Feeding rates, assimilation efficiencies and growth of two amphipod species on biodeposited material from zebra mussels

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SUMMARY

1. Accumulation of organic material by the zebra mussel *Dreissena polymorpha* is assumed to be the source of a biodeposition-based food web. However, only little is known about the importance of the biodeposited material as a food source and its contribution to increased abundances of macroinvertebrates in the presence of *D. polymorpha*.
2. Feeding, assimilation and growth of the amphipods *Gammarus roeselii* and *Dikerogammarus villosus* on food sources directly and indirectly associated with *D. polymorpha* (biodeposited material and chironomids) and on conditioned alder leaves were measured. The stoichiometry of carbon, nitrogen and phosphorus of the diets was measured as an important determining factor of food quality.
3. Chironomids had the highest nitrogen and phosphorus contents, alder leaves were depleted in nitrogen and phosphorus, and the stoichiometry of biodeposited material was intermediate.
4. Both amphipod species had highest feeding rates and assimilation efficiencies on chironomids. *Gammarus roeselii* fed more on biodeposited material than on alder leaves, but assimilation efficiencies were similar; *D. villosus* also had similar feeding rates and assimilation efficiencies on the two diets.
5. Both amphipod species had highest growth rates on chironomids and lowest growth rates on alder leaves. Both grew at intermediate rates on biodeposited material of *D. polymorpha*. The growth rates of the amphipod species were related to food stoichiometry. Overall, the invasive *D. villosus* grew faster than the indigenous *G. roeselii*.
6. Food resources directly and indirectly associated with *D. polymorpha* are potential diets for amphipods, providing further evidence for a *D. polymorpha* biodeposition-based food web.

Keywords: *Dikerogammarus villosus*, feeding strategy, food quality, food web, *Gammarus roeselii*

Introduction

The growth and reproduction of many benthic macroinvertebrates depends on the quality and availability of potential food sources (Willoughby & Sutcliffe, 1976; Fuller, Fry & Roelofs, 1988; Söderström, 1988).

An important determining factor of food quality is the stoichiometry of carbon, nitrogen and phosphorus in the food (Frost *et al.*, 2002). A stoichiometric mismatch between diet and consumer, caused by a low food quality, can lead to lower growth rates of the consumer even under a saturated food quantity (Frost & Elser, 2002). A compensatory feeding response to low-nutrient food is possible but cannot fully compensate food quality-related deficiencies in growth (Fink & von Elert, 2006).

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Allochthonous leaves are an important energy source in many streams, but are a low-quality food because of low phosphorus and nitrogen contents (Kaushik & Hynes, 1971; Anderson & Cummins, 1979; Friberg & Jacobsen, 1994; Cross *et al.*, 2005). Animal matter, in contrast, is a high-quality food source because of high phosphorus and nitrogen contents (Cross *et al.*, 2005; Fink, Peters & von Elert, 2006). Diet quality has often been estimated by assessing feeding rates and assimilation efficiencies (e.g. Bärlocher & Kendrick, 1975; McCullough & Minshall, 1979; Graca *et al.*, 2001). However, these parameters cannot be related directly to growth and the estimation of growth rates is also important (Fuller *et al.*, 1988).

In many freshwater systems in Europe and North America, the littoral habitat and benthic energy flow have been modified by the invasion of the zebra mussel, *Dreissena polymorpha* (Pallas). Following the arrival of zebra mussels, the abundance of many benthic taxa, especially amphipods and chironomids, increases (Stewart & Haynes, 1994; Stewart, Miner & Lowe, 1998; Mörtl & Rothhaupt, 2003). Zebra mussels alter the benthic habitat by increasing surface area and restructuring the substrate in the form of mussel shells. The mussels influenced the benthic community also by biodeposition, the excretion of faeces and pseudofaeces. This causes an accumulation of pelagic resources in the benthos (Stanczykowska *et al.*, 1976; Klerks, Fraleigh & Lawniczak, 1996; Silver Botts, Patterson & Schloesser, 1996; Ricciardi, Whoriskey & Rasmussen, 1997). It is assumed that the availability of this new food resource leads to a biodeposition-based food web (Stewart & Haynes, 1994; Mitchell *et al.*, 1996). The amphipods may benefit from the new resource directly by feeding on the biodeposited matter or indirectly by feeding on associated invertebrates (i.e. those that feed on the matter, such as chironomids). Gammarids are often classified as shredders, but it is usually not possible to classify them into a discrete functional feeding group because their feeding strategy has great plasticity (MacNeil, Dick & Elwood, 1997). Hence, gammarid amphipods are best characterized as omnivores (Bärlocher & Kendrick, 1973; Pöckl, 1992).

