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ORIGINAL PAPER

Environmental and morphological factors influencing predatory behaviour by invasive non-indigenous gammaridean species

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Abstract Predatory behaviour seems to be more frequent in invasive gammaridean species than in native ones. This results in the exclusion of other, mostly native gammaridean species and a change in benthic communities. The present study analysed the influence of environmental factors (water temperature) and morphological factors (sex, body parts involved in catching and holding prey) on the predatory behaviour of *Dikerogammarus villosus*. A diet study of invasive relatives of *D. villosus* showed that predation intensity is especially high in spring and summer, that is, at increasing and high temperatures. Experiments with *D. villosus* in climate rooms at various temperatures, using the native *Gammarus fossarum* as prey, showed that the average predation rate by both sexes gradually increased over the temperature range from 5 to 30°C.

Natural mortality during the experiments was negligible compared to losses due to predation. At each temperature, the predation rate by females was lower than that by males. Males showed a steep allometric growth of body parts involved in the process of catching and holding prey, compared to females at increasing body size in a number of measurements. This may explain the difference in predatory behaviour between males and females, which plays a role in intraguild predation a supposed mechanism for species displacement.

Keywords Species displacements · Predation · *Dikerogammarus villosus* · Invasive amphipods · Sex · Water temperature · Allometric growth · Seasonal effects

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Introduction

Amphipods belong to the most successful invaders in fresh and brackish waters (Jazdzewski 1980; Holdich and Pöckl 2007). Their ability to reach very high densities means they can have a large impact on benthic communities and even ecosystems (Van der Velde et al. 2000, 2002, 2006; Haas et al. 2002; Van Riel et al. 2006). Gammaridean amphipods are considered to be detritivores (phyto-detritophages, detritophages), omnivores (phyto-zooprophages, zoophytophages) or predators (zoophages) (Monakov 2003). During invasions, increased predation on other macroinvertebrates and fish by gammaridean species is sometimes recorded, for instance in the case of the invasion of the North American gammaridean *Gammarus tigrinus* in continental Europe (Schmitz 1960) and the invasion of *Gammarus pulex* in Ireland (Kelly et al. 2003, 2006).

During successful invasions by non-indigenous gammarideans, native gammaridean species often become reduced in abundance or are locally even completely replaced by the non-indigenous relatives. Such species displacements by invasive gammaridean species have been recorded on several occasions all over the world (Pinkster et al. 1977; Dick et al. 1993, 1995; Dick 1996; Dick and Platvoet 1996, 2000; Dermott et al. 1998; Jazdzewski and Konopacka 2000, 2002; Jazdzewski et al. 2002, 2004, 2005; MacNeil and Prenter 2000; Van der Velde et al. 2000, 2002; Van Overdijk et al. 2003; Kelly et al. 2003; MacNeil et al. 2004; Kelly and Dick 2005; Meyer et al. 2005; Grabowski et al. 2006, 2007; Felten et al. 2008a).

Intraguild predation (Polis et al. 1989) is considered to be one of the main factors determining such species replacement processes (Dick et al. 1993, 1995, 1999; Dick 1996; Dick and Platvoet 1996, 2000; Kinzler and Maier 2003). The replacement of native gammarideans by invasives could thus be caused by asymmetry in mutual predation (Kinzler and Maier 2003). However, interference competition for shelter can also play a role (Van Riel et al. 2006, 2007, 2009; Platvoet et al. 2009a). These processes are influenced by body size, while in the field, habitat heterogeneity is also important, as heterogeneous habitats provide refuges that may prevent total replacement (MacNeil et al. 2008; Grabowski et al. 2009; Kestrup and Ricciardi 2009; Piscart et al. 2009; Platvoet et al. 2009a; Van Riel et al. 2009).

