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Interference competition among native and invader amphipods

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ABSTRACT

Aquarium experiments were used to study indications of interference competition, such as substratum choice shifts, swimming activities and mortality of invasive and indigenous gammarids in each other's presence. The more recent invaders *Gammarus tigrinus* and *Dikerogammarus villosus* were more likely to prefer stone substratum, whereas the native *Gammarus pulex* and an earlier invader *Gammarus roeseli* were found more frequently in the water layer. Sand was the least likely substratum to be chosen by any of the species. *G. pulex* and *G. roeseli* did not alter their substratum preference in each other's presence. In the presence of *D. villosus*, *G. pulex* shifted towards smaller stones and increased its swimming activities, whereas *D. villosus* did not change its behaviour in the presence of *G. pulex*. These shifts may indicate interference competition, with *D. villosus* being the stronger competitor. The greatest shifts in substratum preference arose when one species had occupied a substratum before the other one was introduced, especially when *D. villosus* was already present before *G. pulex* was introduced, possibly indicating pre-emptive competition. Swimming activities of *G. pulex* increased in the presence of *D. villosus*, whereas *D. villosus* spent little time swimming. Mortality was comparable between the different experiments without any indication of predation. The effect of Intra Guild Predation (IGP) may not be reflected adequately by short-time experiments as moults occurred seldom during the experiments. Although no IGP was observed during our experiments, habitat shifts occurred, which may indicate that competitive interactions are apparent before IGP starts. Such shifts may serve to avoid intraguild competition.

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1. Introduction

Invasions by closely related species can lead to competition between invading and native species. Changes in gammaridean communities due to invasions by closely related species have frequently been recorded (Dick et al., 1993; Dick and Platvoet, 2000; Van der Velde et al., 2000; Jazdzewski et al., 2004) and thus offer useful opportunities to study the mechanisms of such events. Sharing the same resources, such as food or space, and substantial ecological overlap make competition more likely (Reynoldson and Bellamy, 1970; Schoener, 1983; Chase and Leibold, 2003). Interspecific competition can be categorized as exploitative competition or interference competition. Exploitative competition refers to direct competition for limited resources, whereas interference competition involves behavioural, often aggressive interaction. Examples of exploitative competition are pre-emptive competition, in which individuals occupy a unit of space and inhibit its occupation by others, and consumptive competition, in which a shared resource is being consumed. Interference competition is found during territorial competition, when individuals actively defend a unit of space, and during encounter competition, when individuals harm each other by competitive interactions upon encounters (Schoener, 1983). An extreme form of encounter competition is intraguild predation (IGP), in which competitive interactions between closely related species are combined with predation (Polis et al., 1989). This has frequently been observed for gammaridean amphipod species and occurs most of the time after moults, as specimens with a soft skin are more vulnerable (Dick et al., 1993; Dick, 1996; MacNeil and Platvoet, 2005).

Interspecific competition can also influence habitat utilization, as gammaridean amphipods often increase their activity levels in terms of swimming and seeking shelter in the presence of a strong competitor. Size-mediated habitat utilization (Gee, 1982; Adams et al., 1987; Bollache et al., 2000) and size-mediated competition for habitat have been observed among gammaridean species (Pringle, 1982; Hacker and Steneck, 1990; Olyslager and Williams, 1993), providing the larger species with an advantage in the competition for the larger shelter sites, and driving the weaker species to smaller shelter areas, if available. The outcompeted species may exhibit more risky behaviour due to its shelter opportunities being reduced and may become more vulnerable to top predators in this way (Garvey et al., 1994).

