Density and temperature dependent feeding rates in an established and an alien freshwater gammarid fed on chironomid larvae

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ABSTRACT

We compared feeding rates of the well-established, non-invasive amphipod Gammarus roeselii *with those of the invasive* Dikerogammarus villosus *at different prey densities and different temperatures in laboratory experiments using chironomid larvae as prey. Feeding rates were very variable in both species but higher in the invader species than in the well-established non-invasive species. These results were age independent. At high temperature (18-20 °C) and high prey density (≥1000 prey m⁻²) one large adult* D. villosus *consumed 6-9 prey day⁻¹ on average while one* G. roeselii *consumed 4-7 prey d⁻¹ and one smaller* D. villosus *of a length of 8-10 mm consumed 2-5 prey d⁻¹ while one* G. roeselii *of the same length consumed 3 prey d⁻¹. Predation rate decreased considerably from high (18-20 °C) to low temperature (3±2 °C), from 9 to 4 prey predator⁻¹ d⁻¹ in* D. villosus *and from 7.5 to 2.5 prey predator⁻¹ d⁻¹ in* G. roeselii*. We conclude that both gammarids consumed a biomass in the range of 1/2 to 1/3 to their own biomass and that low predation/feeding rate at low temperature could be a reason why, in some places, indigenous gammarids can re-colonize their former habitats for a short period of time in cold winter and early spring in spite of the presence of the invasive. We further conclude that differences in weight between the species in particular in the experiments with adults can have influenced feeding rates; possibly differences in weight- specific feeding rates are small.*

Key words: consumption rates, carnivory, Dikerogammarus villosus*,* Gammarus roeselii*, prey density, temperature*

1. INTRODUCTION

Formerly, freshwater gammarids were considered as representatives of the functional feeding group of shredders, feeding primarily on fallen leaves and particulate microbia- enriched organic matter (Bärlocher & Kendrick 1973; Haeckel *et al*. 1973; Kostalos & Seymour 1976; Cummins & Klug 1979). More recent investigations of feeding ecology, morphology and biomarkers have shown that freshwater gammarids are omnivorous, feeding on a variety of food (Dick 1996; MacNeil *et al*. 1997; Dick & Platvoet 1996, 2000; Krisp & Maier 2005; Platvoet *et al*. 2006; Maazouzi *et al*. 2007; Mayer *et al*. 2008). Although omnivory seems widespread in freshwater gammarids, differences in preferred food types or feeding modes seem likely. This has already been observed by Ponyi (1956, 1961) who distinguished between "filter feeding" amphipods and "chewing" ones. More recent investigations have shown that several gammarids can be markedly carnivorous (e.g., MacNeil *et al*. 1997).

The Ponto-Caspian amphipod *Dikerogammarus villosus* Sowinsky, 1894 began invading large rivers of Central Europe in the 1990s (Bij de Vaate & Klink 1995; Grabow *et al*. 1998). Meanwhile the species is recorded from various large lakes, e.g., Lake Constance, Germany and lakes in adjacent countries, Lake Leman

and Lake Geneva, Switzerland or Lake Garda, Italy (e.g., Mürle *et al*. 2002; Bollache 2004; Lods-Crozet & Reymond 2006; Casellato *et al*. 2006). Coincidently with the arrival of *D. villosus* a decline of several native macro-invertebrates, including native and established gammarids such as *Gammarus roeselii* Gervais, 1835, was observed (Bollache *et al*. 2004; Kley & Maier 2006; van Riel *et al*. 2006). Laboratory studies suggested that *D. villosus* is markedly carnivorous feeding on a variety of prey types from different taxonomic groups (Dick *et al*. 2002; Krisp & Maier 2005). Isotope analyses even suggested that *D. villosus* could be placed on the same trophic level as some fish species (Marguillier 1998). Although numerous investigations demonstrated that, besides feeding on leaves and detritus, freshwater gammarids are cannibals and predators (e.g., reviewed in MacNeil *et al*. 1997) little is known about the quantity of prey one gammarid can consume per time unit. Krisp & Maier (2005) studied the consumption rate of four gammarid species at high prey density and observed that each individual of these gammarids consumed prey of approximately one third of its own biomass per day.

