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Effects of Adult *Dreissena polymorpha* on Settling Juveniles and Associated Macroinvertebrates

key words: Dreissena polymorpha, macroinvertebrates, gregarious settlement, recruitment, chemical cues

Abstract

The impact of *Dreissena polymorpha* settlement on recruitment of juvenile mussels and density of other macroinvertebrates was studied in field experiments using blank concrete blocks and tiles (control), blocks and tiles with attached empty zebra mussel shells, and blocks and tiles with attached living mussels. On blocks, dominant invertebrate taxa showed colonization patterns coinciding with increased habitat complexity owing to zebra mussel settlement or the biodeposition of faeces and pseudofaeces. Adult and especially juvenile zebra mussels preferred blocks with empty shells to blank blocks and blocks with living mussels; this might possibly be caused by a chemical cue that induces gregarious settlement. Lower recruitment on blocks with attached living mussels compared to blocks with only shells could be the consequence of ingestion of larvae by adult mussels and of competition for food. On tiles, the sediments deposited and the organic content of the sediment were investigated. Sedimentation was significantly higher on shell-only and live-mussel tiles compared to blank tiles. Organic matter differed significantly between blank and live-mussel tiles.

1. Introduction

The settlement of zebra mussels (*Dreissena polymorpha*) strongly influences benthic communities. Basic studies have been carried out in Eastern Europe (KARATAYEV *et al.*, 1997) and in North America, after the Laurentian Lakes were invaded by mussels in the mid-1980s (e.g. GRIFFITHS, 1993). There, the major impacts of the immigration of the zebra mussel are a change in the structure of the substrate and the accumulation of organic matter by biodeposition (BOTTS *et al.*, 1996; STEWART *et al.*, 1998; RICCIARDI *et al.*, 1997). Many benthic taxa increased in abundance, e.g. annelids, gastropods, amphipods, decapods, and insect larvae (STEWART and HYNES, 1994). Invading zebra mussels negatively affect unionids (RICCIARDI *et al.*, 1996). Changes in the benthic community also affect other trophic levels, e.g. plankton (e.g. HOLLAND, 1993) and fish (e.g. MAYER *et al.*, 2001).

Even though the zebra mussel is abundant in many Central European lakes and rivers (GLÖER and MEIER-BROOK, 1994), studies on impacts on the benthic community are lacking. Synecological research has focused mainly on the interactions between zebra mussels and waterfowl (DE LEEUW *et al.*, 1999) and native mussels (BAUER *et al.*, 2002). However, knowing how zebra mussels affect associated macroinvertebrates would be helpful to explain temporal and spatial distributions of macroinvertebrates.

In this study, different substrate complexity and surface area as well as the effect of biodeposition by zebra mussels on macroinvertebrates and sediment quantity and quality were

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evaluated in field experiments in Lake Constance, which was invaded by zebra mussels in 1966 (Siesegger, 1969). In the littoral zone, zebra mussels are common on hard substrates (Streit and Schröder, 1978; Mauch, 1996) and undergo typical annual fluctuations in abundance and biomass through high predation by wintering waterfowl (Cleven and Frenzel, 1993). Zebra mussels also play an important role in the littoral food web of the lake (Walz, 1978). In addition, we are interested in the mechanisms that affect settlement of juvenile zebra mussels, i.e. the completion of their planktonic phase, and movement of adults. Indications of chemical communication of a variety of marine benthic species that propagate by planktonic larvae have been found (Burke, 1986). Evidence of gregarious settlement of zebra mussels or of an attraction, possibly to zebra mussel shells, has also been presented in the literature (Hebert et al., 1991; Wainman et al., 1996).

