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FLEXIBLE OMNIVORY IN *DIKEROGAMMARUS VILLOSUS* (SOWINSKY, 1894) (AMPHIPODA) — AMPHIPOD PILOT SPECIES PROJECT (AMPIS)
REPORT 5

BY

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ABSTRACT

Feeding in *Dikerogammarus villosus* (Sowinsky, 1894) males was observed in the field and recorded on video in the laboratory. The following feeding modes were recognized: detritus feeding, grazing, particle feeding, coprophagy, predation on benthic and free swimming invertebrates, predation on fish eggs and larvae, as well as feeding on byssus threads of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771). The feeding methods are described and illustrated with screenshots of video recordings. The very flexible feeding modes of *D. villosus*, which make diet switches possible, form a trait that must be an important factor in the invasion success of this Ponto-Caspian gammaridean species, and may thus explain for a great deal its high ecosystem impact.

RÉSUMÉ

L'alimentation des mâles de *Dikerogammarus villosus* (Sowinsky, 1894) a été observée dans la nature et enregistrée par vidéo au laboratoire. Les différents modes d'alimentation suivants ont été reconnus: détritivore, broutage, particulaire, coprophage, prédation sur des invertébrés benthiques et nageurs, prédation d'œufs et de larves de poissons, et aussi alimentation sur les amas de la moule rayée *Dreissena polymorpha* (Pallas, 1771).

Les méthodes d'alimentation sont décrites et illustrées avec des photos provenant d'enregistrements vidéos. Le mode d'alimentation très flexible de *D. villosus*, qui permet des changements de

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régime, est un trait qui est peut-être un facteur important dans le succès d'invasion de cette espèce de gammaridé Ponto-Caspien et qui peut expliquer en grande partie son fort impact sur l'écosystème.

INTRODUCTION

Gammaridean amphipods have long been considered purely as shredders of organic material. In a growing number of publications, however, the role of these amphipods in food-webs is put in a different perspective by Gledhill et al. (1993) and Monakov (2003, and literature therein). In Irish river systems, 95% of the macroinvertebrate biomass can consist of *Gammarus p. pulex* (Linnaeus, 1758), an invasive alien species in Ireland (MacNeil et al., 2000). Assuming that the absence of other macroinvertebrates in these rivers is the result of interaction with this species, then a predatory role of this species becomes rational. Intraguild predation has been recognized as a common phenomenon in gammarideans (Dick et al., 1993).

Stable isotope data of *Dikerogammarus villosus* (Sowinsky, 1894) from the river Rhine indicated that this invasive Ponto-Caspian gammaridean clustered with zoobenthivorous fish in contrast to *Gammarus tigrinus* Sexton, 1939, which species occurred on a lower trophic level (Marguillier, 1998; Marguillier et al., 1998; Van der Velde et al., 2000; Van Riel et al., 2006b). The appearance of *D. villosus* in the river Rhine coincided with the decrease of the North American gammaridean, *G. tigrinus* as well as of other macroinvertebrates, in particular on the stones of groynes and river banks (Van der Velde et al., 2000, 2002; Van Riel et al., 2006a, b). In a Rhine-fed lake in the Netherlands, the IJsselmeer, the appearance of *D. villosus* coincided with the total disappearance of the native *G. duebenii* Lilljeborg, 1852 from the stony banks, its only habitat in the lake, whereas *G. tigrinus* disappeared also from these stones but maintained its population in deeper water in the sediment, and in zebra mussel beds (Platvoet, 2007). Predation on a wide range of other invertebrates was first demonstrated by laboratory experiments (Dick et al., 2002), in which *Dikerogammarus villosus* proved to be a formidable predator, preying even on predaceous, hard skinned insects such as water bugs and damselfly larvae. However, in the absence of prey, this species is easily able to switch to particle feeding (Platvoet et al., 2006). Being a food generalist is an important characteristic for an invading species (Van der Velde et al., 2000). To determine how flexible *D. villosus* is with respect to feeding, we studied its feeding-related activities.

We also discuss the position of this species, and of gammaridean species in general, in the classification of species as belonging to various feeding guilds or categories.

MATERIAL AND METHODS

In May 2001, male specimens of *Dikerogammarus villosus* were collected from Lake Gouwzee, a Rhine-fed, slightly brackish lake that is part of the Markermeer/IJsselmeer complex. The specimens were immediately transferred to the laboratory and stored in a large tank with site water at site temperature (16°C).

Four male specimens of *D. villosus* were involved in the observations (body length 21-22 mm). In gammaridean amphipods with a pre-copula stage, males are much larger than females. Therefore, males are far more active food collectors than females.

Recording on video was done with a JVC digital video camcorder GR-DVL100 on mini DV at the highest resolution. Two types of cuvettes were used: the first experiments were performed with two bolted-together plexi-glass plates separated by a plastic hose bent in U-shape, leaving a 9 mm space between the plates with 25 ml of source water, and later a cuvette was developed consisting of a U-shaped plexi-glass plate of 10 by 10 cm of 9 mm thickness lined with two 2 mm thick glass plates of 10 × 10 cm, with 16 ml of source water. Both cuvettes were aerated with a syringe needle connected to a hose and an air pump. Water temperature in the cuvettes was maintained at 19°C during the experiments, the temperature of the climate room.