To shed more light into the feeding rate question, we conducted laboratory experiments about feeding of two gammarid species, the well-established *G. roeselii* and the invasive, alien *D. villosus*, at different prey densities

and different temperatures. We chose chironomid larvae since these belong to the preferred prey organisms of gammarids and since they are consumed entirely (Dick *et al.* 2002; Krisp & Maier 2005). Our expectation was that feeding rate is particularly high in the invasive *D. villosus* since this species is known to exert a high impact on native food webs (van Riel *et al.* 2006). We also expected that the feeding rate of both gammarid species decreases considerably at low temperature. A decrease in feeding rate of *D. villosus* at low temperature could explain that native gammarids, which were displaced by the invasive in many places, can sometimes re-colonize their former habitats for a short time in cold winters and early springs.

2. METHODS

Specimens of *D. villosus* were collected at the shore of Lake Constance near Langenargen (E 9°31'57"; N 47°36'07"), *G. roeselii* was obtained from the Danube near Ulm (E 10°2'; N 48°25'). Upon capture by nets, the individuals were immediately transported to the laboratory, sorted by species and kept at densities similar to that at the collection sites (250-350 ind L^{-1}) in aerated plastic containers ($50 \times 40 \times 40$ cm). Gammarids, which were used in high-temperature experiments, were maintained at 18-20 °C, those used in low temperature experiments were kept at 8-10 and 2-3 °C, respectively. All containers contained aged tap water and were equipped with substrate (gravel and stones with a grain size of 1-3 cm). Dried leaves of alder and living chironomid larvae served as food. Animals which were used in the high-temperature experiments were kept under long-day conditions (approximately 14:10 h light:dark), those which were used in the low-temperature experiments were kept under short-day conditions (approximately 8:16 h light:dark). Chironomid larvae were collected from their natural habitat (generally in the Danube, near Ulm) or bought in aquarium trade, dependent on their availability in the nature. The larvae were kept under the same temperature and light conditions as the gammarids but in smaller plastic boxes ($12 \times 12 \times 6$ cm) at densities that were in the range of densities observed in nature (200-500 ind m^{-2}). Chironomids were collected (or bought) one or two days before they were used in experiments. Only larvae of a body length of 10 (± 2) mm and only those who appeared healthy were used in an experiment.

Experiments were run in boxes of the same size than those, which were used to maintain chironomid larvae. The boxes were provided with stones (grain size: 1-3 cm) and/or filter tubes (length: 1 cm, diameter of holes: 0.5 cm) and filled with tap water to a height of 5 cm. In a first series of experiments, two adult gammarids of *D. villosus* or *G. roeselii* (total length: >12 mm; not size matched) were introduced into a box containing water of 18-20 °C and allowed to acclimatize to experimental conditions for 2 d. After that time, during which the

gammarids were starved, prey organisms were added. Five different prey densities (5, 10, 15, 20 and 25 specimens corresponding to approximately 500, 1000, 1500, 2000 and 2500 ind m^{-2}) were tested. During an exposition time of 24 h, the gammarids were allowed to feed; then they were removed and the remaining chironomids were counted. In a second set of experiments size-matched smaller individuals (total body length: 8-10 mm) of *G. roeselii* and *D. villosus* were used as predators. The experimental design was the same as in the experiments with large adults but feeding rate was tested at three different prey densities (5, 10 and 15 chironomid larvae per box) only. In a third set of experiments feeding rate was tested at low water temperature. Adult specimens (total length: 14-18 mm) of both gammarid species, which had been collected and maintained at low temperature and short day conditions (see above), were allowed to feed on chironomid larvae at two low temperatures (8 and 3 °C ±2°C, respectively). Prey density in the temperature experiments was 2000 m^{-2}. In total 509 experiments (311 with adults, 89 with juveniles and 109 at low temperature) were conducted. In all experiments, gammarids of both sexes were used randomly.

A non-parametric Kruskal-Wallis ANOVA served to test for differences in feeding rate at different prey densities and temperatures. A Wilcoxon test was used to test for differences in feeding rate between species.

3. RESULTS

Feeding rate of adults of both gammarid species was very variable but depended on prey density (Kruskal-Wallis ANOVA; *D. villosus*: H = $75.0_{(4)}$, P <0.0001; *G. roeseli*: H = $18.1_{(4)}$, P <0.0002). Consumption rate of large adult *D. villosus* was significantly higher than consumption rate of adult *G. roeselii* (Wilcoxon: Z = -6.53, P <0.0001). One adult *D. villosus* consumed approximately between 6 and 9 chironomid larvae d^{-1} on average at a prey density $\geq$1000 m^{-2} while one adult *G. roeselii* generally consumed between 4 and 7 larvae on average at a prey density of $\geq$1000 m^{-2} (Fig. 1).

