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Freshwater Biology

Freshwater Biology (2013) **58,** 730–741 doi:10.1111/fwb.12078

There is more than one 'killer shrimp': trophic positions and predatory abilities of invasive amphipods of Ponto-Caspian origin

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SUMMARY

1. Biological invasions are regarded as one of the greatest threats to biological diversity. One of the macroinvertebrate groups with the largest number of invasive species in fresh water are gammarid amphipods. Their omnivorous (including predatory) feeding behaviour may facilitate their spread and establishment in new areas.
2. *Dikerogammarus villosus*, the 'killer shrimp', is a well-known example of a Ponto-Caspian gammarid that is a very effective predator and successful coloniser in Europe. There are, however, other invasive Ponto-Caspian amphipods, which have spread successfully in Northern, Central and Western Europe. Our aim here was to test whether two of such invaders (*Pontogammarus robustoides* and *Dikerogammarus haemobaphes*) are also more predacious than a native species (*Gammarus fossarum*).
3. Stable isotope analysis (δ^{15}N and δ^{13}C) of Ponto-Caspian amphipods coexisting in a reservoir demonstrated that the trophic positions of *P. robustoides* and *D. haemobaphe*s were similar to that of *D. villosus*. *Echinogammarus ischnus* and *Chelicorophium curvispinum* occupied the lowest position in the food web, while the native *Gammarus fossarum* (collected from another waterbody) had an intermediate trophic position.
4. Stomach content analysis of *P. robustoides*, *D. haemobaphes* and *G. fossarum* collected in the field, as well as laboratory feeding experiments, was used to compare diet and feeding preferences among the two invasive and one native species. All three species were omnivorous and predacious. However, the two invasive species (*P. robustoides* and *D. haemobaphes*) were more effective predators than *G. fossarum* and showed a clear preference for animal prey and tissue.
5. *Pontogammarus robustoides* and *D. haemobaphes* may, like *D. villosus*, also be called 'killer shrimps' and could have a similar impact as invaders of European freshwater and brackish waterbodies.

Keywords: aquatic invasive species, ecosystem impact, feeding preferences, omnivory, predation, stomach content, trophic level

Introduction

Assemblages of freshwater and brackish water macroinvertebrates in Europe have changed dramatically over the last few decades, due to ongoing biological invasions (e.g. Bij de Vaate *et al*., 2002; Leppäkoski, Gollasch & Olenin, 2002; García-Berthou *et al*., 2005). Every year, new alien species of freshwater macroinvertebrates are recorded somewhere in Europe (DAISIE, 2009). Amphipods, and particularly gammarids, are strongly represented among non-indigenous species in Europe (Grabowski, Jazdzewski & Konopacka, 2007c). Many studies have been conducted to identify biological traits that may promote their invasiveness, including high fecundity, rapid embryological

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development, relatively short maturation time, short generation time, relatively large or small body size (Van der Velde *et al.*, 2000; Bij de Vaate *et al.*, 2002; Kley & Maier, 2003, 2005; Devin & Beisel, 2007; Grabowski, Bacela & Konopacka, 2007a; Pöckl, 2009), euryoeciousness and euryhalinity (Bij de Vaate *et al.*, 2002; Grabowski *et al.*, 2009). Their feeding is also important, and non-native omnivorous species and/or effective predators may have an advantage over related native species (e.g. Dick & Platvoet, 2000; MacNeil & Platvoet, 2005; Van Riel *et al.*, 2006; Platvoet *et al.*, 2009a,b; Van der Velde *et al.*, 2009).

The most intensively studied example of such a successful invasive gammarid is *Dikerogammarus villosus*, which is of Ponto-Caspian origin (Bij de Vaate *et al.*, 2002). It is now widely distributed in Europe and currently inhabits the largest rivers in Western and Central Europe, as well as some Alpine Lakes (Bollache *et al.*, 2004; Grabowski, Bacela & Wattier, 2007b; Grabowski *et al.*, 2007c; Bacela, Grabowski & Konopacka, 2008), and was first found in Great Britain in 2010 (MacNeil *et al.*, 2010). This species is extraordinarily competitive, and its introduction has led to the decline of other macroinvertebrates, including earlier gammarid colonisers of various origins, probably through intraguild predation (e.g. Dick & Platvoet, 2000; Van der Velde *et al.*, 2000, 2009; MacNeil & Platvoet, 2005; Van Riel *et al.*, 2006; Kinzler *et al.*, 2009; Stoffels *et al.*, 2011). It also feeds on eggs, larvae and juveniles of fish (Casellato, Visentin & La Piana, 2007; Platvoet *et al.*, 2009a). Van Riel *et al.* (2006) showed that *D. villosus* feeds higher in the food web than other gammarids and that its trophic position is similar to that of small benthic fish, which is why this species is also known as the 'killer shrimp' (Dick & Platvoet, 2000). However, as an omnivore, *D. villosus* is capable of feeding on a wide variety of items, using a broad range of feeding behaviour, which means that food is unlikely to be a limiting factor in colonising new habitats (Platvoet *et al.*, 2006, 2009b; Van der Velde *et al.*, 2009).

