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The impact of the invasive amphipod *Dikerogammarus haemobaphes* on leaf litter processing in UK rivers

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Abstract The impact of invasive gammaridean species on native biodiversity is well documented, but the potential for them to disrupt ecosystem functioning is less well understood. Native freshwater amphipods are considered to be archetypal leaf shredders and are considered key to leaf litter processing within rivers. It is possible that invasions may interfere with key ecosystem processes such as leaf litter breakdown, due to behavioural traits displayed by the invasive species. In two laboratory experiments, we compared the leaf shredding efficiency of the native *Gammarus pulex* and *Dikerogammarus haemobaphes*, a recently established Ponto–Caspian invader in the UK. We hypothesised that in isolation *G. pulex* would have a greater shredding efficiency than *D. haemobaphes* and that, in the presence of the invasive, leaf shredding and survival of *G. pulex* would be reduced. The results supported our hypothesis that, in isolated conditions, *G. pulex* consumed significantly more leaves than *D. haemobaphes*. Under mixed treatments, *G. pulex* leaf consumption and survival, although not statistically significant, appeared to be reduced. The implications of our findings suggest that the potential displacement of *G. pulex* from its native range, by *D. haemobaphes*, could lead to a decline in leaf litter processing and recycling in rivers within the UK.

Keywords Alien species · *Dikerogammarus* · Ecosystem functioning · Predation · *Gammarus pulex* · Shredders

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Introduction

Biological invasions of freshwater ecosystems by invasive species continue to be a main driver for native biodiversity loss. Invasive species can have severe impacts on biological communities that are considered to be as strong as human-caused stressors (Strayer 2012). The Ponto–Caspian gammarid *Dikerogammarus haemobaphes* (Eichwald, 1841) is the latest invasive gammarid to invade UK freshwaters. First recorded in May 2012 in the River Severn (Aldridge 2013), it has since spread rapidly throughout rivers and canal networks, establishing significant populations over a wide spatial distribution (Fig. 1). The impacts of *D. haemobaphes* have been little studied, which is in direct contrast to the voracious predator *Dikerogammarus villosus* (Sowinsky, 1894) whose ecological impacts on other macroinvertebrates and amphipod species are well documented (Dick and

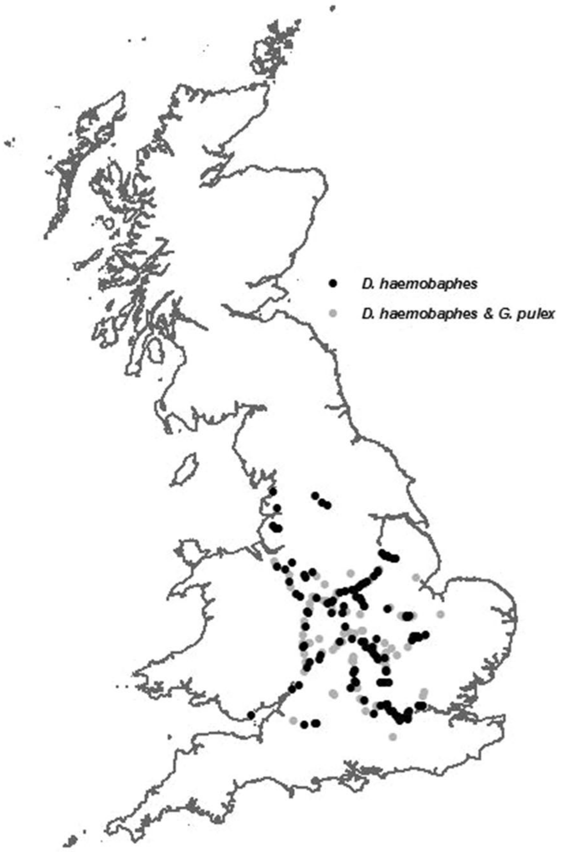

Fig. 1 Map showing current distribution of *D. haemobaphes* and known locations of co-occurrence with *G. pulex* in the UK (Environment Agency data)