2. Methods

2.1. Study Site

The experiments were carried out in the main basin of Lake Constance, a large (surface area: 472 km^2) and deep (maximum depth: 254 m) pre-alpine lake in Central Europe. The mean depth of this basin is about 100 m. The littoral zone (water depth <10 m) comprises 10% (Wessels, 1998). The main tributary is the River Rhine, draining parts of the Swiss, Austrian, and Italian Alps. Annual water-level fluctuations of about two meters are caused by snowfall in the Alps, with continuous low inflow during winter and higher inflow from melting snow in early summer. Experiments were performed on the south-western shore of Lake Constance, close to Konstanz, Germany. At this site, the littoral zone is covered by gravel and stones.

2.2. Colonization Experiment

The experimental design was similar to that of Ricciardi et al. (1997) and Stewart et al. (1998). Concrete blocks (surface area: 121 cm^2) were used as artificial substrates for colonization in three treatments, with nine replicates each: treatment 1 (T1, control), blank blocks; treatment 2 (T2, shell-only treatment), empty shells of adult *Dreissena* fixed to the blocks (10,768 ± 884 shells m^{-2}; mean ± SD) with silicone glue; treatment 3 (T3, live-mussel treatment), living adult zebra mussels fixed to the blocks (8,388 ± 562 ind. m^{-2}) with a two-component adhesive. Mussels were collected from Lake Constance and cleaned before handling. All prepared blocks were stored for several days in an aquarium filled with tap water, thus allowing a biofilm to develop. The blocks were deployed by scuba divers in two meters depth on July 28, 1999, and arranged in an area of 2 m^2 in three rows of nine blocks each. The differently treated blocks were placed in random order.

On August 24, 1999, the blocks were collected by scuba divers. Each block was carefully placed in a bucket covered with a lid. The buckets were transported to the laboratory immediately, and the blocks were processed within 2 h. The blocks were brushed, and the suspension including the lake water in the buckets was sieved through a 200-μm mesh. The samples were preserved in 70% ethanol and counted under a dissecting microscope at 10–15× magnification. With the exception of chironomids, oligochaetes, and members of the trichopteran family Leptoceridae, organisms were identified to the species or genus level. Mussels shorter than 5 mm were counted as newly settled juveniles (young of the year, Cleven and Frenzel, 1993).

Numerical abundances were expressed as individuals m^{-2} and were sqrt $(x + 1)$ transformed to achieve homogeneity of variances. For testing the null hypothesis, an analysis of variance (ANOVA) was used. Dependent variables in the ANOVA were all taxa that had a mean abundance among all blocks of more than 410 ind. m^{-2} or 5 ind. per single block. This value was chosen to reduce the number of ANOVA calculations and refers to Downing's equation of sampler size efficiency (Downing, 1984). The oligochaetes were disregarded because they broke into many pieces after fixation and therefore could not be counted accurately. Tukey-HSD tests were run to determine significant differences between treatments. Since 10 separate ANOVA tests were performed, the sequential Bonferroni adjustment (Rice, 1989) was

Table 1. Mean abundances of the dominant taxa and the total macroinvertebrate abundance settled on blank, shell-only, and live-mussel blocks.

Taxon	Mean abundance [ind. m⁻² (SE)]					
	T1 Blank blocks		T2 Shell-only blocks		T3 Live-mussel blocks	
Dreissena polymorpha (juvenile)	7,897	(1.253)	12,819	(1.223)	7,815	(960)
Chironomids	2,103	(338)	3,921	(678)	6,942	(731)
Potamopyrgus antipodarum	826	(167)	1,653	(433)	2,002	(319)
Bithynia tentaculata	367	(60)	900	(112)	597	(118)
Gammarus roeseli	193	(72)	973	(240)	2,158	(267)
Caenis spp.	551	(171)	1,423	(313)	900	(141)
Dreissena polymorpha (adult)	478	(108)	1,598	(405)	716	(162)
Leptoceridae	542	(85)	872	(168)	725	(117)
Dugesia lugubris	459	(146)	542	(140)	551	(118)
Total	16,171	(1,618)	29,550	(2.305)	27,484	(1,922)

applied to obtain an experiment-wise error rate of $\alpha = 0.05$ across all dependent variables. All statistical analyses were performed with STATISTICA for Windows 5.5 (STATSOFT, Inc., Tulsa, Okla., USA, 1993).

