Effects of zebra mussels on a native amphipod and the invasive *Dikerogammarus villosus*: the influence of biodeposition and structural complexity

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Abstract. In the last decades, zebra mussels (*Dreissena polymorpha*) have invaded many freshwater systems with severe consequences for entire communities. Most benthic macroinvertebrates, especially amphipods and chironomids, increase in abundance in the presence of zebra mussels. Increased structural complexity and an unknown biotic factor lead to this effect. *Dreissena*-associated factors that might influence populations of the native *Gammarus roeselii* and the invader *Dikerogammarus villosus* in Lake Constance, Central Europe, were investigated in laboratory experiments. These factors were: 1) increased structural complexity related to mussel shells, 2) *Dreissena* biodeposition, 3) chironomids, the presence of which is increased by biodeposited matter, and 4) *Dreissena* kairomones. In habitat-choice experiments, the native and omnivorous amphipod *G. roeselii* showed a preference for mussel shells with biodeposited material and for mussel shells with biodeposited material with chironomids, whereas the invasive and predatory amphipod *D. villosus* showed a preference only for mussel shells with biodeposited material with chironomids. In a kairomone y-maze experiment, both amphipods avoided zebra-mussel-conditioned lake water. These results indicate that habitat complexity and food availability, mediated directly or indirectly through biodeposited material, are the factors by which amphipod abundances are increased in the presence of *Dreissena*. Thus, biodeposited material can form an important new food resource, translocated from the pelagic zone to the benthos by zebra mussel filtration, and this biodeposited material might support a new detritus-based food web in the benthos.

Key words: biodeposition, zebra mussel, food web, *Gammarus roeselii*, *Dikerogammarus villosus*, habitat-choice, kairomone, preference.

Zebra mussel invasions in Europe and North America have led to many changes in planktonic and benthic communities in invaded habitats (Stanczykowska et al. 1976, Griffiths 1993, Roditi et al. 1997, Mörtl and Rothhaupt 2003). Filtration by mussels reduces the overall concentration of phytoplankton (e.g., Holland 1993, Nicholls and Hopkins 1993) and alters the makeup of the phytoplankton community. The reduction in phytoplankton leads to higher light levels, which in turn, lead to the proliferation of submersed macrophytes (Skubinna et al. 1995).

Abundances of many benthic taxa, especially amphipods and chironomids, increase in response to zebra mussel invasion (Stewart and Haynes 1994, Mörtl and Rothhaupt 2003). Zebra mussels alter the benthic habitat by increasing the surface area and restructuring the substrate in the form of mussel shells.

The mussels also appear to influence the benthic community by biodeposition, causing an accumulation of pelagic resources in the benthos (Stewart and Haynes 1994, Silver Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998). Zebra mussel density is controlled through predation by diving ducks in some habitats: a reduction of >90% of the zebra mussel density has been observed in Lake Constance during winter (Cleven and Frenzel 1993, Werner et al. 2005). Control of zebra mussel density by waterfowl increases seasonal variation of the habitat structure and the amount, and therefore, the importance of biodeposited matter.

The omnivorous amphipod *Gammarus roeselii* (Bärlocher and Kendrick 1973, Pöckl 1992, 1993, Friberg and Jacobsen 1994) was the dominant species in the littoral zone of Lake Constance (Mörtl 2003) before the Ponto Caspian amphipod *Dikerogammarus villosus* invaded the lake in 2002 (Mürle et al. 2004). Presence

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of the predatory *D. villosus* has been correlated with decreases in abundances of other benthic species in other invaded ecosystems (Dick and Platvoet 2000, Dick et al. 2002). Thus, post-*D. villosus*-invasion decreases in abundances of many benthic species are expected in Lake Constance.

Biodeposition by zebra mussels could lead to the development of a biodeposit-based food web (Stewart and Haynes 1994, Mitchell et al. 1996). Macroinvertebrates can benefit from this resource directly by feeding on biodeposited material or indirectly by predation on other macroinvertebrates. Detritivorous chironomids, the abundances of which increase after zebra mussel invasions (Stewart and Haynes 1994, Mörtl and Rothhaupt 2003), might be a link to higher trophic levels. Zebra mussels also might influence the benthic community through kairomones, which might cause an increase in abundance of the olfactory-sensitive amphipods (Wudkevich et al. 1997, Baumgärtner et al. 2002). A kairomone-based response would result in redistribution of amphipods in the habitat rather than an increase in total amphipod abundance.

