

# Habitat-mediated cannibalism and microhabitat restriction in the stream invertebrate *Gammarus pulex*

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**Abstract** In cannibalistic species, small individuals often shift habitats to minimize risk of predation by larger conspecifics. The availability of diverse size-structured habitats may mediate the incidence of cannibalism by larger individuals on smaller individuals and increase fitness of smaller individuals. We tested these hypotheses in a series of laboratory studies with *Gammarus pulex*, a freshwater amphipod inhabiting substrates with varying interstitial pore space sizes. In the absence of larger, potentially cannibalistic individuals, small *Gammarus* actively used all pore space sizes offered. They used only substrates containing food and preferred food items that provided cover to food items that did not. In the presence of larger *G. pulex*, small individuals almost exclusively used smaller pore spaces from which larger individuals were excluded. Small

individual survival was significantly lower in the presence of larger *Gammarus* than in controls without larger individuals regardless of substrate size, but availability of mixed pore sizes significantly increased survival. Food consumption and growth per individual were not affected by the presence of larger individuals or substrate composition. Our results suggest that the distribution and availability of complex and high-quality habitats may affect the occurrence and significance of cannibalism in size-structured populations.

**Keywords** Substrate · Body size · *Gammarus pulex* · Abiotic–biotic interactions · Microhabitat

## Introduction

Although the role of predation in prey habitat selection has been well documented, much of our understanding comes from interspecific interactions. Considerably less is known regarding influences of intraspecific (cannibalistic) interactions on prey habitat selection. Size-asymmetric cannibalism can have significant effects on population and community dynamics (Orr et al., 1990; Benoit et al., 2000). In cannibalistic species, larger individuals usually eat smaller ones and cannibalism can be a major source of juvenile mortality (Polis, 1981). Size-asymmetric cannibalism has been

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documented in many taxa, but particularly fish (e.g., Skov & Koed, 2004) and aquatic invertebrates (Marshall et al., 2005). Wissinger (1992) suggests that cannibalism is most likely to occur in size-structured species with overlapping generations in time and space.

Habitat quality, including refuge availability for prey, may affect the occurrence of cannibalism and its significance in a population. The occurrence of cannibalism depends on the relative availability of intraspecific prey and other food sources and may therefore be habitat-dependent (Benoit et al., 2000). Both quantity and quality of prey habitat affect prey fitness, with refuge availability reducing the incidence of cannibalism (e.g., Benoit et al., 2000; Marshall et al., 2005). Habitat quality is also important since multiple functions must be served and prey must balance the relative risks and rewards of habitat choices (Sih, 1992). Habitat that provides food or refuge but not both will produce individuals of lower fitness than habitat providing both (Sih, 1987).

Prey organisms shift among habitats as needs, resource availability and risks change. Ontogenetic niche shifts, associated with changing environmental tolerance and resource needs, are common in many species (Werner & Gilliam, 1984) and may reduce cannibalistic interactions by separating age classes (Foster et al., 1988). Under risk of predation, prey shift habitats or reduce time spent in higher risk areas, whereas in the absence of predators prey behavior may approach maximum feeding efficiency (Sih, 1987). Temporary shifts to refuge habitat associated with predator presence has been widely documented (Sih, 1987). Availability of refuge and high-quality habitats and overlap in habitat use between size classes may have profound effects on the incidence of cannibalism in a population.

The freshwater shrimp *Gammarus pulex* (Crustacea: Amphipoda) is common in small slow-flowing lowland streams of Western Europe. They and their North American congeners are associated with the breakdown of detritus and are preferred prey for a variety of fish species (Holomuzki & Hoyle, 1990). Although *Gammarus* are omnivorous and considered detritivorous, cannibalism has been well documented in many

gammarid species (e.g., Dick, 1995). *Gammarus* have been shown to size sort in substrates, with larger individuals associating with larger substrates and interstitial pore sizes (e.g., Gee, 1982; Olyslager & Williams, 1993).