Platvoet 2000; MacNeil and Platvoet 2005; Kinzler et al. 2009). There are forewarnings that the invasion of *D. haemobaphes* poses a significant threat to the native *Gammarus pulex* (Linnaeus, 1758) within the UK, with the species sharing similar characteristics as *D. villosus*, in terms of both life history traits (Kley and Maier 2006; Grabowski et al. 2007a) and intraguild predation (IGP) pressure (Kinzler et al. 2009). In Poland, prior to *D. villosus* colonisation, large populations of *D. haemobaphes* dominated the amphipod fauna of the Vistula River (Jazdzewski et al. 2002; Grabowski et al. 2007b), having mostly replaced a previous invader *Chaetogammarus ischnus* (Stebbing, 1899) (Jazdzewski et al. 2004).

Leaf litter breakdown is a key ecosystem process within rivers in terms of both energy flow and nutrient cycling (Giller and Malmqvist 1998). This is most significant in watercourses that flow through forested catchments that receive abundant allochthonous leaf material (Baldy et al. 1995). In such environments, macroinvertebrate shredders can be pivotal in accelerating and converting coarse particulate organic matter (CPOM; >1 mm in diameter) into fine particulate organic matter (FPOM; 50 μm–1 mm), which forms a major energy resource to other organisms and can affect higher trophic levels within the wider food web (Wallace et al. 1997). Despite being omnivorous, freshwater amphipods, gammarids in particular, are considered key archetypal leaf shredders (MacNeil et al. 1997) and can account for up to 75 % of leaf litter processing within rivers (Piscart et al. 2009). A risk facing native gammarids and their shredding activity contributions comes from the spread and establishment of non-native counterparts. Interactions between native and non-native amphipods can lead to the displacement of the former as a result of IGP (Dick et al. 1993; Dick and Platvoet 2000) or competition interference (van Riel et al. 2007). Examples of amphipod displacement include the invasive *G. pulex* replacing the native *Gammarus duebeni celticus* (Stock and Pinkster 1970) in Ireland (Dick et al. 1993) and the non-native *Dikerogammarus villosus* replacing the native *G. duebeni* (Lilljeborg, 1851) and the non-native *Gammarus tigrinus* (Sexton, 1939) in the Netherlands (Dick and Platvoet 2000). Such displacements have the potential to threaten ecosystem structure and function with previous studies having shown invasive amphipods to have lower leaf shredding efficiencies than natives (MacNeil et al. 2011; Piscart et al. 2011).

The purpose of this study was to investigate (1) whether *G. pulex* has a greater shredding efficiency than *D. haemobaphes* and/or (2) whether the presence of *D. haemobaphes* alters the shredding efficiency and survival of *G. pulex*.

Methods

Collection and maintenance of animals

In October 2014, individuals of *D. haemobaphes* were collected from the River Great Ouse, Bedfordshire (N52°11′55″; W0°36′09″), and *G. pulex* from Duloe Brook, Cambridgeshire (N52°13′58″; W0°22′29″), by a combination of kick and Surber sampling. Three Surber net samples (area 0.1 m^2, mesh size 500 μm) were taken at each site to give an indication of amphipod densities. *D. haemobaphes* densities ranged from 130 to 370 m^2

with an average of 250 m^2, and *G. pulex* ranged from 90 to 220 m^2 with an average of 140 m^2.

