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ORIGINAL PAPER

Substrate preferences of coexisting invasive amphipods, *Dikerogammarus villosus* and *Dikerogammarus haemobaphes*, under field and laboratory conditions

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Abstract Two Ponto-Caspian amphipods, *Dikerogammarus villosus* and *Dikerogammarus haemobaphes*, have expanded their geographical ranges from eastern Europe into Great Britain in recent years. This study represents one of the first examining the distribution and habitat preferences of coexisting populations of *D. haemobaphes* and *D. villosus* via field and laboratory experiments in the UK. Field surveys of a recently invaded lowland reservoir in the UK are complimented with ex situ laboratory mesocosm experiments examining the substrate preferences of coexisting populations of *D. villosus* and *D. haemobaphes*. Results from the field study indicated that *D. haemobaphes* dominated the

macroinvertebrate community within the reservoir and demonstrated a strong affinity for large cobble and artificial substrates. *D. villosus* occurred at lower abundances but displayed a strong preference for coarse cobble substrates. A third invasive amphipod, *Crangonyx pseudogracilis*, was largely confined to sand/silt habitats. Laboratory mesocosm experiments clearly supported the field observations of *D. villosus* and *D. haemobaphes* with both species demonstrating a preference for cobble substrates. Results from the study highlight the importance of characterising physical habitat when investigating biological invasions and suggest that habitat availability may influence the extent and speed at which range expansion of new amphipod invaders occurs.

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Introduction

The Ponto-Caspian region represents one of the most significant sources of invasive taxa within western Europe (Müller et al. 2002; Gallardo and Aldridge 2013a) and North-America (Ricciardi and MacIsaac 2000; Vanderploeg et al. 2002). Ponto-Caspian invaders have been particularly successful in

expanding beyond their native range associated with their wide environmental tolerances to water quality, thermal regime variability and habitat modifications (Havel et al. 2005; Gallardo and Aldridge 2013a; Van der Velde et al. 2009). The rapid expansion of Ponto-Caspian taxa beyond their native habitat range has been accelerated by the anthropogenic connection of river systems in western Europe via extensive canal networks (Bij de Vaate et al. 2002). The opening of the Main-Danube canal in 1992 further facilitated invasions via a new 'southern corridor' (Leuven et al. 2009).

Within the UK, an increasing number of Ponto-Caspian invasive amphipods have recently become established in both lentic and lotic ecosystems (Dobson 2013). The most widely distributed of these is *Dikerogammarus haemobaphes* (demon shrimp), which was first recorded in the UK in 2012 (Bovy et al. 2015). A second invasive amphipod, *Dikerogammarus villosus* (killer shrimp), was first recorded in the UK 2010 (MacNeil et al. 2010) and to date is geographically confined to five known locations (GBNNS 2017). It is likely that the geographical distribution of this species will expand in the future across the globe (Kobak et al. 2016) and it is anticipated that it is only a matter of time before *D. villosus* invades North America (Bollache et al. 2008).

D. villosus and *D. haemobaphes* possess several life history traits which make them highly successful invaders. These include rapid growth rates and early sexual maturation. In addition, both taxa exhibit high fecundity which may be up to three times higher than *Gammarus pulex*, the most widely distributed native amphipod in north-western Europe (Grabowski et al. 2007; Bacela et al. 2009; Pöckl 2009; Koester et al. 2016). Both *D. villosus* and *D. haemobaphes* also have strong competitive advantages over native and other established non-native amphipod taxa associated with their opportunistic and flexible omnivorous feeding characteristics (Dick et al. 2002; Platvoet et al. 2009a; Rewicz et al. 2014). Consequently, the establishment of large populations of invasive amphipods may lead to the replacement and extirpation of native and non-native congeners through inter-specific competition for refuges and resources (De Gelder et al. 2016) and intra-guild predation (Dick and Platvoet 2000; Dick et al. 2002; Kley and Maier 2005).