We hypothesized that presence of larger individuals would restrict habitat use by small *G. pulex* and that availability of diverse habitats would mediate the degree of cannibalism and ultimately fitness of small *G. pulex*. Our objectives were to: (1) characterize small *G. pulex* substrate preference in the absence of larger conspecifics, (2) test for differences in habitat use in the presence of larger individuals, and (3) examine the effects of substrate that provides no predator refuge and no food, on mortality, food consumption, and growth of small *G. pulex*. Findings from our study may contribute to understanding of population dynamics of cannibalistic species.

## Methods

### Animals

*Gammarus pulex* used in all experiments were collected from Heelsumse Beek (5°45' E, 51°59' N), a small lowland stream in the central part of the Netherlands, and transferred immediately to the laboratory. All animals were collected at least 48 h prior to use in experiments, held under experimental conditions, and fed natural leaf food sources. Prior to each experiment, animals were size-sorted and counted into small dishes as necessary per experiment. Care was taken to ensure random placement of animals at all phases of each experiment. Small and large organism total body lengths were 4–6 mm and 10–13 mm, respectively. Body sizes used in Experiment 4 are described more fully below.

### Food

Food consisted of autumn-shed poplar leaves (*Populus nigra*) that were soaked in water for 7 days, air-dried, and then conditioned with an inoculum of pond water for 3 days. Conditioning allows for the colonization of microbial organisms

and fungi; conditioned leaves are preferred over non-conditioned leaves (Willoughby & Sutcliffe, 1976). In most experiments, leaves were finely chopped (~2 mm × 2 mm) and placed under substrate since larger pieces may be used as cover by smaller *G. pulex* (Abjornsson et al., 2000). In experiments using larger leaf pieces, leaf piece sizes were approximately 1.5 cm × 1.5 cm). In experiments with suspended food, large leaf pieces were suspended from a wire approximately 4 cm above the substrate surface.

### General experimental procedures

We conducted all experiments in aquaria at  $15 \pm 1^\circ\text{C}$  on an 11:13 h light:dark regime in a small climate chamber. Experiments were performed in small (18 × 12 × 14 cm, 3 l), medium (24.5 × 15 × 19 cm, 7 l) or large (49.5 × 29 × 29 cm, 40 l) aquaria with a water depth of 5.5 cm. Aquaria were arranged randomly within the climate chamber. Mean gravel substrate sizes ( $\pm$ SD) were: small (S),  $1.52 \pm 0.21$  cm, medium (M1),  $2.03 \pm 0.18$  cm, medium (M2),  $2.39 \pm 0.22$  cm, large (L),  $3.72 \pm 0.20$  cm. Substrate sizes were chosen such that small substrates generally permitted entrance of small but not larger individuals, thereby providing refuge for small *G. pulex*. Large substrates permitted entrance of all individuals. Medium substrates were intermediate: due to shape irregularities of individual particles, some refuge space was likely available and some access to large individuals was likely available. Substrate was placed either directly on the bottom of the aquaria or in small plastic substrate trays (3.5 × 9.5 × 4.5 cm) distributed randomly within the aquaria. We controlled for substrate area by allowing number of pore spaces to vary among substrate sizes while ensuring that excess numbers of pore spaces were available because in a preliminary study we found that

*G. pulex* were responsive to area but not pore number. Experiments lasted either 2.5 or 3.5 days and always included complete light:dark cycles beginning on a dark cycle. Preliminary studies indicated that habitat use did not change after 48 h. Organisms were released into aquaria by distributing them evenly along the edges of the aquaria away from substrates. Animal density ranged from 1.3 to 6.7 organisms/l. We did not control for differences in animal density because food was unlimited, number of pore spaces always exceeded number of animals, and in a preliminary study we found that habitat use by small *G. pulex* did not vary with animal density. All experiments were conducted with four replicates. Evidence of cannibalism included observation of large individuals capturing and consuming live small individuals during experiments and observation of remaining body parts in test containers upon completion of experiments. Experimental details varied among tests; specifics of each test are summarized in Table 1.