Each amphipod species was maintained in separate aerated aquarium tanks (30 × 22.5 × 23 cm) at a water temperature of 15 °C ± 1 and a lighting regime of 10:14 light/dark cycle. Each aquarium was supplied with a 50:50 mixed-source water from the two locations (River Great Ouse 738 $\mu S\ cm^{-1}$ and Duloe Brook 792 $\mu S\ cm^{-1}$), substrate in the form of ceramic filter tubes (1-cm-length, 0.6-cm-diameter aperture) which acted as refugia and food in the form of commercially sourced *Chironomus* sp. (Maidenhead Aquatics, Huntingdon) and decaying river-submersed sycamore (*Acer pseudoplatanus*) leaves. Amphipods were allowed to acclimatise to these conditions for 5 days with both sources of food being supplied in abundance. Prior to each experiment, amphipods were starved for 24 h.

Experiment 1: Leaf shredding by *D. haemobaphes* and *G. pulex*

In Experiment 1, plastic aquaria (9 cm diameter) were supplied with 300 ml of aerated mixed-source water and one ceramic filter tube to act as refuge. Water temperature was maintained at 15 °C ± 1. Thirty replicates were monitored for 4 days in each of the treatment groups: (1) an individual *G. pulex*, (2) an individual *D. haemobaphes* and (3) a control with no amphipod individuals. The 30 individuals for each species treatment were randomly chosen from specimens which were >10 mm, non-gravid, healthy adults. Each individual was weighed prior to the 24-h starvation period. Each replicate then received 5 preweighed (wet mass) 6-mm leaf discs, which had been cut from stream-conditioned sycamore leaves using a cork borer, avoiding central veins and midribs. Freshly fallen sycamore leaves were conditioned by placing them in mesh bags and immersing them in a stream for 14 days to allow sufficient time for microbial colonisation. Replicates were then inspected every 24 h with the number of leaf discs consumed (to the one-fourth disc) and amphipod deaths being recorded. When the number of leaf discs in any aquarium fell to 3, a further 2 leaf discs were added. Faecal matter was removed by pipette daily. At the end of the experiment, the remaining leaf discs for each replicate were weighed to calculate the wet leaf mass consumed per wet mass of amphipod.

The overall 4-day leaf shredding efficiency (g wet mass of leaf consumption/ g wet mass of amphipod) between the two species and control was compared using Welch's ANOVA (Welch 1951). To test for general differences in daily leaf count consumption and any temporal patterns, a generalised linear mixed model (GLMM) with a negative binomial distribution was used, which was chosen due to the data being non-normal (Shapiro–Wilk test; $W = 0.780$, $df = 240$, $p = < 0.001$) and overdispersed (see Table 1a). The main effects were amphipod, time, their two-way interaction and amphipod weight (g wet mass), with time as a repeated measure and individual included as a random factor. Amphipod weight was modelled as a continuous variable and used as a constant within the model. We used a stepwise exclusion method to remove insignificant predictor variables. Models were compared using Akaike's information criterion (AIC). All factors and interactions of the final model are presented here irrespective of significance. Differences in adjusted means and significances between factors were indicated by pairwise comparisons with sequential Bonferroni adjustments for multiple comparisons. Statistical analyses were performed using SPSS statistical software v. 22.0 (SPSS Inc, Chicago, Illinois, USA).

Experiment 2: Presence of *D. haemobaphes* and effect on shredding efficiency and survival of *G. pulex*

In Experiment 2, plastic aquaria (18 × 12 × 7 cm) were supplied with 1200 ml of aerated mixed-source water (as above) and five ceramic filter tubes to act as refuge. Water temperature was maintained at 15 °C ± 1. Each aquarium was subject to one of the three treatments: (1) five adult *G. pulex*, (2) five adult *D. haemobaphes* or (3) five adult *G. pulex* and one adult male *D. haemobaphes* selecting only healthy, >10-mm non-gravid individuals. Similar sized *G. pulex* and *D. haemobaphes* were selected by visual inspection. For the mixed-species treatment, *D. haemobaphes* were kept separately, when starved, prior to the start of the experiment to prevent IGP. Six replicates were undertaken for each treatment. Following the 24-h starvation period, each aquarium received 30 stream-conditioned leaf discs, 6 mm in diameter (disc wet mass $= 5.63 \pm$ SE 0.05 mg, $n = 200$), as in Experiment 1. Replicates were inspected every 24 h for 5 days with the number of