Several more Ponto-Caspian gammaridean species are widely distributed in the larger European rivers and lakes, including *Pontogammarus robustoides* and *Dikerogammarus haemobaphes*. Like *D. villosus*, both are native to the lower courses of rivers such as Volga, Don, Dnieper, Dniester and Danube (Dedju, 1967, 1980; Mordukhai-Boltovskoi, 1969). They have also been recorded from some freshwater and brackish coastal lakes and Black Sea lagoons (Jazdzewski, 1980). In the 1960s, they were introduced to many Ukrainian, Lithuanian and Caucasian lakes and artificial reservoirs, as food for fish (Gasiunas, 1968; Jazdzewski, 1980; Arbaciauskas, 2002). As a result, both species spread westwards and northwards. *Pontogammarus robustoides* colonised waters in Germany (Rudolph, 1997; Zettler, 1998; Martens, Eggers & Grabov, 1999), Poland (Jazdzewski & Konopacka, 2000; Grabowski *et al.*, 2007c), Lithuania (Berezina & Panov, 2003; Arbaciauskas, 2005), Latvia (Grudule, Parele & Arbačiauskas, 2007; Kalinkina & Berezina, 2010) and Russia (Kurashov & Barbashova, 2008). *Dikerogammarus haemobaphes* is even more widely distributed in the waters of Western Europe (the Danube and continental North Sea catchments, the Alpine Lakes) (Ponyi, 1958; Nesemann, Pöckl & Wittmann, 1995; Tittizer, 1996; Bij de Vaate *et al.*, 2002) and Central Europe (Bij de Vaate *et al.*, 2002; Jazdzewski & Konopacka, 2002). In 2012, *D. haemobaphes* was also found for the first time in Britain (http://www.thisisgloucestershire.co.uk/Killer-Shrimp-River-Severn/story-17034289-detail/story.html; http://www.bbc.co.uk/news/uk-england-hereford-worcester-19828575.

Both species are highly tolerant to extreme environmental conditions, such as high salinity (Ponomareva, 1975; Santagata *et al.*, 2008), temperature (Kititsyna, 1980), and low oxygen concentration (Dedju, 1980; Arbaciauskas, 2005). Their life histories have been studied extensively, revealing their high invasive potential resulting from the high fecundity, fast maturation, short embryological development and large number of generations per year (Bacela & Konopacka, 2005; Bacela, Konopacka & Grabowski, 2009). However, their diet and trophic position in invaded systems have not been studied in detail. As these two species are very successful invaders and, like *D. villosus*, can grow to a relatively large size compared to native species, we asked whether they are also effective predators.

The first aim of our study was to assess the trophic position of invasive *D. haemobaphes* and *P. robustoides*, compared to other amphipod species, using stable isotope analysis to test the hypothesis that it would be high. The second aim was to compare their predatory abilities and omnivory with that of the native *Gammarus fossarum*, using stable isotope analysis, gut content analysis and food choice experiments.

Methods

Study sites

To test the trophic position of the invasive gammarids versus a native species, we used stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analysis. For this purpose, samples of both invasive amphipods, *P. robustoides* and *D. haemobaphes*, and other food-web components representing various trophic levels were taken from the Zegrzynski Reservoir, an artificial lake on the Bug River (N 52°27′54″; E 21°01′42″) where *P. robustoides* and *D. haemobaphes* coexisted with *D. villosus*, from the Wloclawski Reservoir (on the Vistula River) in Murzynowo (N 52°35′09.2″; E 19°30′27″) and from the Vistula River at Nieszawa (N 52°50′12″; E 18°54′05″). On each occasion, other amphipod species (*Echinogammarus ischnus* and *Chelicorophium curvispinum,* both also of Ponto-Caspian origin) were also collected. The native *G. fossarum* as well as other food-web components were collected from the small stream Struga Dobieszkowska near the city of Lodz (N 51°50′47.3″; E 19°34′13.4″).

To characterise the diet and for the diet choice experiments, we also collected *P. robustoides* from the Wloclawski Reservoir in Murzynowo (N 52°35′09.2″; E 19°30′27″), while *D. haemobaphes* was taken from the Vistula River at Nieszawa (N 52°50′12″; E 18°54′05″). The native *G. fossarum* was again collected from the Struga Dobieszkowska near the city of Lodz.

Field study – stable isotope analysis

Food-web components (macrophytes, macroinvertebrates, fish and detritus) were collected from the littoral zone using a pond net with a mesh size of 0.5 mm. Samples were sorted, washed with distilled water and dried for 48 h at 60 °C, after which specimens were then frozen with liquid nitrogen and then grounded to a fine powder using a pestle and mortar. In view of the low body mass of some species, a composite sample was prepared by pooling available specimens. Shells of molluscs were removed before grinding their body tissue. Samples of adult fish and larger crustaceans (crayfish) comprised only muscle tissue, which provides a history of food assimilation over months and excludes short-term variability (Gearing, 1991).

Carbon and nitrogen stable isotope ratios were measured with a Carlo Erba NA 1500 elemental analyser, coupled online via a Finnigan Conflo III interface with a ThermoFinnigan DeltaPlus mass-spectrometer. Carbon and nitrogen isotope ratios were expressed in delta notation (δ^{13}C, δ^{15}N) relative to Vienna PDB and atmospheric nitrogen.