Recent laboratory experiments have shown that the biodeposited material of zebra mussels is a food source and affects habitat choice of the native amphipod *Gammarus roeselii* Gervais, whereas the invasive amphipod *Dikerogammarus villosus* (Sowinsky), a predator (Dick & Platvoet, 2000; Dick, Platvoet & Kelly, 2002), is

not attracted by biodeposited material but rather by the associated chironomids (Gergs & Rothhaupt, 2008). Although gammarid amphipods and chironomids can grow on faeces and pseudofaeces of zebra mussels (Izvekova & Lvova-Katchanova, 1972; González & Burkart, 2004), little is known about the quality and utilization of the biodeposited material as food. Since biodeposited matter and chironomids might be important in habitats dominated by zebra mussels, we investigated the feeding, assimilation and growth of *G. roeselii* and *D. villosus* on these resources. We also compared these food sources to allochthonously introduced leaves, which are an important energy source in many aquatic systems (Minshall, 1967; Kaushik & Hynes, 1971; Webster & Benfield, 1986) and a better food source for gammarid amphipods than decaying macrophytes or green algae (Pöckl, 1995).

Methods

Test animals: origin and maintenance

The experiments were conducted with the two dominant amphipod species of Lake Constance, the indigenous *G. roeselii* and the invasive *D. villosus*. The species were obtained from the littoral of Lake Constance and kept separate in a 15 °C climate chamber with a diurnal light rhythm of 12 h : 12 h (day : -night). *Gammarus roeselii* was maintained in tanks filled with water from Lake Constance. *Dikerogammarus villosus* was kept in a flow-through system with water from Lake Constance to minimize their mortality rate. Both were fed on commercially available frozen chironomids. For shelter, a mixture of gravels of different grain sizes was provided. In the experiments, amphipods of both sexes were used randomly.

Food types

Three different food sources were tested: dead animal material (commercially available frozen chironomids), material biodeposited by zebra mussels (*D. polymorpha*) and conditioned alder leaves.

To estimate the quantity of chironomids at the beginning of the feeding experiments, a length–ash-free dry mass correlation was established. The chironomids were measured with a digital sliding calliper (Preisser; Digi-Met, Gammertingen, Germany) to the nearest 0.01 mm, and the ash-free dry mass was

determined by drying the chironomids at 105 °C for 24 h, weighing, combusting at 550 °C for 8 h and weighing again for ash content.

Biodeposited material was collected in the lake using modified sediment traps consisting of a tube of grey PVC (50 cm length; Ø 10 cm) to which a funnel and a 200-mL PET flask were fixed at the lower end to collect the settling sediment. A clamp was used to hold two tiles (4.7 × 4.7 cm) with 15 living mussels (15.01 ± 0.40 mm shell length) each in a vertical position above the upper opening of the sediment trap. The mussels were collected from the littoral of Lake Constance. Five traps were suspended at a depth of 2 m from a pontoon in the pelagic zone of Lake Constance for 7 days. The collected material was centrifuged (1180 g, 6 min), and the supernatant was replaced with enough distilled water to bring the volume to 100 mL. Biodeposited material was stored at 4 °C in darkness. An aliquot was filtered on pre-combusted glass fibre filters (GF/6, Ø 25 mm; Whatman/Schleicher & Schuell, Kent, U.K.), and the ash-free dry mass was determined to estimate the appropriate amount for the experiments.

The alder leaves were conditioned by exposing them for 3 weeks in the littoral of Lake Constance in 200-µm litterbags to exclude macroinvertebrates. From a sub-sample of 16 leaf discs (diameter 1 cm), the ash-free dry mass was determined to estimate the appropriate amount for the experiments.