Table 1 Results from GLMM analysis showing (a) model comparison and (b) best model parameter output

Model type	Model	Model factors	AIC	Δ_i
(a)				
Neg. binomial	1	Intercept + Amphipod + Time + Amphipod: Time + Amphipod weight	773.45	0.00
Neg. binomial	2	Intercept + Amphipod + Time + Amphipod: Time	778.31	4.86
Poisson	3	Intercept + Amphipod + Time + Amphipod: Time + Amphipod weight	790.43	16.98
Poisson	4	Intercept + Amphipod + Time + Amphipod: Time	794.83	21.38

Model factor	*F* value	df 1	df 2	*p* value	AIC
(b)					
Model 1 (neg. binomial)					773.45
Amphipod	213.985	1	137	**<0.001**	
Time	4.788	3	102	**0.004**	
Amphipod: time	11.304	3	102	**<0.001**	
Amphipod weight	0.146	1	28	0.705	

Bold values indicate $p \leq 0.05$

leaf discs consumed (to the one-fourth disc) and amphipod deaths being recorded. When the number of leaf discs in any aquarium fell to 10, a further 10 leaf discs were added. Faecal matter was removed by pipette, and 200 ml of water was replaced with aerated mixed-source water at each 24-h recording period.

A two-way factorial ANOVA with repeated measures was used to compare differences in daily leaf consumption per amphipod and to identify any temporal patterns. The main effects were amphipod, time and their two-way interaction. Data were square root transformed ($\sqrt{x} + 0.5$) for normality and homoscedasticity purposes. Pairwise comparisons for main effects were made using Bonferroni-corrected post hoc tests. Fisher's exact test was used to examine differences in the proportion of amphipod survival between treatments to indicate any significant IGP effects. Statistical analyses were performed using SPSS statistical software v. 22.0 (SPSS Inc, Chicago, Illinois, USA).

Results

Experiment 1: Leaf shredding by *D. haemobaphes* and *G. pulex*

Mean leaf consumption of *G. pulex* (0.792 ± 0.069 g leaf wet mass per g amphipod wet mass) was significantly higher than *D. haemobaphes* (0.056 ± 0.009 g leaf wet mass per g amphipod wet mass) over the 4 days (Welch's ANOVA; $F_{1,\ 30.16} = 110.81$, $p = < 0.001$; Fig. 2). There was no amphipod mortality during the experiment. Although there was a significant difference between leaf mass consumed by *D. haemobaphes* and the control (Welch's ANOVA; $F_{1,\ 30.67} = 17.23$, $p = < 0.001$), a number of *D. haemobaphes* replicates did not exceed the mass loss range observed in the control (≤3.5 %, range 0.7–3.5 %), meaning that microbial/leaching processes cannot be entirely disregarded in the analyses.

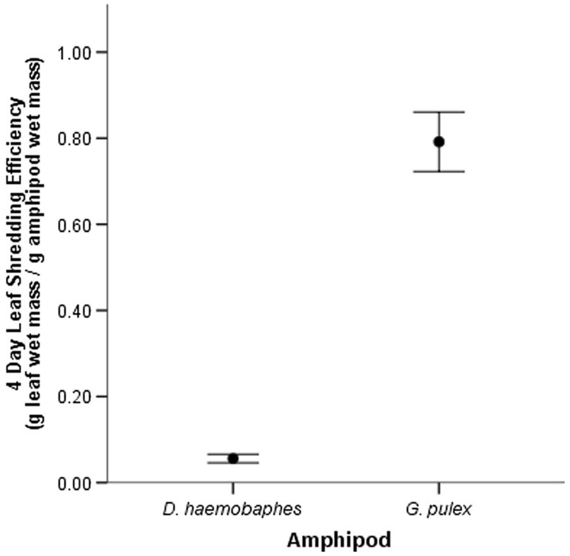

Fig. 2 Mean 4-day leaf shredding efficiency of *D. haemobaphes* and *G. pulex*, ±1 SE

In total, four GLMMs were created and analysed for the data set. Model types and overall AIC values can be found in Table 1a. Models were ranked in relation to each other using ΔAIC values. The parameter output of the best fit model is presented in Table 1b.