The invasive amphipods of *D. villosus* and *D. haemobaphes*, have been reported to display greater

predatory tendencies than native or established non-native amphipod species in the UK (Bacela-Spychalska and Van der Velde 2013; Dodd et al. 2014; Bovy et al. 2015) and have been observed to inflict 'bite' injuries on prey (Dick et al. 2002). In addition, detrital processing efficiency of invasive amphipods has been reported to be lower than that of native amphipod species resulting in a potential modification of energy flows within invaded ecosystems (MacNeil et al. 2011; Piscart et al. 2011; Constable and Birkby 2016; Jourdan et al. 2016). The resulting effects on community structure, resource flow and ecosystem functioning have given rise to *D. villosus* being regarded as one of the most dangerous invasive species across Europe (DAISIE 2009; Gallardo and Aldridge 2013b).

One potential factor which may mediate colonisation and local range expansion of invasive amphipods is substrate availability (Devin et al. 2003; Hessescherdt et al. 2008). Substrate preferences often reflect the body size and age/life stage of an individual; with intra and inter-specific spatial separation being observed among many populations of amphipods (McGrath et al. 2007). Optimum substrates are typically heterogeneous with the particle size or interstitial spaces between them being similar to that of the organisms' body size (Platvoet et al. 2009b; De Gelder et al. 2016). Consequently, smaller individuals often utilize smaller particle sizes which may also serve as refuge from predators (MacNeil et al. 2008). The limited number of experimental studies conducted, and which are primarily focussed on *D. villosus*, suggest that invasive amphipods have a stronger affinity for large cobble habitats (Van Riel et al. 2009; Kobak et al. 2015). However, little is known about how habitat preferences may vary in mixed populations of congeners. There is therefore a need for studies which examine and define invasive amphipod substrate preferences within newly colonised habitats and which determine optimal conditions that may enhance the establishment of invasive amphipod populations (Jermacz et al. 2015).

In this study we specifically examined the field distribution of co-existing populations of *D. villosus* and *D. haemobaphes* in relation to the dominant available substrates at an invaded lentic waterbody in the UK. Substrate preferences were also examined via laboratory mesocosm experiments to examine evidence of; (a) spatial segregation between the two

gammarid species and; (b) spatial segregation associated with the body size of individuals.

Methods

Field sampling

Pitsford Water is a small reservoir in Northamptonshire, UK (52°19'N, 00°53'W; surface area 7.4 km²) which at present supports three invasive amphipods at different invasion stages. *Crangonyx pseudogracilis* (Crangonyctidae), a North American species, was first recorded in the UK in 1930s (Gledhill et al. 1993) but has been shown to have no deleterious effects on the majority of recipient freshwater communities (MacNeil et al. 1997). The first member of the *Dikerogammarus* genus to invade Pitsford was *D. haemobaphes* which was first recorded in 2014 followed by *D. villosus* which was first documented in 2015. As such the reservoir provides a unique opportunity to examine the invasion dynamics of a newly invaded lentic ecosystem supporting mixed populations of invasive congeners.

This study focussed on the southern basin of the reservoir with sampling taking place at 24 littoral sites around the perimeter of the waterbody during May 2016. Littoral samples (< 1.5 m depth) were collected around the margin of the reservoir encompassing the natural variability in mineral substrate composition and as a result the distance between sample sites was variable. Submerged and floating leaved macrophytes occurred around the perimeter of the reservoir in association with fine grained (sand and silt) substrates. Water temperature varied from 14.5 to 17.1 °C (mean 15.4 ± 0.64 °C) reflecting changes in ambient air temperature, conductivity varied from 410 to 434 µS cm (mean 425 ± 5.76 µS cm) and pH ranged from 8.4 to 8.6 (mean 8.42 ± 0.05).

At each sample site, a combination of kick and sweep sampling (standard 1 mm mesh pond net) was conducted over a 90 s time period (comprising three 30-s samples which were subsequently pooled) and at each point the substrate composition noted (percentage contribution of each type). Four substrate categories were recorded: artificial (predominately geotextile matting), material encompassing boulders and cobbles (diameter 256–64 mm; hereafter referred

to as cobbles for brevity), gravel (64–2 mm) and material in the size fraction of sand/silt (< 2 mm).