The organic carbon, nitrogen and phosphorus content of the three food sources were estimated to assess food quality. Aliquots of the biodeposited material were filtered on pre-combusted glass fibre filters (GF/6, Ø 25 mm; Whatman/Schleicher & Schuell). Sub-samples of the conditioned alder leaves and the chironomids were ground. The samples were dried at 55 °C for subsequent analysis of particulate organic carbon and particulate organic nitrogen with an NCS-2500 analyser (Carlo Erba Instruments, Milano, Italy). For determination of particulate phosphorus, aliquots of the biodeposited matter were filtered through acid-rinsed polysulfone membrane filters (0.2 µm pore size, Ø 45 mm; HT-200, Pall, Ann Arbor, MI, U.S.A.). For the conditioned alder leaves and the chironomids, sub-samples as described above were used. The samples were digested with a solution of 10% potassium peroxodisulfate and 1.5% sodium hydroxide at 121 °C for 60 min, and soluble reactive phosphorus was then determined using the

molybdate-ascorbic acid method (Greenberg, Trussel & Clesceri, 1985). Both analyses were replicated five times for each food type.

Feeding rates and assimilation efficiencies

To estimate feeding rates and assimilation efficiencies, single adult test animals (>10 mm body length) were fed a specific amount of a single food source. All food sources were provided in saturated quantity. Chironomid replicates each received seven chironomids (5.2 ± 0.4 mg ash-free dry mass), alder leaf replicates received one leaf disc (4.8 ± 1.0 mg ash-free dry mass) and biodeposition replicates received an aliquot of 4.8 ± 0.1 mg ash-free dry mass.

The weight-specific feeding rate was determined as food ingested per day, being the difference between the ash-free dry mass of offered and remaining food per unit weight (ash-free dry mass) of animal. The assimilation efficiency was calculated as the percentage ratio between assimilated (ingested food – faeces) and ingested food.

The experiments were arranged in containers (10.5 × 10.5 × 3.5 cm) filled with 0.3 L of aerated lake water that had been filtered through a 0.45-µm filter to eliminate potential food for the amphipods. A stone approximately 2 cm in diameter was provided as a shelter. All amphipods used in the experiments were pre-fed on the tested food source for 24 h and pre-starved for another 24 h individually. After 24 h of feeding on the tested food source the remaining food and the faeces were collected separately. Faeces particles were identifiable easily by cylindrical pellets. Subsequent the feeding period, each individual was starved for 24 h to collect faeces. The accumulated faeces produced during the feeding and the post-experimental starving time was pooled for each individual. In every 24-h period described above a new container with new water was provided. For both starving periods, individuals were placed in a PVC cylinder (Ø 6 cm; 8 cm height) with a 1-mm gauze 0.5 cm above the ground, installed in a container filled with lake water. Since amphipods do not empty their gut completely (Bärlocher & Kendrick, 1975), the pre-feeding and pre-starving were integrated into the experiment. We assumed that gut fullness at the start of the experiment equals gut fullness at the end of the starving period when faeces are collected. After 24 h of feeding, the remaining food of each replicate and

the ash-free dry mass were determined. All faeces of each replicate were filtered on pre-combusted glass fibre filters (GF/6, Ø 25 mm; Whatman/Schleicher & Schuell) and their weight determined. All experiments were conducted in April and May 2007. Each diet was replicated 15–16 times, depending on survival of the amphipods. Sixteen additional replicates of each food source without amphipods were installed as controls to estimate the weight decline of food during the experimental period.