The trophic position of the amphipods in the food web was examined using a dual isotope (δ^{13}C, δ^{15}N) method (Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999; Vander Zanden *et al.*, 2000). As the organisms at the base of the food web can differ greatly between sites, trophic position was estimated for each individual sample, based on a primary consumer baseline estimated for each case. We examined the overall δ^{15}N–δ^{13}C relationship following Vander Zanden & Rasmussen (1999) (Equations 1–4):

$$\delta^{15}\mathrm{N}_{\mathrm{e,primary\,consumer}} = 6.34/\{(1+\exp[9.67 + (0.356 * \delta^{13}\mathrm{C}_{\mathrm{m,primary\,consumer}})]\} \quad (1)$$

where $\delta^{15}\mathrm{N}_\mathrm{e}$ is the estimated δ^{15}N value for a taxon, which was calculated from the measured δ^{13}C value ($\delta^{13}\mathrm{C}_\mathrm{m}$) for that taxon in the food web under study, using the overall δ^{15}N–δ^{13}C relationship. The food-web-specific deviation from the general baseline curve was calculated for every primary consumer in the food web of every sample as follows:

$$\mathrm{residual} = \delta^{15}\mathrm{N}_{\mathrm{m,primary\,consumer}} - \delta^{15}\mathrm{N}_{\mathrm{e,primary\,consumer}} \quad (2)$$

where $\delta^{15}\mathrm{N}_\mathrm{m}$ is the δ^{15}N value measured for the taxon in the food web under study. The residual value was calculated for every primary consumer in the food web under study. Subsequently, the mean residual value ($\mathrm{U}_{\mathrm{residual}}$) of all primary consumers in the food web was calculated. The trophic position (TP) of each consumer in the food web was estimated by combining the general baseline curve (1) with the mean residual value:

$$\delta^{15}\mathrm{N}_{\mathrm{corrected}} = 6.34/\{(1+\exp[9.67 + (0.356 * \delta^{13}\mathrm{C}_{\mathrm{consumerX}})]\} + \mathrm{U}_{\mathrm{residual}} \quad (3)$$

where $\delta^{15}\mathrm{N}_{corrected}$ is the food-web-corrected baseline δ^{15}N value. Equation (3) produces an appropriate baseline δ^{15}N value for each taxon based on the δ^{13}C signature of the taxon, the general δ^{15}N–δ^{13}C relationship and the food-web-specific deviation ($\mathrm{U}_{\mathrm{residual}}$). Finally, the TP of the species in the food web in a particular sample (consumer X) was estimated as follows:

$$\mathrm{TP}_{\mathrm{consumerX}} = [(\delta^{15}\mathrm{N}_{\mathrm{consumerX}} - \delta^{15}\mathrm{N}_{\mathrm{corrected}})/3.4] + 2 \quad (4)$$

where 3.4 is one trophic level increment (mean enrichment) in δ^{15}N (Vander Zanden & Rasmussen, 1999). For our overall assessment of the trophic position of the different species, we used the average of all samples collected.

In the case of larger amphipods (*G. fossarum*, *P. robustoides*, *D. haemobaphes*), we analysed juveniles (body length < 7 mm) and adults (> 7 mm) separately, as we suspected that small individuals would be less predacious than the larger adults (Limen, van Overdijk & MacIsaac, 2005; Berezina, 2007). For *D. villosus*, only adults were analysed as we did not catch any juveniles of this species during our sampling.

Field study - diet

Based on stable isotope analysis, we used only adult individuals for the gut content analysis. Individuals of *P. robustoides*, *D. haemobaphes* and *G. fossarum* were taken in the spring, summer, autumn and winter of 2005. Samples were collected with a pond net using the kick sampling method (Hynes, 1950) and were preserved in the field in a formaldehyde solution (4%). Specimens were subsequently sorted and identified using the key by Eggers & Martens (2001).

The gammarids were then measured, from the anterior margin of the head to the posterior margin of the telson, using an ocular micrometer On each occasion, 30 adults with a body length of 10 ± 0.5 mm were taken at random from the sample and sexed. The percentage fullness of the digestive tract was determined for each specimen by estimating the length of intestine that was full as a percentage of the total. Individuals with empty digestive tracts were excluded from the analysis. Next, individuals were dissected, and the contents of the stomach only were mounted in lactophenol on microscopic slides for further analysis using light microscopy (Nikon Eclipse 200).

The following food categories were distinguished: (i) detritus; (ii) plant tissue – remains of higher plants; (iii) algae (mainly diatoms); (iv) animal remains, including (a) unidentified material, (b) chironomid larvae, (c) other insects (e.g. heteropterans), (d) oligochaetes and (e) crustaceans (including gammarids).

Subsequently, the quantity of the various food items was established using the subjective volumetric methods developed by Hynes (1950) and Hyslop (1980), in which the share of a particular food item in the gut is estimated by eye. The percentage of individuals with a particular food item frequency ($\%F_i$) and the share of a particular food item in the diet ($\%V_i$) were estimated and used to calculate the following indices: An index of importance (IOI) was calculated for every food category. This index measures the importance of each prey item relative to the others by taking into account both the share of each prey item and the frequency with which each occurs in the diet (Gray, Mulligan & Hannah, 1997). The IOI for food item i was calculated using the Equation:

$$\mathrm{IOI}_i = 100\,x\,\mathrm{HI}_i/\Sigma\mathrm{HI} \qquad (5)$$

where $\mathrm{HI}_i = \%F_i + \%V_i$, $\%F_i$ is the percentage of individuals which have eaten food item i, and $\%V_i$ is the share of food item i in the total volume of the gut content;

Diet width was calculated as a Simpson diversity index:

$$1 - D_\mathrm{s} = 1 - \Sigma[n_i(n_i - 1)]/[(\mathrm{N}(\mathrm{N} - 1)] \qquad (6)$$

where $\mathrm{n_i}$ is the number of individuals consumed of the ith prey species and N is the total number of individuals consumed by each species analysed; the value of this index ranges from 0 to 1, and the higher the value, the wider is the spectrum of the species' diet.