In the Netherlands, biological invasions have thoroughly altered the macroinvertebrate fauna composition of the river Rhine. Recently, the Ponto-Caspian gammaridean amphipod *Dikerogammarus villosus* invaded the river Rhine through the Main–Danube canal and became the dominant species in this river, after which it spread to connected waters (Dick and Platvoet, 2000; Bij de Vaate et al., 2002; Wijnhoven et al., 2003). Since the invasion by *D. villosus*, the abundance of another invader gammarid species in the main channel of the river Rhine has declined considerably (Van der Velde et al., 2000, 2002). Canalization of the Rhine's streambed has reduced the heterogeneity of its habitats, limiting them to wave-exposed sand and gravel sediments and to groyne-consolidated riverbanks (Admiraal et al., 1993), which offer little refuge for gammaridean species. Since macrophytes are absent from the main stream of the Rhine and most macroinvertebrates inhabit the stone substratum, severe interference competition between successful macroinvertebrates may occur in this ecotope, leading to a decrease in the numbers of the competitively weaker species (Van der Velde et al., 1994; Van Riel et al., 2006a). The native species *Gammarus pulex* and the early invader *Gammarus roeseli* (Karaman and Pinkster, 1977; Jazdzewski, 1980) now jointly occupy smaller waters, such as brooks discharging into the Rhine. *G. pulex* used to be the native gammaridean species in the Rhine, before *Gammarus tigrinus* took over. The North American invader *G. tigrinus* dominated the river Rhine for decades, but declined in numbers after the invasion and population increase of *D. villosus*. *D. villosus* could also impede possible recolonization of the river channel by *G. pulex*. Furthermore, *D. villosus* is expanding its distribution area from rivers to canals and lakes, where it meets *G. pulex* and other gammaridean species. A laboratory study by MacNeil and Platvoet (2005) simulating a lake/pooled area of river found that *D. villosus* differed from *G. pulex* in terms of its habitat preference, that the native species had no influence on the distribution of the invader whereas the invader did influence the distribution of the native species, and that *G. pulex* suffered greatly from IGP by *D. villosus* in mixed species conditions.

The present study tested a number of hypotheses in aquarium experiments using substrata of various sizes, providing different shelter opportunities: (a) substratum choice patterns of recently invaded gammarid species differ from those of native species or early invaders; (b) substratum shifts are influenced by species densities; (c) the outcome of substratum choice experiments is influenced by the sequence of release of species; (d) shifts of substratum choice may be a way to avoid interspecific competition in mixed species conditions.

2. Methods

We used aquarium experiments in the laboratory to examine the single-species substratum choice of *Dikerogammarus villosus, Gammarus tigrinus, Gammarus roeseli* and *Gammarus pulex*, as well as interspecific competition for substratum between the native *G. pulex* and the early invader *G. roeseli*, and between the more recent invader *D. villosus* and *G. pulex*. The experiments used lava stones of various sizes and sand, providing the species with a variety of shelter opportunities. Changing substratum choice patterns and shifts in preferred substratum (the substratum where the animals were most numerous), shifts in swimming behaviour, as well as interspecific predation and mortality after the introduction of another species were assumed to indicate interspecific competition. Swimming behaviour is included in the substrate choice analysis. Mortality is analysed separately as it does not concern a choice.

2.1. Gammaridean species collection

Dikerogammarus villosus were collected from stone substrata in the river Waal, the main Rhine branch in the Netherlands, near the town of Nijmegen (5°48′ E, 51°51′ N). *Gammarus*

tigrinus were collected from lake IJsselmeer (5°32′ E, 52°35′ N). *Gammarus roeseli* were collected from the Kroonbeek brook (5°59′ E, 51°44′ N) and *Gammarus pulex* from the Tielebeek brook (5°58′ E, 51°44′ N), both situated near Milsbeek, south of Nijmegen. Specimens for the single-species experiments on substratum choice were collected during the autumn (October 2001), whereas *D. villosus* and *G. pulex* for the mixed species experiments were collected during the summer (June 2001). While studying interspecific competition, the single-species substratum experiments on *G. pulex* and *D. villosus* were repeated (June 2001) to allow substratum preferences to be compared without seasonal influences.

All species were kept separately, in aerated basins (40 × 40 × 50 cm) at 15 °C, with a 9:15-h dark/light regime, before being released into experimental aquaria. The gammaridean species were fed chironomids during captivity.

2.2.   Experimental design

Experiments were carried out in a climate-controlled room at 15 °C with a 9:15-h dark/light regime (two 36W/840TLD lamps). Aquaria (25 × 25 × 30 cm) were filled to a depth of 20 cm with Rhine water and aerated. Four different types of substratum were put into four plastic cups (diameter 11.5 cm, height 6.5 cm), viz. washed river sand, large lava stones (with a mean diameter of 5.3 cm), small lava stones (mean diameter 3.1 cm) and a mixture of large and small lava stones (mean diameter 3.7 cm), which were placed at random in each aquarium. Fifty specimens of the same species were collected from the stock population and were allowed to choose between the different substrata. Occupying the water column by choosing to swim is also a choice for a spatial habitat and therefore incorporated in substrate choice patterns analysis. Individuals were not used more than once in an experiment. After 24 h, the cups with the substrata were collected and the gammarids inside each cup were counted and their body lengths measured from rostrum to telson. In addition, the numbers of specimens that had been consumed or died were counted and recorded as mortality. All single-species experiments were repeated using new individuals in each experiment: 18 times for *Gammarus pulex*, 18 times for *Gammarus roeseli*, 4 times for *Gammarus tigrinus* and 20 times for *Dikerogammarus villosus*. The same experiment was repeated 12 times for *G. pulex* in the presence of *G. roeseli*. Interspecific competition between *G. pulex* and *G. roeseli* was studied by allowing 25 new individuals of each species per repeat to choose substrata after being simultaneously introduced in the experimental set up described above.