The males were individually filmed in a total of 20 recording sessions of one hour each. In four one-hour experiments, a mix of several food items was offered to give *D. villosus* a choice. Most invertebrates offered were collected from a small inland water body where *D. villosus* is absent, the Oosterpoel bordering the Gouwzee, with equal salinity and temperature as the lake. Water fleas (*Daphnia* sp.) were obtained from an aquarium shop. A pondweed (*Potamogeton pectinatus* L.) was collected from Lake Gouwzee.

In some experiments, the animals were given an abundant supply of vegetation or invertebrate specimens, in others only a single prey. Generally, potential prey or plants were already present in the cuvette for 15 minutes, before a male *D. villosus* was added. The males of *D. villosus* were not starved before the experiments. Coarse sand and gravel served as a substrate in most recordings. Observations were purely qualitative.

RESULTS

In all experiments a response to the food provided was recorded. It became clear that the abundance of food led to a continuous feeding activity, only interrupted by regular cleaning sessions at intervals of, on average, ten minutes. These cleaning sessions are described below in the particle feeding section.

During detritus feeding, grazing, and some forms of predation the individuals actively browsed the substrate, while during predation of free-swimming animals attacks were made from a steady position, like from an ambush (sit and wait strategy).

We identified the following feeding-related activities:

1. detritus feeding
2. coprophagy
3. grazing
4. particle feeding
5. predation of free-swimming animals
6. predation on benthic animals
7. predation on fish eggs
8. feeding on byssus threads of zebra mussels

1. Detritus feeding

In four experiments, four different males were given a choice of decaying and non-decaying parts (ratio 50/50) of pondweed (*Potamogeton pectinatus*). Only feeding on decaying parts was observed, and the non-decaying parts were ignored. The first contact with the plant material was made by the first antennae carefully touching it. In a quick response, the second antennae pulled the food towards the outstretched first and second gnathopods. With additional support from the antennae, the food was brought in line with the mouthparts. Finally, the incisors of the mandibles cut off parts that were then moved to the molars for grinding. Fluids and particles were directed towards the oesophagus through a combined action of the inner rami of the maxilliped, the first maxillae, and of both rami of the second maxillae. The feathered setae that line these parts assisted in maintaining a directed flow.

2. Coprophagy

The process of re-digestion of faeces in *D. villosus* started with bringing the urosome towards the mouthparts (fig. 1A–D). The third uropods were always in a horizontal position, ventral side up. The faeces were forced from the rectum in a quick action, lasting between two and four seconds, and then received by either the mouthparts directly or by the third uropods, after which the gnathopods led the faeces to the mouthparts. The inside setae of the inner rami of the third uropods are lined with long, feathered setae, forming a network. The mouthparts apparently manipulated the faeces in such a way that digestible and indigestible fractions were separated, resulting in a cloud of rejected material. The whole process took about 30 seconds at 19°C. Coprophagy has been observed at least once in all experiments, in four experiments twice.

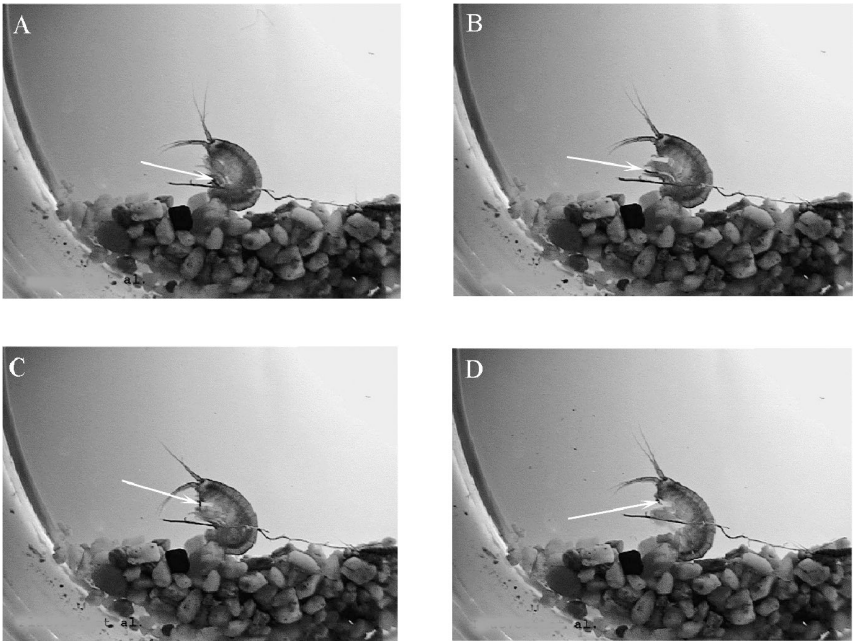


Fig. 1. Coprophagy by *Dikerogammarus villosus* (Sowinsky, 1894): A, the urosome is moved towards the cephalon; B, the faeces are forced from the rectum and received by the third uropods; C, the gnathopods bring the faeces to the mouthparts; D, the mouthparts check the faeces, which are partly taken in and partly rejected (white arrows indicate position of faeces).

3. Grazing

In two experiments, amphipods were found grazing the surface of the gravel. Such gravel may be colonized by bacteria, algae, and protozoans forming a biofilm. These small gravel stones (diameter 2-5 mm) were first lifted from the substrate by the second antennae, taken over by the gnathopods and subsequently manipulated by the mouthparts (fig. 2). To optimize the grazing process, the gravel stone was turned around. Per gravel particle, the grazing action lasted 11 seconds on average (S.D. 6.5 sec.; $n = 18$). On one occasion, the second antennae served as a safety net for a gravel stone that prematurely fell from the gnathopods and was immediately caught and returned to the gnathopods, after which grazing continued.