Dikerogammarus villosus can be studied as a model species of an omnivorous gammaridean showing a high degree of predation on fish eggs, recently hatched fish (Casellato et al. 2007; Platvoet et al. 2009b), on relatives including their own juveniles well as on other macroinvertebrates (Dick et al. 2002). Marguillier et al. (1998) and Van der Velde et al. (2000) noticed that the Ponto-Caspian gammaridean species *D. villosus*, which has invaded the Rhine system since 1994/1995 through the Main–Danube canal (Bij de Vaate et al. 2002), must act as a predator, in view of the high values of $\delta^{15}\text{N}$, which are similar to those measured in zoobenthivorous fish. Van der Velde et al. (2000, 2002) and Haas et al. (2002) noticed that the composition of the communities changed after the arrival of *D. villosus*, and densities of macroinvertebrates, including the non-indigenous *G. tigrinus* on the stones along the River Rhine, were also observed to decrease (Van Riel et al. 2006, 2009; Leuven et al. 2009). Dick and Platvoet (2000) noticed the disappearance of the native *Gammarus duebeni* along the stony shores of Lake IJsselmeer, as well as a decrease in *G. tigrinus* in this zone after the arrival of *D. villosus* (Platvoet et al. 2009a).

It is unknown which factors determine when invasive gammarideans become more or less predatory. Several factors are suspected to play a role, such as differences in morphology, morphological change, genetic change, size, sex, water temperature, the presence of abundant food, etc. The objective of the present study is to unravel the dominant environmental and morphological factors of the predatory behaviour of invasive gammaridean species. We focus on water temperature, including season, and sex including body size and development of body parts involved in predation.

Materials and methods

Seasonal share of animal food in the diet of non-native gammarideans

We analysed the diets of three non-indigenous gammarid species, viz. *Pontogammarus robustoides*, *Dikerogammarus haemobaphes*, and *Gammarus roeseli*. *P. robustoides* and *D. haemobaphes* originate from the Ponto-Caspian region and were sampled in

the middle stretch of the Vistula River. *G. roeseli* originating from the Balkan was sampled in the upper part of the Notec River in Poland.

Gammarideans for the study were collected four times in 2005: in winter, spring, summer and autumn. Thirty adult individuals were taken at random from each sample, after which they were dissected and the gut contents were sealed in lactophenol on a microscopic slide. Qualitative and quantitative analyses were then done following Hynes (1950) and Hyslop (1980). Qualitative analysis was applied to all gut contents, while the quantitative analysis was done only on the stomach content, as hard-to-digest material

could be overrepresented in an intestine. The amount of animal remnants (i.e. oligochaetes, chironomids, crustaceans, mayflies etc.) (Fig. 1a–e) in the stomach was estimated, and an index of importance (IOI) of this category of food in the gammarids' diet was calculated as follows:

$$\text{IOI}_i = 100 \times \text{HI}_i / \Sigma \text{HI}$$

$$\text{where } \text{HI}_i = \%F_i + \%V_i$$

and $\%F_i$ is the share of individuals that had eaten food category i ; $\%V_i$ is the share of food category i in the stomach contents volume. Differences in predation