The body length of specimens used in these experiments was 2–18 mm (mean = 9.1 mm) for *Gammarus roeseli*, 4–15 mm (mean = 7.2 mm) for *Gammarus pulex*, 3–7 mm (mean = 4.0 mm) for *Gammarus tigrinus* and 4–12 mm (mean = 7.0 mm) for *Dikerogammarus villosus*.

A further series of experiments studied the interspecific competition between the native *Gammarus pulex* (GP) and the invasive *Dikerogammarus villosus* (DV). Experiments in which both species were introduced at the same time were conducted at different densities: 25 GP + 25 DV, 25 GP + 50 DV, 50 GP + 50 DV and 50 GP + 25 DV. In addition, experiments were carried out in which 25 individuals of one species were allowed to occupy the substratum for two hours before the other species was added: 25 GP + 25 DV, 25 DV + 25 GP. All experiments in which *G. pulex* was brought together with *D. villosus* were repeated four times, using new individuals in each experiment. The mean body length of individuals of the same species was comparable across the various experiments (P > 0.05, *t*-test), ranging from 3 to 18 mm for *G. pulex* and from 6 to 21 mm for *D. villosus*.

2.3.   Statistical analysis

Differences in substratum choice patterns (i.e. the abundance of individuals on large, medium or small stones, sand, or water column) of single species tests, the influence of *Gammarus roeseli* and *Gammarus pulex* on one another's substratum choice patterns, and differences in substratum choice patterns of *G. pulex* and *Dikerogammarus villosus* under different levels of competitive stress from the presence of the other species (including single-species tests, which were presumed to be no-stress situations) were tested using a 2-way generalized linear model for Poisson distribution (SAS 8.0), further referred to in this paper by the abbreviation 2w-GMP. This analysis was used for the substratum choice patterns derived from counting the surviving specimens present on the substratum types. The Poisson distribution was used in the model because the data were based on counts. The consequences of Bonferroni adjustment on the level of significance have been explored for the 2w-GMP results describing competition between *G. pulex* and *D. villosus*. A Games–Howell post hoc test (SPSS 11.5) was used to analyse significant preference for any of the substratum types within the substratum choice pattern of a gammaridean species in a specific experiment. Differences between experiments in the number of individuals of a species found on one substratum type were tested using a *t*-test (SPSS 11.5). Differences in mortality of *G. pulex*, *G. roeseli* and *D. villosus* in the mixed species experiments were tested within each experiment using one-way ANOVA with a Games–Howell post hoc test. A *t*-test compared the total mortality figures of *G. pulex* and *D. villosus* in this study. Differences in body length of specimens on the different substrata were tested using one-way ANOVA when variances were homogeneous, or Kruskal–Wallis test when the variances were heterogeneous (according to Levene's test, SPSS 11.5).

A PCA ordination diagram, drawn by means of CANOCO software, was used to illustrate changes in the substratum choice of *Gammarus pulex* and *Dikerogammarus villosus* in the various experiments. Differences in body length distribution for each species in the various experiments were tested using a *t*-test, whereas differences in body length distribution of a species on different substrata within the same experiment were tested using one-way ANOVA (SPSS 11.5).

3.   Results

All gammaridean species showed a clear distribution pattern over the substrata by choice (Table 1). A strong interaction was found between substrate choice pattern and species. This interaction did not, however, result in significant differences in substrate choice patterns between species. Substrate

Table 1 – Influences of substratum type, interspecific relations and the interaction between interspecific relations and substratum type on the substratum choice patterns shown by G. pulex, D. villosus and G. roeseli in single species tests and in the presence of a possibly competitive species, analysed by means of a 2-way generalized linear model for Poisson distribution (SAS 8.0)