4. Particle Feeding

Particle feeding, i.e., feeding on suspended organic matter including microscopic organisms, was observed throughout all sessions. In a separate study it was found that specimens of *D. villosus* removed the microscopic unicellular green alga, *Monoraphidium griffithi* (Berkeley) Komárkova-Legnerová offered in containers. Large quantities of these algae were found in the guts of *D. villosus* (cf. Platvoet et al., 2006).

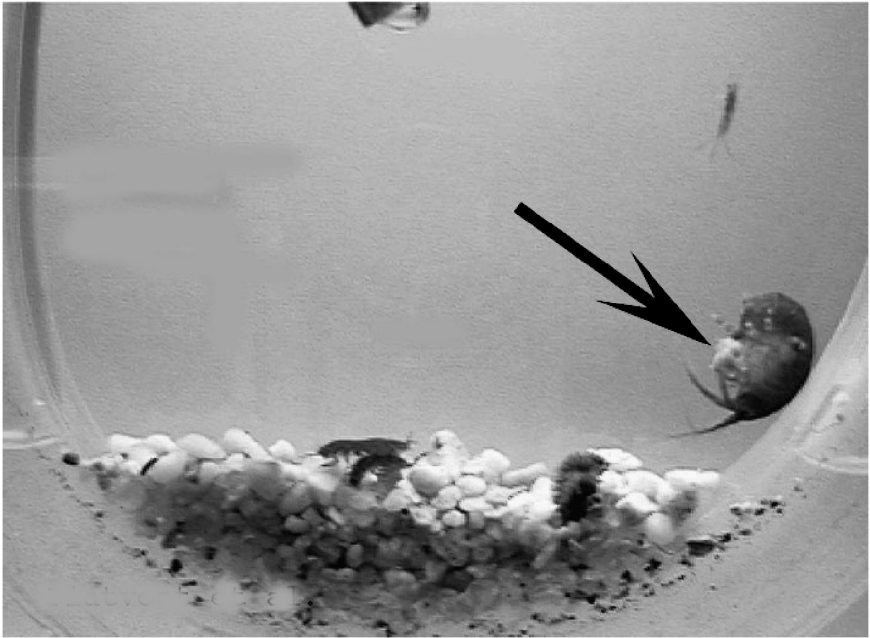


Fig. 2. A gravel particle is turned around by the gnathopods and simultaneously checked for food by the mouthparts of *Dikerogammarus villosus* (Sowinsky, 1894).

The highly setose flagellae of the second antennae (distal whip-like parts) were regularly brought into contact with the mouthparts in a beating action, after which a raised activity of these mouthparts could be observed.

All feeding sessions were followed by a grooming session, where the body and especially the pleopods, the gnathopods, and both pairs of antennae were cleaned of particles by the carpal setation of the gnathopods and by the maxilliped. Also here, the grooming actions were always followed by a raised activity of the mouthparts. The body of *D. villosus* is covered with high numbers of micro-scales (tens of thousands per mm^2). Between these scales micro-algae, bacteria, and other organisms can accumulate. The regularly observed cleaning action by the gnathopods of the body segments, followed by a raised activity of the mouthparts, provided the amphipods with a continuous supply of micro-organisms, probably a welcome addition to their diet.

Predation, general

Several forms of predation were observed: (a) predation on benthic animals; (b) predation on free-swimming organisms; (c) predation on fish eggs; (d) feeding on byssus threads of *Dreissena polymorpha*.

5. Predation on free-swimming animals

Two free-swimming species were found to be preyed on by *D. villosus*: *Sigara* sp. (Insecta, Heteroptera) and *Daphnia* sp., each in two one-hour experiments per species. Both of the two specimens offered of *Sigara*, fast-swimming water bugs, were captured when they were getting too close to the second antennae of *D. villosus*. They were pulled in by the second antennae and eating started instantly. In the first one-hour session a *Sigara* specimen was captured at its posterior end and brought towards the mouthparts of *D. villosus*. A sudden strong rejection of the prey could be observed, possibly the result of a chemical released by *Sigara*. Later the specimen was captured again and partly eaten.

In two experiments (with 20 specimens of *Daphnia* sp. per one-hour experiment), predation on *Daphnia* sp. was recorded. During the first experiment, eleven specimens of *Daphnia* were consumed in the first thirty minutes. After one hour, only three water fleas were left. In the second one-hour experiment, with a different male *D. villosus*, a total of twelve water fleas was eaten within one hour.

The free-swimming water fleas were captured through a high-speed motion of both antennae. In all cases, when the water fleas touched or came too close to the first antennae, an extremely rapid response of the antennae of *D. villosus* was induced. During the video recording with a frame speed of 20 frames/second it took four frames (fig. 3A–D) from the first movement of the second antenna till securing the prey with the gnathopods. Thus, at 19°C this action was taking only a fraction of a second.

After the first contact of one or both of the second antennae the prey was forced into a space between the outreaching gnathopods, a space lined with the long, ornamented setae of the inner ventral edge of the propodal articles of both pairs of gnathopods. These setae form a receptive 'basket' for small prey like water fleas. It was very clear that the dactyls play no role in the initial capturing action. Only after the prey was secured in the 'basket', the subchelae of the gnathopods were used to bring the prey towards the mouthparts.

