribution, data were analysed using non-parametric statistics [42,43]. Results were considered significant at $P < 0.05$. Two-tailed tests of significance are used throughout.

Overall, 1087 gammarids were collected in April 1999. The prevalence of *P. laevis* in the river Ouche did not differ between *G. pulex* (8.78%; $n = 1036$) and *G. roeseli* (7.84%; $n = 51$; Fisher's exact test: $P = 1$).

Overall, 194 *G. pulex* individuals (39 uninfected and 50 infected males, 35 uninfected and 70 infected females) and 265 *G. roeseli* individuals (60 uninfected and 38 infected males, 101 uninfected and 66 infected females) were used in the experiments.

We first considered the influence of parasite load on reaction to light. Infected *G. pulex* were assigned to three different categories corresponding to individuals harboring one ($n = 63$), two ($n = 32$) or three and more ($n = 25$) cystacanths. We found no effect of parasite load on reaction to light (Kruskal–Wallis: $H_2 = 2.720$, $P = 0.26$). Infected *G. roeseli* were assigned to two categories corresponding to individuals harboring one ($n = 86$) or two and more ($n = 18$) cystacanths. We found no effect of parasite load on reaction to light (Mann–Whitney U -test: $Z = 1.657$, $P = 0.1$). Therefore, for each gammarid species, data from all infected individuals were pooled in subsequent analyses.

Sex had no influence on reaction to light in either *G. pulex* (Mann–Whitney U -test, non-infected individuals: $Z = -0.268$, $P = 0.788$; infected individuals: $Z = 0.749$, $P = 0.454$) or *G. roeseli* (non-infected individuals: $Z = 0.527$, $P = 0.60$; infected individuals: $Z = -1.108$, $P = 0.27$). To investigate if size influences reaction to light, we created three size classes, each one including about the same number of individuals. Because *G. roeseli* individuals are bigger than *G. pulex* ones, the groups were defined as presented in Table 1. Size has no effect on reaction to light in *G. pulex* (Kruskal–Wallis, healthy individuals: $H_2 = 0.733$, $P = 0.69$; infected individuals: $H_2 = 2.640$, $P = 0.27$) and in *G. roeseli* (Kruskal–Wallis, healthy individuals: $H_2 = 4.431$, $P = 0.11$; infected individuals: $H_2 = 1.348$, $P = 0.51$). Therefore, data for both sex and size were pooled for subsequent analysis.

Table 1
Number of gammarids (infected and uninfected) in each class size. Sizes correspond to the height of the metacoxal plate

| Class size (mm) | Infected | Uninfected |
|-------------------|----------|------------|
| <i>G. pulex</i> | | |
| 1.843–2.315 | 26 | 27 |
| 2.316–2.673 | 55 | 21 |
| 2.674–3.845 | 39 | 26 |
| <i>G. roeseli</i> | | |
| 2.108–2.508 | 35 | 54 |
| 2.509–2.853 | 46 | 54 |
| 2.854–3.762 | 23 | 53 |

There was a significant difference in reaction to light between infected and uninfected *G. pulex* and *G. roeseli* (Kruskal–Wallis analysis of variance: $H_3 = 48.295$, $P < 0.00001$). Among all categories, the only non-significant comparison was found between infected and uninfected *G. roeseli* individuals (Table 2, non-parametric multiple comparison analysis between groups corrected for tied ranks [43]). However, infected *G. pulex* individuals were far more photophilic than uninfected ones (Fig. 1). *G. roeseli* individuals (either infected or not) were significantly less photophilic than infected *G. pulex* but also significantly less photophobic than uninfected *G. pulex*.

In the Ouche River (Parc de la Colombière), the prevalence of *P. laevis* did not differ between the resident *G. pulex* and the invading *G. roeseli*. Our results somehow contrast with those obtained by Dunn and Dick [17] who found in an Irish river that the prevalence of the acanthocephalan *Polymorphus minutus* was significantly higher in the native *G. duebeni celticus* than in the invader *G. tigrinus*. However, a marked difference in prevalence of *P. laevis* (*G. pulex*: 11.56% ($n = 450$), *G. roeseli*: 2.69% ($n = 253$)) has been observed in a population (Les Maillys) distant from about 30 km from Parc de la Colombière (A. Bauer, unpublished results). More importantly, our results from the experiments on reaction to light suggest that the influence of *P. laevis* was actually lower in the invading host species than in the resident one. Infected *G. roeseli* individuals showed no altered behaviour in reaction to light compared to uninfected individuals of the same species, whereas infected *G. pulex* individuals were markedly less photophobic than uninfected ones. Although our results must be treated with caution since they are only based on one population, they contrast with a previous observation [44]. In this study, *Pomphorhynchus laevis* induced in the amphipod *Echinogammarus stammeri* the same behaviour as in *G. pulex*, characterized by a significant preference for lighted areas. However, Maynard et al. [44], unlike the present study, did not compare directly the effect of *P. laevis* on two host species coexisting in sympatry.