Substrate choice patterns of	Source	num DF	den DF	F value	Pr > F	Chi-square	Pr > ChiSq
G. roeseli, G. pulex, G. tigrinus and	Substrate type	4	215	44.69	<0.001	178.74	<0.001
D. villosus in single species tests	Species	3	215	1.28	0.281	3.85	0.2779
	Substrate * species	12	215	7.77	<0.001	93.26	<0.001
G. roeseli in presence of G. pulex	Substrate type	4	120	68.86	<0.0001	275.45	<0.0001
	Competition	1	120	1.24	0.267	1.24	0.2649
	Substrate * competition	4	120	1.81	0.132	7.22	0.1247
G. pulex in presence of G. roeseli	Substrate type	4	120	32.91	<0.0001	131.64	<0.0001
	Competition	1	120	1.37	0.244	1.37	0.2418
	Substrate * competition	4	120	1.04	0.387	4.18	0.3824
G. pulex in presence of D. villosus	Substrate type	4	105	61.31	<0.0001	245.25	<0.0001
	Competition	6	105	3.22	0.006	19.29	0.0037
	Substrate * competition	24	105	2.82	0.0001	67.67	<0.0001
D. villous in presence of G. pulex	Substrate type	4	105	58.04	<0.0001	232.18	<0.0001
	Competition	6	105	0.64	0.701	3.82	0.7016
	Substrate * competition	24	105	3.32	<0.0001	79.64	<0.0001

choice patterns of *Gammarus pulex* and *Gammarus roeseli* were highly similar, and seemed less similar to those of the recent invaders *Gammarus tigrinus* and *Dikerogammarus villosus*. The recent invaders also demonstrated highly similar substratum choice patterns. *G. roeseli* and *G. pulex* equally occupied the water layer and the stone substratum, and showed no preference within the differently sized stones (Fig. 1), whereas *G. tigrinus* and *D. villosus* both strongly preferred mixed and small sized stones. These invasive gammaridean species were less likely to swim than the 'native' species. All gammaridean species showed the lowest preference for sand. The

differences in substrate choice patterns between species were, however, not evident enough according to statistical analysis (Table 1). When *Gammarus pulex* and *Gammarus roeseli* were introduced to the aquaria simultaneously, neither showed any changes in substratum choice patterns in the presence of the other species (Table 1, Fig. 1a,b).

Dikerogammarus villosus and *Gammarus pulex* both showed a distinct substratum choice pattern during the mixed species experiments ($P < 0.001$, 2w-GMP) and a strong interaction was found between the substratum choice pattern and the presence of the other species ($P < 0.001$, 2w-GMP). The different
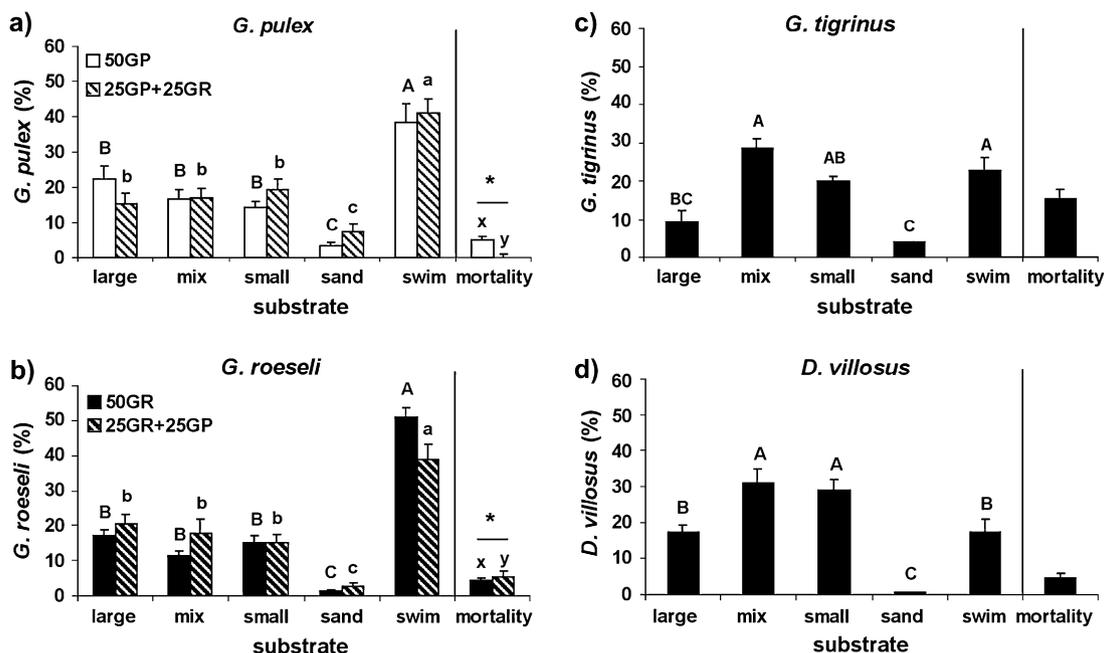
Fig. 1 – Substratum choice patterns (mean ± SEM) of the native gammarids *Gammarus pulex* (a) and *Gammarus roeseli* (b) in aquarium experiments in each other's absence or presence, and substratum choice patterns of the invasive gammarids *Gammarus tigrinus* (c) and *Dikerogammarus villosus* (d) in single species tests. Different letters indicate significant differences within the same experiment. Bars marked with asterisks indicate significant differences between the experiments for the same substratum.