We hypothesized that either the availability of additional food from biodeposition or zebra mussel kairomones are responsible for the increase in amphipod abundance near living zebra mussels. We tested these hypotheses by investigating the importance of biodeposited material, living chironomids, and kairomones produced by zebra mussels on the behavioral response of 2 amphipod species, the native and omnivorous *G. roeselii* and the invasive and predatory *D. villosus*. These results could help to elucidate the importance of zebra mussel biodeposition for the benthic food web of lake littoral zones (Walz 1978).

Methods

Origin and maintenance of the animals

The amphipod species *G. roeselii* and *D. villosus*, living zebra mussels, and mussel shells were obtained from the littoral zone of the prealpine and oligotrophic Lake Constance (Central Europe, on the border of Germany, Switzerland, and Austria). Water levels fluctuate annually within 2 m, depending largely on the unregulated alpine system of the Rhine River. The main basin of Lake Constance has a mean depth of 100 m and covers 473 km² (IGKB 2004).

In the laboratory, the 2 amphipod species and the zebra mussels were kept separately in a 15°C climate chamber with a diurnal light rhythm of 12 h:12 h (day:night). Habitat-choice and y-maze experiments also were conducted in this climate chamber. Zebra mussels and *G. roeselii* were 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. Gravels of different grain sizes were provided for shelter for amphipods. Both amphipod species were fed commercially available frozen chironomids. In all experiments, only adult amphipods (0.7–1.7-mm length) of both sexes were used. Different amphipods were used in each replicate in both experiments.

Habitat-choice experiment

The attractiveness of food sources provided directly or indirectly by zebra mussels was examined in a 2-chamber habitat-choice arena (Fig. 1). Each 9- × 9- × 7-cm chamber was constructed of gray polyvinyl chloride (PVC), and chambers were separated by a removable dividing wall (3.5 × 7 cm). Each chamber featured a notch to hold an unglazed 4.7- × 4.7-cm tile. The reference habitat for all tests was a tile with 15 mussel shells attached to the tile with superglue (UHU plus 2-components epoxy resin glue; UHU, Bühl, Germany).

Five different habitat treatments were tested against the reference habitat: 1) tiles with mussel shells (reference habitat = mussel shells), 2) bare tile, 3) tiles with living mussels (living mussels), 4) tiles with mussel shells and biodeposited material produced by zebra mussels (biodeposited material), and 5) tiles with mussel shells, biodeposited material, and 30 living chironomids (biodeposited material with chironomids). The number of mussel shells or living mussels in test habitats was the same as the number of mussel shells in the reference habitat. The 5 treatments were chosen to measure the attractiveness of factors that might influence the amphipods in their natural lake environment. Mussels shells acted as a control, and bare tile tested the habitat effect caused by the mussel shells. The remaining 3 treatments specified the biotic influences of the zebra mussel, i.e., the presence of living mussels without biodeposited material and the availability of different food sources. Each treatment was replicated 8×, except for treatments 1, 2, and 3 for *G. roeselii*, which were replicated 16×. The higher number of replicates in these 3 treatments was necessary for better precision. All habitat-choice experiments were conducted in a period of 1.5 mo in August and September 2006. Four replicates from 2 different treatments (8 replicates in all) were run at the same time. Food treatments (4, 5) of each amphipod species were done within a single 1-wk period.