Because we used amphipods with natural infections in our experiments, there is a possibility that the observed modified behaviours lead to increased likelihood of infection, rather than the converse. However, previous studies of similar host-parasite systems (e.g. Bethel and Holmes [45])

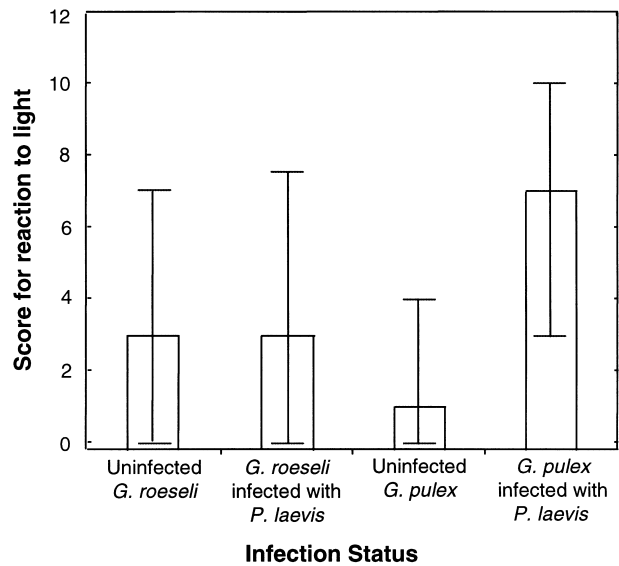


Fig. 1. Median values for reaction to light according to infection status. Bars show the interquartile range.

have shown that modified behaviours are observed only after the cystacanths have become infective to the definitive host, indicating that the observed alterations of infected hosts behaviour are the consequence and not the cause of infection. We thus consider that the differential influence of the parasite between host species is the result of the interaction between the parasite's ability to manipulate its hosts and the ability of the hosts to resist manipulation [46,47]. We thus consider that the observed variation between host species in the virulence of the parasite is the result of the interaction between the parasite's ability to manipulate its hosts and the ability of the hosts to resist manipulation [46,47]. Therefore, both aspects of the interaction must be considered. Firstly, host specificity by the parasite might well account for the results obtained in this study. Although cases of infection of *G. roeseli* by *P. laevis* have been reported in eastern Europe [31,32] there is, to our knowledge, no detailed account of the influence of the acanthocephalan parasite on the behaviour of its host in this part of its geographic range. One possibility is that *P. laevis* is able to infest *G. roeseli* but is unable to alter its photophobic behaviour. The absence of enhanced photophily in *G. roeseli* infected with *P. laevis* in Burgundy may correspond to an adaptation of *P. laevis* to the predominant host species that might to some extent preclude its adaptation to the invading gammarid species. This would be in accordance with a recent theoretical study predicting that in a heterogeneous host population (composed of two host types) specialist parasite strains will evolve if the switch from one host to the other is connected with a high cost for the parasite [48]. Similarly, parasite-induced alterations in behaviour in insects are dependent [49,50] upon the species or even the genetical strain considered [50].

Finally, the inability of *P. laevis* to alter the behaviour of

Table 2
Results from multiple comparison between groups for reaction to light

| Comparison | Observed Q value | P |
|--|--------------------|-----------|
| Uninfected <i>G. roeseli</i> vs infected <i>G. roeseli</i> | 3.6654 | > 0.500 |
| Uninfected <i>G. roeseli</i> vs uninfected <i>G. pulex</i> | - 3.9760 | < 0.002 |
| Uninfected <i>G. roeseli</i> vs infected <i>G. pulex</i> | 3.0741 | < 0.001 |
| Infected <i>G. roeseli</i> vs uninfected <i>G. pulex</i> | - 3.9319 | < 0.020 |
| Infected <i>G. roeseli</i> vs infected <i>G. pulex</i> | - 6.7270 | < 0.001 |
| Uninfected <i>G. pulex</i> vs infected <i>G. pulex</i> | 0.3757 | < 0.001 |

G. roeseli might also be the consequence of the invasion process. According to Hynes [51], parasitised gammarids are more likely to die under stress than uninfected ones. If the colonisation of a new habitat involves a stress, then the invasion process may have selected for more vigorous individuals, or individuals resistant to acanthocephalan parasites [17]. Dobson and May [19] have indeed suggested that such a loss of parasites may confer a competitive advantage to the invading species. Comparative data on the behavioural effect of the parasite on *G. roeseli* in other areas of the geographic range and reciprocal cross-infection experiments are therefore necessary to determine whether resistant individuals were selected during the recent extension of the geographic range of *G. roeseli*, or if different strains of parasites are involved in the observed differential susceptibility of the two gammarid species to the parasite, as Munro et al. [52] mentioned in the British Isles.

Our results also pointed out, however, that *G. roeseli*, whether infected or not, were slightly less photophobic than healthy *G. pulex*. A change in behaviour induced by the parasite might thus be of little value, if the normal behaviour of *G. roeseli* already predisposes it to predation by an appropriate final host of *P. laevis*. However, *G. roeseli* clearly remained photophobic, although less so than *G. pulex*, and thus should be less exposed to predation than infected *G. pulex*. Direct experiments comparing the susceptibility of each gammarid species, whether infected or not by *P. laevis*, to predation by fish should help to clarify this point.

The overall study seems to indicate that these gammarid species, which share the same trophic niche and which have been recently found in sympatry, might be involved in an ‘apparent’ competition [18] potentially mediated via *P. laevis*. The absence of photophilic behavioural alteration in infected *G. roeseli* suggests less intense predation on the invading gammarid than on the resident one. This may have consequences on the population dynamics of the two species in the study area. Thus, long-term survey of both parasites and hosts should be undertaken to determine the role that parasites can play in regulating the success of invading species and hence shaping the structure of amphipod communities.

Acknowledgements

Financial support was provided by the Programme National Diversité Biologique, volet Interactions Durables and the Contrat de Plan Etat-Région Bourgogne. We thank Jérôme Comte, Marilyne Duval and Laurent Landré for field and laboratory assistance.

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