levels of competition had no effect on the substratum choice pattern of *D. villosus* ($P = 0.70$, 2w-GMP), whereas *G. pulex* did show different substratum choice patterns at different levels of competition ($P = 0.006$, 2w-GMP, Table 1) by shifting from large stones to smaller stones and increasing its swimming activities (Fig. 2a–c). Introducing one species two hours prior to the other had the most significant effect on the substratum choice pattern of *G. pulex* (Table 2), which resulted in more individuals of *G. pulex* swimming in the water layer than occupying the substrata when *D. villosus* was released first (Fig. 2c).

The numbers of *Gammarus pulex* on large stones declined significantly ($P = 0.004$, *t*-test) when densities of *Dikerogammarus villosus* were higher or lower than those of *G. pulex* (Fig. 2a). At lower densities of *D. villosus*, *G. pulex* preferred to occupy smaller stones and spent more time swimming, whereas at high densities of *D. villosus*, *G. pulex* showed no significant preference for any substratum or for swimming and did not suffer significantly higher mortality. *D. villosus*, on the other hand, showed less preference for mixed stones ($P = 0.03$) and greater preference for large stones ($P = 0.02$) when densities

of *G. pulex* differed from that of *D. villosus* (Fig. 2d) or when *G. pulex* had already occupied the substratum when *D. villosus* was introduced (Fig. 2f). When both species were present in equal densities, no major changes in substratum preference were found for either species (Fig. 2b,e), although *D. villosus* became less likely to prefer mixed stones (Fig. 2e). When *G. pulex* was allowed to settle first, *G. pulex* shifted from the larger stone substrata to the smaller stones ($P = 0.02$), whereas *D. villosus* became less likely to prefer mixed stones. When *D. villosus* was the first species to occupy the stones, more specimens of *G. pulex* occurred in the water layer ($P = 0.04$), whereas *D. villosus* became more numerous on the large stones ($P = 0.01$) and less so on the mixed stone substratum ($P = 0.01$). There was no significant difference in body length distribution for either species in the various experiments. Substratum choice did not depend upon body size ($P > 0.05$ for all cases) (Fig. 3). After adjusting the significance level according to the Bonferroni method, significant differences between various situations of competition between *G. pulex* and *D. villosus* became minor (Table 2).
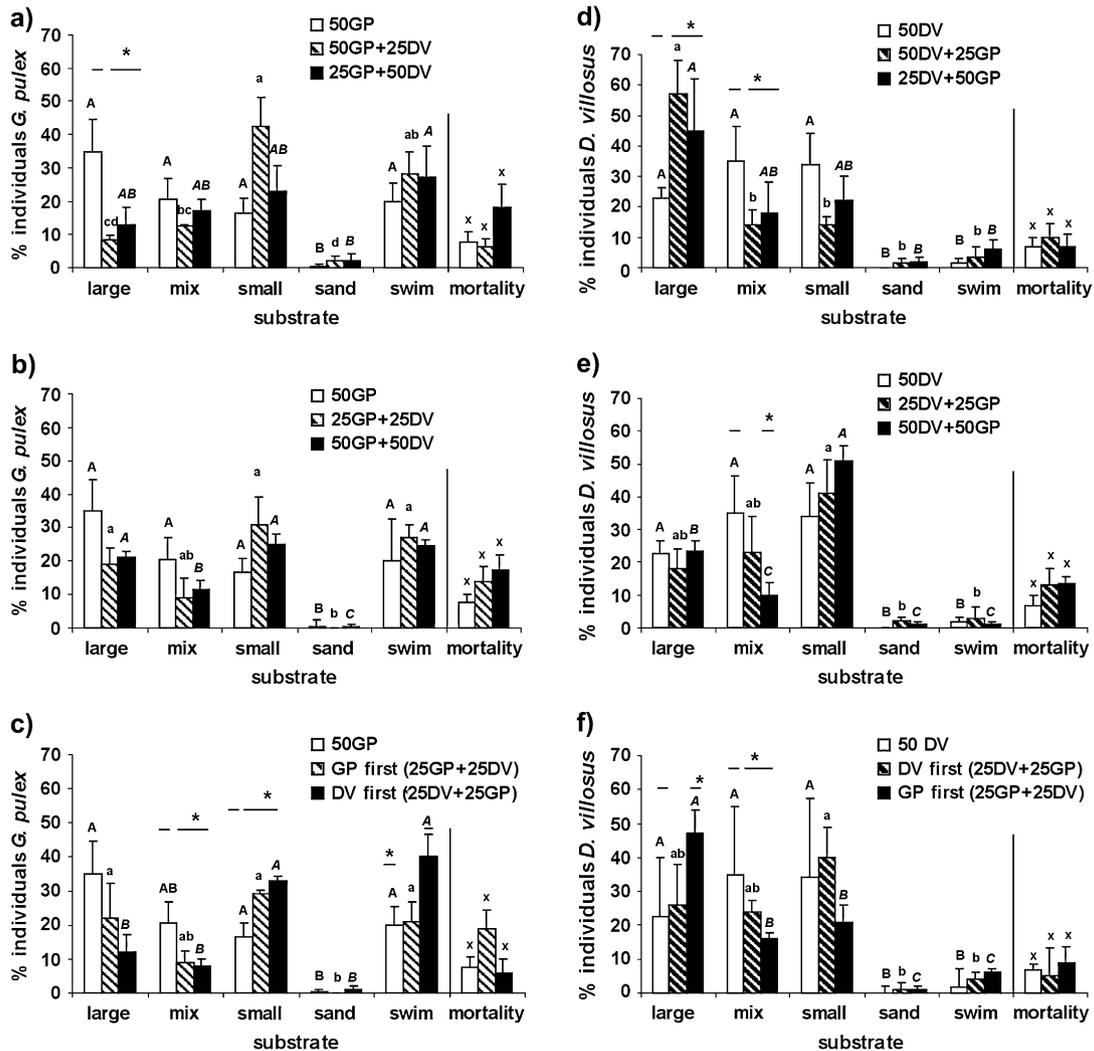