2.3. Sedimentation Experiment

In a second experiment, tiles (surface area: 33.64 cm²) were prepared as in the colonization experiment (six replicates each). Tiles were attached to concrete blocks to ensure recovery and placed in the lake at the same location between February 2 and March 14, 2001. Scuba divers transferred tiles carefully into plastic bags and sealed them with clips. Some replicates were disregarded for following reasons: one control tile was completely covered with sediment; two plastic bags, one with a shell-only tile and one with a live mussel tile, were damaged and leaked; and one shell-only tile could not be recovered.

In the laboratory, tiles were cleaned with distilled water, macroinvertebrates were removed and discarded, and suspensions were filtered through pre-weighed 0.45-µm cellulose acetate filters (SARTORIUS). Mass (g m⁻²) was determined after drying for 24 h at 105 °C (dry weight), and organic matter [ash-free dry matter (AFDM), g m⁻²] was determined as the difference between dry and ash weight, the latter achieved by ignition at 550 °C for 2.5 h. The percentage of loss on ignition (LOI) was calculated as the ratio between organic matter and dry mass. The data for dry mass and organic matter were sqrt (x + 1) transformed and differences between treatments were calculated by ANOVA and Tukey-HSD tests.

3. Results

3.1. Colonization Experiment

The most abundant taxa in our study were juvenile zebra mussels (*Dreissena polymorpha*), followed by chironomids, snails (*Potamopyrgus antipodarum, Bithynia tentaculata*), amphipods (*Gammarus roeseli*), mayflies (*Caenis* spp.), adult zebra mussels, caddiesflies (Leptoceridae) and flatworms (*Dugesia lugubris*, Table 1). Miscellaneous taxa include molluscs (*Pisidium*), water mites, leeches (*Erpopdella octoculata, Helobdella stagnalis, Glossiphonia complanata*), and caseless caddisflies (*Polycentropus flavomaculatus, Tinodes waeneri*). Those were less abundant (less than 410 ind. m⁻² or 5 ind. per block) and were not considered further.

Total density of macroinvertebrates was nearly twice as high on blocks with dead shells and live mussels than on blank blocks ($p < 0.0001$; Tables 1, 2). Abundances of amphipods

Table 2.   Differences in taxon abundance on the differently treated blocks, as shown by results of ANOVA. Significant results after sequential Bonferroni adjustment of p-values ($p \leq 0.05$; Rice, 1989) are marked with *. Rank order between treatments T1, T2, and T3 (blank blocks, shell-only blocks, and live-mussels blocks, respectively) was determined using a Tukey-HSD test. n.s.= no significant differences.

| Taxon | Rank order | Results of ANOVA | | |
		F	$df_{eff, err}$	p
Dreissena polymorpha (juvenile*)*	T1 < T2 > T3	5.90	2, 24	0.008*
Chironomids	T1 < T2 < T3	17.61	2, 24	<0.0001*
Potamopyrgus antipodarum	n.s.	3.10	2, 24	0.06
Bithynia tentaculata	T1 < T2	6.90	2, 24	0.004*
Gammarus roeseli	T1 < T2 < T3	28.02	2, 24	<0.0001*
Caenis spp.	T1 < T2	3.62	2, 24	0.04
Dreissena polymorpha (adult)	T1 < T2 > T3	5.84	2, 24	0.009*
Leptoceridae	n.s.	1.20	2, 24	0.32
Dugesia lugubris	n.s.	0.07	2, 24	0.93
Total	T1 < T2 = T3	14.24	2, 24	<0.0001*

and of chironomids were significantly different among the three treatments ($p < 0.0001$), with the lowest numbers of individuals on blank blocks, intermediate numbers on the shell-only blocks, and highest numbers on live-mussel blocks (Tables 1, 2). Abundances of juvenile and newly settled adult zebra mussels colonizing blocks were similar on the blank blocks and live-mussel blocks, but significantly higher on shell-only blocks (Table 2). May-fly larvae of the genus *Caenis* and the snail *B. tentaculata* were more abundant on shell-only blocks than on blank blocks, but after Bonferroni adjustment, the result for *Caenis* spp. was shown to be insignificant. Other macroinvertebrates showed no preference for any of the treatments.