Consumption rate of specimens of a length of 8-10 mm also depended on prey density (Kruskal-Wallis ANOVA: *D. villosus*: H = $17.3_{(2)}$, P <0.0002; *G. roeselii*: H = $20.8_{(2)}$, P <0.0001). Specimens of *D. villosus* also consumed more prey than *G. roeselii* specimens (Wilcoxon: Z = -2.72, P <0.007). Again consumption rate was very variable (Fig. 2). At high density ($\geq$1000 prey m^{-2}), specimens of *D. villosus* consumed 2 and 5 prey d^{-1} on average while *G. roeselii* consumed 3 prey d^{-1}.

Feeding rate strongly depended on temperature in both species (Kruskal-Wallis ANOVA: *D. villosus*: H = $41.7_{(2)}$, P <0.0001; *G. roeselii*: H = $37.7_{(2)}$, P <0.0001). In *D. villosus*, feeding rate decreased from approximately 9 prey $predator^{-1}$ d^{-1} at 18-20 °C to 4 prey $predator^{-1}$ d^{-1} at 3 °C and in *G. roeselii* from 7.5 prey
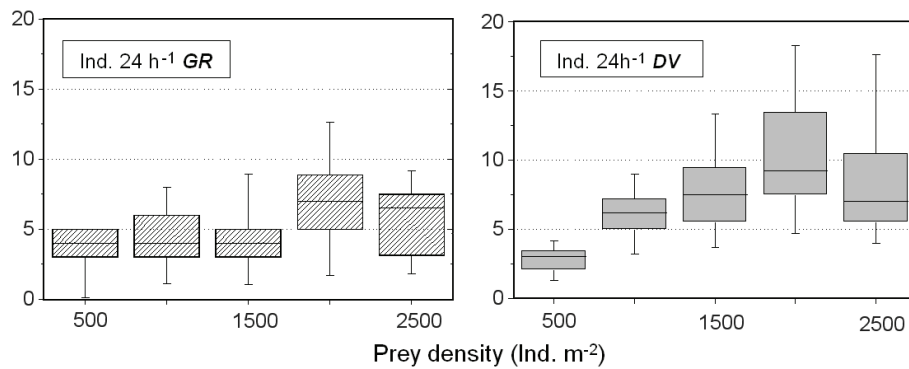
Fig. 1. Consumption rate of adult *Gammarus roeselii* GR and *Dikerogammarus villosus* DV (size >12 mm) at 5 different densities of chironomid larvae.
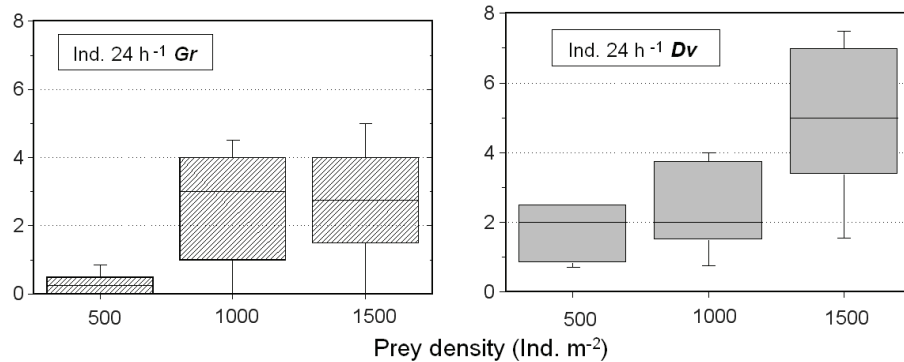