### Substrate use in the absence of large individuals

#### Experiment 1

We tested the effects of food (presence/absence) and substrate (S, M1, M2, and L) on small *G. pulex* substrate choice. Substrate trays, each containing one combination of substrate size X food availability (eight combinations) were placed in the center of each aquarium. At test completion, individuals in each tray and outside the trays were enumerated.

#### Experiment 2

Organisms use habitat for multiple benefits. *G. pulex* are commonly found associated with

**Table 1** Details of experiments described in the text. Experiments are numbered in the order they appear in the text

Experiment	# Aquaria	Aquarium size	# Substrate trays	# Organisms/aquarium	Organism density (#/l)
1	4	L	8	50	1.3
2	16	S	0	10	3.3
3	8	M	3	15, 25	2.1, 3.6
4	20	S	0	20	6.7

detritus that has the potential to provide both shelter and food. In order to distinguish between substrate use for refuge and for food provision, we tested the effect of food presentation and location on use of large substrate by small *G. pulex* by placing three large rocks (large substrate) in a substrate tray in the center of each aquarium. Four food treatments were tested: (1) 1–2 large leaf pieces cut to fit the bottom of the tray, (2) finely chopped poplar leaves, (3) one large leaf piece suspended in the water above the substrate, and (4) no food. Large substrate in these treatments potentially provides (1) shelter and food, (2) food only, (3) shelter only, where organism must choose between food and shelter, and (4) neither, respectively. Food in treatments 1 and 2 were placed under the substrate. At test completion, individuals within and outside each substrate tray were enumerated.

Effects of large individuals on substrate use

### Experiment 3

We examined the effect of presence of large *G. pulex* on substrate selection by small *G. pulex* by placing three small substrate trays, one each containing S, M2 and L substrate, in the center of each aquarium. Half of the aquaria received only small *G. pulex* and half of the aquaria received 15 small and 10 large *G. pulex*. At test completion, individuals were enumerated in each substrate tray and outside all trays.

Effects of substrate and large individuals on fitness characteristics

### Experiment 4

We examined the effects of large *G. pulex* presence and substrate size composition on small *G. pulex* survival, food consumption, and growth by placing a single layer of substrate on the bottom of each aquarium. Substrate size compositions tested were (1) 100% L and (2) 50% L on one half and 50% M2 on the other half of the tray. Because we could not refresh food supplies under the substrate for the duration of the

experiment without disrupting experimental animals, two leaves per experimental chamber were suspended into the water from above and replaced approximately weekly. To document the total weight of leaf matter consumed during the experiment, pre- and post-use dry weight of each leaf was recorded.

Either 20 small or 15 small and 5 large *G. pulex* were released into each aquarium at the beginning of the experiment. Five large individuals were released into an additional four aquaria to document food consumption of large animals. Additional individuals of each size were immediately preserved and later measured. Head capsule and total body length were measured; head capsule length was used in all analyses. Mean ( $\pm$ SD) head capsule for small and large *G. pulex* in each experimental aquarium were  $0.73 \pm 0.06$  mm and  $1.28 \pm 0.09$  mm, respectively.

To calculate leaf consumption rate per small individual, we first subtracted average food consumption by large individuals from total consumption for the treatment aquaria containing large individuals. We interpolated survival at each time period for which leaf consumption was measured from total survival for each aquarium to calculate food consumption per individual for each time period.