Schoener's index (PSI) was used to estimate differences in the diet between species and was calculated as:

$$\mathrm{PSI} = 1 - 0.5\left[\Sigma(P_{xi} - P_{yi})\right] \qquad (7)$$

where P_{xi} is the share of food category i in the diet of species x, and

P_{yi} is the share of food category i in the diet of species y. The index ranges from 0 (no overlap of diet between species) to 1 (complete overlap of diets), and the overlap is significant when PSI > 0.6 (Schoener, 1970; Wallace, 1981).

Experiment 1 – food preferences

The aim of the first choice experiment was to verify the preference of the three species among living prey (chironomid larvae and *Tubifex* sp.), dead animal tissue (pork and fish) or cyanobacterial material (*Spirulina* sp.). Gammarids were collected in the field and transported in containers to the laboratory, where they were kept at 15 °C under a 12-h light, 12-h dark regime for 1 week to acclimatise. These conditions are appropriate for the three species (*P. robustoides*, *D. haemobaphes* and *G. fossarum*) and induce relatively rapid feeding that could be easily recorded (e.g. Van der Velde *et al.*, 2009). During this period, they were fed decaying plant material collected from the sampling sites, as well as live oligochaetes and commercial fish food. Before the experiment started, the gammarids were starved for 24 h.

A container (50 × 50 × 20 cm) filled with aerated water was prepared. The bottom of the container was divided into 20 equal squares by drawing lines on the bottom (Fig. 1a). One of five possible food items was placed in each square: 15 living oligochaetes (*Tubifex tubifex*), 15 living chironomid larvae, five food pellets consisting of the cyanobacterium *Spirulina* sp. (SERA commercial fish food), pieces of pork (2 cm in diameter) and pieces of roach *Rutilus rutilus* (2 cm in diameter). The food items

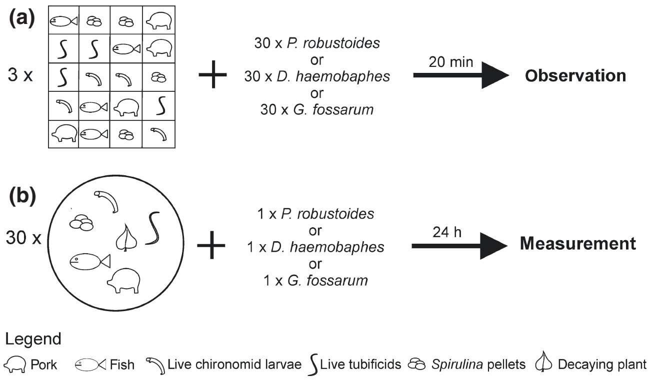

Fig. 1 Design of food preference experiments: (a) Experiment 1 – food preferences; and (b) Experiment 2 – food consumption.

were allocated to positions randomly. Subsequently, 30 adult individuals (each with a body length of 10–12 mm) of one species were placed in the tank and were observed for 20 min, during which time, the number of specimens feeding on each food item was noted. They did not switch to other food items while feeding and remained on the food item they chose during the 20 min, so were easy to count. The experiment was repeated three times for each species, each time using a different distribution of food items but using the same three configurations for all three gammarid species.

Experiment 2 – food consumption

The aim of the second experiment was to estimate the proportion of different food items consumed by individuals of each species in 24 h. This experiment used the same food items as in experiment 1, but decaying plant material was added (collected from a field just before the experiment). Thirty adult individuals (body length 10–12 mm), including both sexes of each gammarid species, were used in this second experiment. Individuals of *P. robustoides*, *D. haemobaphes* and *G. fossarum* collected from the field were transported to the laboratory and allowed to acclimatise for a week to the experimental conditions of temperature (15 °C) and light–dark period (12 h : 12 h). During the period of acclimatisation, they were fed with commercial fish food (SERA) and living chironomid larvae. Before the experiment started, the gammarids were starved for 24 h. After this period, 90 pots (60 mm in diameter, 20 mm water level) were prepared (30 individuals of each species, one individual per pot). To each pot, a known quantity of food was added (mean wet mass given in brackets): four living chironomid larvae (15 mg), four living oligochaetes (*Tubifex tubifex*) (14 mg), a piece of pork (25 mg), a piece of fish (*Rutilus rutilus*) (11 mg), pellets of the cyanobacterium *Spirulina* sp. (SERA commercial fish food) (5.6 mg) and decaying plant material (3.6 mg). One gammarid was then placed in each pot, and after 24 h, the amount of material that had been consumed was estimated by weighting each food item (Fig. 1b).

The data allowed us to estimate frequency ($\%F_i$) – the number of stomachs containing a food item i divided by the total number of non-empty stomachs as well as the volumetric share of a particular food item i in the diet ($\%B_i$), the index of importance of each food item (*IOI*) and Ivlev's electivity index (*I*) according to Ivlev (1961):

$$I = (r_i - p_i)/(r_i + p_i) \tag{8}$$

where r_i is the share of food item i in the diet and p_i is the share of food item i in the environment. The index ranges from −1 (avoidance of food item i) to +1 (high positive electivity), and an index of 0 means neither selection nor avoidance.