All macroinvertebrate samples were preserved in the field in 10% formaldehyde and returned to the laboratory for identification. Within the laboratory, macroinvertebrates were identified to the lowest practical taxonomic resolution, in most instances species or genus level with the exception of Diptera which were recorded to family level, Corixidae, Caenidae (cf *Caenis luctuosa*), small specimens of Baetidae (dominated by *Cloeon dipterum*), Planariidae, Zygoptera and Ostracoda which were recorded as such.

Laboratory experiments of substrate preferences

Replicated substrate preference experiments were conducted over a 24-h period under controlled conditions within four mesocosms (77 × 45 × 18 cm) during July 2016. Mesocosms were filled with dechlorinated tap water, aerated throughout the experimental period via the use of aquaria pumps and water temperatures were held at an ambient temperature of 14.5 ± 1.5 °C reflecting the natural water temperature of the reservoir at the time of study. Experiments were subject to shaded natural ambient light conditions (16 h light:8 h dark cycle). Each mesocosm comprised eight plastic containers (8 × 13 × 6 cm) filled with different substrates (a) large gravel (64–32 mm); (b) medium gravel (16–8 mm); (c) fine gravel (8–4 mm) and; (d) sand (2–0.125 mm). In addition two large cobbles (120–150 mm) were placed in each mesocosm. Each substrate treatment was replicated twice within each mesocosm with 20 individual experiments being conducted in total (n = 20).

Specimens were collected from Pitsford Water on the morning of each 24-h experiment. On each occasion, individuals were collected from locations dominated by boulder and cobble sized clasts known to support mixed populations of *D. haemobaphes* and *D. villosus*. 50 random individuals of mixed size classes and species (*D. haemobaphes* and *D. villosus*) were released into the mesocosms and left to redistribute for 24-h. Mixed populations of *D. haemobaphes* (70%) and *D. villosus* (30%) were used in the experiments reflecting the natural proportions recorded at the collection site where the two species co-existed. At the termination of the experiments, individuals were collected from each substrate

treatment by washing the contents of each container through 0.25 mm sieves. Size classes for each substrate treatment were subsequently determined by passing individuals through a sieve nest (8, 4, 2 and 1 mm) which were classified into the following four mesh size classes > 8 mm, < 8 to > 4 mm, < 4 to > 2 mm and < 2 to > 1 mm. Individuals were preserved in 70% industrial methylated spirit and subsequently identified to confirm species and abundance per substrate. Recapture rates of individuals for all experiments were high (average 97.4%, range 94–100%) and did not vary between experiments.

Statistical analysis

Field sampling

Littoral distribution maps of the three invasive amphipod species recorded in Pitsford Water (*D. haemobaphes*, *D. villosus* and *C. pseudogracilis*) and dominant substrates were created in ArcMap 10.3. To assess differences in macroinvertebrate community composition associated with substrate type, non-metric multidimensional scaling (NMDS) plots were examined. Similarity matrices were created using Bray–Curtis coefficients on square root transformed data. One way analysis of similarities (ANOSIM) were used to examine statistical differences in community composition associated with the different substrate types. Application of the similarity percentage (SIMPER) enabled the assessment of taxa which drove any dissimilarity in communities and whether this was associated with the populations of invasive amphipod species recorded (*D. haemobaphes*, *D. villosus* and *C. pseudogracilis*). All multivariate analyses were performed in PRIMER (version 7.0.11, PRIMER-E Ltd, Plymouth, UK).

Laboratory experiments

Statistical analysis was conducted to determine whether there was a significant difference in the number of invasive amphipods inhabiting the different substrate types and whether this varied as a function of body size and/or species. To account for the mixed co-existing populations of *D. haemobaphes* and *D. villosus* and the differences in individual body sizes utilized in the experiments (reflecting the natural population dynamics at Pitsford), a binomial general

linear model (GLM) with a logit error distribution was fitted to raw count data via the ‘*glm*’ function in the ‘*stats*’ package. The model was built using the terms ‘substrate × amphipod size × species’. All statistical tests were run in R version 3.2.2.