Fig. 2 – Substratum choice patterns (mean ± SEM) of the indigenous *Gammarus pulex* (a–c) and the invasive *Dikerogammarus villosus* (d–f) in each other's presence at unequal densities (a, d), equal densities (b, e) and equal densities with different timing (c, f). Different letters indicate significant differences in substratum preferences within the same experiment. Bars marked with asterisks indicate significant differences between the experiments for the same substratum.

Table 2 – Substrate choice patterns of *G. pulex* in the experiments mentioned in the first column are compared to substrate choice patterns of *G. pulex* in the experiments mentioned in the second column. The third column shows the Differences of Least Squares Means (analysed by means of 2-way GLM for Poisson distribution, SAS 8.0) between the substrate choice patterns of *G. pulex* in the different experiments. The column at the right shows what the critical level of significance ought to be according to Bonferroni

Compared experiments		Pr > ChiSq	Bonferroni level of significance
50GP	25GP + 25DV	0.043	0.008
50GP	50GP + 50DV	0.757	0.008
50GP	50GP + 25DV	0.887	0.008
50GP	25GP + 50DV	0.053	0.008
50GP	GP first	0.036	0.008
50GP	DV first	0.034	0.008
50GP + 25DV	25GP + 25DV	0.025	0.008
50GP + 25DV	25GP + 50DV	0.013	0.008
50GP + 25DV	GP first	0.020	0.008
50GP + 25DV	DV first	0.010	0.008