3.2. Sedimentation Experiment

Sedimentation differed significantly between the control (blank tiles) and tiles with altered structure (shell-only, live mussels). The amount of dry mass was lowest on blank tiles and about five times greater on shell-only and live-mussel tiles (Table 3). Organic matter (g AFDM m^{-2}) was lowest on the blank tiles and highest on the live-mussel tiles. The results of the Tukey-HSD test revealed a weak significant difference between the shell-only tiles and the live-mussel tiles ($p = 0.08$). The ratio between organic matter and dry mass, i.e. the loss on ignition, was significantly lower on the shell-only tiles than on the live-mussel tiles. In the control treatment (blank tiles), intermediate values were obtained (Table 3).

4. Discussion

4.1. Intraspecific Effects

Juvenile and adult zebra mussels reached highest abundances on the shell-only blocks, possibly because of the increased surface area provided by the shells compared to the blank blocks. However, lower abundances of juveniles on the live-mussel blocks indicate that the

Table 3. Results of sediment analyses. Dry mass, organic matter, and loss on ignition are given for the different treatments. T1, control treatment (blank tiles); T2, shell-only tiles; T3, live-mussel tiles. Results of ANOVA indicate significant differences among treatments. Rank order was calculated using a Tukey-HSD test. SE is given in parentheses.

	T1 Blank tiles (n = 5)		T2 Shell-only tiles (n = 4)		T3 Live-mussel tiles (n = 5)		Rank order	Results of ANOVA		
								F	$df_{eff, err}$	p
Dry mass (g m^{-2})	130.7	(57.1)	620.7	(113.5)	639.4	(198.2)	T1 < T2 = T3	7.99	2, 11	0.007
Organic matter (g AFDM m^{-2})	4.9	(1.9)	17.9	(0.8)	30.0	(4.1)	T1 < T2 = T3	25.2	2, 11	<0.0001
Loss on ignition (%)	4.10	(0.27)	3.06	(0.36)	5.56	(0.70)	T2 < T3	6.08	2, 11	0.017

adult mussels may have influenced settlement of the juveniles. Several factors affect settlement and recruitment of benthic macroinvertebrates from planktonic larvae (e.g. CONNEL, 1985); larvae might be transported to the substrate in different densities, chemical cues in the water may influence settlement, or predation and locomotion after settlement can affect the number of recruits.

In our experiment, homogenous concentrations of veligers in the water column at our study site were assumed because of the small-scale area (about 2 m^2) to which the treated blocks were exposed. This should theoretically allow larvae to settle randomly on our substrates.

Attraction by chemical cues has been discussed for several marine taxa. A wide taxonomic range of planktonic larvae prefer locations colonized by conspecific adults. BURKE (1986) argues that gregarious settlement and metamorphosis is mediated by chemical cues in different phyla, e.g., cnidarians, molluscs, annelids and arthropods. Attracting substances operate either in solution or are adsorbed on a surface (ZIMMER-FAUST and TAMBURRI, 1994) and are often produced by bacterial films that are specifically adapted to those surfaces (HATFIELD and PAUL, 2001). Settlement of *D. polymorpha* might be cued by a substance that works as an attractant at low concentrations and a repellent at high concentrations (HEBERT *et al.*, 1991). WAINMAN *et al.* (1996) observed a lower settling rate of juvenile zebra mussels on mussel-sized stones than on shells or living mussels. They concluded that gregarious settlement of zebra mussel larvae mediated by a substance in the shells lead to comparable abundances on the shell-only blocks and on the live-mussel blocks. Although in their data no significant difference between these two treatments was observed, their data indicate a higher average and maximum recruitment on shell-only blocks. Perhaps this may be due to higher surface area provided by interior and exterior shell surface, covered by the biofilm.