Mussels were measured with a digital sliding calliper (Preisser; Digi-Met, Gammertingen, Germany) to the nearest 0.01 mm. The mean length of empty

FIG. 1. Diagram of the arena used in the 2-chamber habitat-choice experiment. The passage between the chambers was closed with a removable dividing wall during the set-up phase of each trial. A tile was placed into a notch in each chamber. Fifteen mussel shells (MS) were glued to the surface of the reference tile in 1 chamber. One of 5 habitat treatments (MS, bare tile, living mussels, MS plus biodeposited material, or MS plus biodeposited material and chironomids) was presented on the surface of the tile in the 2nd chamber.

mussel shells and living mussels was 14.99 ± 0.46 mm and 14.95 ± 0.49 mm, respectively. Shell length did not differ significantly between the empty mussel shells and living mussels (Mann-Whitney *U*-test, $p = 0.31$). The mussel shells and the living mussels were cleaned before use in the experiments.

Biodeposited material was collected in the lake using modified sediment traps. The sediment trap consisted of a tube of gray PVC (50-cm length; 10-cm diameter). A funnel and a 200-mL polyethylene terephthalate (PET) flask were fixed at the lower end of the tube to collect the settling sediment. A clamp was used to hold 2 tiles (4.7×4.7 cm) with 15 living mussels (14.91 ± 0.48 -mm shell length) each in a vertical position above the upper opening of the sediment trap. Biodeposited material was collected twice between the end of August and the beginning of September 2006. Five traps were suspended at a depth of 2 m from a pontoon in the pelagic zone of Lake Constance for 7 d. The collected material was centrifuged ($1180 \times g$, 6 min), and the supernatant was replaced with enough pure water to bring the volume to 100 mL. Biodeposited material was stored at 4°C in darkness. Ash-free dry mass (AFDM) of biodeposited material was determined on an aliquot of this material (combustion at 550°C, 8 h). An amount of biodeposited material equivalent to 8.0 ± 0.9 -mg AFDM was added to the tile of one chamber in each replicate of the treatments with added biodeposited material of the habitat-choice experiment.

All animals were starved for 24 h over a mesh (1-mm-mesh size) before the test to allow them to empty their guts. Thus, the presence of feces in a chamber indicated food uptake by the amphipods during the test. Each replicate in all tests consisted of a single arena separated by the dividing wall into 2 chambers, each of which had 1 tile of the appropriate treatment and 0.5-L aerated lake water prefiltered through a 0.45- μ m filter to prevent biodeposition by zebra mussels during the test. The treatments were randomly assigned to the left or right chamber. Arenas were set up with the dividing wall in place. Ten amphipods of one species were added to each chamber (20 amphipods of the same species per replicate). This quantity of amphipods was equivalent to a density of ~ 1200 individuals (ind.)/m², which is slightly higher than natural densities (Mörtl et al. 2005). To avoid stress for the amphipods, the experimental arena was shaded by a black curtain. Thirty minutes after the amphipods were added to the chambers, the dividing wall was removed. After 24 h, the dividing wall was re-inserted to inhibit crossing to the other chamber. The amphipods in each chamber were counted after the dividing wall was inserted.

Y-maze experiment

In September 2006, the influence of zebra mussel kairomones on both amphipod species was tested in a y-shaped flow-through system according to the protocol of Baumgärtner et al. (2002, 2003). The y-maze

(length $\times$ width of root: 36×13 cm, and of each y-arm: 30×9 cm) consisted of gray PVC. Similar to the setup in Baumgärtner et al. (2002, 2003), the y-maze was shielded from the light in the climate chamber by a black curtain and was dimly illuminated with 2 fluorescent lamps (Osram Lumilux Plus, 18 W; Osram, München, Germany). Inflow of water took place near the surface at the ends of both y-arms. The outflow at the end of the mixing zone was covered by a 1-mm net so that animals could not drift away. Inflow was provided from 2 basins with taps, and the inflow volume was adjusted to 0.5 L/min for each y-arm. In each replicate, 30- μ m-filtered and aerated lake water was used as a reference. Fresh kairomone water was prepared on every experimental day by holding 1000 zebra mussels from a natural population (13.2 ± 1.6 mm in length) of zebra mussels in 60 L of lake water for 24 h. The conditioned water was purified through a 30- μ m-size filter to remove potential food for the amphipods before it was used in the experiment.