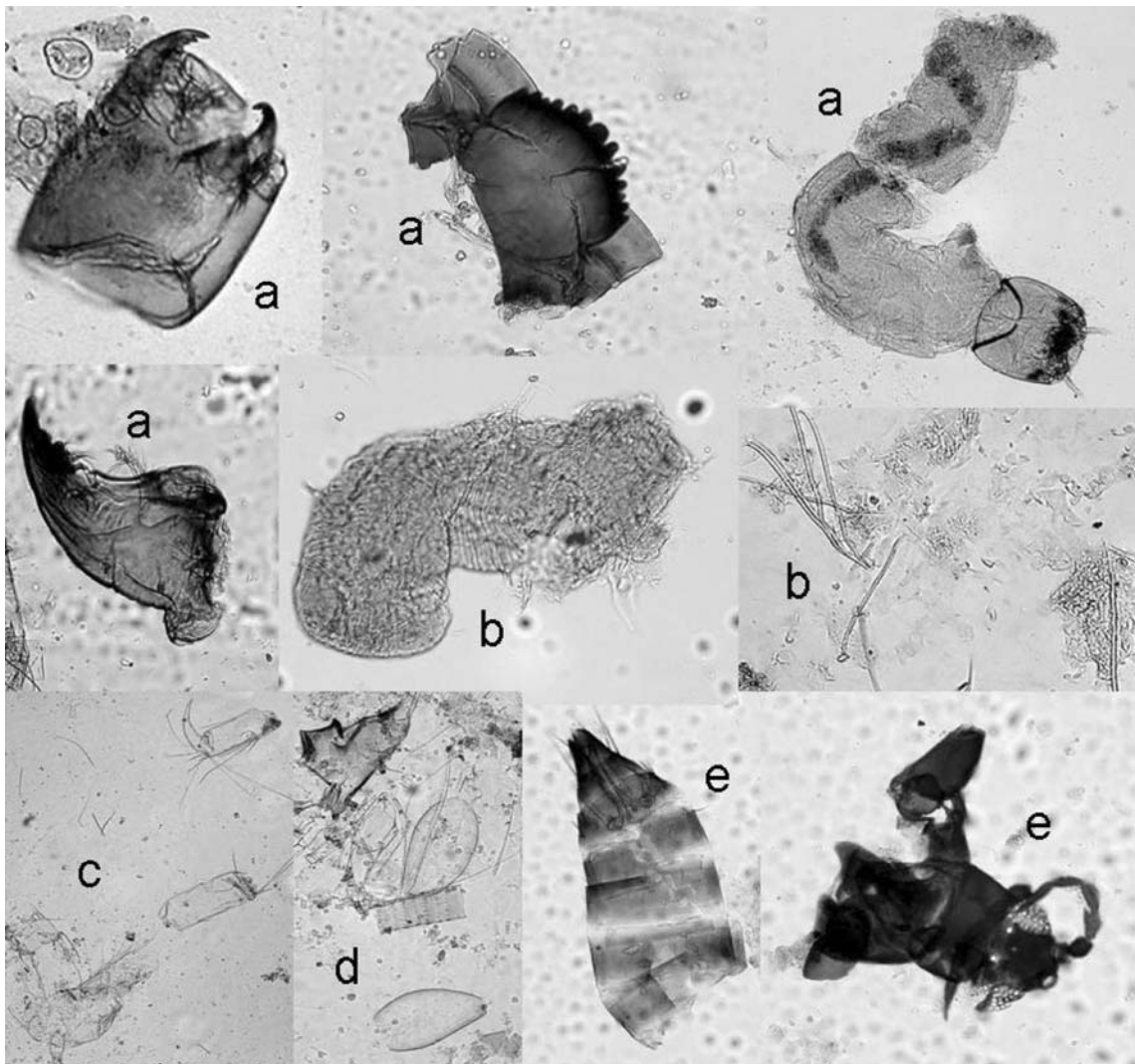


Fig. 1 Examples of animal remnants (a chironomids, b oligochaetes, c crustaceans, d mayflies and e other insects) found in gammaridean stomachs

intensity of the various invasive gammaridean species were tested by a Kruskal–Wallis test.

Predation experiments in climate rooms

Predation by adult *D. villosus* (body length range 10–20 mm) on the native *Gammarus fossarum* (body length 5–15 mm) was studied at six water temperatures, viz. 5, 10, 15, 20, 25 and 30°C, in climate rooms at a 50% light–dark regime, in order to assess the predation capabilities of *D. villosus* at various temperatures. The temperature range of 5–30°C should be tolerated by both species, as demonstrated by Wijnhoven et al. (2003a, b). We used 33 numbered plastic beakers per temperature, filled them with water (115 ml) and added to each beaker one adult individual of *D. villosus* and one individual of *G. fossarum*. The duration of the experiments, which took place at constant temperature conditions, was 10 days. On each day during the experiment, the number of partly or totally consumed *G. fossarum* was recorded and they were replaced by new specimens from a stock. Remnants of *G. fossarum* were removed. Dead specimens of *D. villosus* were also recorded. Water was regularly refreshed when detritus particles became visible at the bottom of the beakers.

After each experiment at a particular temperature was finished, the individuals of *D. villosus* were separately preserved in 70% ethanol, in tubes labelled with the same number as the beakers, after which their sex was established by the presence of male genital papillae and female brood plates. Body length was assessed by measuring the length from the apex of the rostrum to the base of the telson.

As a control for the mortality of *G. fossarum* at the six temperatures, we used the 33 numbered plastic beakers also with one single *G. fossarum* each. This experiment was carried out once at each temperature, under light–dark conditions similar to those described above. No food was added to the beakers, and water was regularly renewed. Dead individuals were recorded daily over a period of 10 days.