PCA ordination clearly showed that the substratum choice patterns of *Gammarus pulex* in the presence of *Dikerogammarus villosus* deviated more from those in the single-species experiments than those of *D. villosus* deviated in the presence of *G. pulex* (Fig. 4). In the presence of *D. villosus*, *G. pulex* preferred smaller stones and showed more active swimming behaviour (Fig. 4, Fig. 2a–c).
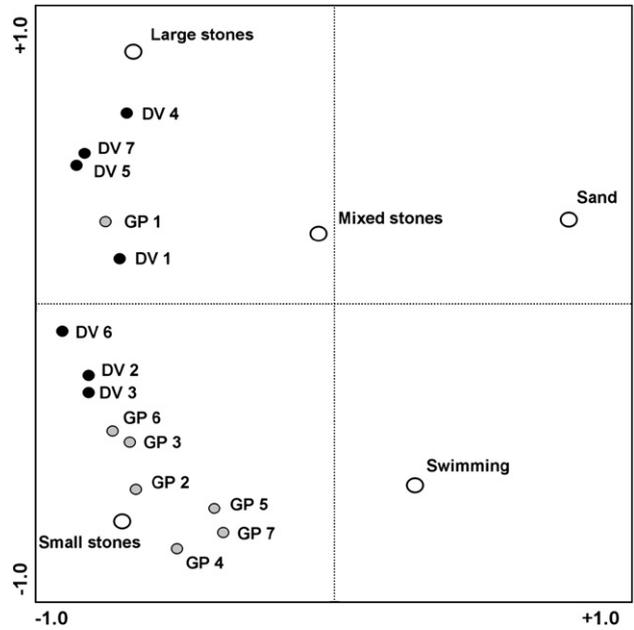

Fig. 4 – Ordination diagram (PCA) showing differences in substratum choice patterns for *Gammarus pulex* (GP) and *Dikerogammarus villosus* (DV), in various situations of interspecific competition. The different experiments are coded by numbers (1–7): 1 = single-species preference, 2 = equal low densities, 3 = equal high densities, 4 = lower competitor densities, 5 = higher competitor densities, 6 = different timing: added first, 7 = different timing: added last.

4. Discussion

The invasive gammaridean species *Gammarus tigrinus* and *Dikerogammarus villosus* seem to be more attracted to stone substratum than the native *Gammarus pulex* and the early invader *Gammarus roeseli*, both of which were most frequently found in the water layer. These divergences in habitat use are however not underpinned by statistics (P > 0.05). *G. pulex*
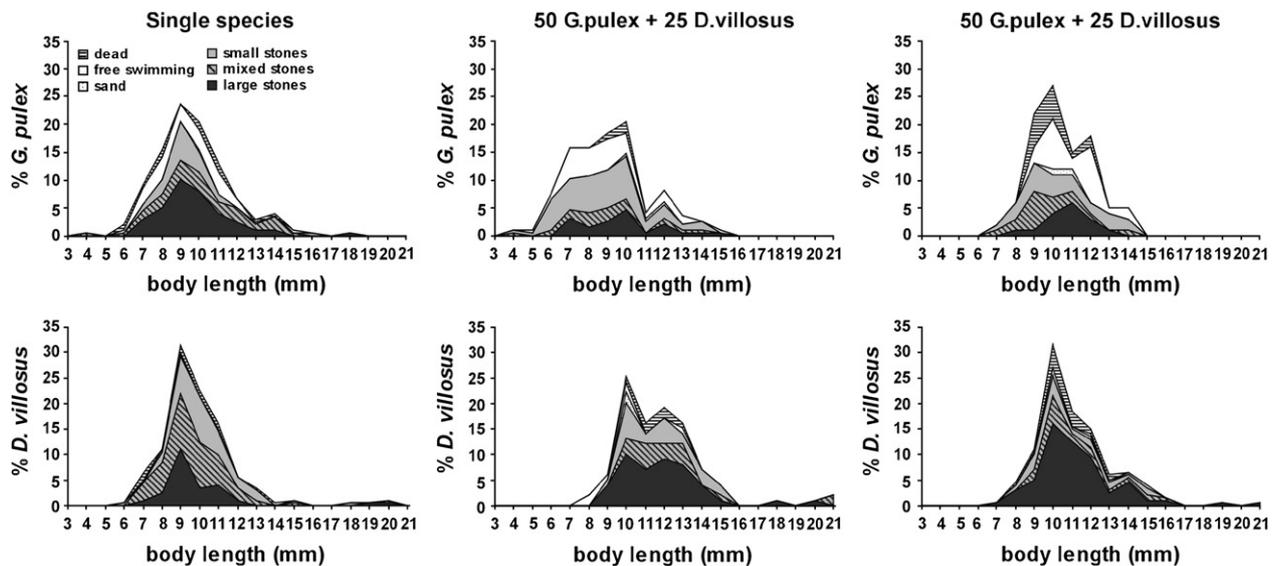
Fig. 3 – Body length frequency distribution (%) of *Gammarus pulex* (GP) and *Dikerogammarus villosus* (DV) on the different substrata in single-species tests, and in tests with unequal densities of *G. pulex* and *D. villosus* (50 GP + 25 DV and 25 GP + 50 DV).