At the beginning of each trial, the y-maze was filled with reference water, and the inflow was adjusted. After 1 min of preflow time, 20 individuals of one amphipod species were placed in the mixing zone near the outlet of the y-maze. Each replicate test lasted 30 min, and the number of the amphipods in each y-arm was determined every 2 min. Only the values from minute 10 to minute 30, the period when water in the root of the y-maze was fully mixed (Baumgärtner et al. 2002), were included in our calculations. Reference water was tested against reference water as a control to demonstrate that neither arm of the y-maze was preferred by the amphipods. The order of the replicates was random, and treated water and reference water were alternated between the y-arms for every replicate. Both treatments (control and kairomone water) were repeated 8 $\times$.

Statistical analysis

Habitat-choice experiment.—Some animals died during the habitat-choice experiments. Therefore, the difference in the number of amphipods in the test and in reference habitats relative to the number of amphipods in the reference habitat (% difference) at the end of the experiment was the dependent variable in the analysis. Percentages rather than actual counts were used so that replicates in which amphipods died during the experiment could be included in the analysis without introducing bias. Percent difference described the preference of amphipods for the test habitat treatment. The strength of the influence of the test habitat was assessed by ignoring the direction of habitat choice and comparing the absolute value of the

% difference to 0 (equal numbers on both habitats). Percentages were arcsine($\sqrt{x}$)-transformed to satisfy assumptions of normal distribution and homogeneity of the variances (Underwood 2006). Homogeneity of variances was tested with a Levene test. Differences in preference of a single species between habitat treatments were evaluated using a 1-way analysis of variance (ANOVA) with subsequent Tukey's Honestly Significant Difference (HSD) post-hoc tests. Differences between species were evaluated using a 2-way ANOVA.

Y-maze experiment.—No animals died during these experiments. Therefore, the difference in the number of individuals between the 2 y-arms at each time point was used as the dependent variable in the analysis. Homogeneity of variances was tested with a Levene test. Differences in preference between species and kairomone treatments were analyzed with a repeated-measures ANOVA (rm-ANOVA). All analyses were done with Statistica software (version 6.1; StatSoft Inc., Tulsa, Oklahoma) as described in Baumgärtner et al. (2002, 2003).

Results

Habitat-choice experiment

Habitat preferences differed significantly between species (2-way ANOVA, $p = 0.048$; Table 1). However, the species $\times$ habitat interaction term was not significant ($p = 0.13$). Preferences of *G. roeselii* differed significantly among the 5 treatments (ANOVA, $p = 0.002$; Table 1). Amphipods were equally distributed when reference habitat and mussel shells and when reference habitat and living mussels were compared (Fig. 2A). Preferences for mussel shells and living mussels over reference habitat did not differ significantly from preferences for bare tile or biodeposited material with or without chironomids over reference habitat. Preferences for biodeposited material and biodeposited material with chironomids over reference habitat were significantly greater than preferences for reference habitat over bare tile (no food). The color of feces of *G. roeselii* was similar to that of the food offered, indicating that amphipods ate the biodeposited material.

Preferences of *D. villosus* also differed significantly among the 5 habitat treatments (ANOVA, $p < 0.001$; Table 1). Amphipods were equally distributed when reference habitat and mussel shells and when reference habitat and biodeposited material were compared (Fig. 2B). Amphipods preferred reference habitat over bare tile. Preferences for reference habitat over living mussels and preferences for mussel shells and biodeposited material over reference habitat were not

TABLE 1. Analysis of variance results comparing responses to habitat treatments of 2 amphipod species, *Gammarus roeselii* and *Dikerogammarus villosus*, in the habitat-choice experiment. The dependent variable, % difference, was calculated between pairwise combinations of habitats on reference (15 mussel shell [MS]) and test (MS, bare tile, living mussels, MS with biodeposited material, or MS with biodeposited material and chironomids) tiles in 2-chamber arenas.

Factor	Species	F	df	p
Habitat	Both	15.893	4	<0.001
Habitat	<i>G. roeselii</i>	4.757	4	0.002
Habitat	<i>D. villosus</i>	13.260	4	<0.001
Species	Both	4.030	1	0.048
Species $\times$ habitat	Both	1.826	4	0.13

significantly different, and preferences for biodeposited material with and without chironomids over reference habitat were not significantly different. Preference for biodeposited material with chironomids over reference habitat was significantly greater than preference for reference habitat over living mussels and bare tile. Only a few *D. villosus* feces matched the color of the biodeposited material, indicating that amphipods ate little biodeposited material.