Statistical analysis

Following confirmation that data were normally distributed, we analyzed short-term experiments through one-way or two-way analyses of variance (ANOVA), as appropriate. Raw data were animal counts; percent use was analyzed for all habitat use experiment results. Because some individuals were always outside of any substrate, numbers within substrates were independent. Food consumption data were analyzed first in a repeated measure ANOVA. Temporal autocorrelation was addressed by examining results per time period. The Bonferroni *P*-value adjustment was used to identify significant treatment pairs. All analyses were conducted in Systat (Systat Version 8.0, SPSS, Inc., 1998). In the final experiment, a Kolmogorov-Smirnov (K-S) test for differences in distribution (DeGroot, 1991)

was conducted on the different size frequency distributions of surviving *G. pulex*.

## Results

Substrate use in the absence of large individuals

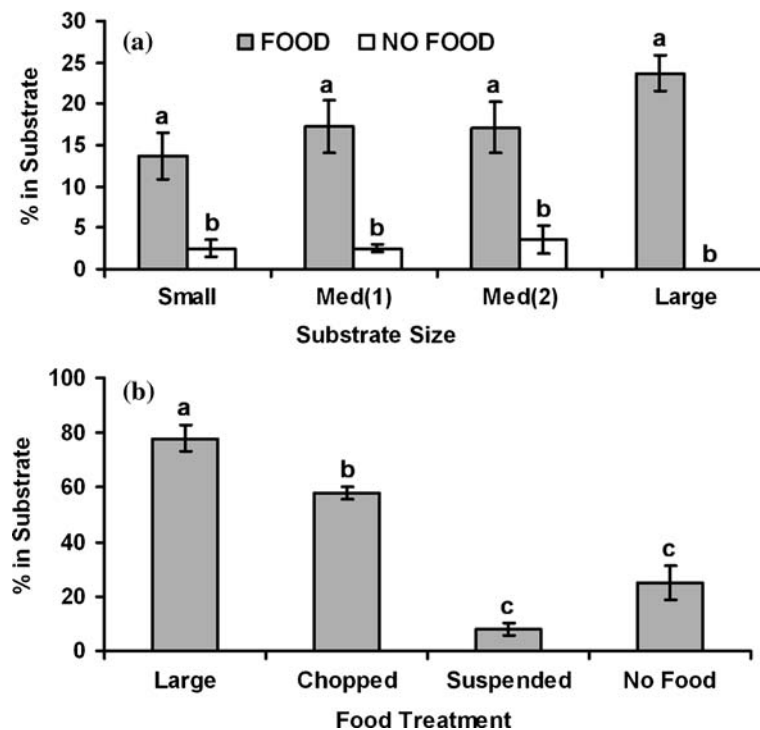
### Experiment 1

Small *G. pulex* used substrate significantly more frequently when it contained food than when it did not ( $N = 32$ ,  $F_1 = 111.15$ ,  $P < 0.0001$ ; Fig. 1a). Substrate size did not significantly affect use ( $N = 32$ ,  $F_3 = 1.06$ ,  $P = 0.38$ ). However, the interaction term of these variables was also significant ( $F_3 = 3.34$ ,  $P = 0.04$ ), indicating a trend of increased use of larger substrates with food and a decline of larger substrate use without food. Use was extremely low (<5% of individuals) in all trays not containing food and did not differ

among substrate sizes. Although use of large substrates containing food appeared to be higher than other substrate sizes containing food, the paired treatment comparison between large and small substrate was not significant ( $P = 0.16$ ). Use of the open water column was also high (12–32% across all four replicates), although some disruption of individuals from substrates occurred during the termination of the experiment.