Results

Field distributions and substrate preferences

A total of 15,828 individuals representing 44 taxa were recorded from the 24 sample sites. Numerically the most abundant family of macroinvertebrates were Chironomidae (comprising 73.8% of total abundance). *D. haemobaphes* was the second most abundant taxon (9.82% of total abundance; average abundance 125 per-sample; range 5–1555) and was also the most widely distributed, occurring at all 24 sites (Fig. 1a). *C. pseudogracilis* was the third most abundant taxon (2.15%; average 27.2 per sample; range 0–340) and occurred at 15 sample sites (Fig. 1a). *D. villosus* occurred in low abundances (0.59%; average 3.9 per sample; range 0–33) and was recorded at 6 sites.

When habitat preferences were considered (based on the dominant substrate recorded at the sample site), *D. villosus* displayed a strong preference for habitats comprised of large clasts (large cobble and gravel; Fig. 1b) and was confined to these substrates. The greatest abundances of *D. haemobaphes* were also recorded on coarse grained cobble substrates, but individuals were recorded across all substrate types. In marked contrast, *C. pseudogracilis* were recorded predominantly on substrates dominated by sand and silt sized particles. *C. pseudogracilis* coexisted with mixed *D. villosus* and *D. haemobaphes* at only one site (Fig. 1). *C. pseudogracilis* coexisted with *D. haemobaphes* populations at 15 sites (predominantly in low abundances—seven sites at abundances < 5 individuals) and *D. villosus* at three sites. *D. villosus* and *D. haemobaphes* coexisted at 6 sites.

NMDS analysis clearly indicated that when dominant substrate type was considered, sample sites reflected a gradient from coarse to fine grained substrates on the first axes (Fig. 2). Cobble and sand habitat patches were the most distinct communities (ANOSIM $R = 0.914$; $p = 0.002$), with SIMPER indicating that *C. pseudogracilis* (4.97% dissimilarity) and *D. haemobaphes* (3.86%) were the key taxa