In our experiments in Lake Constance, a significant lower abundance on living mussel blocks was observed. Therefore, we assume that additional negative interactions play a role. In field observations and laboratory experiments, intraspecific predation has been demonstrated as a regulatory mechanism for *Dreissena* settlement (MACISAAC *et al.*, 1991). Adult *D. polymorpha* are able to ingest particles up to 750 µm in length (TEN WINKEL and DAVIDS, 1982), although the preferred size spectrum is between 0.4 µm and >40 µm (RODITI *et al.*, 1996; COTNER et al., 1995; SILVERMAN *et al.*, 1995). In Lake Constance, the shell length of settling zebra mussels is 250 µm (WACKER, 2002). Thus, veligers are a potential prey for adults; this might explain considerable larval mortality, which is assumed to be as high as 99% (LEWANDOWSKI, 1982), but has not yet been clarified.

In addition to the above-mentioned adult-larva interactions before and during settlement, post-veliger movements and mortality also affected numbers of recruits (RODRIGUEZ *et al.*, 1993). Early postmetamorphic stages of the zebra mussel can disperse in the water column.

Drifting juveniles up to 800 µm in length and some even up to 2 mm have been observed (Martel, 1993). Chase and Bailey (1996) have reported an avoidance of high densities of adult mussels in recruitment experiments in the field. Their results show that the mean length of the recruits decreases with increasing number of conspecific adults, which suggests that increased competition for food in the high-density treatments results in reduced growth of recruits. Obviously, there is a trade-off between adult numbers that are high enough to provide an attachment site and a post-veliger protection, and numbers that are low enough to enhance growth and possibly survival (Chase and Bailey, 1996).

In our field experiments, several factors may have affected settlement and recruitment during the experimental period of 27 days. Possibly mediated by a chemical cue, the abundances of recruits and immigrated adults were significantly increased on shell-only blocks. Predation and food-competition may have reduced their settlement on live-mussel blocks to the same extend as on blank blocks. Therefore, at high densities (>8000 ind. m^{-2}), living adult mussels negatively influenced the recruitment of juveniles and immigration of adults.

4.2. Interspecific Effects

Increased surface area and complexity on the shell-only blocks corresponded to a significant increase in density of macroinvertebrates compared to the blank blocks. Biodeposition of living mussels caused no significant difference in overall abundance of macroinvertebrates between the shell-only blocks and the live-mussel blocks, but qualitative differences in species assemblage were observed.

Density of chironomids significantly increased as the surface of the blocks became more complex (blank→empty shells→living mussels). This group benefited from the enhanced surface area, the complexity of the surface, and biodeposition by the living mussels. Similar results have been described by Izvekova and Lvova-Katchanova (1972), Ricciardi et al. (1997), and Stewart et al. (1998) (Table 4). Enhanced amount of bacteria and algae in the faeces and pseudofaeces (Roditi et al., 1997) is assumed to account for this phenomenon (Izvekova and Lvova-Katchanova, 1972).

Compared to results of other studies (Table 4), we observed a significant lower abundance of amphipods on shell-only blocks than on live-mussel blocks. In our study, the data were sqrt-transformed because homogeneity of variances could not be achieved by a logarithmic transformation. Hence, differences at higher numbers are more pronounced than in other studies (Ricciardi et al., 1997; Stewart et al., 1998). Nevertheless, the feeding habit of Gammarus roeseli makes it plausible that it also benefits from biodeposition by D. polymorpha (Gonzalez and Downing, 1999). G. roeseli ingests various types of food, such as bacteria, fungi, algae, and particulate organic matter (Delong et al., 1993; MacNeil et al., 1997). Therefore, an increase in organic matter by biodeposition of the mussels affects the density of the amphipods. The gammarids might profit from enhanced algal growth, stimulated by the excretion of nitrogen and phosphorus by zebra mussels (Arnott and Vanni, 1996; Heath et al., 1995; James et al., 1997). Results of sediment analyses support these findings. The mass of organic matter reached highest values on the live-mussel tiles, intermediate values on the shell-only tiles, and lowest values on the blank tiles. Loss on ignition analysis yielded significant differences between shell-only tiles and live-mussel tiles, confirming enrichment of sediment with organic compounds by biodeposition of zebra mussels. Additionally, gammarids feed as predators and might benefit from higher abundances of their prey (e.g. chironomids) on the live-mussel blocks (MacNeil et al., 1997).