and *G. roeseli* have both been reported to prefer waters with a rich vegetation or vegetational debris (Den Hartog, 1964; Kern-Hansen, 1978; Welton, 1979; Bollache et al., 2000). This preference has presumably complicated their survival in the Rhine, since the available ecotopes in the river channel are limited to streambeds dominated by wave-exposed sand and gravel, and riverbanks which are mostly consolidated by groynes made of basalt stone (Admiraal et al., 1993). The available habitat structure in the Rhine, combined with the distinct substratum preferences of the natives and invaders, may have provided *G. tigrinus* with an advantage over the native *G. pulex* in the interspecific interference competition. Other competitive advantages for *G. tigrinus* compared to *G. pulex* are its higher physiological tolerance for ion-rich, polluted water (Savage, 1982; Wijnhoven et al., 2003), its higher reproduction rate and its more aggressive behaviour (Pinkster et al., 1977). Interspecific competitive stress from *G. tigrinus* combined with physiological stress from the ion-enriched Rhine water may have restricted the distribution of *G. pulex* to the ion-poor ditches and brooks discharging into the Rhine. Our experiments demonstrated that *G. pulex* and *G. roeseli* seem to have similar habitat requirements, and probably exhibit a low level of direct interspecific competition. Furthermore, the microdistribution of *G. pulex* is thought to be size-assortative, with larger animals associating with larger substratum particles (Gee, 1982; Pringle, 1982; Bollache et al., 2000). This may also be a result of current avoidance, as it has mainly been observed in studies using flowing water habitats (Adams et al., 1987) and was not apparent in the present study.

The shift of *G. pulex* towards smaller stones, which offer more shelter opportunities, and increased swimming of *G. pulex* when *D. villosus* was present indicate that *G. pulex* probably suffered interspecific interference competition from *D. villosus*. Statistical analysis showed significant changes in the substrate choice pattern of *G. pulex* in presence of *D. villosus* for several competitive situations. We chose to maintain $P < 0.05$ as significant standard and not adjust the level of significance to the method of Bonferroni, because Bonferroni correction increases the probability of a Type II error and makes it likely that legitimately significant results will fail to be detected (Perneger, 1998). *G. pulex* is known to move into the water layer rather than seek refuge in alternative patch types when it is displaced from its optimal patches by interspecific or intraspecific competition (Adams et al., 1987). It could be likely that in our study, *D. villosus* forced *G. pulex* from its preferred large stone substratum, as *G. pulex* showed behaviour similar to that observed by Adams et al., (1987). Furthermore, *G. pulex* was also found more abundant between the smaller stones whenever *D. villosus* was present. Dahl and Greenberg (1996) also observed *G. pulex* seeking shelter in the presence of a predator.

Although *D. villosus* is known to be a predator (Dick and Platvoet, 2000; Van der Velde et al., 2000; Dick et al., 2002; Van Riel et al., 2006a), it was not found to prey directly upon *G. pulex* in our experiments. MacNeil and Platvoet (2005) proved that *D. villosus* could engage in intraguild predation on *G. pulex*. Our experiments studying substrate choice only lasted for 24 h, which may have been too short for actually studying IGP. Moulting makes specimens vulnerable to IGP, as their skin is soft during this process. If IGP depends on

moults, experiments studying IGP should last several weeks. The mortality of *G. pulex* and *D. villosus* during the experiments did not increase significantly in presence of the other species. Dead specimens were undamaged and showed thus not any sign of mortality by IGP.

Responses to competition in the form of substratum choice shifts were most prominent for *Gammarus pulex* when densities of *Dikerogammarus villosus* exceeded those of *G. pulex* or whenever one of the species had already occupied the substratum, resembling a natural situation in west European river areas. Pre-emptive competition could thus eventually determine whether these species can co-exist. Choosing to shift substratum may additionally be effective in avoiding potential IGP and increase the chances of competitive species to coexist.

As habitat heterogeneity is poor in the Rhine and very few smaller refugia are found on the stone groynes, *Gammarus pulex* is presumably unable to recolonize this river as long as *Dikerogammarus villosus* dominates the macroinvertebrate communities on the stones (Van Riel et al., 2006a,b) preying on other gammaridean species (MacNeil and Platvoet, 2005). Restoring habitat heterogeneity and complexity could have a profound effect on gammaridean amphipod species interactions, as it would generate more microhabitat types and more potential refugia (Crowder and Cooper, 1982), potentially allowing more gammaridean species to co-exist in areas of sympatry and allowing species to interact to determine the community structure.

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