Statistics

The trophic positions of the amphipods were compared using the Kruskal–Wallis *H*-test. The sources of differences among the species were identified using the Mann–Whitney *U*-test with *P*-value adjusted for multiple comparisons. The same tests were used for the comparison of the amount of food intake of three gammarids studied in experiment 2, as normal distribution was not assumed for these data.

Differences among the species in terms of the consumption of animal material were assessed using nonparametric tests, the Kruskal–Wallis test (for amounts) and the Pearson chi-square test for independence (for frequencies), as the data did not fit assumptions of homogeneity of variances. The presence of a correlation between the frequency of feeding by the individuals on animal material and the size of the individuals was verified using logistic regression.

The Pearson chi-square test for goodness of fit was used to test whether the frequencies of various items taken by a particular species deviated from a random pattern in experiment 1.

All calculations were performed using the JMP, Version 5.0.1 Software (SAS, 2002) and the Statsoft 8.0 statistical software package (StatSoft, Inc, 2007) with *P* values < 0.05 considered significant.

Results

Field study – stable isotope analysis

Trophic position (TP) differed among the species ($H_{8,91} = 46.332$, $P < 0.001$) (Fig. 2). Adult *P. robustoides* and *D. haemobaphes* took a high and similar trophic position ($U_{44} = 198$, $P < 0.30$), while the native *G. fossarum* was at a lower trophic position ($U_{35} = 25$, $P < 0.001$; $U_{32} = 43$, $P < 0.001$, respectively), similar to juveniles of the two invasive species and *E. ischnus* (*U*-tests, $P > 0.09$ in all cases).

Similar to juveniles of *P. robustoides* and *D. haemobaphes* compared to their respective adults ($U_{32} = 25$, $P < 0.05$ and $U_{32} = 58$, $P < 0.05$, respectively), the juveniles of *G. fossarum* fed at a lower position in the food web than the adults ($U_{42} = 4$, $P < 0.01$), but at a higher position than *C. curvispinum* ($U_{15} = 0.01$, $P < 0.01$) (Fig. 2).

We analysed only one sample of *D. villosus*, which had a TP of 3.696. In the same sample, *D. haemobaphes* and *P. robustoides* had TP values of 3.434 and 3.569, respectively.

Field study – diet

Stomach content analysis demonstrated that all gammarid species were omnivorous. For all species, detritus was the most frequently found food category (83–94%), and its share did not differ between the species (Kruskal–Wallis test $H_{2,314} = 3.027$, $P = 0.220$). However, there were significant differences between the species in terms of the importance of other food items. The frequency of occurrence of all animal remains, including animal tissue, chironomid larvae, oligochaetes and crustaceans, varied significantly between the species (Pearson test $\chi^2_{2,314} = 35.071$, $P < 0.001$). Animal remains were most common in the stomachs of *D. haemobaphes* (Dh) and *P. robustoides* (Pr), with frequencies of 73.1% and 65.6%, respectively, compared to only 32.8% in *G. fossarum* (Gf) (Pearson test $\chi^2_{\text{Dh-Gf}[209]} = 33.64$, $P < 0.001$ and $\chi^2_{\text{Pr-Gf}[222]} = 12.78$, $P < 0.001$). The animal material constituted, on average, 31.3 and 30% of the stomach volume, respectively, in the two Ponto-Caspian species, compared to only 3% in *G. fossarum* ($H_{2,314} = 56.80$, $P < 0.001$), whereas plant tissue was found in 84% of *G. fossarum* individuals. The frequency of animal remains (all categories) in the stomach content of these three species did not depend on sex [Pearson test $\chi^2_{93} = 1.035$, $P = 0.39$ (Dh); $\chi^2_{106} = 0.215$, $P = 0.643$ (Pr) and $\chi^2_{116} = 0.700$, $P = 0.40$ (Gf)] nor on size [logistic regression: $\chi^2_{93} = 3.61$, $P = 0.057$ (Dh); $\chi^2_{106} = 3.20$, $P = 0.073$ (Pr) and $\chi^2_{116} = 0.10$, $P = 0.750$ (Gf)].

The greater fraction of animal material in the stomachs of the two Ponto-Caspian species was confirmed by the IOI (Fig. 3). Although detritus constituted the most important food item for all gammarids, the highest index values for animal material (all prey remains and unidentified material) were found for *P. robustoides* and

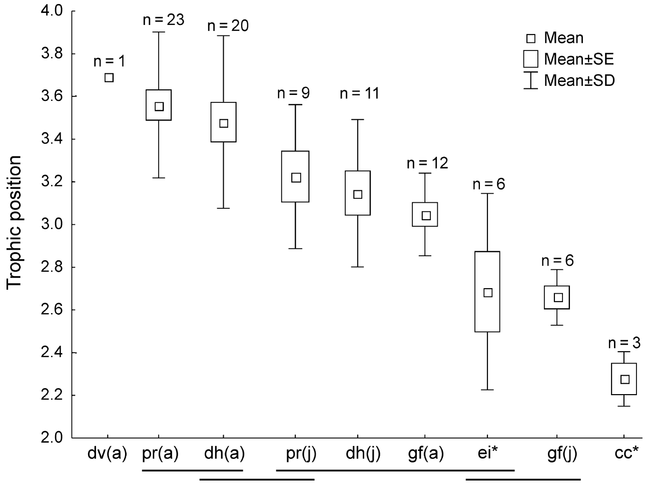

Fig. 2 Trophic position of amphipod species: [dv(a) - *Dikerogammarus villosus*, adults; pr(a) – *Pontogammarus robustoides*, adults; dh(a) – *Dikerogammarus haemobaphes*, adults; pr(j) – *Pontogammarus robustoides*, juveniles; dh(j) – *Dikerogammarus haemobaphes*, juveniles; gf(a) – *Gammarus fossarum*, adults ei – *Echinogammarus ischnus*; gf(j) – *Gammarus fossarum*, juveniles; cc – *Chelicorophium curvispinum*]. Species connected by a line or indicated by * do not differ regarding their trophic position (TP) (*P* > 0.05), n means the number of samples analysed per species.