The best model (lowest AIC value) used for the GLMM analysis was a negative binomial model that included the factor amphipod weight (Model 1), despite it being statistically non-significant ($p = 0.705$). The weight of amphipod individuals was therefore considered a substantive contributor to model fit, with an AIC Δ_i 4.86 improvement over Model 2 (which excludes amphipod weight as a factor). According to Burnham and Anderson (2002), there is considerably less support for adopting Model 2 given that AIC Δ_i is between 4 and 7. The inclusion of weight in selecting the best model also has a strong theoretical basis, with the size of an individual being related to how much it consumes. This model selection approach is supported by Gelman and Hill (2007). A Pearson residuals vs. fit plot of Model 1 indicates that it appears reasonably unbiased and homoscedastic (Fig. 3).

Daily leaf consumption differed significantly between *D. haemobaphes* and *G. pulex,* with the latter species consuming more leaves. Holding body weight constant (mean = 0.0451 g), there was a significant difference between time–amphipod interaction of the two species, indicating differing daily patterns of leaf consumption (GLMM, $p = < 0.001$). *D. haemobaphes* showed a gradual increase in leaf consumption from day 1 to day 4, with pairwise comparisons (Table 2), showing significant differences between day 1 and 4 ($p = 0.001$) and day 2 and 4 ($p = 0.01$). In contrast, *G. pulex* consumption showed a decrease following day 2 with a significant difference between day 2 and 4 being observed ($p = <0.01$). Despite the different pattern of leaf consumption, *G. pulex* consumed significantly more leaves than *D. haemobaphes* on any particular day (Fig. 4).

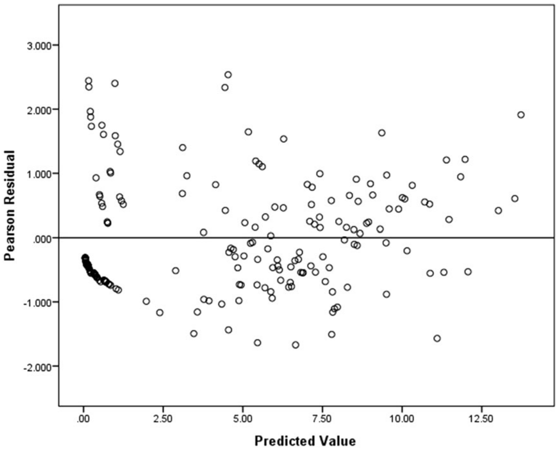

Fig. 3 Diagnostic plot for negative binomial GLMM 1. Pearson's residuals plotted against predicted values

Experiment 2: Presence of *D. haemobaphes* and effect on shredding efficiency and survival of *G. pulex*

Leaf shredding efficiency was significantly different among the three species treatments (ANOVA $F_{2,15} = 7.75$, $p = <0.01$; Fig. 4). Significantly more leaf discs were consumed by *G. pulex* and mixed-species treatments in comparison with *D. haemobaphes* (Bonferroni, both $p = <0.05$). No significant difference was observed between *G. pulex* and mixed-species treatments indicating that *G. pulex* leaf consumption was not significantly affected by the presence of a male *D. haemobaphes* individual (Bonferroni, $p > 0.05$). There was also no significant effect of time and the interaction between time and species on leaf shredding activity ($F_{4,60} = 1.08$, $p = 0.38$ and $F_{8,60} = 1.14$, $p = 0.35$ Fig. 5). The survival rates of *G. pulex* between isolated (96.7 %) and mixed treatment (86.7 %) groups also indicated that no significant predation effect of *D. haemobaphes* on *G. pulex* was observed (Fisher's test, $p = 0.353$; Fig. 6). No individuals of *D. haemobaphes* died in either of its treatment groups indicating no significant cannibalism or IGP effect by *G. pulex*.