### Experiment 2

Small *G. pulex* used large substrate for cover and to obtain food (Fig. 1b). Use of large substrate differed significantly with food location in the substrate ( $F_3 = 51.5$ ,  $P < 0.0001$ ). Substrate was used most when food was within the substrate and in large pieces (food + cover), and used least when food was suspended above the substrate (choice of food or cover). Examination of treatment pairs indicated that all pairs were significantly different ( $P < 0.05$ ) except between the



**Fig. 1** Habitat choice of small *Gammarus pulex* in the absence of larger individuals: (a) effects of food availability and substrate size, (b) effects of nature and location of

food. Med = medium, see text for description of substrate sizes. Error bars are  $\pm 1$ SE. Treatments sharing letters are not significantly different

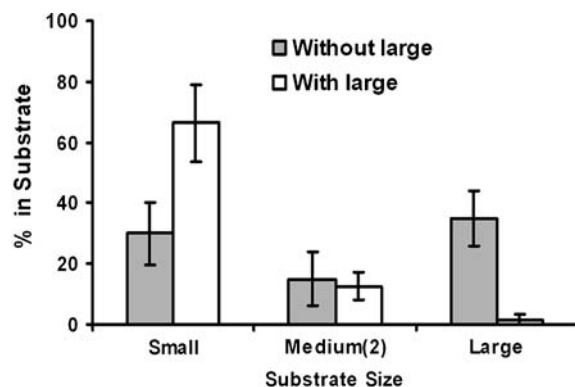
treatments with food suspended above the substrate and with no food provided. Although more animals used substrate when no food was available than when food was suspended, the difference was not significant ( $P = 0.09$ ).

Effects of large individuals on substrate use

### Experiment 3

There was a significant difference in substrate use with respect to substrate size ( $F_2 = 9.33$ ,  $P = 0.002$ ; Fig. 2), but not presence of large *Gammarus* ( $F_2 = 0.001$ ,  $P = 0.979$ ). However, the significant interaction term ( $F_4 = 8.14$ ,  $P = 0.003$ ) indicates that small *G. pulex* use of small substrate was relatively high when large individuals were present, but use of large substrate was relatively low when large individuals were present. Separate one-way ANOVA analyses of small and large substrate use revealed altered substrate use in the presence of larger individuals. Large substrate use changed significantly among *Gammarus* size treatments ( $N = 8$ ,  $F_2 = 12.75$ ,  $P = 0.02$ ,  $r^2 = 0.680$ ) and small substrate use was marginally non-significantly different among *Gammarus* size treatments ( $N = 8$ ,  $F_2 = 4.99$ ,  $P = 0.07$ ,  $r^2 = 0.454$ ).

Large individuals were most likely to be located in the water column (65%), with 10, 12.5, and 12.5% located in small, medium, and large substrates. In most replicates containing large individuals, small substrate did permit



**Fig. 2** Small *G. pulex* use of substrate in the presence of larger individuals. Error bars are  $\pm 1SE$

limited access of larger individuals and was therefore not an absolute refuge for smaller individuals. Survival of small individuals with and without large individuals was 86.7% ( $\pm 10.9$ , 2SE) and 100.0% ( $\pm 0.0$ , 2SE), respectively.

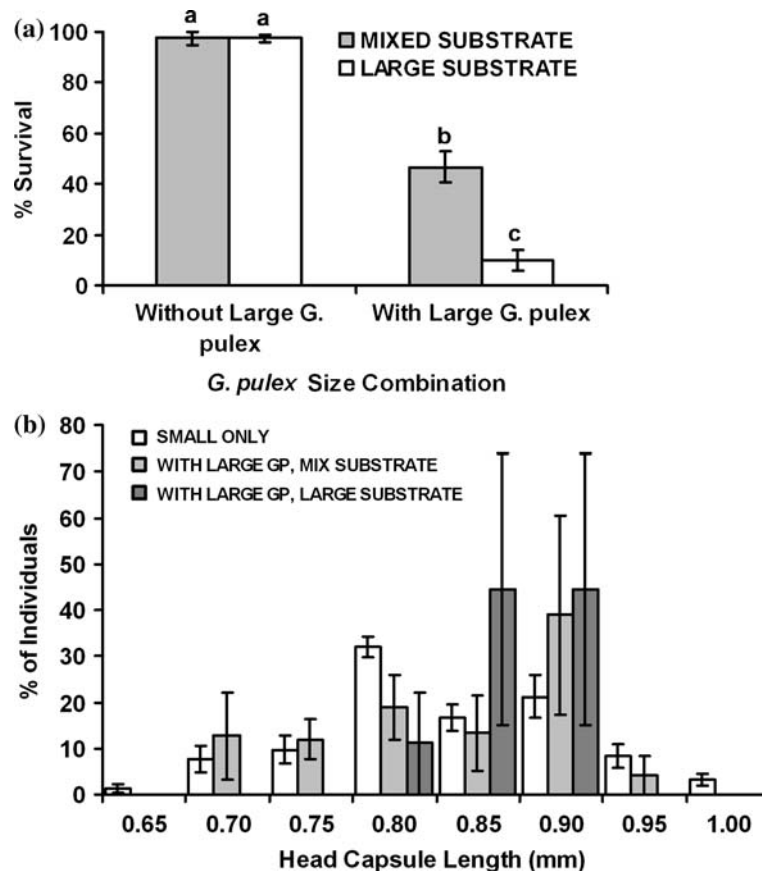
Effects of substrate and large individuals on survival, food consumption, and growth