Predation by the sexes related to temperature

The average predation rate of *G. fossarum* by the sexes of *D. villosus* (average number consumed per

day), was related to the temperature using logistic regression, as the average predation rate varies between 0 and 1 day⁻¹ (Everitt and Dunn 2001):

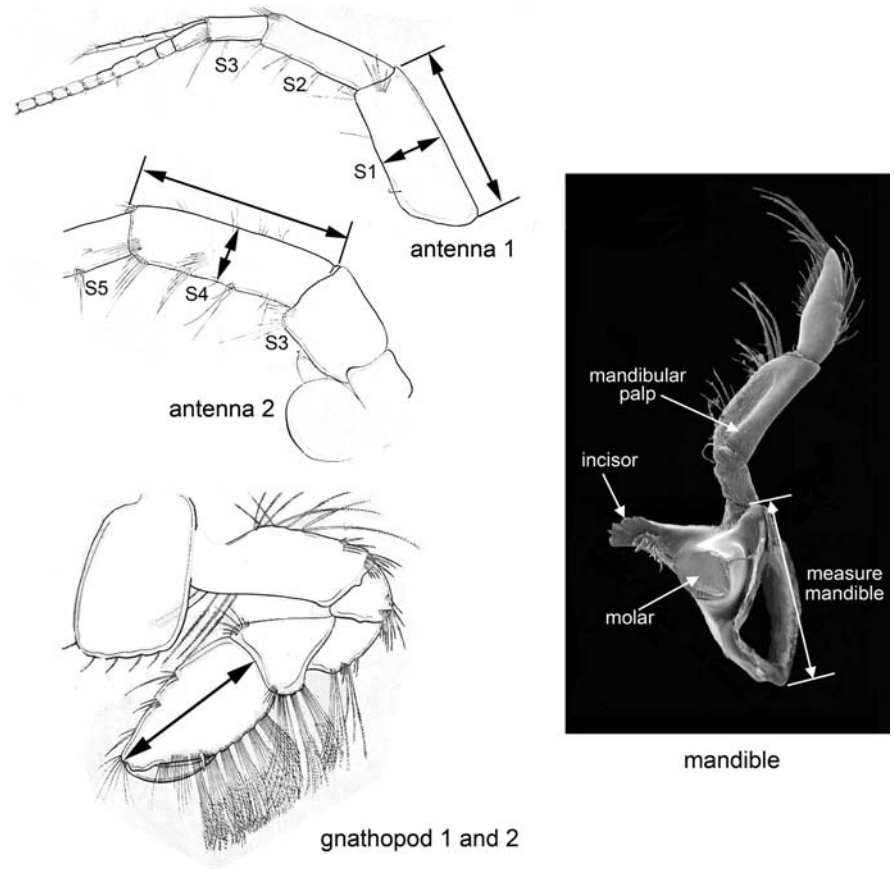
$$\ln\left(\frac{p}{1-p}\right) = a \cdot \text{TEMP} + b$$

where p is the average predation rate of *G. fossarum* by *D. villosus* (day⁻¹), TEMP is the environmental temperature (°C), a the slope and b the intercept of the regression equation. The regression equation was optimized using a linear least squares fit to find appropriate values for the slope (a) and intercept (b). This was done for males and females, respectively, with $N = 14$ –24 for females and $N = 8$ –15 for males for each temperature.

Morphological measurements on sexes of *D. villosus*

The antennae, in particular the well-developed second antennae, in combination with the pereopods and mouthparts, play a major role in gathering and processing food (Platvoet et al. 2009b). This means that these body parts may show morphological adaptations to a more predatory life style in *D. villosus*. We therefore studied the allometric growth of these body parts. A population of *D. villosus* in Lake Gouwzee (The Netherlands) was sampled and the sample transferred to 70% alcohol. Random samples of 10 males and 10 females were taken by placing them on a grid and using a random table. First the body lengths of the selected specimens were determined (see above), by means of a camera lucida, a piece of string and a scale fitted with an Olympus glass micro-measure. The piece of string was fitted around the contours of the dorsum of the specimens and then stretched out on the scale. The same method was used to measure the length of both first and second antennae. The width of the first peduncular article of antenna 1 was measured with the camera lucida and callipers. The width of the fourth peduncular article of the second antennae, the length of the basal body of the left mandible and the lengths of the propodi of pereopods 1 and 2 (gnathopods 1 and 2) were determined in a similar way, at an accuracy of 0.1 mm (Fig. 2). The mandibles were dissected and mounted on a slide in glycerine.