On twelve occasions, *Daphnia* specimens escaped the first attack, after which a frantic search action of the second antennae followed, in seven cases leading to capture of the prey. During these search movements the second antennae beat in turn, which probably increases the success rate by provoking a strong return flow in the direction of the predator, a flow that may be hard for small animals, like water fleas, to escape from.

6. Predation on benthic animals

In two experiments, each with one male and one female of *Gammarus tigrinus*, the females were preyed on by *D. villosus*. In one of the experiments *D. villosus* was able to pull a female *G. tigrinus* from the substrate in which she had sought

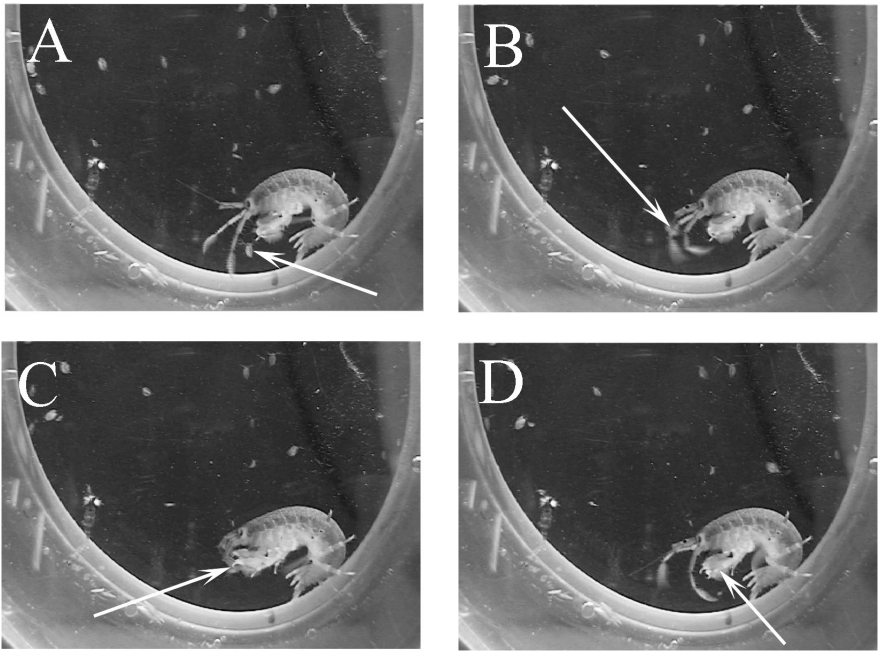


Fig. 3. Preying of *Dikerogammarus villosus* (Sowinsky, 1894) on *Daphnia* sp. A, *Daphnia* sp. detected by *D. villosus*; B, flagella of the second antennae are moved towards the prey; C, second antennae bring prey to the gnathopods; D, prey secured by the gnathopods (white arrows indicate position of *Daphnia* sp.).

shelter. Presumably, she was discovered by *D. villosus* using the first antennae that were inserted in the interstitial spaces of the substrate. After their capture by the second antennae, the two *G. tigrinus* females were immediately consumed by *D. villosus* (fig. 4A–D). Both *G. tigrinus* males were ignored.

In a more or less similar way several specimens of *Tubifex* worms were collected from the substratum and quickly consumed. After each consumed worm, a cleaning session by *D. villosus* took place.

Also larvae of midges, *Chironomus* sp. (bloodworms), were easy prey and were removed from the substrate by the digging action of the second antennae.

In three experiments, each with one specimen of *Asellus aquaticus* (Linnaeus, 1758) (2 males, 1 female, respectively), *D. villosus* rapidly captured the isopods. The second antennae of *D. villosus* pulled these slow moving animals towards the amphipod's outreaching gnathopods. *D. villosus* always started eating that part that was closest to the mouthparts, thus without any selection with respect to the body part at issue. In the last of these experiments, a female isopod was eaten till only one half of the body was left (fig. 5A–D). The head with some anterior somites was released after four minutes, and walked away to live on for another 15 minutes. At the end of all three experiments the specimens were almost completely eaten, and

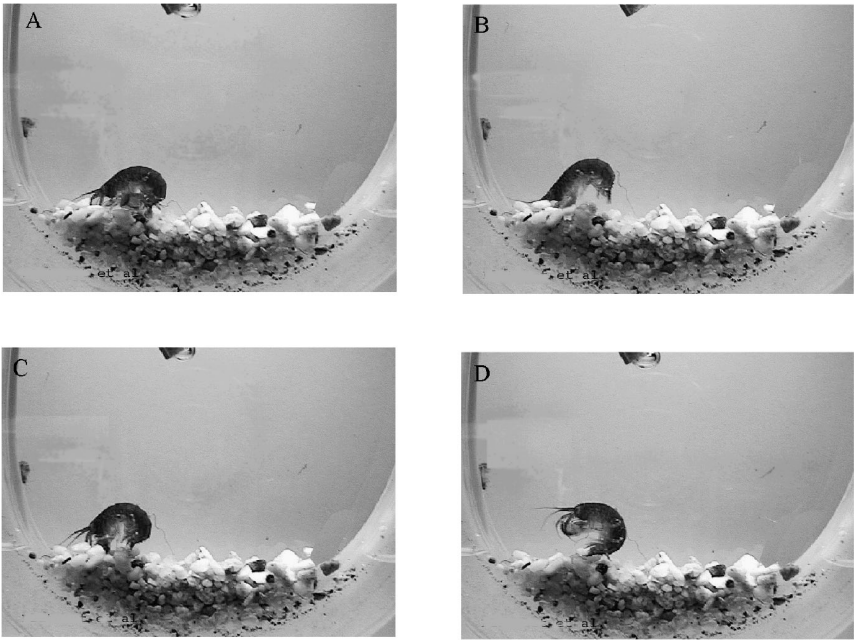


Fig. 4. Predation on *Gammarus tigrinus* Sexton, 1939 by *Dikerogammarus villosus* (Sowinsky, 1894): A, the substrate is checked by the antennae; B, the female *G. tigrinus*, hiding in the substrate, is detected; C, the female *G. tigrinus* is collected by the second antennae from the substrate; D, the female is immediately eaten by *D. villosus*.