Fig. 2. Consumption rate of size matched 8-10 mm individuals of *Gammarus roeselii* Gr and *Dikerogammarus villosus* Dv at 3 different densities of chironomid larvae.
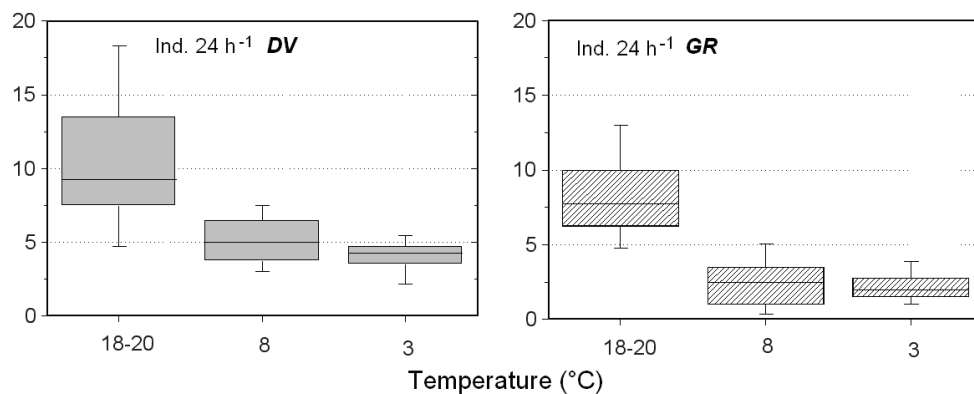

Fig. 3. Consumption of large adult specimens of *Gammarus roeselii* GR and *Dikerogammarus villosus* DV fed chironomid larvae at 3 different temperatures.

predator^{-1} d^{-1} at 18-20 °C to 2 prey predator^{-1} d^{-1} at 3 °C (Fig. 3).

4. DISCUSSION

Our results show that both gammarids consumed considerable amounts of prey at least at high water temperature and prey density, which highlights the findings of many authors during the last decade that gammarids can be markedly carnivorous. That *D. villosus*, which is known for its predatory habit (e.g., Dick & Platvoet 2000; Dick *et al*. 2002; Krisp & Maier 2005; van Riel *et*

al. 2006), consumed slightly more prey than *G. roeselii* was expected. Recent investigation of mouthpart morphology indicated that, although both species have tools for carnivorous feeding, *G. roeselii* is more adapted to feed on plant material and adherent food (Mayer *et al*. 2009). This species has, unlike *D. villosus*, chisel-like cuspidate setae on the endites of its maxillulae and specialized setae on the maxillipeds, which are suited for scraping off adherent algae from plants or the substrate; its mandibular molars have rasp-like structures on the surfaces, which are well suited for grinding firm plant
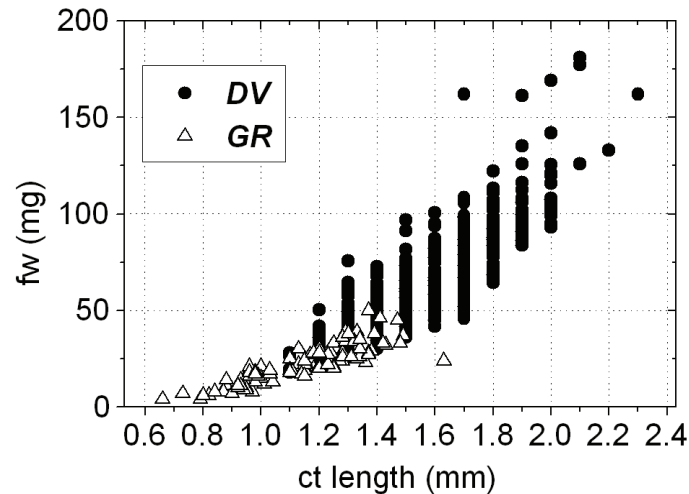
Fig. 4. Length from the anterior margin of the cephalothorax until the posterior margin of the third pleomer (ct) *versus* fresh weight (fw) of randomly selected adult specimens of *Gammarus roeselii* (open symbols) and *Dikerogammarus villosus* (full symbols).

material, whereas those of *D. villosus* are only little structured (Mayer *et al.* 2009). Platvoet *et al.* (2006), who studied *D. villosus* feeding on micro-algae, found intact algae in its foregut, which supports the opinion that the species has no tools for grinding plant material. The specialization to a more herbivorous mode of feeding in *G. roeselii* may explain the somewhat lower feeding rate of this species compared to that of *D. villosus* when only animal prey is present. Moreover, the higher consumption rate in large adult *D. villosus* compared to adult *G. roeselii* may originate from the higher food demand of the former species which per se originates from its greater body mass. Although in our experiments with large adults we tried to use individuals of similar size, *D. villosus* individuals, in overall, were most probably larger on average than individuals of *G. roeselii*. We did not analyse fresh weights of test specimens because handling during the weighing can lead to injuries. Adult specimens of *D. villosus* can have fresh weights of approximately 80 mg in female to 120 mg in male sex (Kley & Maier 2006; Pöckl 2007) or even higher (Kley & Maier 2003), while in *G. roeselii* the fresh weights can rise to only 60 and 90 mg, respectively (Pöckl 1993, 1995). It is, therefore, most probable that differences in weights between large adult specimens of the two species may have influenced feeding rates. Further, we do not know whether the proportion of males, which are more carnivorous than females (Kinzler & Maier 2003), was the same in *G. roeselii* and in *D. villosus* test specimens because we did not distinguish between sexes in our experiments. Gergs & Rothhaupt (2008) studied feeding rate, assimilation efficiencies and growth of *G. roeselii* and *D. villosus* using chironomid larvae, bio-deposited material from zebra mussels and alder leaves as food. These authors found that weight-specific feeding rate of *G. roeselii* on chironomid larvae was higher than weight-specific feeding rate of *D. villosus* on the same prey. Yet, as we in our

