Substrate mediated predator–prey interactions between invasive crayfish and indigenous and non-native amphipods

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Abstract The increasing number of taxa being translocated across the globe is leading to many non-native species encountering indigenous taxa as well as other non-native species. Environmental heterogeneity may strongly influence the spatial distribution, habitat use and refuge availability for these taxa. Using a series of 24-h mesocosm experiments we examined the predator–prey interactions between an invasive crayfish (*Pacifastacus leniusculus*) and four amphipod taxa, one indigenous (*Gammarus pulex*) and

three non-native species (*Crangonyx pseudogracilis*, *Dikerogammarus villosus* and *Gammarus tigrinus*) to Great Britain. The potential mediating effect of physical habitat on predator–prey interactions was examined via the use of different substrate particle sizes; cobbles, gravels and, sand. Survivorship of amphipods in response to crayfish predation varied significantly with the highest rates recorded for the non-native species *D. villosus*, followed by *G. tigrinus*, and *C. pseudogracilis*, with the lowest survivorship recorded for the indigenous species *G. pulex* for all substrates except cobble. However, total biomass consumption of the indigenous *G. pulex* and the non-native *D. villosus* by *P. leniusculus* were similar suggesting that crayfish may have been satiated by larger *D. villosus* individuals. Substrate size had a significant influence on the predation success of *P. leniusculus*, with larger substrate clasts typically resulting in increased survivorship rates for all species except *C. pseudogracilis*, which displayed lower predation rates for sand substrates. The findings of this study highlight the risks that naïve indigenous taxa may face from new invasive species and the importance of characterising physical habitat (complexity and refugia potential) when considering the potential ecological effects of invaders on predation success.

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Introduction

The introduction and establishment of non-native invasive species outside of their endemic geographical range is recognised as one of the most significant threats to biodiversity globally (Early et al., 2016; Turbelin et al., 2017; Reid et al., 2019). Freshwater ecosystems are particularly vulnerable to such pressures, with biodiversity losses currently far exceeding those of terrestrial systems (Dudgeon et al. 2006; Martinuzzi et al., 2014). The establishment of non-native invasive species within receiving ecosystems typically leads to the homogenisation of communities via the replacement and predation of native biota (Olden and Poff, 2004). This may ultimately lead to the loss of regional biodiversity and the disruption of natural ecosystem functioning (Vitousek et al., 1997; Lodge et al., 2012).

There is increasing evidence that range expansions of multiple non-native species are occurring simultaneously (Clinton et al., 2018; Zhang et al., 2019). This is leading to growing concerns that a hypothesised “invasional meltdown” of aquatic ecosystems could occur in the future, in which the presence of existing non-indigenous species may facilitate the colonisation and establishment of additional invasive species, thereby magnifying the effects on indigenous communities further (Simberloff and Von Holle, 1999; Green et al., 2011; Hohenadler et al., 2018). Several regions across the globe are currently experiencing the successful establishment of populations of significant numbers of invasive organisms originating from the Ponto-Caspian region, in particular a number of amphipod crustacean species (Ricciardi and MacIsaac, 2000; Gallardo and Aldridge, 2015; Borza et al., 2017). Whilst the acceleration of species invasions has been widely observed (Hellmann et al., 2008; Rahel and Olden, 2008), the interspecific interactions among non-native species requires further investigation (Ermgassen and Aldridge, 2011; Fort et al., 2019) especially where new combinations of species occur.

Crayfish represent one of the most widely translocated groups of freshwater organisms globally (Gallardo et al., 2016), and where populations have successfully become established, they may have detrimental effects on all trophic levels associated with their polytrophic and omnivorous feeding habits (Dorn and Wojdak, 2004; Carvalho et al., 2018). Crayfish are keystone species and can dominate

benthic biomass where they occur in both lentic and lotic ecosystems (Momot, 1995; Crandall and Buhay, 2008). Signal crayfish, *Pacifastacus leniusculus* (Dana, 1852), one of the most successful invasive species, have established large non-native populations throughout the globe, including most of Europe (Lodge et al., 2000; Holdich, 2002; Usio et al., 2009). Ecosystem invasion by signal crayfish has been associated with changes in the community structure of fish (Guan and Wiles, 1997; Peay et al., 2009), macroinvertebrates (Crawford et al., 2006; Mathers et al., 2016; 2018), macrophytes and periphyton (Creed, 1994; Nyström and Strand, 1996), in addition to the extinction of many indigenous populations of crayfish (Holdich et al., 2014).