only some scattered body parts were found on the substrate. In two experiments, after capturing an isopod, the amphipod took the prey to the corner of the tank, moving backwards to find shelter.

In a separate study (Dick et al., 2002) the species was found preying on zygopterans and ephemeropterans as well (fig. 9).

Two freshly hatched fish larvae of the bullhead (*Cottus perifretum* Freyhof, Kottelat & Nolte, 2005) were immediately attacked and eaten after adding an adult male of *D. villosus* into the cuvette (fig. 8). One fish larva was eaten head-first, the other tail-first.

7. Predation on fish eggs

Field observation. — In the field, predation on eggs of *Cottus perifretum*, a bottom-dwelling fish that deposits yellow clumps of eggs on hard substrate that are guarded by the male, was indirectly observed. After turning a boulder, a clump of eggs was found, covered with a number of male *D. villosus* and twelve empty eggshells.

Laboratory observation. — Four eggs of *Cottus perifretum* were taken to the laboratory and released in a cuvette. It took one minute and twelve seconds before

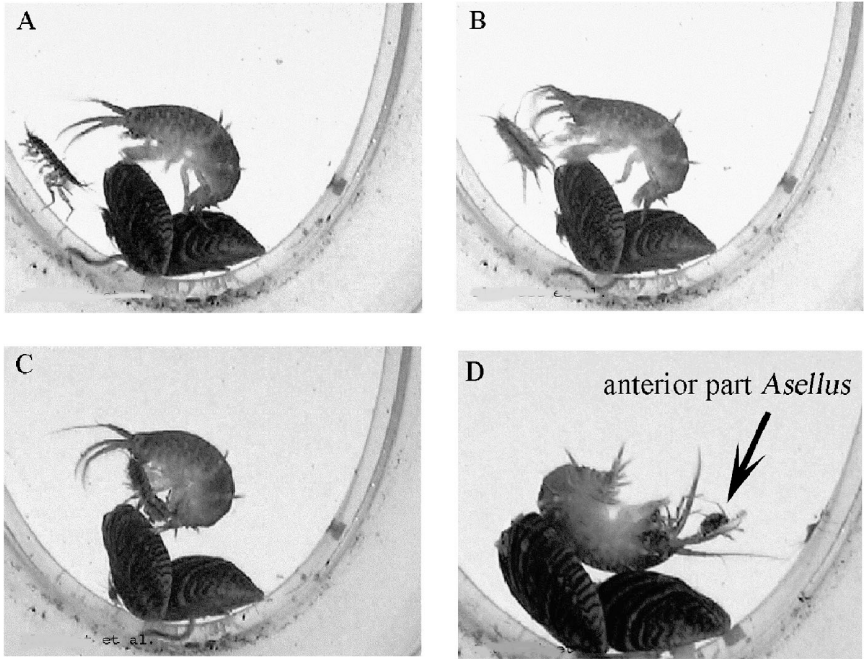


Fig. 5. *Asellus aquaticus* (Linnaeus, 1758) attacked and eaten by *Dikerogammarus villosus* (Sowinsky, 1894). A, *A. aquaticus* detected by *D. villosus*; B, the second antennae of the amphipod pull the isopod towards the gnathopods; C, the amphipod starts eating the isopod; D, the anterior part of the isopod body is released four minutes after capture.

D. villosus detected the eggs, probably by their odour: the first antennae were pointed in the direction of the eggs, and subsequently brought to the mouthparts. A very rapid approach of the eggs followed and eating the eggs started instantly. The eggs were first opened by the incisors of the mandible, after which the content was guided to the oesophagus through a combined action of the mouthparts as described in the detritus feeding section. Within 17 minutes, all four eggs were eaten. The shells were only partly eaten, and shell fractions could be recognized on the substrate at the end of the experiment (fig. 7A–L).

8. Feeding on byssus threads

In one experiment, where two small specimens of *Dreissena polymorpha* (Pallas, 1771) were combined with one male *D. villosus*, it was found that the amphipod started to consume the byssus threads (fig. 6). These byssus threads were very translucent, indicating their recent production. For this experiment, the bivalves were removed from the stock tanks and were in the process of reattachment when the experiment started and *D. villosus* was added.