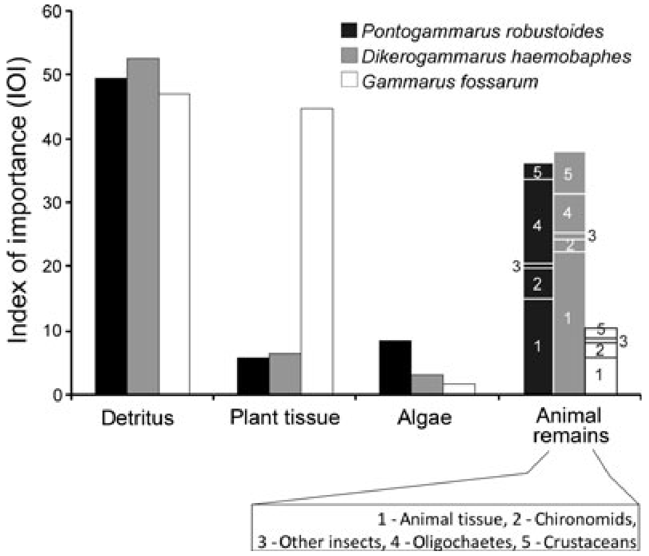

Fig. 3 Importance of specific food items in the diet of *Pontogammarus robustoides*, *Dikerogammmarus haemobaphes* and *Gammarus fossarum*, assessed by gut content analysis.

D. haemobaphes (36.3 and 37.8, respectively). However, the highest index value in *D. haemobaphes* was found for unidentified animal tissue, whereas the analysis for *P. robustoides* showed many remains of oligochaetes. The index showed that plant tissue formed the most important food item in the diet of *G. fossarum* (Fig. 3). This was not because of a lack of potential prey in the environment, as the site where *G. fossarum* was collected harboured larvae of chironomids, mayflies and stoneflies.

All three species had a relatively wide dietary niche, according to Simpson's index. However, the invasive species seemed to be more omnivorous than *G. fossarum*, the index taking values of 0.73 for *P. robustoides* and 0.63 for *D. haemobaphes*, against 0.51 for *G. fossarum*. Schoener's index was used to examine whether there was a potential dietary overlap among these species. Detritus was excluded from the analysis, as it constituted more than 45% of stomach content volume in all three gammarids species. There was a significant dietary overlap between the two Ponto-Caspian species *P. robustoides* and *D. haemobaphes* (Schoener's index: 0.69), whereas both species differed considerably from *G. fossarum* in terms of their diet (Schoener's index was 0.19 for *P. robustoides* and 0.40 for *D. haemobaphes*)

Experiment 1 – food preferences

The two Ponto-Caspian invaders preferred animal prey and tissue as their first food choice, in contrast to the native *G. fossarum* (Fig. 4). *Gammarus fossarum* consumed SERA fish food (*Spirulina* sp., a cyanobacterium) most frequently (Pearson $\chi^2 = 29.5$, $P < 0.001$), while chironomid larvae were eaten most frequently by *P. robustoides* and *D. haemobaphes* (Pearson $\chi^2 = 19.1$, $P < 0.001$).

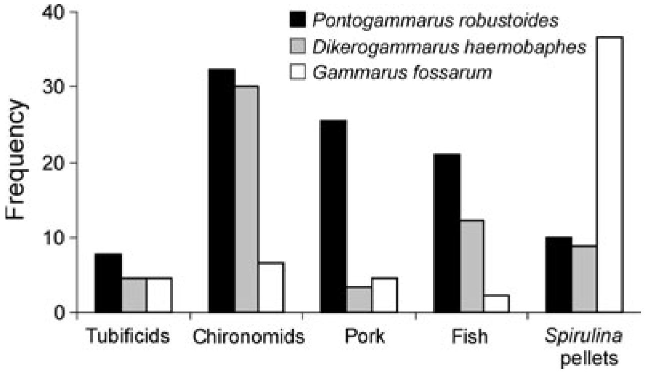

Fig. 4 Feeding frequencies indicating preferences of *Pontogammarus robustoides*, *Dikerogammmarus haemobaphes* and *Gammarus fossarum* for food items offered under laboratory conditions (Experiment 1).