### Experiment 4

Survival of small *G. pulex* was significantly reduced in the presence of larger *G. pulex* (Fig. 3a), but small substrate availability increased survival ( $N = 16$ , *Gammarus* size:  $F_1 = 311.20$ ,  $P < 0.0001$ , substrate:  $F_1 = 23.29$ ,  $P < 0.0001$ , model  $r^2 = 0.968$ ). The interaction between these variables was also significant ( $F_1 = 23.29$ ,  $P < 0.0001$ ) due to the difference in effect of substrate on survival in the presence versus absence of large individuals. One-way ANOVA with each combination of the two variables as a separate treatment confirmed these relationships. Survival of small *G. pulex* was significantly different among all treatment combinations ( $P < 0.05$ ) except between the two treatments without large individuals and differing in substrate ( $P = 1.0$ ).

Although the size frequency distributions of small *G. pulex* among treatments appear to differ (Fig. 3b) with treatments containing cannibalistic individuals skewed toward larger individuals within the small *G. pulex* size class, the K-S test for differences in cumulative distribution was not significant ( $N = 189$ ,  $D = 0.143$ ,  $P = 0.60$ ).

Food consumption by all small *G. pulex* within a treatment was significantly different among *Gammarus* size treatments but did not differ among substrate treatments ( $N = 15$ , *Gammarus* size combination:  $F_1 = 8.16$ ,  $P = 0.016$ , substrate:  $F_1 = 1.37$ ,  $P = 0.27$ ). The interaction between these variables was not significant ( $F_1 = 0.33$ ,  $P = 0.58$ ). Total food consumption varied significantly over the duration of the experiment (temporal autocorrelation:  $F_3 = 3.47$ ,  $P = 0.03$ ), as did the interaction between *Gammarus* size combination and the temporal variable ( $F_3 = 3.52$ ,  $P = 0.03$ ). Food consumption was lower in treatments with large individuals in the



**Fig. 3** Effects of larger individuals and substrate on (a) percent survival and (b) size distribution of surviving small *G. pulex*. Error bars are  $\pm 1$ SE. Treatments sharing letters are not significantly different. GP = *G. pulex*

beginning of the experiment, but by the end of the experiment there was no difference among treatments (Fig. 4a). *Gammarus* size combination was significantly different on days 11, 19, and 26, but not on day 33 of the experiment ( $P = 0.003$ , 0.0001, 0.01, 0.880, respectively).