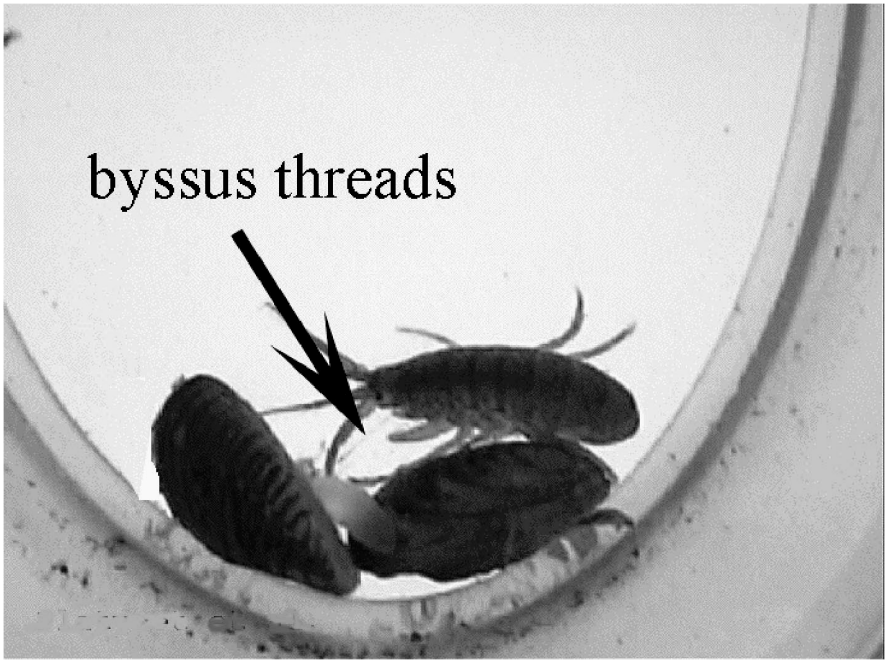


Fig. 6. *Dikerogammarus villosus* (Sowinsky, 1894) feeding on freshly produced, translucent byssus threads of *Dreissena polymorpha* (Pallas, 1771).

DISCUSSION

The laboratory experiments indicate many aspects of feeding in *D. villosus*. All observed feeding methods will be discussed below.

By offering both decaying and living plant material, it became clear that there is a strong preference for decaying material. Detritus feeding is common amongst most freshwater gammarideans, and has labelled the members of this family as pure shredders for a long time. In fact, more and more information is emerging, indicating that detritus feeding is only one of the feeding methods in gammarids.

In all sessions, single or multiple coprophagy events were observed. It may be assumed that recycling of the own faeces is very common in amphipods, and in fact in all animals that have to deal with limited food resources and with food that is hard to digest, e.g., rabbits produce two types of faecal pellets, one of which is produced especially for recycling. The short digestive tract of amphipods is probably not able to break down all ingested food, and recycling is the answer to the potential loss of nutrition. Re-introduction of digestive agents, vitamin K, and bacteria into the anterior gut may also play a role (F. R. Schram, pers. comm.). Coprophagy shows, as no other food-related activity, the efficiency developed in the exploitation of food, and fits perfectly in an opportunistic feeding behaviour.

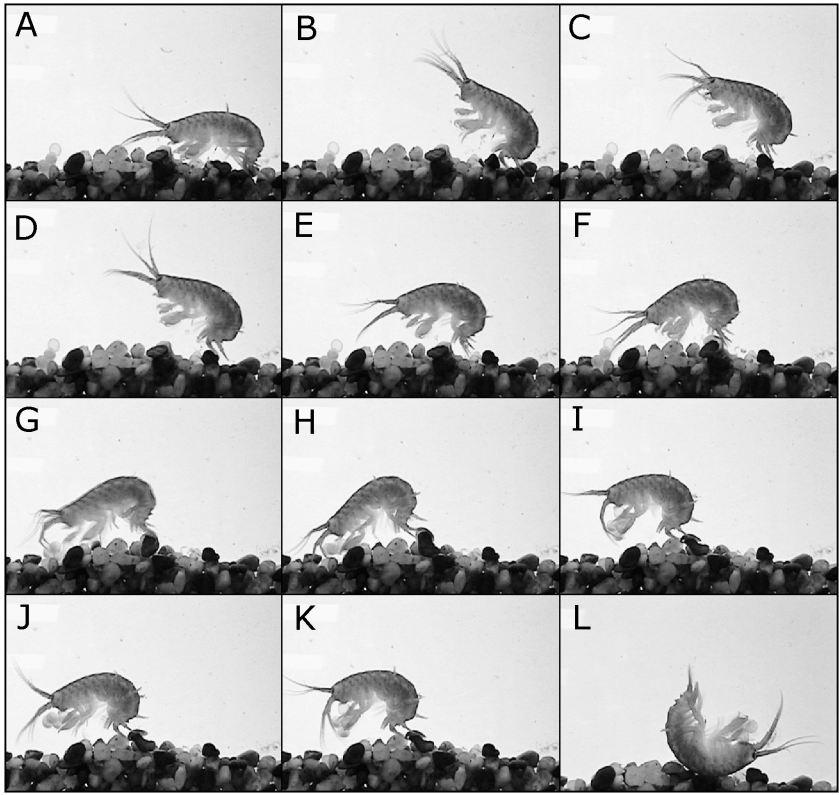


Fig. 7. Male *Dikerogammarus villosus* (Sowinsky, 1894): A–F, detects; G–I, collects; and J–L, eats four eggs of *Cottus perifretum* Freyhof, Kottelat & Nolte, 2005.

Coprophagy is also known for isopods, such as *Asellus aquaticus* (cf. Lammens & Van der Velde, 1978).

Grazing by *D. villosus* has been observed on many occasions and appears a normal part of the species' feeding pattern. Being able to scrape periphyton from the substrate provides the amphipod with a large food stock.