The bare tile treatment had a significantly stronger effect than the other treatments on the distribution of *D. villosus* (ANOVA, $F = 9.159$, $p < 0.001$). Treatment effects on *G. roeselii* differed significantly (ANOVA, $F = 2.829$, $p = 0.032$), but the Tukey HSD post-hoc test did not identify a specific treatment that differed significantly from the others. However, the effect of the bare tile treatment appeared to be stronger than the effect of other treatments because the bare tile effect did not differ between amphipod species (ANOVA, $F = 3.679$, $p = 0.105$), and the bare tile treatment did affect *D. villosus* significantly.

Y-maze experiment

The habitat-choice experiments revealed no preference for living mussels (*G. roeselii*; Fig. 2A) or avoidance of living mussels (*D. villosus*; Fig. 2B), but the elicitor of the avoidance reaction was unknown. The y-maze experiment tested whether kairomone produced by the zebra mussels was a possible elicitor. The presence of kairomones in water elicited significant negative responses from both amphipod species (Fig. 3A, B). The mean difference in abundance of individuals between y-maze arms with reference and kairomone water was $16.2 \pm 4.3\%$ for *G. roeselii* (rm-ANOVA, $p < 0.001$) and $10.4 \pm 3.1\%$ for *D. villosus* (rm-ANOVA, $p < 0.01$).

FIG. 2. Mean % difference (± 1 SE) of *Gammarus roeselii* (A) and *Dikerogammarus villosus* (B) for habitats in pairwise choice experiments comparing responses to 1 of 5 test habitat treatments (mussel shells [MS], bare tile, living mussels, MS plus biodeposited material from zebra mussels, and MS plus biodeposited material and 30 living chironomids) against a reference habitat (MS). Percent difference was calculated based on the distribution of amphipods at the end of the experiment. Negative values indicate a preference for the reference habitat; positive values indicate a preference for the test habitat. Bars with the same uppercase letter are not significantly different ($p > 0.05$).

Discussion

Zebra mussels increase the amount of benthic organic matter by filtration and biodeposition (e.g., Stanczykowska et al. 1976, Klerks et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998). Benthic organic matter is an appropriate food source for detritivores and omnivores, and its increase often is hypothesized to be the direct biotic factor that causes abundances of detritivores and omnivores to increase in habitats that have been invaded by zebra mussels. Moreover, predators might benefit indirectly from organic matter deposition if it increases the abundance of detritivores, such as chironomids. Zebra mussels also increase the structural complexity of benthic habitats, and the additional structure is hypothesized to be an abiotic

FIG. 3. Mean (± 1 SE) difference in the number of individuals (ind.) of *Gammarus roeselii* (A) and *Dikerogammarus villosus* (B) in 2 arms of a y-maze experiment testing responses to lake water conditioned with zebra mussels, i.e., containing kairomones, and unconditioned water. Values are the difference in the number of individuals between the arms of the y-maze, averaged at 10-min intervals from 10 to 30 min after initiating the experiment. Positive values indicate preference for the conditioned water; negative values indicate avoidance of the conditioned water. ** $p < 0.01$, *** $p < 0.001$.

factor that causes abundances of benthic invertebrates to increase in habitats that have been invaded by zebra mussels. Our results support both of these hypotheses and indicate that the native *G. roeselii* and invasive *D. villosus* both responded (either directly or indirectly) to the increased food supply associated with biodeposited material in Lake Constance. Therefore, the biodeposition of invading zebra mussels could lead to the formation of new food webs and increase secondary production in benthic systems.