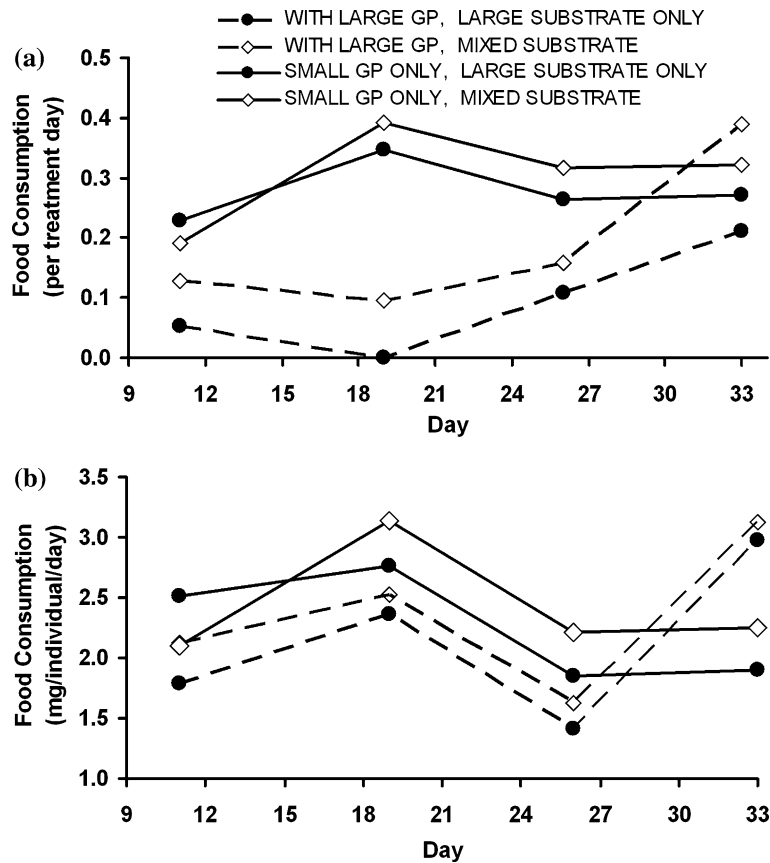
Per individual food consumption did not differ among *Gammarus* combination or substrate treatments ( $N = 15$ , size combination:  $F_1 = 0.00$ ,  $P = 0.98$ , substrate:  $F_1 = 0.14$ ,  $P = 0.72$ ). Although per individual food consumption was higher in treatments that did not contain large individuals (Fig. 4b), variation among replicates was very high, and on Day 33, consumption was highest in treatments containing large individuals.

Growth of small *G. pulex* was not significantly different among *Gammarus* size treatments or substrate combinations ( $N = 15$ , *Gammarus* size

combination:  $F_1 = 0.58$ ,  $P = 0.46$ , substrate:  $F_1 = 0.11$ ,  $P = 0.74$ , model  $r^2 = 0.147$ ).

## Discussion

Our findings clearly demonstrate the influence of biotic interactions, including intraspecific size composition, on habitat use by small *G. pulex* as well as the importance of controlling for or documenting these factors in habitat use investigations. That small *G. pulex* demonstrate a preference for smaller substrates only in the presence of larger individuals provides a mechanism for the size assortative substrate selection observed in field (Gee, 1982; Elliott, 2005) and laboratory (Olyslager & Williams, 1993) studies. Those studies examined mixtures of *Gammarus*



**Fig. 4** Total food consumption per treatment (a), and per individual (b), of small *G. pulex* over time when provided with only large substrate or mixed substrate, and in the

presence or absence of larger *G. pulex*. Error bars were omitted to improve clarity; see text for detailed presentation of results. GP = *G. pulex*

sizes, and may therefore reflect restricted micro-habitat use by small *G. pulex* in the presence of potential predators, cannibalistic *G. pulex*. As we observed, outcomes can be vastly different depending on the nature of the biotic environment in which target organisms are studied.