Discussion

It is important that the ecological impacts of invasive species are better understood. In these experiments, we showed that the leaf shredding activity of the invasive amphipod *D. haemobaphes* was notably lower than the native amphipod *G. pulex*. This result concurs with previous studies which have shown invasive amphipods to have inferior leaf shredding rates compared to native congeners (MacNeil et al. 2011; Piscart et al. 2011). This could be a result of *D. haemobaphes'* predaceous behaviour and preference

Table 2 Day pairwise comparisons of leaf consumption for each amphipod species, the sequential Bonferroni-adjusted level of significance is 0.05

Amphipod	Day pairwise contrasts	Sequential Bonferroni level of significance
D. haemobaphes	1–2	0.273
	1–3	0.059
	1–4	0.001*
	2–3	0.273
	2–4	0.010*
	3–4	0.273
G. pulex	1–2	0.524
	1–3	0.524
	1–4	0.054
	2–3	0.107
	2–4	0.003*
	3–4	0.524

* Significant contrasts are starred

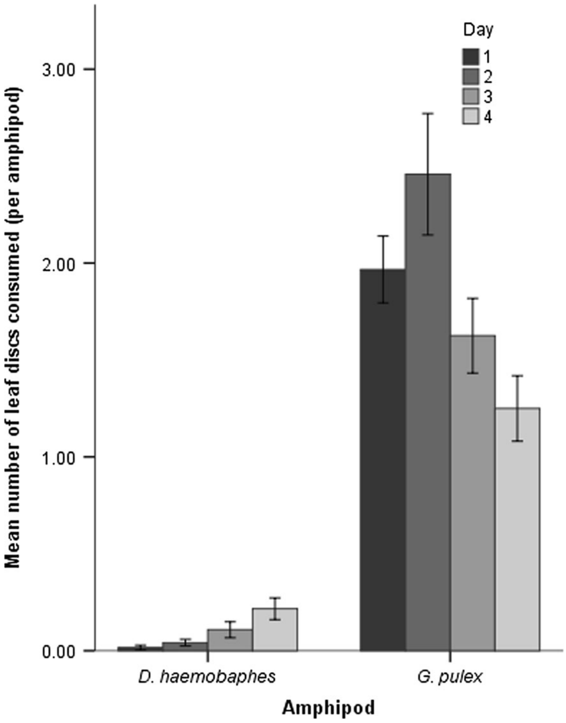

Fig. 4 Mean daily leaf shredding consumption (number of leaf discs per amphipod) of *D. haemobaphes* and *G. pulex*, ±1 SE

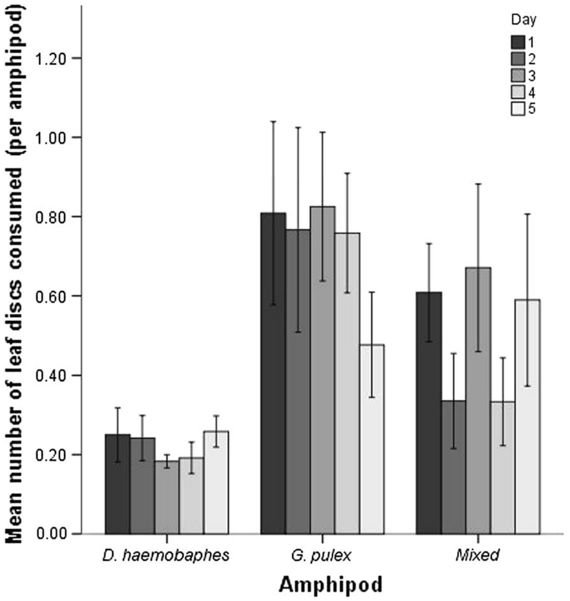

Fig. 5 Mean daily leaf consumption (number of leaf discs per amphipod) over 5 days, ±1 SE. Mixed: *G. pulex* with one *D. haemobaphes*