Fig. 2 Measurements on body parts of *Dikerogammarus villosus* involved in feeding: antennae 1 and 2, gnathopods 1 and 2 and mandible. Double arrows indicate measurements



Allometric regression

Allometry means the disproportionate development (in terms of size) of some structure in relation to the rest of the body. Allometric relations for a number of morphological characteristics were derived via linear regression on the basis of the body length of males and females, respectively:

$$C_{j,i} = a_{j,i} \cdot BL_i + b_{j,i}$$

where $C_{j,i}$ is morphological characteristic j of gender i , BL_i the body length of gender i , a the slope and b the intercept of the regression equation for morphological characteristic j of gender i . The regression equation was optimized using a linear least squares fit to find appropriate values for the slope (a) and intercept (b). For each morphological characteristic, we analysed whether the slopes of the allometric

regressions differed significantly between males and females.

Results

Seasonal changes in animal food in the diet of non-native gammarideans

Gut contents analysis of the non-indigenous gammarids studied showed that predation intensity increased with higher temperatures. In the case of *P. robustoides* and *D. haemobaphes*, the predation intensity was lower in winter (Kruskal–Wallis test, $P = 0.0012$ in both cases) than in spring and summer (Fig. 3). The largest amounts of animal remnants in the stomachs of *Gammarus roeseli* were found in summer (Kruskal–Wallis test, $P = 0.0022$) (Fig. 3).

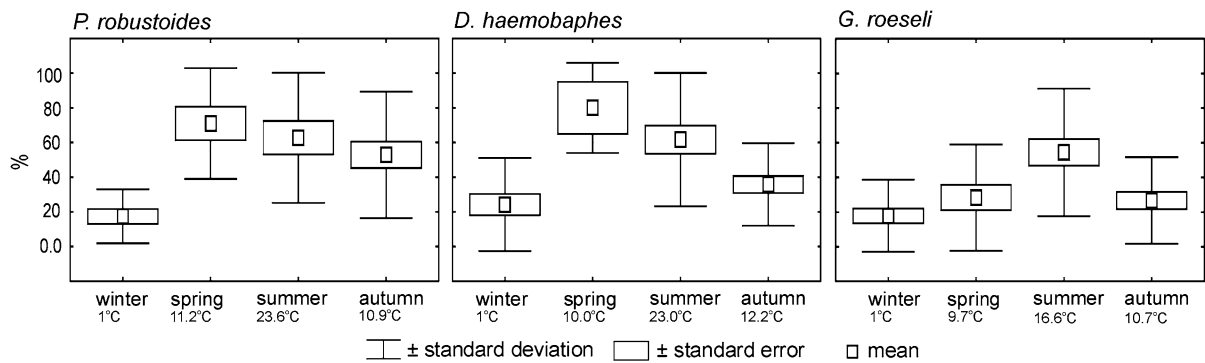


Fig. 3 Average percentage of animal tissue in the stomachs of *Pontogammarus robustoides*, *Dikerogammarus haemobaphes* and *Gammarus roeseli* during various seasons

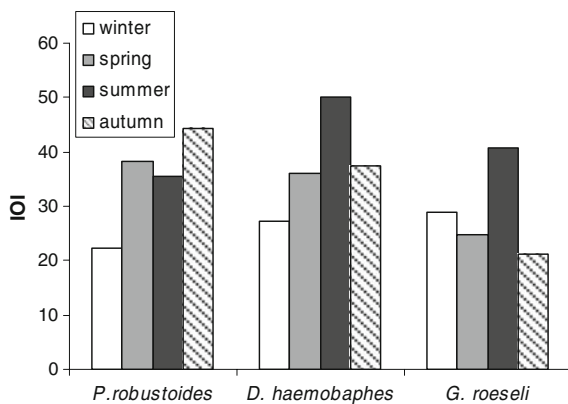


Fig. 4 Values of index of importance (IOI) of animal tissue in the diets of *Pontogammarus robustoides*, *Dikerogammarus haemobaphes* and *Gammarus roeseli* in various seasons

A similar phenomenon was observed when applying the index of importance (IOI) to the data. This index takes frequency into account (Fig. 4).

Predation rate by sexes versus temperature

A significant positive relationship between the average predation rate of *G. fossarum* by *D. villosus* and the temperature was found for both males and females (Fig. 5). The slopes and intercepts of the regressions significantly deviated from 0 ($P < 0.05$), meaning that feeding rate and temperature were significantly related for males as well as females.

$$\ln\left(\frac{p_m}{1-p_m}\right) = 0.14 \cdot \text{TEMP} - 2.0$$

$$\ln\left(\frac{p_f}{1-p_f}\right) = 0.14 \cdot \text{TEMP} - 3.8$$

where p_m and p_f are the predation rates by males and females, respectively.