Our results suggest that small *G. pulex* may be more vulnerable to cannibalism in homogeneous and poor quality natural environments since they require refuge substrates for survival and are willing to leave refuges to obtain food when forced to make a choice. Habitat complexity has previously been associated with reduction of predation risk for vulnerable individuals (Silleet & Foster, 2000), including *G. pulex*, which selected complex habitats that provided refuge from predators (Dahl & Greenberg, 1996). Low-quality habitat forces prey to move between

refuge habitat and more productive foraging areas, and by doing so increases their risk of predation (Sih, 1992). In our first experiments, we found small *G. pulex* strongly preferred substrates that contained food over those that did not and substrate that did not contain food to the unstructured open water of our experimental aquaria. Substrate treatments that contained food were used preferentially (~8X) over identical substrates not containing food, and treatments providing both shelter and food were approximately four times more likely to be used than treatments providing only one function. In our final experiment, availability of smaller substrates from which larger individuals were excluded by body size significantly increased survival of small individuals. Survival was significantly reduced when no refuge substrate was offered and when



refuge substrate contained no food, forcing small *G. pulex* to forage in high risk open water. Incidence of cannibalism may therefore be higher in simple low-quality habitats that provide for refuge or food provision but not both.

Small *G. pulex* restricted their use of larger substrates in the presence of larger individuals. Microhabitat restriction by smaller individuals to reduce predation risk by larger conspecifics has been well documented in a variety of taxa, particularly fish (Skov & Koed, 2004). Our finding is consistent with Elliott (2005), who found that small *G. pulex* changed substrate size preference between day and night, preferring smaller substrates during the day but demonstrating no size preference at night. This behavior may reflect avoidance of larger individuals, who take refuge in substrate during the day to avoid predation by sight-feeding fishes and emerge to forage at night (Andersson et al., 1986). With larger individuals actively foraging out of the substrate at night, small *G. pulex* can potentially occupy a wider range of substrate (pore space) sizes without risk of cannibalism, whereas when larger individuals are sheltered within larger substrates, those spaces become risky to small individuals. This is consistent with Hunte & Myers (1984), who found that change in phototactic behavior of juvenile *Gammarus* coincided with the age (body size) at which they became less vulnerable to cannibalism by larger individuals. They found that as juveniles grew, they were more likely to exhibit negative phototaxis, associating more closely with the substrate. Our finding is also consistent with Dahl & Greenberg (1996), who found that *G. pulex* moved to refuge habitat in the presence of a fish predator. Although other factors may be involved in the size assortative substrate use observed in field experiments, considerable evidence suggests that vulnerable *G. pulex* change habitats to avoid predation risk from cannibalistic conspecifics.

Limiting activity under predation risk is a common response to the presence of predators in many species (Andersson et al., 1986; Sih, 1987; Kats & Dill, 1998), including *Gammarus* (e.g., Friberg et al., 1994). We expected to see differences in food consumption and growth between treatments that contained large individuals and those that did not. Several factors may be

responsible for the lack of difference we observed. First, our results suggest that larger individuals of our small size class were more likely to survive in the long-term experiment, due either to size-selective survival and/or growth out of the most vulnerable size range. Second, because our experimental conditions provided only low-quality habitat with refuge habitat and food separated, hunger may have forced small *G. pulex* to feed under a high risk of predation to avoid starvation whereas in a shorter-term experiment they may not have reached a hunger threshold and limited activity to avoid predation (Sih, 1987).

Our study contributes to the understanding of factors affecting cannibalism in an aquatic invertebrate. We provide evidence for three important factors influencing size-mediated habitat use in the aquatic environment. First, the presence of larger, cannibalistic individuals can have dramatic effects on the fitness (survival) and habitat use of smaller, vulnerable individuals. Second, the availability of size-structured substrate providing refuge space for vulnerable individuals mediates the incidence of cannibalism. And third, habitat quality, including the spatial and temporal distribution of high-quality habitats that affect the tradeoffs vulnerable individuals must make, as well as their ultimate fitness, has important effects on the incidence and outcome of cannibalism. These factors may strongly influence the significance, occurrence, and effects of cannibalism on population structure and community dynamics.

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