for high energy food, e.g. animal prey and tissue (Kinzler et al. 2009; Bacela-Spychalska and van der Velde 2013; Bovy et al. 2015). It is known that more nutritious animal diets lead to accelerated growth and maturity in amphipods (Delong et al. 1993; Berezina et al. 2005; Gergs and Rothhaupt 2008) which allows rapid population expansion, an advantageous trait of invading species. This is supported by Bacela-Spychalska and van der Velde (2013), who examined amphipod food preference and diets, and observed that *D. haemobaphes* consumed no decaying plant material and favoured live prey (chironomids and oligochaetes). A potential consequence of the significant disparity in leaf litter consumption between *D. haemobaphes* and *G. pulex* could be a considerable reduction in leaf litter breakdown and recycling within rivers, in situations where the invading species

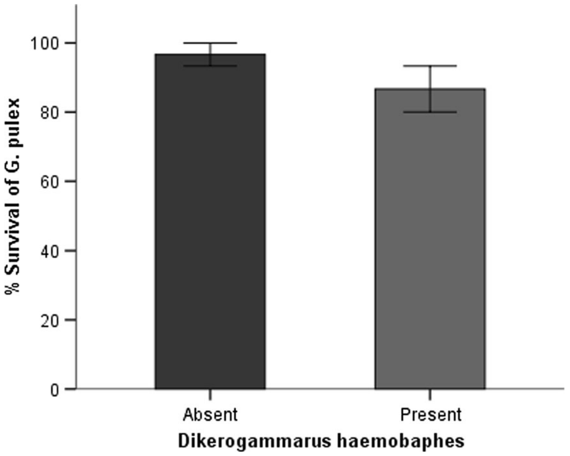

Fig. 6 Percentage survival of *G. pulex* in the absence and presence of one male *D. haemobaphes* ±1 SE

displaces the native. In the UK, *D. haemobaphes* is known to co-occur with *G. pulex* in a wide range of locations (see Fig. 1). These locations include some small, shallow wooded rivers (e.g. <6 m wide, <0.5 m deep), for example the River Tove, Northamptonshire, Loughton Brook, Buckinghamshire and Carlton Brook, Leicestershire. At Loughton Brook, it has been observed that the arrival of *D. haemobaphes* has led to reduced population numbers of *G. pulex* within collected samples (D. Constable and N. Birkby pers. obs.). This displacement of the native could therefore have a significant impact on leaf litter recycling, which is important for facilitating nutrient and energy transfer to the wider food web (Vannote et al. 1980).

In the presence of *D. haemobaphes*, a tendency towards decreased leaf litter consumption by *G. pulex* was observed, which was most apparent when comparing days 2 and 4 across treatments in Experiment 2 (see Fig. 5). The results indicated a mild impact on *G. pulex* shredding efficiency, which might be a response to predator avoidance creating a trade-off between feeding and risk of predation (Pettersson and Brönmark 1993; Viherluoto and Viitasalo 2001). Whilst not statistically significant ($p = >0.05$) it is possible that had the experiment been conducted over a greater duration or had a greater sensitivity to measuring leaf consumption been employed, a significant effect may have been observed. MacNeil et al. (2011) conducted experiments with similar design (aquaria number = 6 per experimental group) using *D. villosus* and *G. pulex*. They found that the presence of one male *D. villosus* had a strong (significant) impact on leaf consumption of *G. pulex* within 24 h of interaction over a 4-day period. Comparison of the two studies would indicate that the interference on *G. pulex* feeding behaviour by *D. villosus* is superior to that of *D. haemobaphes*. Further study would be required to substantiate this notion, however.