The 2 species differed significantly in their habitat preferences (Table 1), which indicated different responses to food sources. *Gammarus roeselii* responded positively to the structure associated with mussel shells and to any additional food source (biodeposited material with or without chironomids), as was evident

from the feces at the end of the experiment. However, our data did not provide evidence that *G. roeselii* actually fed on chironomids. Moreover, chironomids were added only in combination with the biodeposited material, so a true preference for one food source over the other could not be determined. On the other hand, *D. villosus* responded positively to biodeposited material with chironomids but not to biodeposited material without chironomids. These results agree with the known feeding strategies of both amphipod species. *Dikerogammarus villosus* is a predator (Dick et al. 2002), and *Gammarus* is a shredder or omnivore (Bärlocher and Kendrick 1973, Pöckl 1992, 1993, Friberg and Jacobsen 1994).

Both species avoided bare tile. The response of *D. villosus* to bare tile was significantly stronger than its response to any other habitat treatment, and the response of *G. roeselii* to bare tile tended to be stronger than its response to any other treatment. Thus, the high structural complexity provided by the mussel shells was a clear driver of habitat choice for both species. This strong response might be associated with reduced predation risk with increasing habitat complexity (González and Downing 1999). It is not specific to amphipods, and the potential explanation can be applied to most benthic macroinvertebrates (Stewart et al. 1998).

Both amphipods species showed a significant negative response to lake water conditioned with zebra mussels in the y-maze experiments. *Dikerogammarus villosus* also avoided tiles with living mussels in the habitat-choice experiment. These results indicate that kairomones released by living zebra mussels cannot explain the increase in abundance of amphipods in the field and that kairomones might actually provoke an avoidance reaction. Zebra mussels excrete NH_4^+ as an end product of their metabolism, and NH_4^+ accumulates in the surrounding water (Heath et al. 1995). Amphipods are very sensitive to NH_4^+ contamination, which can be lethal at high concentrations (Williams et al. 1986, Berenzen et al. 2001). Thus, the amphipods in our experiments might have avoided living mussels because of NH_4^+ accumulation in the chamber.

Implications for the benthic community

Our experiments were carried out under standardized laboratory conditions and cannot reproduce the variability of environmental conditions in the lake. Under natural conditions, the habitat preference of amphipods varies seasonally, and high-complexity substrates are not preferred over low-complexity substrates throughout the year (González and Down-

ing 1999). Living mussels are preferred by gammarids only in late summer, possibly because late-summer peaks in phytoplankton concentrations cause maximum biodeposition by zebra mussels and high food availability (Reeders and Bij de Vaate 1992). During winter and spring, abundances of zebra mussels are low in Lake Constance because of predation by diving ducks (Werner et al. 2005). Thus, structural complexity and biodeposition vary seasonally, and both are less important in winter and spring than in summer and autumn. The abundances of amphipods also are lowest during winter (Mörtl et al. 2005). Mörtl and Rothhaupt (2003) observed an increase in abundance of *G. roeselii* and chironomids on zebra mussels in July 1999, during a period when habitat complexity and biodeposition rate presumably were high. Our results suggest that this increase might be attributable to the structural complexity and additional food source from biodeposition by zebra mussels.

In Lake Constance, the benthic food web has been disturbed by the Ponto Caspian invader *D. villosus*, which has colonized the lake rapidly since 2002 (Mörtl et al. 2005). One consistent response in many freshwater systems during the establishment of *D. villosus* is the decline or extirpation of native amphipods because of predation by *D. villosus* (Ponyi 1956, Dick and Platvoet 2000, Kinzler and Maier 2003, Josens et al. 2005). Other benthic macroinvertebrates are also prey of *D. villosus*, and their abundances decrease after its invasion (Dick et al. 2002, Krisp and Maier 2005).

In conclusion, our results provide strong indications that amphipods are involved in a *Dreissena*-biodeposit-based food web. To our knowledge, ours is the first study that indicates how biodeposition by zebra mussels might influence habitat choice by benthic macroinvertebrates. The effects of zebra mussels on amphipods differ between species. Omnivorous *G. roeselii* was attracted to biodeposited material and to mussel shells, whereas the predatory invader *D. villosus* was attracted to shells only when added animal prey was present. Therefore, the invasive amphipod species is influenced indirectly by zebra mussels through their effect on other species that feed on biodeposited material. The other species involved in this possible food web and the ways in which they are influenced by invading species, such as *D. villosus*, remain to be clarified.

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