The intercepts differed significantly between males and females ($P < 0.1$, two-sided confidence interval), whereas no significant differences were found for the slopes ($P > 0.9$, two-sided confidence interval). This implies that the slope dependency of the temperature and feeding rate did not differ significantly between males and females. However, the basic level of feeding was significantly higher for males than for females at any given temperature. Body size distribution did not differ significantly between the animals of the same sex used in the temperature tests (Mann–Whitney U test; SPSS 18.0.1), which means that the increase in predation rate with increasing temperature is not due to differences in body sizes within the sexes used for the experiments.

Mortality versus temperature

Average daily mortality of *D. villosus* during the experiments at all temperatures together, was very low, viz. 0.5% (SD 0.5%). Average daily mortality was highest at 30°C, but still low (on average 1.4%). The range of average values at the other temperatures was 0–0.6%. Daily mortality of *G. fossarum* without *D. villosus* was clearly increased at 30°C, with an average mortality of 15.2%. The range of average values at the other temperatures was 0.3–4.2%.

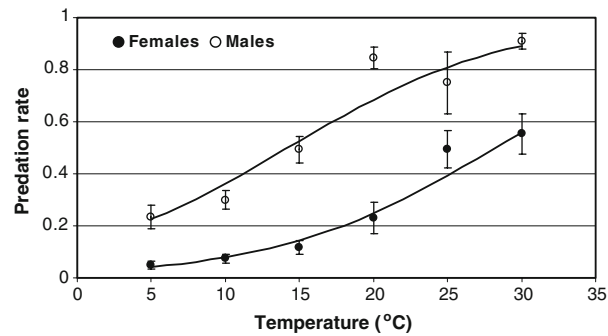


Fig. 5 Logistic fit of predation rate of *Gammarus fossarum* by *Dikerogammarus villosus* males (open circles) and females (filled circles) (average number of *G. fossarum* per *D. villosus*

consumed per day). The error bars refer to \pm standard error of the mean due to the spread in the individual predation rates per specific ambient temperature in the experiments

Allometric regressions of body parts involved in predation

The sexes of *D. villosus* also significantly differed in terms of the slopes of the regressions of various measurements (Table 1) at $\alpha = 0.1$ (two-sided), viz., the diameter of antenna 1, the length of antenna 2, the diameter of antenna 2 and the lengths of propodus 1 and propodus 2 (Fig. 6). The slopes of the regressions of the length of antenna 1 and the length of the basal body of the mandible were not significantly different between the sexes. Differences in the measurements tended to be larger at larger body lengths of both sexes. Males grew to a larger size than the females, demonstrating a much stronger allometric growth in the body parts involved in predation.

Table 1 Slopes of the allometric regressions between body length and a number of species characteristics for males and females, and results of the test of significance between the male and female allometric regressions

Species characteristic	Male	Female	Significance
Length of antenna 1	0.357	0.348	NS
Diameter of segment 1 of antenna 1	0.022	0.014	*
Length of antenna 2	0.386	0.296	**
Diameter of segment 3 of antenna 2	0.023	0.007	***
Length of propodus gnathopod 1	0.092	0.061	**
Length of propodus gnathopod 2	0.123	0.083	**
Length of basal body of mandible	0.061	0.050	NS

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant

Discussion

The diet analyses of three non-indigenous invasive gammarideans revealed that animal food increases in spring and summer thus at increasing and higher temperatures. Our experiments show that higher temperatures stimulate *D. villosus* to increase the predation rate. At lower temperatures the animals become slow and prey less. However, at each temperature, there was a considerable variability in the predatory behaviour of the various specimens. Some specimens were regularly catching *G. fossarum*, eating them every day, while there were also individuals which did not eat any of these gammarideans during the whole experiment. Another source of variability was that some specimens of *D. villosus* were able to immediately catch their prey, while others could not, in spite of attempts, because *G. fossarum* were swimming around out of reach of the antennae of *D. villosus*, or because they kept to the rear of *D. villosus*, delaying the time that the latter could catch them. Furthermore, some specimens moulted during the experiments, and in this state they made few or no attempts to prey on *G. fossarum*. In spite of this variability, there was a significantly positive trend demonstrating that *D. villosus* increase their predation efficiency with increasing temperatures, even up to 30°C. The low figures for daily mortality of *G. fossarum* hardly influenced the predation rate values, because they are negligible compared to the losses by predation at all temperatures except 30°C.