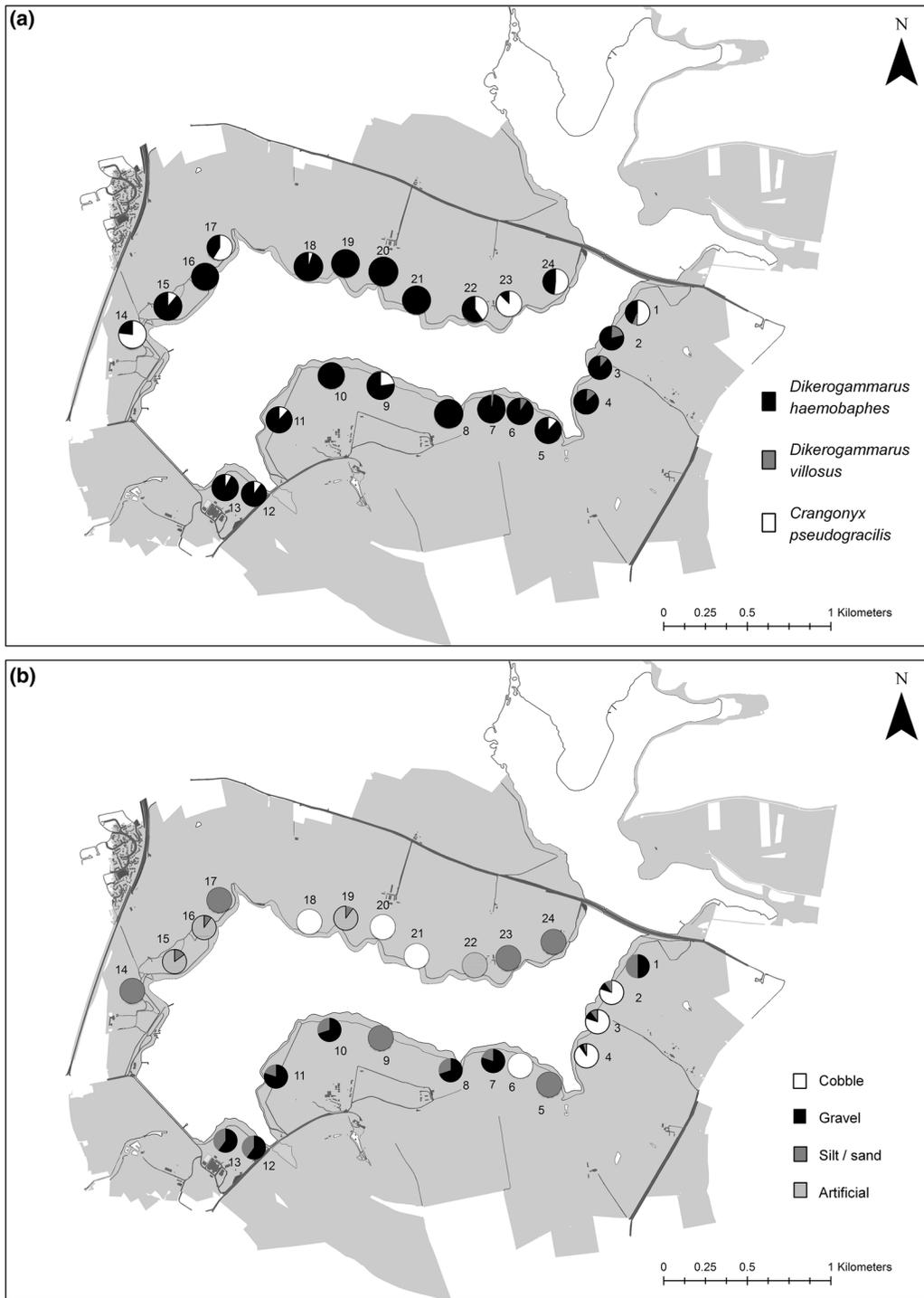


Fig. 1 **a** Invasive amphipod distributions in Pitsford Water; UK and **b** habitat map of dominant substrate distributions in Pitsford Water, UK

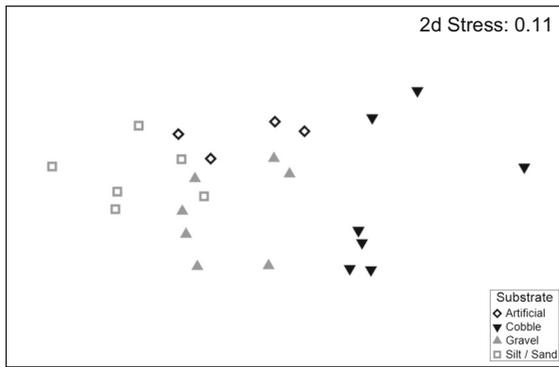


Fig. 2 Non-metric multidimensional scaling (NMDS) of littoral macroinvertebrate community data from Pitsford Water by substrate type based on Bray–Curtis similarity coefficients. Open rhombus = artificial; black triangles = cobble; grey triangle = gravel and; open square = silt/sand

Table 1 Summary of pairwise ANOSIM analysis by substrate type

Pairwise comparison	<i>R</i>	<i>p</i>
Gravel:cobble	0.654	0.001
Gravel:silt/sand	0.425	0.002
Gravel:artificial	0.278	0.061
Cobble:silt/sand	0.914	0.002
Cobble:artificial	0.484	0.006
Silt/sand:artificial	0.341	0.057

Pairwise comparisons which are significant are emboldened ($p < 0.05$)

driving the differences between habitats. Pairwise comparisons of the other substrates indicated that the following substrate patch communities were different to each other (gravel: cobble, artificial: cobble; gravel: sand; all $p < 0.006$; Table 1). In all instances *D. haemobaphes* (average dissimilarity of 5.77, 6.06 and 3.45% respectively) and *C. pseudogracilis* (average dissimilarity 2.23, 2.43, 3.32%) were determined to be driving dissimilarity between the pairwise communities. *D. villosus* was identified as one of the top taxa driving dissimilarity in the first two pairwise comparisons (gravel: cobble, 2.57% and cobble: artificial 3.25%). No significant differences were identified between communities associated with gravel and artificial substrates (ANOSIM $R = 0.278$, $p = 0.061$) or silt/sand and artificial substrates ($R = 0.341$, $p = 0.057$; Table 1).