Growth experiment

During the growth experiment, all amphipods (juveniles, c. 5 mm body length at the beginning of the experiment) were kept individually in 100-mL wide-necked flasks. Each flask was filled with 90 mL lake water (30-µm filtered, held at 17 °C) with a flow-through of approximately 6 mL min⁻¹. The outflow passed through a 1-mm net to avoid drift of animals. The same food sources as in the feeding experiments were offered *ad libitum*. Additionally, individuals of both species were kept without food as controls. The growth experiment lasted 8 weeks from June to August 2007. All food tests and controls were replicated 10 times for each species. Flasks were cleaned, new food was added and the survival of the amphipods was noted weekly. Body length, the distance between the anterior of the head and the posterior of the final abdominal segment (Baumgärtner & Rothhaupt, 2003), was measured at the beginning of the experiment and then every 2 weeks. Length was determined from photographs taken under a stereomicroscope (Zeiss Stemi 2000-C, Jena, Germany) with an attached fire-wire camera (Imaging Source, Bremen, Germany) connected to a computer. Each amphipod was measured three times using a computer program developed by the electronics facility of the University of Konstanz (G. Heine, pers. comm.). The mean value of the three measurements was used for further analyses.

Statistical analysis

All statistical analyses were made using the statistical package SPSS (version 15.0/2006; SPSS Inc., Chicago, IL, U.S.A.).

Weight-specific feeding rates were calculated as the dry weight of food ingested per animal body mass

and day. To homogenize variances, all values were logarithmically transformed [$\ln(x + 1)$] and checked with the Levene test. Assimilation efficiency was calculated if the feeding rate was >0.05 mg food (mg amphipod)⁻¹ day⁻¹. At lower feeding rates, the systematic error in the determination of faeces and ingested food was a limiting factor. It was not necessary to transform the assimilation efficiency data to homogenize variances; the values were checked directly with the Levene test. Intraspecific differences between the food sources were analysed using a one-way ANOVA with subsequent Scheffe *post hoc* tests for unequal number of replicates. Interspecific differences between *G. roeselii* and *D. villosus* were evaluated using a two-way ANOVA to test for food and species effects. The C : P and the C : N ratios were the factors used to determine food quality. Differences in stoichiometry were analysed using a one-way ANOVA with subsequent Tukey-HSD *post hoc* test.

To analyse time effects on body lengths measured in the growth experiment, two-way ANOVAs with the factors time and food for both amphipod species were conducted. The control treatment without food was excluded from the analyses because of the high mortality of both species. We calculated weekly growth rates [$\text{body length}_{(\text{week } n)} - \text{body length}_{(\text{week } n - 2)}/2$] for each food and species using amphipods that survived until the following measurement. Intraspecific differences in food resources were analysed using a repeated-measures ANOVA with subsequent Scheffe *post hoc* tests for unequal numbers of replicates. Interspecific differences between *G. roeselii* and *D. villosus* were evaluated using a two-way ANOVA to test for food and species effects. For all ANOVAs, all values were logarithmically transformed [$\ln(x + 1)$] and homogeneity of variances was checked with the Levene test. Survival of the amphipods was recorded weekly and analysed using a nonparametric Gehan-Wilcoxon test for estimating survival distribution (Pyke & Thompson, 1986). We tested for intraspecific differences among food tests and interspecific differences within each food test.

Results

Food stoichiometry

The organic carbon, nitrogen and phosphorus stoichiometry (C : N and C : P ratios) of the three food

Fig. 1 Organic carbon, nitrogen and phosphorus stoichiometry of the three tested food sources, as indicated by (a) the C : N ratio and (b) the C : P ratio. Mean values $\pm$ SD are shown. Capital letters indicate homogenous subgroups detected by ANOVA with subsequent Tukey-HSD *post hoc* tests.

sources differed significantly (Fig. 1; ANOVA; $P < 0.001$). Chironomids had the highest nitrogen content, as indicated by a low C : N ratio of approximately 5. The biodeposited material of zebra mussels contained less nitrogen (C : N ratio of 18), and conditioned alder leaves had the lowest nitrogen content (C : N ratio of 22). Chironomids also had the highest phosphorus content (C : P ratio of 120). The biodeposited material of zebra mussels contained less phosphorus (C : P ratio of 320), and conditioned alder leaves were severely depleted in phosphorus (C : P ratio of nearly 1000).