Experiment 2 – food consumption

Under experimental conditions, living prey (oligochaetes and chironomid larvae) were the most important food item in the diet of the Ponto-Caspian species *P. robustoides* and *D. haemobaphes* (Fig. 5a). In the case of *D. haemobaphes*, dead animal tissue (pork and fish) also had a high *IOI*. In contrast to these Ponto-Caspian species, *G. fossarum* preferred decaying plant material, although the second most important food item consumed by this species was living animal prey (Fig. 5a). During the experiment, the

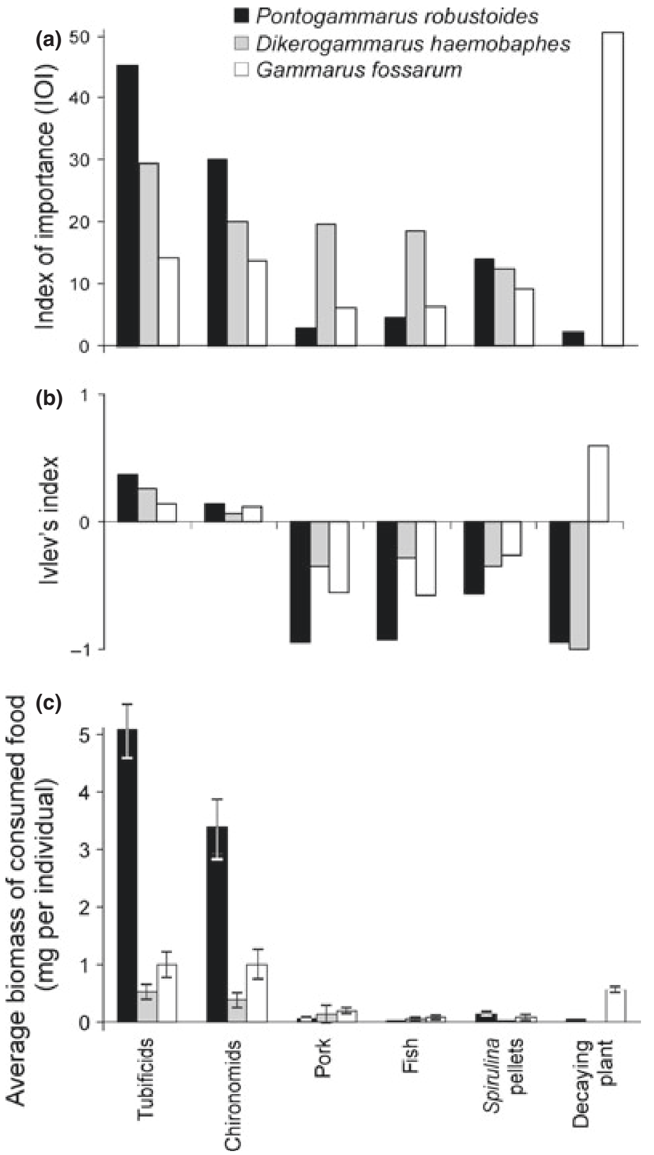

Fig. 5 Food consumption by *Pontogammarus robustoides*, *Dikerogammmarus haemobaphes* and *Gammarus fossarum* under laboratory conditions – experiment 2: (a) index of importance (IOI) of particular food items in the diet; (b) Ivlev's selectivity index; (c) average biomass of item eaten within 24-h period, per individual of each species. Standard error is indicated above each bar.

species fed on all food categories, with the exception of *D. haemobaphes*, which consumed no decaying plant material. The values of Ivlev's index showed that *G. fossarum* preferred decaying plant material, unlike the two Ponto-Caspian species (Fig. 5b).

We estimated the mean biomass of food material consumed by one individual of each species within 24h (Fig. 5c) and found that the three species differed in this respect ($H_{2,90} = 31.89$, $P < 0.001$). The largest amount of food (mean, 8.68 mg) was consumed by *P. robustoides* ($U_{\text{Pr-Gf}[59]} = 13.52$, $P < 0.001$; $U_{\text{Pr-Dh}[60]} = 25.88$, $P < 0.001$), and 96.5% of it consisted of living prey. This species consumed the largest amount of both types of living prey ($U > 7.8$, $P < 0.01$ in all cases). *Gammarus fossarum* consumed an average of 2.83 mg of food, which was about twice as much as *D. haemobaphes*. However, this was a result of the relatively high food intake by only four individuals, which also preyed effectively on the live tubificids and chironomid larvae. Nevertheless, the index of importance clearly showed that the preferred diet of *G. fossarum* was decaying plant material, which constituted 14% of the biomass eaten, as it was the food item consumed most frequently (72% of individuals). *Dikerogammarus haemobaphes* had the lowest feeding rate over 24 h ($U_{\text{Pr-Dh}[60]} = 25.88$, $P < 0.001$; $U_{\text{Gf-Dh}[59]} = 9.76$, $P < 0.005$). This species consumed an average of 1.14 mg of food per individual, 86% of which consisted of living prey (chironomids and oligochaetes) (Fig. 5c).

Discussion

Our findings confirm the functional role of gammarids as omnivores and effective predators, as reported previously (MacNeil, Dick & Elwood, 1997; Kelly, Dick & Montgomery, 2002). We also found that the predatory abilities of the two large-bodied invasive species *P. robustoides* and *D. haemobaphes* were greater than that of *G. fossarum*.

Experiments by Berezina, Golubkov & Gubelit (2005) showed that amphipods raised on an animal diet grew and attained maturity faster than those fed on plants. Animal food delivers much more energy and is digested faster than plant material and also has a 'better' stoichiometry, although the cost of catching prey may reduce this advantage.