Laboratory experiments

Substrate preferences did not vary between species ($Z_{6,548} = -0.105$, $p = 0.916$), but *D. haemobaphes* and *D. villosus* demonstrated significant differences in the proportion of the population inhabiting different substrates ($Z_{4,548} = -2.761$, $p = 0.006$). The majority of individuals were recorded on the cobble substrates (59.2 and 68.4% respectively) with a reduction in individuals with decreasing substrate size (Fig. 3). No individuals were recorded in the sand substrates during any of the mesocosm experiments (Fig. 3). Size class did not have significant effect on substrates utilised by either *D. haemobaphes* or *D. villosus* individuals ($Z_{12,548} = 1.395$, $p = 0.163$). However, the largest adult amphipods were recorded on the coarsest grained substrates and smaller individuals were typically located on finer substrates.

Discussion

The results from the field survey and ex situ mesocosm experiments in this study indicate that the invasive amphipods *D. villosus* and *D. haemobaphes* display a strong preference for coarse cobble substrates. These

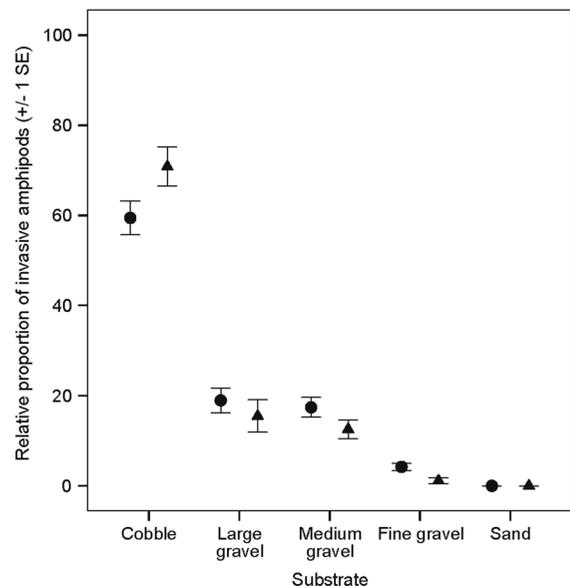


Fig. 3 Mean relative proportion (± 1 SE) of *Dikerogammarus haemobaphes* (circles) and *Dikerogammarus villosus* (triangles) recorded on the five substrate types at the end of the 24-h mesocosm experiments

results support the findings of previous studies centred on *D. villosus* (Devin et al. 2003; Hesselschwerdt et al. 2008; Kley et al. 2009; Van Riel et al. 2009) but also extend our knowledge of substrate preferences for *D. haemobaphes*.

The results of the field survey indicated that *D. haemobaphes* and *D. villosus* coexist at sites in Pitsford Water where coarse boulder and cobble substrates form the littoral substrate. *D. haemobaphes* was the most widely distributed invasive amphipod in the reservoir, being recorded on all sampled substrates and dominated overall littoral community composition. In contrast, *D. villosus* was recorded in much lower abundances than *D. haemobaphes*, probably as a function of its more recent invasion of the site (2015); the current distribution being confined to the area closest to the presumed point of entry into the system. Within many European countries *D. haemobaphes* has been the first member of the *Dikerogammarus* genus to invade waterbodies. In southern Germany, *D. haemobaphes* was first recorded in the Danube in 1976, however following the arrival of *D. villosus* in 1992 it has since been displaced and *D. villosus* now dominates amphipod populations (Kley and Maier 2006). As the population of *D. villosus* expands within newly invaded habitats, spatial segregation among congeners and conspecifics may occur in response to inter- and intra-specific predation.

Within predatory and cannibalistic species, size-asymmetric predation may have significant effects for community dynamics (Benoît et al. 2000; Kinzler et al. 2009) and smaller individuals often select habitats to avoid conspecific predation (McGrath et al. 2007; De Gelder et al. 2016). Adult amphipods often inhabit large stony substrates with smaller individuals seeking refuge in suitable substrate crevices or macrophytes to shelter (Boets et al. 2010; Kobak et al. 2015). Although the field and laboratory investigations did not indicate a statistical effect of size class on the distribution of individuals (most likely due to the naturally low number of individuals in the upper and lower size classes and the presence of pre-copulatory pairs), the mesocosm experiments did indicate that the largest individuals were located on the coarsest and the smallest on the finest grained substrates. Freshwater systems, such as Pitsford Water, which support heterogeneous habitats therefore currently provide a range of refuge sites for smaller individuals and other macroinvertebrate taxa. However, if the population of

D. villosus at Pitsford increases, as it has in other locations where it has invaded, it is likely that its habitat range will expand and the potential effect of intra and inter specific competition may become more evident.