Feeding rates and assimilation efficiencies

The weight-specific feeding rates of *G. roeselii* on the three food sources differed significantly (ANOVA; $P < 0.001$; Table 1). Chironomids resulted in the highest feeding rates; the feeding rates on biodeposited

Table 1 ANOVA results comparing feeding rates, assimilation efficiency and growth rates of the 2 amphipod species, *Gammarus roeselii* and *Dikerogammarus villosus*

Factor	Species	Effect	F	d.f.	P-value
Feeding rate	<i>G. roeselii</i>	Diet	43.8	2	<0.001
	<i>D. villosus</i>	Diet	11.2	2	<0.001
	Both	Species	26.6	1	<0.001
		Diet	51.0	2	<0.001
		Species $\times$ diet	7.4	2	0.001
Assimilation efficiency	<i>G. roeselii</i>	Diet	30.8	2	<0.001
	<i>D. villosus</i>	Diet	10.4	2	<0.001
	Both	Species	0.2	1	0.69
		Diet	32.0	2	<0.001
		Species $\times$ diet	0.1	2	0.87
Growth rate	<i>G. roeselii</i>	Diet	5.0	2	0.03
	<i>D. villosus</i>	Diet	61.2	2	<0.001
	Both	Species	15.2	1	<0.001
		Diet	41.8	2	<0.001
		Species $\times$ diet	8.3	2	0.001

The differences between the three food types, chironomids, material biodeposited by zebra mussels (*D. polymorpha*) and conditioned alder leaves were analysed.

material of *D. polymorpha* were intermediate and lowest on conditioned alder (Fig. 2a). The feeding rate of *D. villosus* was also highest on chironomids, and the rates on the other two food sources were lower, respectively (ANOVA; $P < 0.001$). The interspecific comparison showed significant differences between the feeding rates of the amphipod species (ANOVA; $P < 0.001$; Table 1) and significant species $\times$ diet interactions (ANOVA; $P = 0.001$). The weight-specific feeding rate of *G. roeselii* on chironomids was two-fold higher than that of *D. villosus* and three-fold higher on biodeposited material. The feeding rates of the two amphipod species on conditioned alder leaves did not differ.

The assimilation efficiencies of the two amphipod species did not differ (ANOVA; $P = 0.69$; Table 1) and no significant species $\times$ diet interactions (ANOVA; $P = 0.87$) were found. However, assimilation efficiencies on the food sources differed for *G. roeselii* and *D. villosus* (ANOVA; both species: $P < 0.001$). Assimilation efficiency was highest with chironomids as the food source (c. 70%) and lowest on biodeposited material of *D. polymorpha* and conditioned alder leaves (c. 40% each; Fig. 2b).

Growth experiment

Both species increased in body length during the 8-week experiment on all food sources (Fig. 3; ANOVA;

Fig. 2 (a) Feeding rate, (b) assimilation efficiency and (c) growth rate of the amphipod species *Gammarus roeselii* and *Dikerogammarus villosus* on three different food sources: chironomids, biodeposited material of zebra mussels, and conditioned alder leaves. Mean values $\pm$ SD are shown. In (a) and (c), upper case letters indicate homogenous subgroups for *G. roeselii* and lower case letters indicate homogenous subgroups for *D. villosus*, as detected by the ANOVA with subsequent Scheffe *post hoc* tests for unequal number of replicates. In (b), no significant differences were found between species and the upper case letters indicate homogenous subgroups for both species.

both species: $P < 0.001$; Table 2). Growth differed on the different food source (ANOVA; both species: $P < 0.001$) and significant diet $\times$ time interactions were found (ANOVA; both species: $P < 0.001$). The body length of *G. roeselii* and *D. villosus* increased the

Fig. 3 Body length (mean $\pm$ SD) of (a) *Gammarus roeselii* and (b) *Dikerogammarus villosus* fed chironomids, biodeposited material of zebra mussels, and conditioned alder leaves for 8 weeks and in the control without food.

Table 2 ANOVA results comparing increase in mean body length of the 2 amphipod species, *Gammarus roeselii* and *Dikerogammarus villosus* for the duration of the growth experiment of 8 weeks

Species	Effect	F	d.f.	P-value
<i>G. roeselii</i>	Time	29.8	4	<0.001
	Diet	23.9	2	<0.001
	Diet $\times$ time	14.1	8	<0.001
<i>D. villosus</i>	Time	17.2	4	<0.001
	Diet	62.1	2	<0.001
	Diet $\times$ time	30.0	8	<0.001

Differences depending on time and the three food source chironomids, material biodeposited by zebra mussels (*D. polymorpha*) and conditioned alder leaves were analysed.

most when fed chironomids, followed by biodeposited material of *D. polymorpha*. The increase in body length was lowest when both species fed conditioned alder leaves.