Otherwise, it is interesting that flatworms (Dugesia lugubris), which are also predators, are not significantly affected by the availability of small invertebrates on live-mussel blocks in our experiment; by contrast Stewart et al. (1998), Botts et al. (1996) and Ricciardi

Table 4. Rank order of total macroinvertebrate biomass (g AFDM m^{-2}), total macroinvertebrate density (ind. m^{-2}), and densities of taxa in studies distinguishing effects of shell-generated habitat from biodeposition by *Dreissena polymorpha* (modified from STEWART, 1998). T1, control treatment (blank blocks); T2, shell-only blocks; T3, live-mussel blocks. Names of taxa are provided as reported in the present study[1], BOTTS *et al*. 1996[2], RICCIARDI *et al*. 1997[3], and STEWART *et al*. 1998[4].

	Reference			
Taxon	Present study	BOTTS *et al*. (1996)	RICCIARDI *et al*. (1997)	STEWART *et al*. (1998)
Total biomass[4]/ Total density[1, 3]	T1 < T2 = T3	Not reported	T1 < T2 < T3	T1 < T2 < T3
Chironomids[1, 2, 3]/ *Microtendipes pedellus*[4]	T1 < T2 < T3	T1 < T2 < T3	T1 = T2 < T3	T1 < T2 < T3
Amphipoda[2]/*Gammarus roeseli*[1]/*G. fasciatus*[3, 4]	T1 < T2 < T3	T1 < T2 = T3	T1 < T2 = T3	T1 < T2 = T3
Turbellaria[2]/*Dugesia* sp.[3]/ *D. lugubris*[1]/*D. tigrina*[4]	T1 = T2 = T3	T1 < T2 = T3	T1 = T2 < T3	T1 < T2 = T3
Bithynia tentaculata[1]/ Physidae[3]/*Physella* sp.[4]	T1 < T2	Not reported	T1 < T2 = T3	T1 < T2 = T3

et al. (1997) found higher numbers of *Dugesia* sp. on live-mussel blocks than on blank blocks (Table 4). Further studies of predator-prey interactions within the macroinvertebrate community are needed to interpret these patterns.

The snail *Bithynia tentaculata* benefited from altered physical structure of shell-only blocks. However, their density on live-mussel blocks was lower. This contrasts with the results of RICCIARDI *et al*. (1997) and STEWART *et al*. (1998), who found comparable densities of the gastropod *Physella* sp. on shell-only blocks and live-mussel blocks (Table 4). This difference might be attributed to the different feeding types of these two taxa. *Physella* sp. (Pulmonata) feeds mainly as a scraper, whereas *B. tenatculata* (Prosobranchiata) is able to filter (COLLING and SCHMEDTJE, 1996). Food competition with filtering adult zebra mussels could therefore result in reduced numbers of *B. tentaculata* on blocks with live mussels.

In summary, zebra mussels have a strong impact on the composition of the benthos. We found indications of a chemical communication between adult and larval *D. polymorpha* and subsequent trophic and competitive interactions. On one hand, there is a positive interaction between settling juveniles and living adults or empty shells, possibly triggered by a chemical cue present in the shells or released by biofilm bacteria. On the other hand, there is a negative interaction between settlers and habitats occupied by living adults in high densities because of potential food competition or predation by conspecific adults. In addition, amphipods and chironomids benefited from the altered physical structure and biodeposition of the mussels.

5. Acknowledgements

6. References

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