In marked contrast to the *Dikerogammarus* species, *C. pseudogracilis* occupies a much lower trophic level (MacNeil and Dick 2014) and was confined to fine grained sand and silt substrates. Fine sand and silt particles lack the interstitial spaces that are essential in the provision of refuge from higher predators (particularly fish) and are therefore most likely to be the least preferred habitat substrate of amphipods. Resource partitioning can enable the co-existence of multiple invasive species within the same area, with organisms modifying their diet and switching to another habitat type to avoid competition (Robinson and Wilson 1996; Jermacz et al. 2015). It is therefore likely that within Pitsford reservoir *C. pseudogracilis* has already been displaced from coarse grained substrates and has become restricted to less suitable habitats. Field studies have observed a shift in habitat use of the native amphipod *G. pulex* from optimal cobble/gravel habitat to those comprised of smaller grain sizes or macrophyte patches to reduce interspecific competition pressure (Krisp 2004; Van Riel et al. 2007). Interspecific competition is an important process which shapes the relationships between ecologically homogenous species and may lead to a broadening of the ecological niche of invasive taxa beyond that realised in their native range (Medley 2010).

Waterbodies with heterogeneous habitats which provide complex substrate patches, potentially offer native organisms a greater number of opportunities for active avoidance of invaders (Platvoet et al. 2009a, b) and may reduce the speed of the invasion process. Within the River Main-Danube catchment in Germany, the presence of complex substrate facilitated the co-existence of *G. pulex* and *D. villosus* due to niche partitioning of different life cycle stages (Kley and Maier 2005). In areas of relatively simple habitat/substratum complexity, native amphipods may be more vulnerable to the effects of invader niche overlap, potentially leading to regional extinctions of native taxa (MacNeil et al. 2010). Habitat homogenisation and anthropogenic modifications may even enhance the successful colonisation and future expansion of populations of invasive taxa (Johnson et al. 2008; MacNeil and Platvoet 2013).

Within the mesocosm experiments, both *D. villosus* and *D. haemobaphes* demonstrated a strong affinity for coarse grained substrates and actively avoided sand substrates (Devin et al. 2003; Kley et al. 2009; Van Riel et al. 2009). A slightly larger proportion of *D. villosus* individuals were recorded on the coarsest substrate (cobbles) which may indicate some limited form of intraguild competition. Evidence from experimental studies suggests that *D. villosus* is the strongest competitor of all Ponto-Caspian amphipod invaders and, as a result, intraguild predation (IGP), is likely to be responsible for the displacement or eradication of ecologically homogenous amphipods (Kobak et al. 2015, 2016). In the River Odra in Poland, *D. villosus* was observed to displace and dominate *D. haemobaphes* (Gruszka and Woźniczka 2008). In contrast, within the current experiments, the two taxa appeared to co-exist with little evidence of predation and no bite marks were observed on the small number of cadavers. However, the current experiments, reflecting the natural population proportions recorded in the field, were conducted over a relatively short time period (24-h) with De Gelder et al. (2016) observing IGP only after 48-h. Consequently, future experiments should consider the effect of varying proportions of *D. villosus* and *D. haemobaphes* and experiment duration on amphipod survival rates and spatial segregation patterns.

As the number of invasive species continues to increase internationally, the interaction of multiple co-existing invaders is of growing importance (Jackson 2015) and has been hypothesised as potentially leading to an ‘invasional meltdown’ (Simberloff and Von Holle 1999). This meltdown implies a positive feedback and additive effect amongst invasions over time, especially when the invaders are from the same region (Ricciardi 2001; Simberloff 2006). This study illustrates the benefits of conducting multi-approach studies. Field observations and data are important tools for determining the extent of contemporary invasions and effects on the recipient system, whilst controlled laboratory experiments provide further valuable insights into specific factors which may structure co-existing populations of invasive amphipods.

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