Growth rates of both amphipod species on the different food sources differed significantly (Fig. 2c; repeated-measures ANOVA; *G. roeselii*: $P = 0.03$; *D. villosus*: $P < 0.001$; Table 1). The growth rate of *G. roeselii* fed chironomids twice as high as *G. roeselii* fed conditioned alder leaves; growth of *G. roeselii* fed

biodeposited material was intermediate. The growth rate of *D. villosus* fed chironomids was twice and triply higher than *D. villosus* fed biodeposited material and conditioned alder leaves respectively. The growth of the two species differed (ANOVA; $P < 0.001$), and there were significant species $\times$ diet interactions (ANOVA; $P = 0.001$). *Dikerogammarus villosus* fed chironomids and biodeposited material had higher growth than *G. roeselii* fed on the same diets respectively. The growth rates of the two species fed conditioned alder leaves did not differ.

The survival of the two species on the different food sources also differed (*G. roeselii*: Wilcoxon–Gehan statistic = 42.19, $P < 0.001$; *D. villosus*: Wilcoxon–Gehan statistic = 121.88, $P < 0.001$). In the controls lacking food, survival of both species was significantly lower than when food was available (Fig. 4). Survival of both *G. roeselii* and *D. villosus* was highest when fed conditioned alder leaves. Survival of *G. roeselii* fed chironomids and biodeposited material was lower. For *D. villosus* the same order in survival as described for *G. roeselii* occurred among the three diets. Survival of the two species in the controls lacking food did not differ (Wilcoxon–Gehan statistic = 0.02, $P = 0.897$).

Fig. 4 Survival of (a) *Gammarus roeselii* and (b) *Dikerogammarus villosus* fed chironomids, biodeposited material of zebra mussels, and conditioned alder leaves for 8 weeks and in the control without food.

The survival of *D. villosus* on all three food sources was higher than that of *G. roeselii* (chironomids: Wilcoxon–Gehan statistic = 9.31, $P = 0.002$; biodeposited material: Wilcoxon–Gehan statistic = 21.01, $P < 0.001$; conditioned alder leaves: Wilcoxon–Gehan statistic = 6.32, $P = 0.012$).

Discussion

The growth and feeding of the amphipod species *G. roeselii* and *D. villosus* differed on the three food sources offered in our experiments. In general, however, both amphipod species responded according to the nutritional gradient proposed by Anderson & Cummins (1979), with animal material as a high-quality food and leaf litter as a low-quality food. The animal material food source, chironomids, led to the highest feeding rates and assimilation efficiencies of both amphipod species, resulting in high growth rates. The high nitrogen and phosphorus contents of the chironomids food source also indicate its high food quality. Similar C : N and C : P ratios have been found for *G. roeselii* in Lake Constance (Fink *et al.*, 2006). The leaf litter food source, conditioned alder leaves, had the lowest food quality, and the quality of biodeposited material of zebra mussels as a food source was intermediate between that of the animal material and the leaf litter.

Gammarus roeselii fed at a higher rate on higher quality food sources, which resulted in faster growth. *Gammarus roeselii* had higher feeding rates than *D. villosus* on chironomids and biodeposited material at similar assimilation efficiencies. This implies a higher assimilated food biomass per animal biomass for *G. roeselii*. However, the growth rate of *D. villosus* was higher, which indicated that energy allocation differed between the two amphipod species. Since the native amphipod *G. roeselii* has a higher activity than the invasive *D. villosus* (Kinzler & Maier, 2006), *G. roeselii* probably requires a larger proportion of available energy for motility, whereas *D. villosus* possibly allocates more energy to somatic growth. The growth rate of *D. villosus* fed chironomids in our experiments corresponds well with the calculated field growth rates in spring and summer of Piscart *et al.* (2003). Compared to indigenous amphipod species, the invader *D. villosus* has rapid growth, a bigger brood size, earlier sexual maturity and a shorter egg development time (Piscart *et al.*, 2003; Pöckl, 2007).