The upper temperature tolerance for pleopod activity of *D. villosus* was about 31°C, as its pleopod

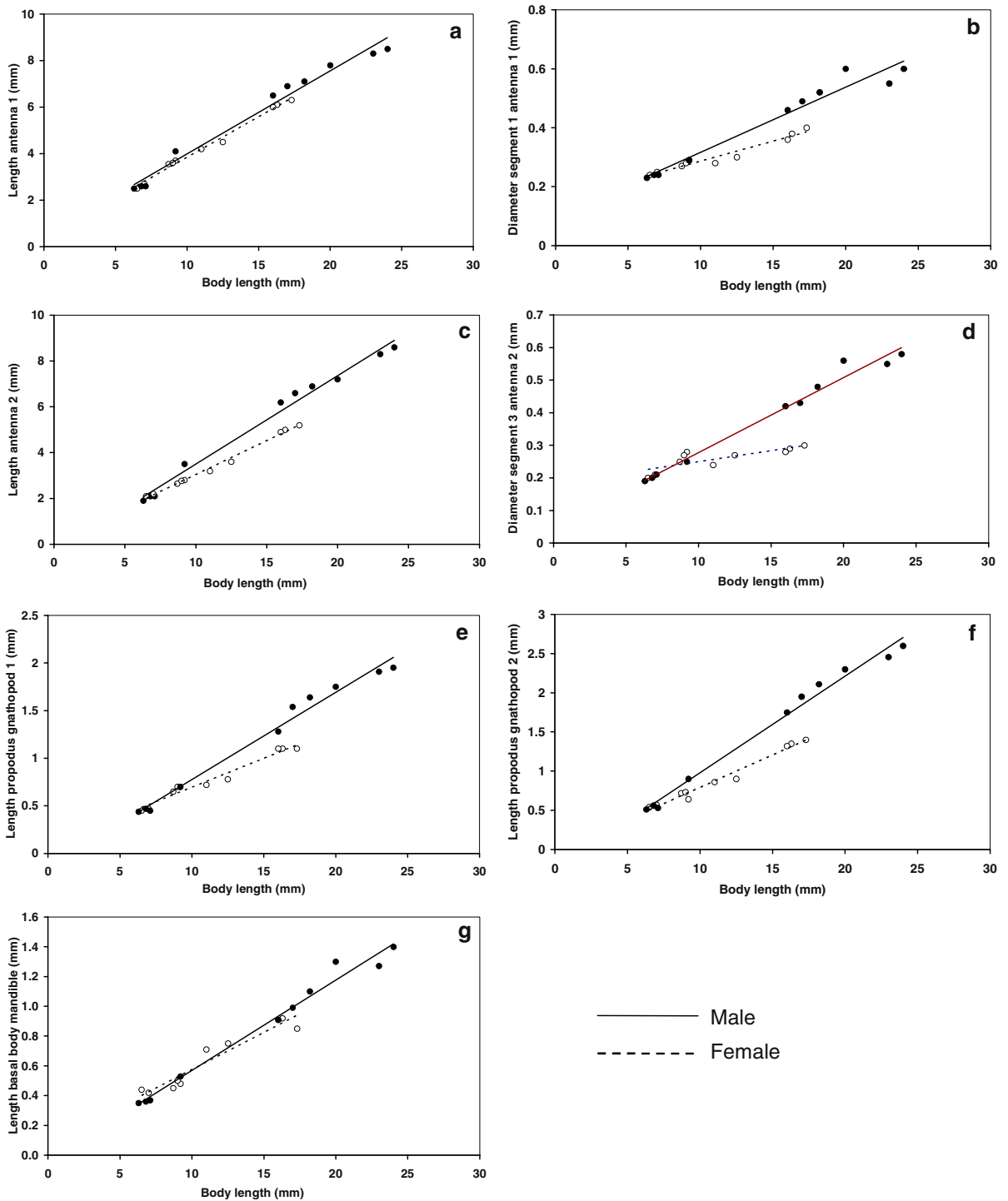


Fig. 6 Measurements of body parts of *Dikerogammarus villosus* involved in predatory feeding (see Fig. 2 for the parts measured) in relation to sex and body length (filled circles; females open circles)

activity increased up to this temperature, whereas pleopod activity decreased quickly above 31°C, indicating a tolerance limit. The upper temperature tolerance for pleopod activity of *G. fossarum* is 29°C (Wijnhoven et al. 2003a, b). This means that the increased mortality at 30°C may have been caused by suboptimal conditions for *G. fossarum*, which may also have contributed to the higher predation rate by *D. villosus* at that temperature.