In all sessions, periods of grooming by *D. villosus* followed feeding. This grooming is done by especially designed setae on the carpal articles of the gnathopods that clean the antennae, the pleopods, and the body surface, always followed by increased activity of the mouthparts. This grooming attributes to the nutrition of the amphipods (Platvoet et al., 2006). Ponyi (1961) described filtration feeding for *Dikerogammarus haemobaphes* (Eichwald, 1841), a species living in crevices. In the illustration of this process, active participation of the antennae is suggested. This method probably is common in both *Dikerogammarus* species and, perhaps, many other gammarideans with setose antennae from different families.

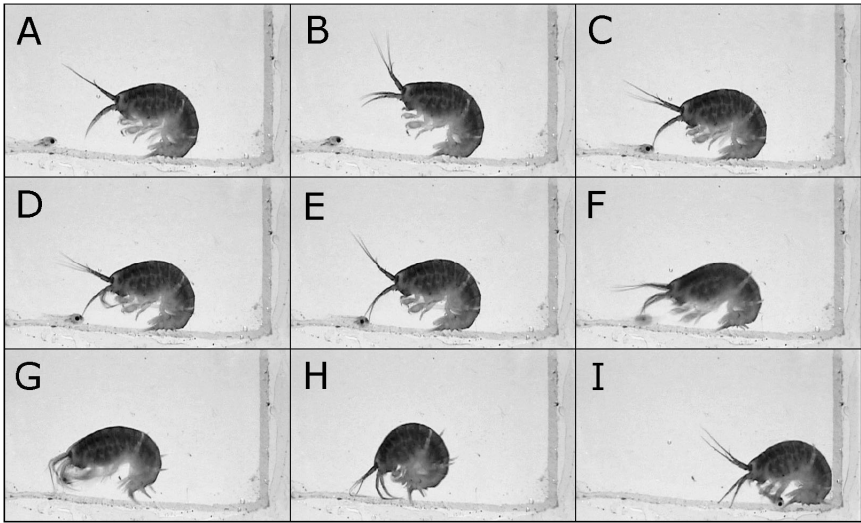


Fig. 8. Male *Dikerogammarus villosus* (Sowinsky, 1894): A–E, detects; F–G, collects; and H–I, eats a juvenile of *Cottus perifretum* Freyhof, Kottelat & Nolte, 2005.

Grazing must affect the position of other settling organisms as well, and may form the steppingstone to predation of domicolous animals, like the amphipod, *Chelicorophium curvispinum* (G. O. Sars, 1895), or tube building Oligochaeta and chironomids. In a study on the foodweb of the River Rhine, it was found that the arrival of *D. villosus* coincided with a strong decline in *Chelicorophium curvispinum* from the surfaces of stones (Van Riel et al., 2006a, b).

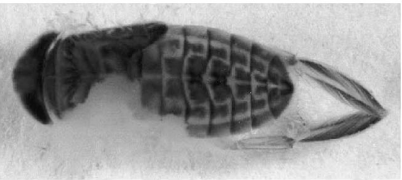
Before the occurrence of *D. villosus* in the Gouwzee in 1996, *Dreissena polymorpha*, the zebra mussel, abundantly covered most of the boulders that form the protection of the shores against wave erosion (D. Platvoet, pers. obs.). In the years following the invasion of *D. villosus*, the number of zebra mussels decreased rapidly, leaving a patchy distribution of these mussels on the rocks. The decline of zebra mussels was generally assumed to be associated with major waterworks that took place during the development of a new suburb of the town of Amsterdam, named IJburg. The raised amount of silt in the water column allegedly would hinder the respiratory systems of the mussels and diminish chances for settlement of their larvae. When observing grazing in *D. villosus*, however, another explanation emerged: post-veliger larvae may be massively preyed on while settling to the substrate after their pelagic dispersal stage. Thus, there may be several factors involved in the decline of the mussels: (a) presence of *D. villosus*, which is abundant in the boulder zone; (b) virtually no other potential prey is present in this zone as a result of the presence of *D. villosus*; (c) the soft shells of the settling mussels form no match for the strong mouthparts of *D. villosus*; and (d) *D. villosus* systematically grazes the surface for the presence of attached



Caenis robusta Eaton, 1884



Asellus aquaticus (L. 1758)



Sigara sp.



Ischnura elegans
(Vander Linden, 1820)

Fig. 9. Several victims of *Dikerogammarus villosus* (Sowinsky, 1894) with bitewounds: *Caenis robusta* Eaton, 1884, *Asellus aquaticus* (L. 1758), *Ischnura elegans* (Vander Linden, 1820), and *Sigara* sp.

organisms. After about one decade of presence of *D. villosus* in the lake, zebra mussels can still be found, but they are not as abundant as before the arrival of the amphipod (D. Platvoet, pers. obs.). The major waterworks were finished in 2001 and no major recovery of the zebra mussel population has occurred in the Gouwzee.

During the experiments, almost all benthic animals offered were attacked and eaten. This may explain the low species diversity in the boulder zone of Lake Gouwzee in the presence of *D. villosus*.

During predation on free-swimming animals, the second antennae are actively involved in food collecting. In contrast to the native gammaridean species, the second antennae are extremely well developed. The relative diameter of the

peduncle and the flagellar segments of the second antennae are much higher than in native species, indicating a strong musculature (Platvoet, 2007). The relative length of these antennae is also greater, giving the animal a much further reach during an attack. The rich setation of the flagellae and the similarity of these setae with Velcro can be considered to be adaptations for a predatory lifestyle.