study, they did not distinguish between males and females. Differences in feeding rate between sexes should be considered more strongly in future experiments. Another difference between our study and that of Gergs & Rothhaupt (2008) is that we used living chironomid larvae while the latter authors used dead (commercially available frozen) larvae. Possibly usage of dead larvae compared to usage of living larvae may have an effect on consumption rate of both gammarids. Kinzler & Maier (2006) showed that *G. roeselii* is more active than *D. villosus*. High activity in *G. roeselii* may result in high encounter rates with the prey and differences in this effect between species may be greater when using dead, larvae compared to when using conspicuous, moving ones.

The fact that in the experiments with size-matched smaller specimens, *D. villosus* also consumed more prey than *G. roeselii* suggests that feeding rate differences between species were not simply an effect of size but also an effect of the more predacious habit of *D. villosus*. This assumption is supported by earlier investigations, in which *D. villosus* showed a remarkable broad prey spectrum encompassing macro-invertebrates from various taxonomic groups (Dick *et al.* 2002; van Riel *et al.* 2006). *Gammarus roeselii* instead seems to be limited to more soft-bodied invertebrates, such as some dipteran larvae (Krisp & Maier 2005). However, results of weighing of males and females indicated that *D. villosus* specimens are slightly heavier than *G. roeselii* specimens of the same size (Fig. 4). Thus the observed differences in feeding rate between the test species may be lower when referring to a weight basis.

Consumption rates reported here are within the range of consumption rates reported in the literature. Roberts (1995), e.g., reported that *Gammarus duebeni* killed 4-8 mosquito larvae day[-1] under laboratory conditions; Krisp & Maier (2005) showed that *D. villosus* consumed on average 7 chironomid larvae day[-1] while

G. roeselii consumed only three larvae day^{-1} at a prey density of approximately 700 individuals m^{-2}. *Echinogammarus ischnus*, a further non-indigenous species originating from the Ponto-Caspian Region, and the native species *Gammarus pulex* had intermediating consumption rates (Krisp & Maier 2005). That the feeding rate decreased with decreasing temperature was also expected since it is a commonplace in invertebrates. Van der Velde *et al.* (2009) also observed lower consumption rates in three gammarid species in winter compared to consumption rates in the warm season. Low predation rate of *D. villosus* at low temperature may be the reason that native gammarids are sometimes able to re-colonize their former habitat for a short time in the cold season. We occasionally observed small numbers of native gammarids in the River Danube in early spring. These native gammarids, which may have migrated from tributaries during winter were subsequently displaced by *D. villosus* so that no or only few specimens were present in late spring / early summer.

Taking into account the above described weights of gammarids together with the observation that one chironomid larva of 1 cm length has a mean fresh weight of approximately 3.6 mg (Krisp & Maier 2005) and that, at high temperatures and high prey density, one adult gammarid specimen consumed up to 9 (*D. villosus*) and 7.5 (*G. roeselii*) chironomid larvae per day, respectively, one could speculate that one gammarid can consume biomasses per day in the range of 1/2 to 1/3 of its own biomass. Yet, this is a rough estimate, which has to be tested by further investigations. Considering this estimation one should note that gammarids are not simply predators but omnivores feeding on plants, detritus and live and dead animals (e.g., Ponyi 1956, 1961; MacNeil *et al.* 1997; Platvoet *et al.* 2006; Mayer *et al.* 2008). This plasticity in feeding mode, which may vary from species to species (Mayer *et al.* 2009), may be one reason for the success of these animals in freshwaters.

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