The experiments comparing the predation rates between the two sexes showed the same trend for both sexes, but the average predation rates for the females were always lower than those for the males, across the temperature range. This means that sex-related morphology may be important in terms of predation rate.

Although the mouthparts of *D. villosus* were studied by Mayer et al. (2008), they did not distinguish between males and females. They concluded from their extensive study that the mouthparts of this species show no particular specialisation for carnivory and predation, although the well-developed incisors are able to kill prey. The mouthparts also allow other modes of feeding, as was also demonstrated by Platvoet et al. (2006, 2009b). Kinzler and Maier (2003), who did predation experiments with *D. villosus* on *G. fossarum*, at 18°C found that males of *D. villosus* consumed more *G. fossarum* than the females did. In our study we found a difference between males and females with respect to predation rate, with males showing a higher predation rate over the whole temperature range tested. Allometric relationships of body parts involved in prey catching and holding differ between the sexes, with differences becoming larger at larger body sizes. The measurements of the body parts involved in detecting (first antennae) and processing (mouth parts), however, showed no difference between the sexes. Differences in allometry may explain why the predatory impact at the start of an invasion is more evident than later on. Invasive species in their newly invaded area are often released from predators and/or competitors and/or meet abundant suitable food such as animal prey, allowing them to grow faster and larger than in the area of origin. *D. villosus* is the largest gammaridean species in the area, reaching a size of up to 30 mm in the Rhine delta area, which is 6 mm larger than recorded in the River Danube (Platvoet 2007). In a study of a Danube population of *D. villosus*, Pöckl

(2009) found no males larger than 22 mm and no females larger than 18 mm. *D. villosus* in the Rhine delta is thus much larger than recorded in the Danube from where it originated, although Nesemann et al. (1995) also mention 30 mm as the maximum size of *D. villosus* in its native area. This means that the predatory impact of *D. villosus* is determined by local and seasonal conditions determining increasing allometric growth differences between both sexes, including temperature and food availability. Felten et al. (2008b) carried out a study on the diet of *G. fossarum* in streams, which indicated its main role as collector and shredder. However, animal food was taken up by the larger specimens (6–8 mm) and was evident in submersed root and bryophyte but not in detrital pool habitats. Unfortunately they made no distinction between females and males, because the size difference can have caused this difference in predatory behaviour in relation to sex-related allometric growth. This approach can further elucidate such differences in diet and the mechanisms causing this difference.

Conclusions

The predatory behaviour of *D. villosus* is influenced by various factors, a main factor being the water temperature. Predation rate increased with increasing temperature over a temperature range of 5–30°C. Perhaps this is a characteristic of more invasive gammaridean species, as we found that the food of the three other invasive species we analysed contained more animal prey in spring and summer than in wintertime. Males, which can grow larger than females were significantly more predatory than females indicating a sex-dependent predatory behaviour. We found a relation with the allometric growth of body parts involved in feeding, with the size of these body parts increasing faster during growth in males than the same body parts did in females.

These findings provide new information on the mechanisms and conditions of the predatory impact of gammaridean invasive species. We also know that size is important for the reproductive capacity of these gammarideans. When gammarideans are released from predation and find numerous easy preys in the areas they invade, their growth will make them more predaceous, as allometric growth of body parts involved in feeding allows them to feed on stronger

prey, including relatives. This leads to the exclusion of competitors (intra- and interguild predation), particularly by males. Greater food availability under these conditions may accelerate growth and lead to higher densities through increased reproduction by females. Gammarideans seem to be all omnivores with a difference in sex and species specific predation abilities and intensities. Differences in predation rate, body size and allometric growth of body parts of both sexes involved should be studied also in other gammaridean species, native as well as invasive to predict their impact and competitive capacity.

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