To date the majority of research on the implications of invasive signal crayfish has focused on indigenous communities (e.g. Crowl and Covich, 1990; Alexander and Covich, 1991; Dorn, 2013), whilst few have sought to investigate interactions with other non-native / invasive prey taxa. This is particularly important to consider as invasive species are often highly adaptive, competitively strong, demonstrate high dispersal capabilities and are tolerant of a wide range of environmental conditions (Rewicz et al., 2014). Predation pressure and the behaviour of both predator and prey are important drivers of evolutionary change (Vermeij, 1982), and the interactions of two species may differ depending on length of co-occurrence and region of origin (Sih et al., 2010; Haddaway et al., 2014).

Typically, predator-avoidance strategies develop over evolutionally timescales, however the rapid spread of invasive taxa has the potential to disrupt normal behavioural responses or render them ineffective. It is therefore highly likely that many indigenous taxa may be ill-equipped to respond to predators with novel feeding / predatory strategies within an ecosystem. In contrast, the greater environmental flexibility of many non-native invasive taxa, may enhance their avoidance of predation by other taxa by being highly adaptable and successful in sub-optimal habitats. Large populations of invasive amphipods may provide a significant resource for invading populations of invasive crayfish which could facilitate their range expansion (*sensu* Dorn and Hafsadi, 2016) and / or limit the population size of amphipods. Obtaining a greater understanding of the potential interactions among non-native invasive species is therefore

imperative to help inform future conservation and management practices where range expansion of invasive species is likely to occur in the future (Ermgassen and Aldridge, 2011; Jackson et al., 2014; Jackson, 2015).

Within freshwater ecosystems, benthic substrate (encompassing sedimentological characteristics, habitat heterogeneity and refugia potential / availability) is a primary abiotic determinant of community structure and biodiversity (Culp et al., 1983; Verdon-schot et al., 2016; Mathers et al., 2017). Habitats dominated by complex macrophytes or large mineral particle substrates typically support greater species richness and abundance through the provision of habitat heterogeneity (Rezende et al., 2014). Habitat heterogeneity may provide enhanced refuge potential which prey may use to evade predation and reduce biotic pressures. For example, studies within a variety of aquatic ecosystems have demonstrated that complex habitats can reduce the foraging efficiency of predators (Diehl, 1988; Alexander et al., 2012; Smith, Johnston, and Clark, 2014). In contrast, habitats with low habitat heterogeneity may support a limited number of taxa with appropriate adaptations or traits allowing them to interact most effectively with the physical habitat (Beisel et al., 1998). The effects of predation may therefore be influenced and in some instances be controlled by the presence of different physical habitats, with the effects of invasion varying between different habitats / substrate types (Nyström and Perez, 1998; Ruokonen et al., 2014; MacNeil, 2019).

In this study we examined the potential interaction between signal crayfish and four amphipod taxa, one native, *Gammarus pulex* (Linnaeus, 1758), and three non-native species present in Great Britain *Crangonyx pseudogracilis* (Bousfield, 1958), *Dikerogammarus villosus* (Sowinsky 1894) and *Gammarus tigrinus* (Sexton and Cooper 1939), within substrates of varying particle size and refuge potential (cobble, gravel and sand substrates) in a study design sensu Beggel et al., (2016). We hypothesised that survival rates would be greatest for: (i) non-native species and; (ii) larger substrate particle sizes.

Methods

Experiments were undertaken in five 42 L capacity opaque plastic mesocosms (32 cm diameter × 42 cm height) filled with 30 cm depth of dechlorinated water (pretreated with AquaSafe®, Tetra®, Virginia). Experimental mesocosms were aerated via aquarium aeration pumps and held at a constant water temperature throughout the 24-h experimental period ($20\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$). Experiments were undertaken during summer to early autumn (June–September 2017) to coincide with the period of crayfish activity in the Northern Hemisphere.

Three substrate treatments were investigated within each mesocosm: (1) cobble particles (64–256 mm), (2) medium sized gravel (8–16 mm) and; (3) coarse sand (0.5–1 mm). One particle depth of cobble (ca. 64–70 mm) or approximately 50 mm depth of gravel and coarse sand substrate was placed in each mesocosm. In addition, control experiments with no substrate present were undertaken. Each sediment and control treatment were examined for four amphipod species (a) *Gammarus pulex*; (b) *Crangonyx pseudogracilis*; (c) *Dikerogammarus villosus*; and (d) *Gammarus tigrinus*. Sediment treatment and amphipod species were combined in a random full factorial design giving twelve treatment combinations. Each combination was replicated five times to give a total of 60 individual trials (with a further 20 control trials).

Animals used in the experiments

Gammarus pulex is indigenous to Great Britain and has a widespread distribution (Sutcliffe, 1991). *G. pulex* is a sexually dimorphic species, with males reaching up to 21 mm body length, whilst females can reach a maximum of 14 mm in length (Pinkster, 1970). *Crangonyx pseudogracilis* originates from eastern North America and was first recorded in the UK in 1935 (Gledhill et al. 1993; GBNNSS 2019). *C. pseudogracilis* is a small, sexually dimorphic amphipod, with males typically ranging between 3–4 mm in body length, whilst females are larger and can reach lengths of up to 11 mm (Gledhill, Sutcliffe, and Williams, 1993). *Dikerogammarus villosus* is indigenous to the Ponto-Caspian region and was first recorded in the UK in 2010 (MacNeil et al., 2010). It is currently confined to five known areas (GBNNSS

2019), however, there is a high potential for the distribution of this species to expand in the future (Kobak et al. 2016). *D. villosus* is the largest amphipod within this study, with juveniles reaching sizes up to 6 mm (Devin et al., 2003) and adults reaching a maximal body length of 30 mm (Rewicz et al., 2014). *Gammarus tigrinus* is indigenous to the Atlantic coast of North America, first invading the UK in 1931 (Sexton and Cooper, 1939) and has established populations in rivers, lakes and canals. *Gammarus tigrinus* reaches a maximum body size of 14 mm in length (Van Riel et al., 2009; GBNNSS 2019).

Amphipod specimens were collected from local waterbodies where they occur in high abundances using a standard pond net (1 mm mesh). *G. pulex* were collected from Burleigh Brook, Loughborough, UK (52° 76' 72" N., – 00° 12' 35" W), *C. pseudogracilis* from Stonebow Washlands, Loughborough, UK (52° 77' 98" N., – 01° 25' 29" W), *D. villosus* from the southern basin of Pitsford Reservoir, Northamptonshire, UK (52° 32' 00" N., – 00° 85' 41" W), and *G. tigrinus* from Branston Water Park, Burton Upon Trent, UK (52°, 78' 66" N, – 01° 67' 96" W). Once in the laboratory, each amphipod species was allowed to acclimatise to laboratory conditions in separate aerated holding tanks (32 cm diameter x 42 cm height) filled with water from the source waterbody for a minimum of 12-h prior to the start of experiments. Holding tanks were maintained at water temperatures of 20 °C ± 1 °C, with no substrate present and food (pre-conditioned leaves and detritus; Joyce et al., 2007) was supplied in abundance to ensure amphipods were satiated prior to experiments commencing thereby limiting intraguild predation.

Pacifastacus leniusculus is endemic to North America west of the Rocky Mountains and has been introduced to aquaculture facilities in over 20 countries in Europe since 1959. It is now considered to be the most prevalent non-indigenous crayfish species in Europe (Kouba et al., 2015; Ruokonen et al., 2018). All *P. leniusculus* individuals used in the experiments were collected using baited traps from Gaddesby Brook (Twyford, Leicestershire, UK, 52° 68' 40" N., – 0.9° 19' 95" W) during June 2017 ca. 2 weeks prior to commencing experiments. To limit variability associated with differing size and age, individuals with a carapace length of 45 ± 5 mm were selected. Selected individuals did not display any obvious injury (such as damaged carapace or loss of chelae,

legs or antennae), or regenerating chelae which might have affected their foraging behaviour (Basil and Sandeman, 2000; Koch et al., 2006). Only intermoult individuals were used in the experiments (Kuhlmann et al., 2008) because activity and feeding behaviour is known to be modified during ecdysis (moulting; Reynolds, 2002). Both males and non-gravid females were used in the experiment but it should be noted that some behavioural differences in activity patterns have been documented associated with sex which were not tested here (Wurtz and Geist, 2013). Five crayfish were used for all experimental trials (3 males and 2 females) and each individual crayfish was used once for each substrate: species treatment to capture natural variability in predation rates and to ensure no undue influence of sex related predator performance on each treatment outcome. Between experimental trials, crayfish were kept in individual black aquaria (17.5 cm × 40.5 cm × 67.5 cm held at water temperatures 20 °C ± 1 °C) fitted with water pumps and fed on a diet of crustacean pellets (Tetra: TetraCrusa Menu) and carrot. Crayfish were not fed for 24-h prior to the experimental trials to standardise hunger levels.

Experimental procedure

For each substrate experiment, 100 individuals of one amphipod species of prey were placed with one signal crayfish, giving a predator–prey ratio of 1:100. For control trials (where no substrate was present), 25 of each amphipod species were selected at random and added to the mesocosm, giving a predator–prey ratio of 1:25. Preliminary trials and observations indicated that in the absence of any refugia habitat, the behaviour of both the crayfish and amphipods were modified at 1:100 predator–prey ratios. Observations indicated that in the absence of refugia / substrate *D. villosus*, and to a lesser degree *G. pulex*, displayed aggregation behaviour at higher densities around the crayfish resulting in unnatural behaviour of the crayfish and limited predation activity. As a result, control trials were undertaken with lower densities to enable the direct effects of predation to be ascertained. Consequently data from control trials are not included in the statistical analyses comparing substrate treatments.

For all experimental trials, amphipods were released into the mesocosms and left to acclimatise for one hour prior to the addition of *P. leniusculus*. A

single piece of carrot (c.10 g) was provided in each mesocosm as an alternative food source for both amphipods and signal crayfish to avoid excessive predation associated with an absence of sedentary food sources and reduce the likelihood of intraguild predation (Dorn, 2013; Mathers et al., 2016; 2018). Shelter / refugia was provided for each crayfish in the form of one PVC tube (11 cm diameter $\times$ 14 cm length). Mesocosms were covered for the duration of the trials to reduce any disturbances and to simulate low ambient light conditions to encourage the nocturnal foraging strategy and feeding of signal crayfish (Guan and Wiles, 1998). Experiments were undertaken over 24-h, and at the end of the experimental trial crayfish were removed and mesocosms deconstructed by washing the contents through 250 μ m sieves to enable the number of live amphipod individuals to be counted.

To account for differences in the body-size of the four amphipod species examined, the average biomass ($\pm$ SD) for each species was calculated (*G. pulex* = 0.001595 ± 0.000388 g; *C. pseudogracilis* = 0.000257 ± 0.000041 g; *D. villosus* = 0.005104 ± 0.000828 g and; *G. tigrinus* = 0.000298 ± 0.000066 g). 100 individuals of each species were dried on Whatman 0.42 μ m glass microfiber filters and Loss-on-Ignition conducted at 550 °C to obtain the average biomass for one individual (Heiri et al., 2001). Total biomass consumption for each experiment was calculated by multiplying the number of amphipods consumed per experiment by the average biomass of a single individual and is provided as supplementary material (Figure S1). No experiments were undertaken to examine natural mortality and intra-specific predation as rates from literature suggest that these are typically limited (all species recorded > 99% survivorship in intra-specific populations over 24-h, Bailey et al., 2006; MacNeil et al., 2008; Vadher et al., 2018; Cuthbert et al., 2018) compared to direct predation of amphipods by crayfish which can be up to 60% over 24-h (Mathers et al., 2019).

Statistical analyses

All statistical analyses were undertaken in the R environment (R Development Core Team, 2017). Differences in amphipod survivorship were tested within a generalized linear model (GLM) fitted with a binomial error distribution and logit link structure

using the ‘glm’ function in the ‘stats’ package. Two models were constructed, one which examined the statistical differences in the absence of substrate which was fitted with species as a factor. A second model which examined the effect of substrate was fitted with substrate and species as factors, as well as their interaction. The response variable was inputted as a matrix of the proportion of individuals that survived and the proportion that were consumed. Post-hoc pairwise comparisons of the species factor for the control model, and for the substrate $\times$ species interaction for the substrate model, were examined using least-square means with *p-values* adjusted for multiple comparisons via Tukey tests within the ‘lsmeans’ package (Lenth, 2016).

Results

Control experiments

Amphipod survivorship varied significantly as a function of amphipod species ($X_{3,16} = 147.73$, $p \leq 0.001$; Fig. 1). *D. villosus* demonstrated the highest survivorship whilst *G. pulex* displayed a significantly lower survivorship compared to all other amphipods. All pairwise comparisons between species were significant (Table 1).

Fig. 1 Mean ($\pm$ 1 SE) amphipod survivorship in the presence of *P. leniusculus* and at the end of the 24-h experiment for control experiments (no substrate)

Table 1 Pairwise post-hoc comparisons of amphipod survivorship to signal crayfish predation over 24-h under no substrate (control) conditions

Species	<i>Crangonyx pseudogracilis</i>	<i>Dikerogammarus villosus</i>	<i>Gammarus tigrinus</i>
<i>Gammarus pulex</i>	< 0.001	< 0.001	< 0.001
<i>Crangonyx pseudogracilis</i>		< 0.001	0.020
<i>Dikerogammarus villosus</i>			0.024

Significant ($p < 0.05$) results are emboldened. p values adjusted using the Tukey method

Substrate experiments

Amphipod survivorship varied significantly among amphipod species ($X_{3,48} = 354.04$, $p \leq 0.001$), substrate ($X_{3,48} = 88.11$, $p \leq 0.001$) and the interaction of these factors ($X_{6,48} = 199.56$, $p \leq 0.001$; Fig. 2). Greater numbers of *G. pulex* were consumed on gravel and sand substrates with less than 50% of individuals surviving the experiments, whilst survivorship was over 75% on cobble substrates. *C. pseudogracilis* demonstrated significantly enhanced survivorship within sand substrates compared to gravel and cobble substrates. *D. villosus* demonstrated no differences in survivorship as a function of substrate type and had the greatest survivorship rates (over 80%) among all amphipods for all substrates. *G. tigrinus* displayed greater survivorship within cobble and gravel substrates (over 80%) and was reduced to just over 50% on sand (Fig. 2; see Table 2 for all post hoc comparisons).

Fig. 2 Mean (± 1 SE) amphipod survivorship in the presence of *P. leniusculus* and at the end of the 24-h experiment for cobble, gravel and sand substrates

Discussion

This study sought to investigate the predation of *P. leniusculus* on four amphipod species in the presence of different substrates characterized by different particle sizes and refuge potential. We found evidence in support for our first hypothesis, that survival rates would be greater for non-native taxa than for the indigenous species. The indigenous amphipod, *G. pulex*, demonstrated the lowest survivorship rates among all four species, with all three non-native amphipod species displaying significantly higher survivorship in all experiments except the cobble treatment (and sand for *G. tigrinus*). *D. villosus* consistently demonstrated the highest rates of survivorship ($> 80\%$) of all species for all substrates and for control conditions. This species is highly adaptable to heterogeneous and anthropogenically modified habitats (Platvoet et al., 2009) with survivorship being high on both the preferred coarse substrates, but also on sub-optimal substrates such as sand (MacNeil et al., 2010; Rewicz et al., 2014). However, we also found that despite significant differences in the survivorship rates of non-native *D. villosus* and the indigenous *G. pulex*, there were no differences in the biomass consumed for the two species among all substrates (Figure S1). This may indicate that *P. leniusculus* were satiated due to the larger body size of *D. villosus* rather than exhibiting a strong ability to preferentially predate individuals.

We found evidence to partially support our second hypothesis, that large substrates (with larger particle sizes and interstitial spaces) would support the greatest survivorship of amphipods. Cobble substrates had the greatest survivorship rates for *G. pulex* and *D. villosus* and supported comparable numbers following the 24-h experiments as gravels for *G. tigrinus*. For these species, cobble substrates resulted in survivorship

Table 2 Pairwise post-hoc comparisons of amphipod survivorship to consumed by signal crayfish predation over 24-h under different substrate scenarios

Species	<i>Gammarus pulex</i>			<i>Crangonyx pseudogracilis</i>			<i>Dikerogammarus villosus</i>			<i>Gammarus tigrinus</i>		
	Substrate	Cobble	Sand	Gravel	Cobble	Sand	Gravel	Cobble	Sand	Gravel	Cobble	Sand
<i>Gammarus pulex</i>	Gravel	< 0.001	1.000	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.084
	Cobble		< 0.001	0.413	0.460	0.938	0.049	< 0.001	0.125	0.038	0.972	< 0.001
	Sand			< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.285
<i>Crangonyx pseudogracilis</i>	Gravel			1.000	1.000	0.006	< 0.001	< 0.001	< 0.001	< 0.001	0.011	< 0.001
	Cobble					0.008	< 0.001	< 0.001	< 0.001	< 0.001	0.013	< 0.001
	Sand						0.823	< 0.001	0.952	0.774	1.000	< 0.001
<i>Dikerogammarus villosus</i>	Gravel							0.148	1.000	1.000	0.730	< 0.001
	Cobble								0.060	0.181	0.002	< 0.001
	Sand									1.000	0.906	< 0.001
<i>Gammarus tigrinus</i>	Gravel										0.672	< 0.001
	Cobble											< 0.001

Significant ($p < 0.05$) results are emboldened. p values adjusted using the Tukey method

rates of 70% or greater. All three species (*G. pulex*, *G. tigrinus* and *D. villosus*) have habitat preferences for larger mineralogical particle-sizes which provide refuge within the relatively large interstitial pore spaces (Platvoet et al., 2009; Kobak et al., 2014; Clinton et al., 2018); although all will utilize smaller substrate particles. In marked contrast, *C. pseudogracilis* displayed higher survivorship from predation on sand substrates. *C. pseudogracilis* has typically been recorded inhabiting littoral habitats comprising soft substrates such as silt and locations with dense macrophyte cover (Mayer et al. 2012; MacNeil and Dick, 2014).

It is likely that a combination of factors contributed to the varying survivorship rates recorded in this study, including predator avoidance strategies and substrate characteristics which provide varying refugia potential (Barrios-O'Neil et al., 2015). Aquatic invertebrate prey are able to modify their behaviour in the presence of predators (Lima and Dill, 1990), and the presence of crayfish has been previously shown to elicit avoidance behaviours in freshwater gastropods, including complete emergence from the water (Alexander and Covich, 1991) or moving vertically out of the reach of crayfish if there is sufficient water depth to provide a spatial refuge (Covich et al., 1994). For freshwater amphipods three avoidance strategies have been hypothesized: (i) becoming less motile and migrating into the substrate to seek refuge (Wudkevich et al., 1997); (ii) avoidance by actively swimming in the water column (Beggel et al., 2016) and; (iii) aggregation behavior (Kullmann et al., 2008). However, the vertical zonation of amphipod taxa within the water column and submerged substrates has also been reported as a result of inter-specific competition (e.g., Plavoet et al., 2009; Kobak et al., 2017).

In its invaded range, *D. villosus* has been observed to be less active than indigenous *G. pulex* in the presence of predatory fish (Beggel et al., 2016) and this 'immobile' characteristic may act as an effective predator avoidance mechanism by reducing the probability of being targeted. Similarly, a number of faunal groups have been reported to aggregate as a predator evasion behavior (e.g. Morgan and Colgan, 1987) or by confusing predators due to the large numbers present (e.g. Krakauer, 1995). We observed aggregation of *D. villosus* individuals within the sand substrate experimental trials providing support for the observations of Jermacz et al. (2017). They observed that *D.*

villosus avoided predation by reducing activity levels and seeking refuge under large substrate clasts in the presence of the predatory racer goby (*Babka gymnotrachelus*, Kessler, 1857). However, in Jermacz et al.'s (2017) experiments, where shelter was absent *D. villosus* were observed aggregating together; this strategy deterred and reduced goby attacks on *D. villosus* and resulted in comparable survivorship rates as experiments in which shelter was provided.

The non-native amphipod *C. pseudogracilis* also displayed high survivorship in most experimental treatments. We observed that a number of individuals remained swimming in the water column, close to the water's surface. This avoidance strategy was also observed for *G. tigrinus*, particularly for cobble and gravel treatments, and this physical spatial separation between predator and prey is a similar strategy to that reported for gastropods in the presence of predatory crayfish (Alexander and Covich, 1991; Covich et al., 1994), and reported by Macneil (2019) between the predatory *D. villosus* and *C. pseudogracilis*. *C. pseudogracilis* also displayed burrowing behavior within the sand substrate treatment in our experiments. This dual predator avoidance strategy resulted in the sand substrate supporting the highest survivorship for *C. pseudogracilis* compared to the cobble and gravel. This marked difference in substrate preference in contrast to the other amphipod species considered in this experiment provides a mechanism for *C. pseudogracilis* to reduce competitive and predatory encounters. This suggests *C. pseudogracilis* may be more resistant to future pressures associated with the colonization of new non-native invasive amphipod species.

Similarly, *G. tigrinus*, the third non-native amphipod in this study, displayed high survivorship in gravel and cobble substrates, but not sand substrates. *G. tigrinus* has been recorded to demonstrate spatial habitat segregation in the presence of the invasive amphipod *D. villosus* (Platvoet et al., 2009; Van Riel et al., 2009) and co-exists with this species in Lake Gouwee (Netherlands). In contrast the invasion of *D. villosus* resulted in the local extinction of the indigenous *Gammarus duebeni* (Dick and Platvoet, 2000). Within these experiments, we observed that some *G. tigrinus* individuals remained close to the water surface to evade predation in the experiments, providing spatial segregation from the predatory invasive crayfish.

In marked contrast to the non-native amphipod species, *G. pulex* demonstrated low survivorship rates for gravel and sand substrate treatments, whilst survivorship was greater and comparable to the other taxa for cobble substrates. We expected *G. pulex* to utilize gravel substrates more efficiently than observed, with average survivorship being only 44% (compared to 80% observed by Mathers et al., 2019). It is possible that the 50 mm depth of substrate did not provide sufficient depth to evade predation given that signal crayfish are capable of displacing gravels up to 38 mm in size and excavating deeper pits (Johnson et al., 2010). Mathers et al., (2019) reported active avoidance behavior of *G. pulex* in the presence of *P. leniusculus* via vertical migration into gravel substrates 100 mm deep. When vertical migration of *G. pulex* was impeded due to fine sediments blocking interstitial pore spaces, survivorship rates were reduced. The low survivorship rates recorded for *G. pulex* in the sand treatment provides further evidence that interstitial pore spaces potentially represent an important refuge when substrate depth and size is sufficient.

The combined effect of phenotypic plasticity to environmental variability, flexible habitat utilisation, variable locomotory activity (including reduced movement) and aggregation behavior in response to the presence of a predator, resulted in greater survivorship of all of the non-native amphipods compared to the indigenous amphipod (*G. pulex*) in this study. The results of this study provide evidence to suggest that the presence of multiple invaders may not necessarily result in interactions that facilitate the spread of the invading species (e.g., as a food resource) but that invasive predators may significantly affect indigenous communities such that waterbodies have the potential to be dominated by multiple coexisting non-native invasive species (Ricciardi, 2001; Simberloff, 2006). The experiments also demonstrate the importance of characterising physical habitat when considering the ecological effect of invaders with substrate characteristics (complexity and refugia potential) influencing predation success. Further studies are required to examine the mechanisms influencing species interactions and the physical environment, so they can be modelled and used to predict the effects on the wider population and community structure.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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