These ecological traits are important for successful invasion (Ricciardi & Rasmussen, 1998; Kolar & Lodge, 2001).

The preference of gammarid amphipods for various leaf litters and the role of aquatic fungi on leaves have been well investigated (e.g. Bärlocher & Kendrick, 1973), but the predatory impact of gammarids has often been neglected until recently (Kelly, Dick & Montgomery, 2002). In contrast to *G. roeselii*, the invader *D. villosus* is clearly a predator (Dick & Platvoet, 2000; Dick *et al.*, 2002), which may also explain its high growth rate on chironomids in our experiments. Although the feeding rates and assimilation efficiencies of *D. villosus* on biodeposited material of zebra mussels and conditioned alder leaves did not differ, the amphipods grew better on the biodeposited material. The higher growth rate on this food source may be attributed to the higher phosphorus content, which can enhance growth under limiting conditions (Frost & Elser, 2002; Frost, Cross & Benstead, 2005).

Food constituents can be assimilated with different efficiencies, and consumers limited by nutrients (N or P) have been shown to assimilate the limiting element with a higher efficiency than carbon (Rothhaupt, 1995; Sterner & Elser, 2002). Gross growth efficiencies and hence assimilation efficiencies can be close to 100% for elements that are deficient in the food (Sterner & Elser, 2002). In our experiments, the C : P ratio of biodeposited material was 320 : 1, whereas that of alder leaves was about 1000 : 1. If we assume that the assimilation efficiencies that we determined for both food types (c. 40%) reflect the assimilation of carbon and that the deficient element phosphorus was assimilated with a high efficiency of 90%, the resulting assimilated C : P ratios would be 140 : 1 for the biodeposited material and 440 : 1 for the alder leaves. A C : P ratio of 140 : 1 is close to the body stoichiometry of *Gammarus* (Fink *et al.*, 2006).

In the control lacking food, the survival of both amphipod species was lowest; only a few individuals survived after 3 weeks. The flow through of lake water in the flasks did not contain enough food for growth or survival of the amphipods. Hence, all growth effects observed in our experiments can be attributed to the offered food sources.

Both amphipod species had the highest survival and the lowest growth rate on conditioned alder leaves. This apparent paradox can be explained as

follows. Individual growth of crustaceans requires moulting, and animals may be less resistant to toxicants in the post-moult stage, caused by high metabolic stress and the not yet hardened exoskeleton (Carlisle & Knowles, 1959). The intermoult interval increases with decreasing growth rates caused by lower food quality (Willoughby & Sutcliffe, 1976; Pöckl, 1995). Therefore, at lower growth rates, fewer individuals are in the vulnerable moulting phase, and survival should increase, as we observed.

Our results indicate that biodeposited material of the zebra mussel *D. polymorpha* is a potential intermediate-quality food source for both *G. roeselii* and *D. villosus*. In line with this result, González & Burkart (2004) found that mussel faeces and pseudofaeces were a valuable food source for *Gammarus fasciatus* Say. These findings support the assumption of a biodeposition-based food web originating from food sources provided by the zebra mussel (Stewart & Haynes, 1994; Mitchell *et al.*, 1996). Furthermore, chironomids feed well on this food source (Izvekova & Lvova-Katchanova, 1972). Hence, predators such as *D. villosus* can benefit indirectly from the biodeposition of the zebra mussel by predation on macroinvertebrates. Thus, the increase in abundance of many benthic taxa after the invasion of *D. polymorpha* might to some extent be an effect of increased food availability. However, the significance the accumulation of organic matter by zebra mussels under natural conditions remains unknown although stable isotope analyses have indicated that this food source constitutes a part of the diet of the amphipod *G. fasciatus* (Limén, van Overdijk & MacIsaac, 2005). Our results on the feeding and growth of the two amphipods *G. roeselii* and *D. villosus* on resources associated with zebra mussels provide further evidence for the importance of zebra mussel biodeposited material under natural conditions.

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