Cottus perifretum, the bullhead, is a bottom dwelling fish that prefers the same habitat as *D. villosus*. This fish species deposits clumps of yellow eggs in crevices of the substrate. In the laboratory, it was observed that in only a few seconds after adding *D. villosus* in a cuvette with a small cluster of eggs, these eggs were located and immediately eaten. In one field observation a large cluster of eggs of *Cottus perifretum* was found under a boulder, mixed with a number of *D. villosus*. Since some of the outside eggs at one side of the cluster were empty, the amphipods must have been feeding on these eggs, regardless of the presence of a guarding male *Cottus*, and probably out of its view. Casellato et al. (2007) found in laboratory experiments in which *Chironomus* larvae, *Asellus aquaticus*, *Echinogammarus stammeri* (S. Karaman, 1931), and fish eggs of *Coregonus lavaretus* (Linnaeus, 1758) were offered, that *D. villosus* had a clear consumption preference for fish eggs, followed by *Chironomus* larvae. *C. lavaretus* lays many eggs on gravelly bottoms, which are also preferred by *D. villosus*, and *D. villosus* was also observed in abundance at these spawning sites. From these observations it is clear that in this way *D. villosus* forms a threat for several fish species and for the aquaculture of freshwater fish.

The observed consumption of byssal threads of *Dreissena polymorpha* may have consequences for the zebra mussel. On a local scale, the mussel shows a strong mobility (Toomey et al., 2002). Every change of position is followed by the production of a new set of byssus threads, an energy consuming activity. By constant feeding on the freshly produced byssus by *D. villosus*, the mussel may be hindered in its development. Furthermore, settlement of this mussel could be prevented totally by the consumption of its spat by *D. villosus*.

In most highly developed predators, the prey is manipulated into a standard position before eating starts, (a) to kill it quickly to avoid escape or problems during transport (e.g., birds of prey), or (b) to accommodate easy ingestion (e.g., headfirst as in snakes), or (c) to commence feeding on preferred body parts. No manipulation of the kind described above was observed in *D. villosus*. Eating started immediately after capture and at any part of the body that was close to the mouthparts.

On several occasions during the predation experiments it was found that the prey was taken to the corner of the cuvette, where *D. villosus* obviously sought shelter against food competitors or predators. During a habitat simulation experiment, where a grid of holes was offered to several size-classes of *D. villosus*, it was found

that there was a very strong correlation between specimen size and crevice size. As a result of this experiment it became clear that the animals positioned themselves in a way that both provides protection, and accommodates a quick attack action best (D. Platvoet, pers. obs.). Even one of the fingers of the first author was attacked and rejected, after which action the attacker returned to its 'den'. The combination of primitive predatory behaviour (no manipulation of prey) and derived behaviour (attacking from a 'den') makes it hard to determine whether the adaptation to the predatory lifestyle is a (relatively) recent development or not.

Observed morphological adaptation to a predatory lifestyle:

- (a) the very well-developed second antennae play a role in virtually all feeding activities, but especially in predation (see Predation section);
- (b) the setae on the flagellar segments of the second antennae are hooked, probably to increase friction with prey, analogous to Velcro (Platvoet et al., 2006);
- (c) the steep allometric growth of the mouthparts allows the species to prey on intermolt invertebrates (Dick et al., 2002);
- (d) the setae on the especially adapted gnathopods form a dense network that, in combination with the second antennae, facilitates capture of small free-swimming prey;
- (e) the very large body-size of the males (up to 29 mm from tip of rostrum to base of telson) and the very large second gnathopods allow the species to attack large prey (Dick et al., 2002).

As in *Dikerogammarus villosus*, gammaridean amphipods in general may have a much wider range in feeding habits than hitherto presumed, especially when becoming invasive. The large size of invaders (Stokstadt, 2001) in combination with specific allometric growth of body parts and selection can change the position of gammarideans in food webs, and a harmless shredder may (temporarily or permanently) change into a formidable killer due to this 'size-effect'.

A virtually uninterrupted feeding activity of *D. villosus* was found during all experiments. As mentioned in the method section, the amphipods were not starved before the experiments, sustaining the assumption that feeding is an almost continuous process and only limited by food supply and the temperature-dependent metabolism.

In his paper, Monakov (2003) mentions six categories of feeding according to food type: (1) phytophagous, (2) phyto-detritophagous, (3) detritophagous, (4) phyto-zoopagous, (5) zoo-phytophagous, and (6) zoophagous. The feeding methods and food choice found in *Dikerogammarus villosus* demonstrate that this species fits into all of these six categories, depending on the availability of food resources. Therefore, we hypothesize that such a classification is only applicable in stable biotopes, but not in situations where recent invaders form a large portion

of the biomass. In this situation, shifts in the presence and niche occupation of species take place, resulting in alterations of the menu for most of the animals in the ecosystem (MacNeil et al., 2002; Kelly et al., 2002).

The observed feeding-related activities of *Dikerogammarus villosus* in the laboratory are indicative for an opportunistic lifestyle, in which virtually all available food resources contribute to the species' survival. Our observations are coherent with the present field distribution of *D. villosus* in western Europe and reflect the strong interactions of this invader with indigenous and already established alien fauna, found in earlier studies. In dynamic ecosystems with recent invaders, categorizing species according to food choice is not possible, due to (sometimes forced) shifts in menu.

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