

ORIGINAL ARTICLE

The zebra mussel (*Dreissena polymorpha*) and the benthic community in a coastal Baltic lagoon: another example of enhancement?

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Keywords

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Conflicts of interest

The authors declare no conflicts of interest.

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Abstract

The zebra mussel (*Dreissena polymorpha*), a sessile suspension feeder, has been known to enhance the benthos in the sediment around mussel beds and druses. The enhancement is mainly due to biodepositing activity of the mussel and the resultant organic enrichment of the sediment. In addition, mussel beds increase habitat complexity. In June 2007, we studied the distribution of *D. polymorpha* beds and their effects on the benthos in Kleines Haff, the western part of the Szczecin Lagoon, a Southern Baltic coastal water body. We expected that: (i) the sediment near a *Dreissena* bed will support meio- and macrobenthic assemblages more abundant than those living away from the bed, and (ii) the meio- and macrobenthic assemblages close to the *Dreissena* bed will show a stronger dominance of the taxa relying on the organic enrichment (nematodes among the meiofauna; oligochaetes and chironomids among the macrobenthos). Meio-benthos was sampled at two localities, one (MB4) featuring *D. polymorpha* druses and the other (MB5) supporting a distinct zebra mussel bed. The two localities differed in their meiobenthic communities: whereas no difference in abundance and composition was observed between the sets of samples collected at MB4, MB5 showed a distinctly more abundant meiobenthos in the uppermost sediment layer near the zebra mussel bed, but the overall abundance was lower than that away from the bed. We conclude that the meiobenthic response to the presence of *D. polymorpha* was, at least in part, mediated by site-specificity of sediment characteristics. Macrozoobenthos was sampled at four stations in the vicinity of MB5 and around another *Dreissena* locality (MB10), and was also identified in the sediment samples collected for the meiobenthos. The macrobenthic abundance was higher by a factor of 2.4 (sandy sediment) to 4.9 (silty bottom) near the *Dreissena* beds than away from them. Irrespective of their situation relative to *Dreissena* aggregations, both meio- and macrobenthos were dominated by the taxa associated with organic enrichment. The macrobenthos associated with *Dreissena* beds included *Gammarus tigrinus*, a non-indigenous amphipod, whereas another non-native species, the polychaete *Marenzelleria neglecta*, was present in the macrobenthos of sandy sediments of the area.

Problem

Sessile suspension feeders, particularly bivalves, are commonly regarded as keystone species in aquatic ecosystems (Covich *et al.* 1999) due to the variety of effects they produce. Their feeding mode renders them important in benthic-pelagic couplings (Newell 2004) via the effects they produce both in the water column and on the bottom. The effects observed in the water column include changes in seston flux (Asmus & Asmus 1991; Muschenheim & Newell 1992; Baker *et al.* 1998), improvement of water quality and nutrient removal (Nakamura & Kerciku 2000; Yamamuro *et al.* 2000; Newell *et al.* 2002) as well as removal of bacteria (Silverman *et al.* 1997). In the benthic system, they modify the bottom architecture (Buschbaum *et al.* 2009; Crooks & Khim 1999) and provide additional habitats for various other taxa (e.g. Morgado & Tanaka 2001), including alien species (Çinar *et al.* 2008), but their major role there is through the formation of biodeposits, silt production, and sediment organic enrichment, whereby the energy transfer to the benthos is facilitated (Kautsky & Evans 1987; Jaramillo *et al.* 1992; Haven & Morales-Alamo 1996; