Behavioural responses of invasive (*Gmelinoides fasciatus*) and native (*Gammarus lacustris*) amphipods to predators on different bottom substrates

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Abstract

The amphipod *Gmelinoides fasciatus* has invaded and established in numerous large lakes in Eurasia and, in the process, has displaced the native amphipod, *Gammarus lacustris*. The mechanism behind its invasion success is unclear and remains an important topic for invasion ecology. Three laboratory experiments were conducted to determine if superior predator avoidance and different types of bottom substrate could be important factors contributing to the invasion success of *G. fasciatus*. Our results indicate that, on gravel and sand substrates, *G. fasciatus* exhibited superior digging behaviour to avoid predation by fishes (perch and common roach), contrary to *G. lacustris*. On sandy substrate only 9% of *G. fasciatus* individuals were consumed, whereas *G. lacustris* were consumed much more intensively at 74%. In addition, *G. fasciatus* exhibited a more substantial reduction in activity, where the time spent in motion reduced from 37.6% to 20.8% compared to *G. lacustris* (from 21.8% to 17.4%) when in the presence of predatory fish kairomones. *G. fasciatus* movement speed was also reduced in the presence of kairomones (from 57.1 mm/s to 39.3 mm/s). However, the presence of kairomones

had little effect on digging behaviour of *G. fasciatus*. *G. fasciatus* consistently demonstrated superior predator avoidance abilities over *G. lacustris*, suggesting that this mechanism might play an important role in the invasion success of *G. fasciatus*.

Keywords macroinvertebrate ecology・freshwater fish・locomotor activity・predator avoidance・kairomones ・ alien species

Introduction

Amphipods are an important link in freshwater food webs. They help decompose detritus and often are an important prey item for various fish species (Kostrzewa and Grabowski 2003; Grabowska and Grabowski 2005; Lobanova et al. 2017). In the last century, numerous invasive amphipods have established in Europe's freshwater ecosystems (Dick 1996; Bij de Vaate et al. 2002; Spikkeland et al. 2020). In many instances, invasive amphipods have outcompeted and replaced native amphipod populations (Timm and Timm 1993; Packalén et al. 2008; Reisalu et al. 2016; Šidagyte et al. 2017), mostly due to biological traits such as high fecundity (Berezina and Panov 2004; Jänes et al. 2015) and tolerance to a wide range of abiotic factors (Berezina and Panov 2004; Devin and Beisel 2007).

Gmelinoides fasciatus (Stebbing 1899), an amphipod originating from Lake Baikal, is one of the most successful invaders in Eurasia (Gherardi 2007; Berezina 2009). Waterbodies populated by *G. fasciatus* differ greatly in biotic and abiotic characteristics, indicating an ability to tolerate a wide range of environmental conditions. Many large lakes and rivers, such as Lake Ladoga (Panov 1996) and River Volga reservoirs (Berezina and Strelnikova 2010) have been invaded by *G. fasciatus*. *G. fasciatus* also inhabits Lake Peipsi, the fifth largest lake in Europe, where it was introduced in the early 1970s to improve fish food quantity. By 1990, it was well established in littoral areas of Lake Peipsi, while dominating over the native amphipod species, *Gammarus lacustris* and *Pallasea quadrispinosa* (Timm and Timm 1993). In the littoral area of Lake Peipsi *G. fasciatus* represents approximately 43% of total macrozoobenthos abundance (Kangur et al. 2010). Furthermore, at a suitable depth (< 0.2 m) and substrate (gravel and sand), *G. fasciatus* comprises up to 97% of total macrozoobenthos abundance, excluding other macroinvertebrates and effectively forming a zoobenthos “monoculture” (Kangur et al. 2010).

In its native Lake Baikal, *G. fasciatus* is common prey for many species of fish, including perch (*Perca fluviatilis)*, ruffe (*Gymnocephalus cernua)*, whitefish (*Coregonus lavaretus)*, and dace (*Leuciscus leuciscus*) (Bekman 1962). *G. fasciatus* has also successfully invaded Lake Onega (Russia), representing more than 50% of prey items found in perch stomach contents (Lobanova et al. 2017; Georgiev et al. 2022). Similarly, in Lake Otradnoye (Russia), perch consumed mainly *G. fasciatus* (up to 63% of stomach contents; Berezina and Strelnikova 2010).

G. fasciatus inhabits shallow littoral areas in lakes (Berezina et al. 2009; Kangur et al. 2010; Kumari et al. 2007), replacing their native counterparts once established in the same habitat. Prior to the *G. fasciatus* invasion in Lake Peipsi, *P. quadrispinosa* inhabited sand bottom habitats, and *G. lacustris* inhabited stony and vegetated littoral areas (Timm and Timm 1993). Both habitats are now dominated by *G. fasciatus,* which has established high abundances in all types of bottom substrate, particularly gravel and sand. One possible explanation for the success of *G. fasciatus* in littoral areas could be its ability to avoid fish predation, especially in the presence of macrophytes and stony substrates. Pennuto and Keppler (2008) proposed that superior predator avoidance behaviour in non-native amphipods may cause increased predation on native amphipods.

The native gammarid *G. lacustris* has been displaced from its habitat in Lake Peipsi (and many other lakes) due to the invasion and establishment of *G. fasciatus*. Additionally, significant loss of biodiversity manifested as reduced abundances and biomass of indigenous macroinvertebrates, has been recorded (Panov et al. 2000; Gherardi 2007). In recent decades, the reasons for the invasion success of *G. fasciatus* have been explored. For instance, Berezina et al. (2009) suggested that direct predation by *G. fasciatus* on native *G. lacustris* could be one of the reasons for the native species replacement. Furthermore, *G. fasciatus* exhibited greater ability to reproduce quickly under favourable conditions than its native counterpart (Berezina 2004, 2005). However, the mechanisms behind the invasion success of *G. fasciatus* remain poorly explained.

The aims of this study were to explore factors that promote the success of this invasive species in invaded lake ecosystems, and to test the following hypotheses: 1. *G. fasciatus* exhibits superior predator avoidance behaviour to *G. lacustris* by digging into substrates to avoid predation by fishes. 2. *G. fasciatus* is more behaviour sensitive to predatory fish cues (kairomones) than its native counterpart *G. lacustris*. 3. *G. fasciatus* is more prone to digging when in the presence of fish kairomones compared to *G. lacustris*.

Materials and methods

Sampling and experiment set-up

Experiments were conducted in an indoor laboratory setting in the Centre for Limnology, Estonian University of Life Sciences. *Gammarus lacustris* and *Gmelinoides fasciatus* were obtained with a kick net from two Estonian lakes: Lake Võrtsjärv and Lake Peipsi, respectively. The amphipods used in the experiment were adults ranging from 7-10 mm for *G. fasciatus* and 8-12 mm for *G. lacustris*. Amphipods were picked randomly to avoid size bias.

Perch and roach were obtained from Lake Võrtsjärv and Lake Peipsi with a fyke net. Perch specimens chosen for the experiment were aged 2+ with a standard length of 11 cm (±1 mm), and roach individuals were aged 3+ with a standard length of 10 cm (±1 mm). After capture, gammarids and fish were immediately sorted and put into 200 L (gammarids) and 800 L (fish) aquariums. Aquariums were fitted with stones and sand for shelter and aerated continuously. Both amphipods and fish were acclimated to laboratory conditions for seven days prior to the experiment, whilst also being fed with *Chironomous plumosus* larvae (fish) and a commercial food mixture, TetraMin flakes (amphipods). Amphipods were checked for acanthocephalan parasites prior to experimentation since these parasites can affect amphipod responses to kairomones (Baldauf et al. 2007).

Light (450 lx), temperature (14.1 ± 0.2 °C), and oxygen (>90% dissolved oxygen) conditions were kept constant. At the end of the experiments, mortality was low (< 10%), indicating satisfactory conditions for amphipods.

Fish feeding experiment

In a climate-controlled room, smaller (20 l) aquaria were filled with preconditioned tap water. One fish (perch or roach) was placed in the aquarium to acclimate for 48 hours. During this time, no food was provided. Ten individuals each of *G. fasciatus* and *G. lacustris* were simultaneously released into the aquarium and left undisturbed for one hour. After one hour, the fish was removed, and the remaining amphipods were counted and identified. If no amphipods were consumed by the fish, the result was excluded (16% of trials). The experiment was carried out with four different bottom substrates – control (no substrate), sand, gravel, and cobble stones. Substrate sizes were classified according to Jowett et al. (1991), with the following parameters: 0.5-2 mm sand, 2-64 mm gravel, and 65-256 mm cobble stones. All substrates were thoroughly cleaned of periphyton, debris, and macroinvertebrates prior to use and placed in the experimental aquariums in a layer 3-4 cm thick. This approach resulted in a total of eight combinations of treatments, with each combination replicated ten times.

Amphipod activity response to fish chemical cues

This experiment was designed to test the behavioural response of amphipods to predatory fish cues (kairomones) in the water. To obtain kairomone affected water, live perch were held (concentration 0.01 g of fish per 1 ml of water) in non-chlorinated tap water for 24 h (following Mathis and Hoback 1997; Bollache et al. 2006). The filtration unit was removed 24 h prior to each experiment, and aeration was provided by an air stone. For the control experiment, non-chlorinated and aerated tap water was used.

One individual amphipod (*G. fasciatus* or *G. lacustris*) was placed in a petri dish (11 cm diameter) filled with either fish scented or regular water. The amphipod was left to adjust to experimental conditions for five minutes, then filmed from above (using a Canon 5D mark II camera) for an additional five minutes. The experiment was conducted 30 times for each gammarid species, each time using a new gammarid specimen. The films were analysed with LoliTrack (Loligo Systems, Denmark) video tracking software to assess how the chemical cues affected the locomotor activity and velocity of the amphipods.

Effect of chemical cues on digging behaviour

To assess if digging behaviour was affected by fish chemical cues, round glass dishes (11 cm diameter) were filled with non-chlorinated tap water and fish scented water (kairomones). In the bottom of the dish, a 3 cm layer of sterilised sand was added, and five individuals of *G. lacustris* and five individuals of *G. fasciatus* were released separately. Immediately after the release of amphipods, their behaviour was filmed with a Canon 5D mark II camera (fixed on a tripod) for ten minutes and later assessed visually. Five replicates were conducted using water with and without fish scent and the two amphipod species. In total, the behaviour of 50 individuals were assessed per species. Upon reviewing the films, any digging behaviour was recorded.

Statistical analysis

Statistical analyses were conducted using R, version 4.1.3 (R Core Team 2020). Before any test, data were checked for normality and homogeneity assumptions. Since normality assumptions were not met, a non-parametric Wilcox-Mann-Whitney test was used to test for differences between amphipod species consumption in each substrate type, fish feeding, and behavioural responses to fish chemical cues. To test for differences in amphipod consumption between the four different substrate treatments, the non-parametric Kruskal-Wallis test was performed. When a robust difference was found, the pairwise Mann-Whitney U test was used to make pairwise comparisons between substrate treatments.

Results

Substrate influence on fish feeding

Results showed that both fish species consumed more *G. fasciatus* individuals in the control group with no substrate than in the sand and gravel groups ($p<0.001$; Fig. 1). The same pattern was recorded between cobbles and control ($p = 0.04$) and between cobbles and gravel ($p < 0.001$), with higher consumption of *G. fasciatus* in the control and cobbles, respectively (Fig. 1). However, no such differences were found for *G. lacustris* between substrates, except a slightly higher consumption in the control versus cobbles ($p = 0.05$; Fig. 1).

Results also showed differences in consumption of invasive and native amphipod species within substrate treatments. On sandy and gravel substrates, perch and roach preferentially consumed *G. lacustris* over *G. fasciatus* ($p < 0.001$ for both; Fig. 1). On the sand substrate, perch consumed only 9% of *G. fasciatus* individuals after an hour, whereas 74% of *G. lacustris* individuals were consumed (Fig. 1). Visual inspection after each experiment showed that *G. fasciatus* individuals were buried within the sand, whereas *G. lacustris* were lying on top of the substrate or swimming in the water column. Gravel substrate showed similar results, with perch and roach indicating a clear preference for *G. lacustris*. On gravel, perch consumed 8% of *G. fasciatus* and 58% of *G. lacustris* individuals (Fig. 1), and visual inspection after each experiment showed, once again, that *G. fasciatus* were buried into the gravel, and *G. lacustris* were swimming in the water column or lying on top of the substrate. However, in the tank with cobbles, there was no difference in consumption of either amphipod species (Fig. 1).

Roach consumed more *G. fasciatus* on sand and gravel substrates compared to perch ($p = 0.02$ and $p = 0.004$, respectively), while perch consumed more *G. lacustris* compared to roach only with sand substrate ($p = 0.008$; Fig. 1). In the control aquarium, perch and roach exhibited a slight preference ($p = 0.037$) for *G. lacustris*, indicating that without refuge, fish may prefer *G. lacustris* as prey (Fig. 1).

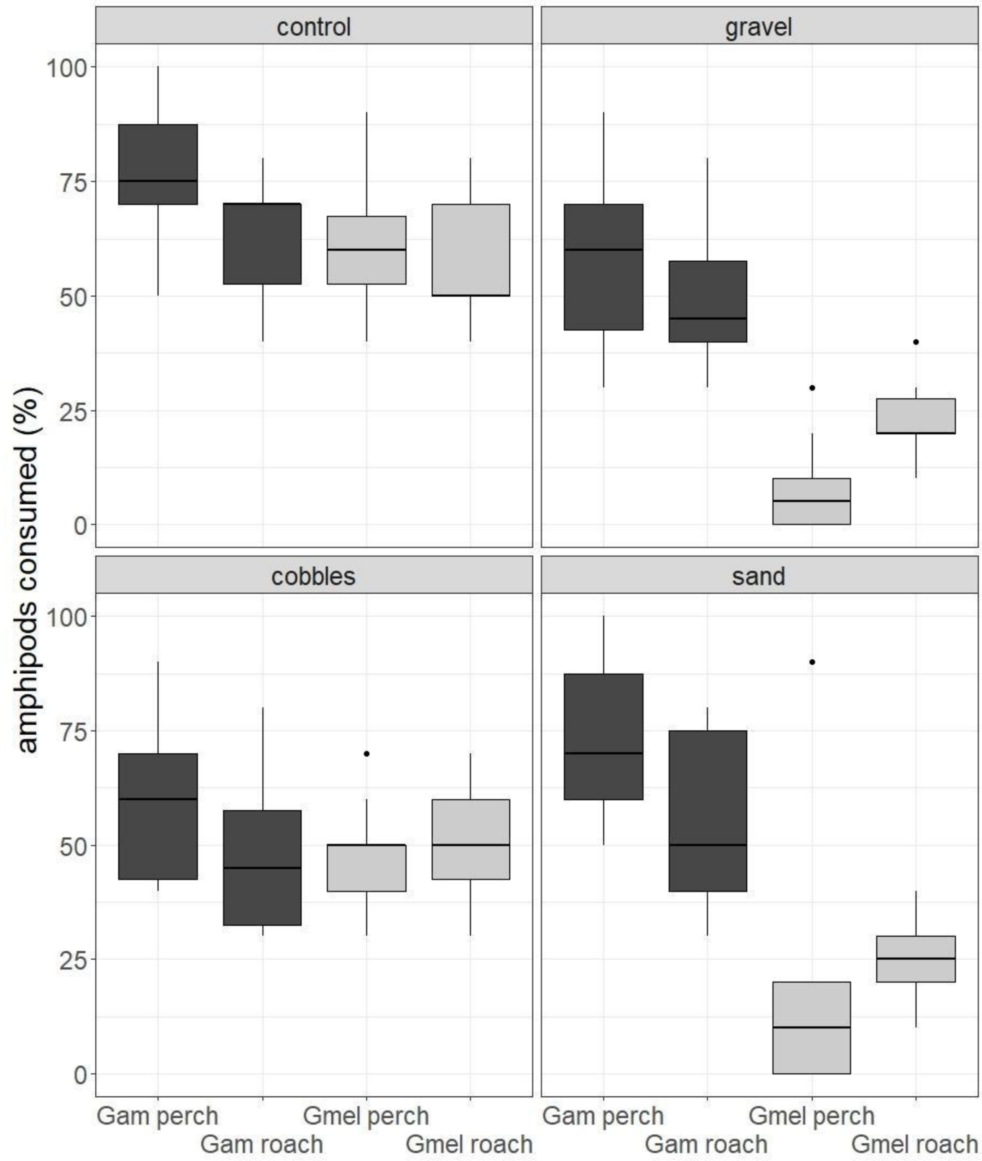

Fig. 1 Percentages of consumed *G. lacustris* (Gam) and *G. fasciatus* (Gmel) on different substrates (control, gravel, cobbles and sand) in the presence of either perch or roach (replicates = 10). Dark box plots represent *G. lacustris* (Gam) ± standard deviation, and light box plots represent *G. fasciatus* (Gmel) ± standard deviation

Gammarid locomotor activity response to fish chemical cues

In general, gammarids responded to fish chemical cues with a decrease in activity (Fig. 2). The average time spent in motion during the 5-minute filming period of *G. fasciatus* (N = 30) decreased from 37.6% to 20.8% in the scented water (kairomones; Fig. 2), indicating a decrease in activity ($p < 0.01$) compared to the control group. *G. lacustris* (N = 33) also decreased in activity in the fish scented water ($p = 0.03$), from 21.8% to 17.4% (Fig. 2), although less so than *G. fasciatus*.

No difference was found in the movement velocity for *G. lacustris* between control (average velocity = 42.6 mm/s) and kairomone treated water (average velocity = 41 mm/s; $p > 0.05$; Fig. 2). *G. fasciatus*, however, exhibited decreased movement speed ($p < 0.05$) between the control and kairomone groups (average velocity = 57.1 mm/s and 39.3 mm/s, respectively; Fig. 2).

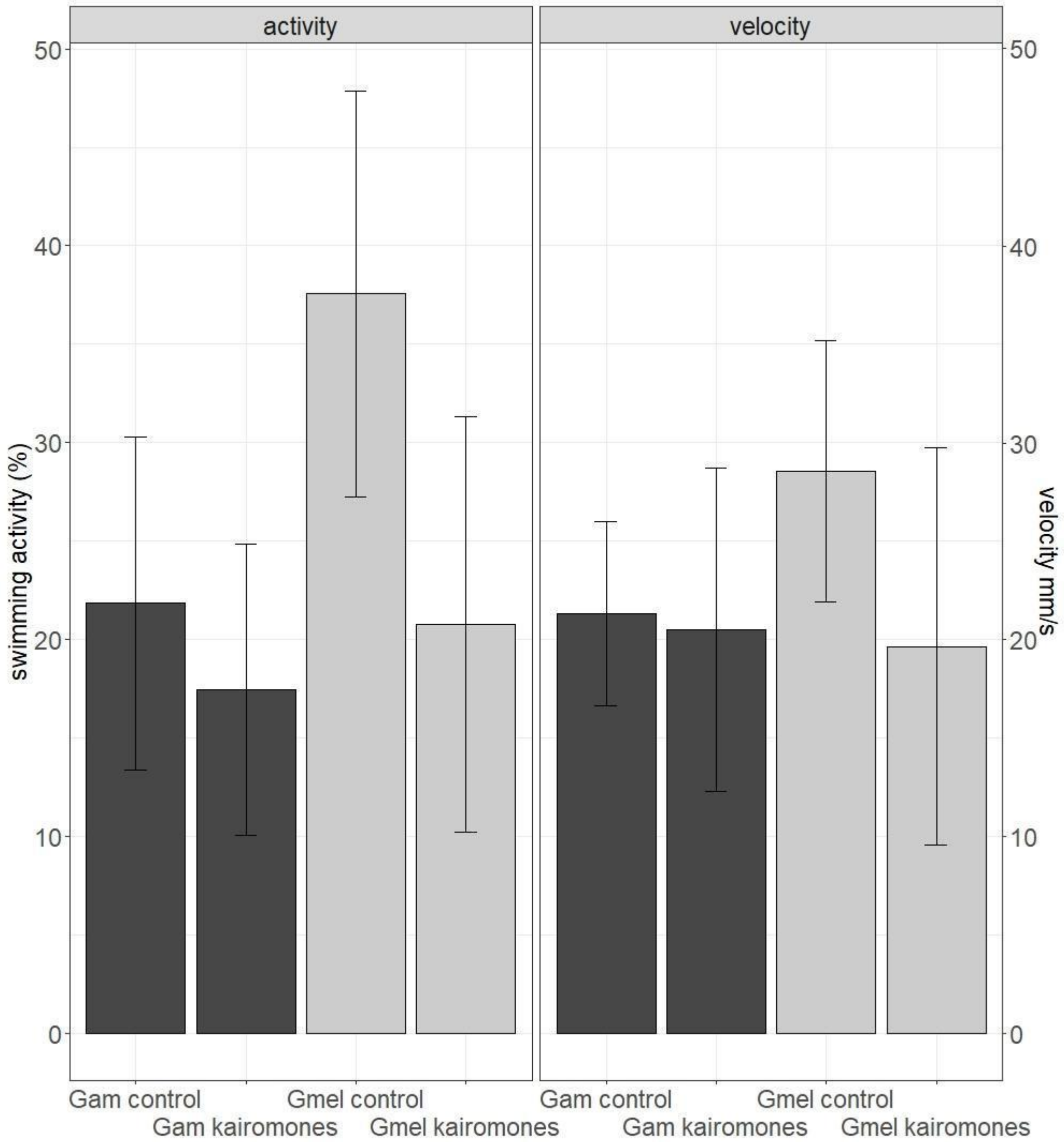

Fig. 2 Effects of chemical cues on swimming activity (percentage of time spent in motion) and velocity (mm/s) of *G. fasciatus* (Gmel; replicates = 30) and *G. lacustris* (Gam; replicates = 33) in water with (kairomones) and without (control) chemical cues. Dark grey and grey columns (± standard errors) represent *G. lacustris* and *G. fasciatus* activities, respectively

Effect of chemical cues on digging behaviour

Visual inspection of gammarid digging responses to chemical cues showed that not a single individual (0/50) of *G. lacustris* dug into the sandy substrate during the experiment in either of the water treatments (Table 1). *G. fasciatus*, on the other hand, demonstrated digging behaviour in both water treatments. In the tap water treatment, 9 of 25 individuals exhibited digging behaviour, while in fish scented water, 12 of 25 individuals were buried into the substrate.

Discussion

Our experimental results support our first hypothesis, suggesting that invasive *G. fasciatus* is more successful at burying within gravel and sand substrates compared to the native *G. lacustris*; thus, *G. fasciatus* can more readily avoid fish predation. In contrast, smaller grain-size substrates did not provide refuge for native *G. lacustris,* which instead seems to be more effective at hiding in larger cobbles. Gammarus species have been reported to avoid bare substrates and prefer physical structures for refuge (Dahl and Greenberg 1996; Starry et al. 1997; Baumgärtner et al. 2003; Franken et al. 2006). However, in some instances, less coarse substrates are preferred for shelter (Baumgärtner et al. 2003). Amphipods are known to prefer distinct substrates and the use of optimal microhabitats can reduce the risk of being preyed upon (Kley et al. 2009). In our study *G. lacustris* seemed to use larger cobble stones as hiding structures, while *G. fasciatus* preferred less coarse substrate as shelter, indicating differences in hiding behaviour strategies.

Differences in predation success were noted for *G. fasciatus* and *G. lacustris* between perch and roach. In sand and gravel substrates, *G. fasciatus* was consumed more by roach than perch, while *G. lacustris* was preyed on by perch more than roach with sand substrate. Adult perch are predatory fish that rely on visual cues for catching prey, and in its earlier stages of life, it feeds primarily on macroinvertebrates (Yazicioğlu et al. 2016). Our results indicate that perch were less effective at preying on *G. fasciatus* individuals on sand and gravel substrates, most likely because they were unable to locate them based on visual cues. Roach, on the other hand, was a more effective predator, due to cyprinids having a greater sense of smell than percids and relying to a greater extent on their sense of smell for finding prey (Malyukina et al. 1999). The ability of *G. fasciatus* to dig into substrates likely benefits this invasive species, which can hide from predatory fish, especially those that locate prey using visual cues, such as perch. However, even in the control tank, perch preyed more on *G. lacustris*, which were larger than *G. fasciatus*, making the former a more suitable prey for perch. Fish typically prefer larger prey for maximal feeding efficiency. For example, mean gammarid lengths in trout stomachs were always larger than those sampled from a river bottom (Newman and Waters 1984).

With benthic feeders, such as bream or roach, increased sediment size was associated with decreased feeding efficiency due to clogged branchial channels (Hoogenboezem et al. 1991; Hoogenboezem 2000). Therefore, the ability of *G. fasciatus* to bury within coarse substrate could provide an effective strategy to escape predation, including from fish that rely primarily on sense of smell for finding prey, like roach. This strategy is not limited to escaping fishes that rely on visual cues, but also for benthic feeding fishes that use sieving of bottom substrate to forage. In this study, *G. fasciatus* was more efficient than *G. lacustris* in the use of fine-grained substrates for hiding from predation, suggesting that the latter were more susceptible to predation in these substrates compared to its invasive counterpart. Indeed, consumption of *G. lacustris* on cobbles was lower than on other substrates.