Although *D. haemobaphes* is known to be a predator (Kinzler et al. 2009; Bovy et al. 2015), our experiment showed a small but non-significant predation impact upon *G. pulex*. The minimal IGP impact on *G. pulex* is in direct contrast to its congener *D. villosus* whose predation impacts on *G. pulex* are well documented (MacNeil and Platvoet 2005; Kinzler et al. 2009; MacNeil et al. 2011). The superior predatory impacts of *D. villosus* in relation to *D. haemobaphes* have been shown via functional response experiments using *Chironomus* sp. and the amphipod *Chelicorophium curvispinum* (Sars, 1895) as prey items (Bovy et al. 2015). Low feeding rates for *D. haemobaphes* have also been observed when compared to *Pontogammarus robustoides* (Sars, 1894) and *Gammarus fossarum* (Koch, 1836), with the species consuming less animal tissue and live prey (Bacela-Spychalska and van der Velde 2013). This does not dispel the predatory risk of *D. haemobaphes,* as 1:1 mutual predation experiments have shown equal IGP pressure between itself and *D. villosus* (Kinzler et al. 2009) and functional response studies have shown the species to have a higher predatory impact towards tubeless and tubed *C. curvispinum* than *G. pulex* (Bovy et al. 2015). It is possible that there was insufficient time or high enough densities of the species within the experiments to observe any significant IGP effect. Both van Riel et al. (2007) and Truhlar et al. (2014) found insignificant *D. villosus* IGP effects on *G. pulex* during short experiments (≤4 days), and van der Velde et al. (2009) observed considerable predation variability of *D. villosus* on *G. fossarum*, with some individuals exhibiting daily IGP and others eating no amphipod prey over the entire 10-day experiment.

In both sets of experiments, *D. haemobaphes* was observed to spend very little time swimming and remained hidden in refugia, whilst *G. pulex*'s behaviour was very energetic, actively foraging and feeding on leaf litter. Such disparity in behavioural activity has been reported for *D. villosus* when observed against *G. pulex*, with the former being significantly less active and less explorative (Maazouzi et al. 2011; Truhlar and Aldridge 2015). This could be indicative of nocturnal, predator evasion and/or ambush predatory behaviours and could partially contribute to the reduced leaf litter consumption and lack of IGP effect observed. Dodd et al. (2014) found that *G. pulex* had a greater maximum feeding rate than *D. villosus* on *Asellus aquaticus* (Linnaeus, 1758) in the presence of substrate. The maximum feeding rates of the two species were, however, reversed when the substrate was absent. Such sedentary behaviour is favourable in conserving energy and reducing mortality, but is at the expense of sourcing food. The results of this study did indeed show a significant increase in leaf consumption by *D. haemobaphes* over time, but only in single individual amphipod treatments, indicating that leaf litter consumption does occur in the absence of live prey.

The wide distribution of *D. haemobaphes* within the UK poses a significant threat to native *G. pulex* populations whether that risk is IGP, interference competition, parasitism, alternative factors or a combination of these. The Ponto–Caspian species is known to have formed very large and dominant populations at the expense of *G. pulex* and/or *Gammarus roeseli* (Gervais, 1835) in parts of the Danube in South Germany (Kley and Maier 2006) and the invasive *Chaetogammarus ischnus* in the Vistula River in Poland (Jazdzewski et al. 2002, 2004; Grabowski et al. 2007b). Given its proficient ability to rapidly spread and establish dominant populations, it is important that there is greater focus on understanding its potential ecological impacts on invaded systems. Our study builds upon the current paucity of data on ecological impacts caused by *D. haemobaphes*, showing that if it were to significantly displace *G. pulex*, this could lead to a decline in leaf litter processing and recycling in rivers within the UK.

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