We found the adults of *P. robustoides* and *D. haemobaphes* to be much more effective predators than those of *G. fossarum*. Chironomid larvae and oligochaetes were most heavily preyed upon; these animals are relatively easy to catch as they are not very mobile and are buried in the substratum. Although our experiment did not use any type of substratum, these Ponto-Caspian gammarids are known to dig into the substratum, so hidden prey can easily be caught (Zaiko & Olenin, 2004; Platvoet *et al.*, 2009a; Poznanska *et al.*, 2012). Feeding on nutritious (in terms of energy and nutrients) and vulnerable prey results in rapid growth and early maturity, as well as in high fecundity. All of this leads to a rapid population growth by the invasive species, which can result in other taxa being outcompeted for resources, such as shelter against predators (Van Riel *et al.*, 2007; Platvoet *et al.*, 2009a). Hence, if these Ponto-Caspian species coexist with the native *G. fossarum*, the indigenous species may be outcompeted (Bacela & Konopacka, 2005; Bacela *et al.*, 2009). Predatory feeding offers *P. robustoides* and *D. haemobaphes* an additional advantage in terms of colonisation compared to less predatory species such as *G. fossarum*. The two predatory invasive species also generally had a broader food spectrum than *G. fossarum*, which is probably advantageous in colonising a variety of new systems.

Earlier studies had classified gammarids only as shredders in the functional feeding group (FFG) classification system (Cummins & Klug, 1979). *Pontogammarus robustoides* has been regarded as a primary consumer by many authors (Briskina, 1952; Ioffe & Maximova, 1968; Gasiunas, 1972; Kititsyna, 1975; Dedju, 1980), although some studies did report its predatory behaviour (Ioffe & Maximova, 1968; Kititsyna, 1975; Berezina & Panov, 2003; Berezina *et al.*, 2005). Monakov (2003) classified *D. haemobaphes* and *D. villosus* as phyto-detritophages and *P. robustoides* as a zoo-phytophage. Monakov's (2003) classification of *P. robustoides* was based on experiments by Kititsyna (1975), in which the green alga *Cladophora* sp. and the oligochaete *Tubifex* sp. were offered to this species, and a much higher intake and assimilation rate was found for *Tubifex* sp. There are very little literature data on the diet of *D. haemobaphes*. Dedju (1980) regarded it as a detritivore and/or shredder. All the methods used in our study (stable isotope analysis, gut content analysis, diet choice experiments) showed that both Ponto-Caspian gammarids, *P. robustoides* and *D. haemobaphes*, to be much more effective predators than the native *G. fossarum* and that their trophic position is close to that of *D. villosus*. Juveniles of the Ponto-Caspian species were less predatory, and this was also true of *G. fossarum*. Thus, we may conclude that predatory behaviour increases during the ontogeny and the growth of the individual. With respect to predation, the Ponto-Caspian juveniles occupied the same trophic position as adults of *G. fossarum*.

As yet we cannot draw direct conclusions about the impact of *P. robustoides* and *D. haemobaphes* on invaded communities, but both species are known to have established very abundant populations at invaded sites (Bacela

& Konopacka, 2005; Grabowski *et al*., 2007c). Based upon the studies showing the dramatic influence of *D. villosus* on colonised assemblages via predation (e.g. Dick & Platvoet, 2000; Krisp & Maier, 2005; MacNeil & Platvoet, 2005; Van Riel *et al*., 2006; Platvoet *et al*., 2009a; Van der Velde *et al*., 2009; Stoffels *et al*., 2011), as well as by its other biological traits (Grabowski *et al*., 2007a; Pöckl, 2009), we may also expect such strong pressure from the two Ponto-Caspian species used in our study. They occupied a similar trophic position as *D. villosus,* being equally effective predators. Further, they have a similarly high fecundity, each has three to four generations per year and matures fast (summarised in Bacela *et al*., 2009). In addition, they are the equally tolerant to environmental conditions (summarised in Grabowski *et al*., 2007a). These two species, disturbing balance in the invaded communities, could also have an influence on key ecosystem processes, such as leaf decomposition, as has been already demonstrated in the case of the 'killer shrimp' (MacNeil *et al*., 2011; Piscart *et al*., 2011).

Several field studies have showed the ability of *P. robustoides* and *D. haemobaphes* to outnumber the native species in the invaded waterbodies (e.g. Berezina & Panov, 2003; Jazdzewski, Konopacka & Grabowski, 2004; 2005; Grabowski *et al*., 2006; Orlova *et al*., 2006). Moreover, their expansion is still ongoing. *Dikerogammarus haemobaphes* recently spread successfully in the some Alpine Lakes and in the Great Masurian Lakes (own unpublished data), and it has been already introduced to the U.K. *Pontogammarus robustoides* is also colonising the Great Masurian Lakes (Jazdzewska & Jazdzewski, 2008; own unpublished data) and is advancing to Northern Europe (i.e. Kalinkina & Berezina, 2010).

In conclusion, our results show that the two successful invaders are much more effective predators than the native species we investigated. The trophic positions of the other alien species we studied were intermediate. Moreover, *P. robustoides* and *D. haemobaphes* are omnivorous, with a wider diet spectrum than observed in the native species. This may imply optimisation of the feeding depending on the resources available in the ecosystem, with a preference for high-energy food items that, together with other biological features, make the term 'killer shrimp' just as appropriate for these two species as it is for *D. villosus*.

Acknowledgments

We thank the late Anna Kostecka for her assistance with the field work, Marij Orbons for helping to prepare the stable isotope samples and Jelle Eygensteyn for measuring the stable isotopes. We also thank Miroslaw Przybylski for his advice on data analysis. Two anonymous reviewers and the editor Alan G. Hildrew made useful comments and suggestions. The research was supported by the Polish Ministry of Sciences and Higher Education (grant no 2 P04C 090 29) and from internal funds of Radboud University, Nijmegen.

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(Manuscript accepted 10 November 2012)