In Lake Peipsi, *G. fasciatus* was most abundant on coarse particle substrates, most notably gravel and sand, while their abundance on silt was minimal (Kangur et al. 2010). This result suggested that coarser substrates provided the best refuge from predators. Our results support those findings and indicate that *G. fasciatus* preferred sand and gravel substrates, instead of cobbles, to hide from fish predation. *G. fasciatus* concentrates in shallow littoral areas (Panov et al. 2000; Berezina 2008; Berezina et al. 2009, Kangur et al. 2010), while *G. lacustris* inhabits a variety of habitats, commonly hiding underneath stones in the uppermost littoral zone of lakes and rivers, where there is often a strong predator presence (Matafonov 2007; Chertoprud and Chertoprud 2004). *G. lacustris* also occupies open water pelagic zones of fishless lakes (Wilhelm et al. 2000; Zadereev et al. 2010). Our results indicated that fish fed equally on both amphipods on cobbles, suggesting that *G. lacustris* was not disadvantaged compared to the invasive species. However, its consumption was lower on cobbles than in the control, suggesting that the larger substrate protected *G. lacustris* from fish predation, since was unable to dig into finer substrates as efficiently as *G. fasciatus*.

Amphipods are sensitive to the scent of fish (Baldauf et al. 2007, Pennuto and Keppler 2008, Jermacz et al. 2017), crayfish (Hesselschwerdt et al. 2009), and injured individuals of the same species (Wudkevich et al. 1997). Previous studies showed that Gammarus spp. exhibit reduced activity and a greater use of refuge (Wudkevich et al. 1997; Schäffer et al. 2013) when exposed to predator kairomones. In general, our results from both amphipods species indicate the same pattern, although *G. fasciatus* exhibited greater response behaviour compared to *G. lacustris,* supporting our second hypothesis. In the presence of chemical cues from perch, *G. fasciatus* reduced its locomotor activity by 16.7%, while *G. lacustris* reduced its activity by only 4.4%. *G. fasciatus* also reduced its movement velocity in kairomone treated water, but this reduction was not observed for *G. lacustri*s. In the presence of pike (*Esox lucius*), *G. lacustris* reduced its time within the water column and spent more time near the bottom, displaying different habitat use under predation pressure (Wudkevich et al. 1997). Our results indicated the same behaviour for *G. lacustris*, but gammarids might react differently to different predatory species, and burying behaviour was not studied by Wudkevich et al. (1997). Baumgärtner et al. (2003) showed that, in the presence of kairomones, *Gammarus roeseli* preferred less coarse substrates for hiding, exhibiting a response similar to that of *G. fasciatus* in our experiments. In line with our third hypothesis, results showed that *G. fasciatus* is more prone to digging into sand substrate compared to *G. lacustris* in the presence of kairomones. However, *G. fasciatus* indicated only slight differences in digging behaviour between the tap water and kairomone water treatments. In addition to kairomones, amphipods also react visually and mechanically to approaching fish (Starry et al. 1998); thus, fish kairomones might not be the only trigger for antipredator responses. To our knowledge, the behavioural response of *G. fasciatus* in the presence of kairomones has not been previously documented. In agreement with our hypothesis, *G. fasciatus* reduced its swimming activity and velocity in the presence of chemical cues from predators. This behavioural response likely provides an advantage for avoiding predation for the invasive species compared to the native amphipod (*G. lacustris*).

In conclusion, *G. fasciatus* demonstrated superior predator avoidance abilities by digging within substrates and having a more significant response to fish kairomones. Further insights into the abilities of benthic feeders to successfully prey upon *G. fasciatus*, using different benthivorous fish species, could explain the invasion success of *G. fasciatus*. In addition to this, a depth selection experiment, similar to Kobak et al. 2017, could shed light to niche overlapping between *G. fasciatus* and *G. lacustris*. The results of this study showed that invasive *G. fasciatus* has advantages in terms of anti-predator responses and behaviours, thus helping to explain its invasion success over the native amphipod.

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Author contributions

All the authors conceived the study and contributed to the revision of the paper. P.T. carried out the experiments and wrote the paper, with contributions from A.T. and F.E. A.T. and P.T. performed field work by collecting the necessary fish and amphipod samples, and set up the laboratory experiment. Statistical analysis was performed by F.E. All authors approved the final version of the manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Conflicts of interest

The authors declare that they have no conflict of interest.

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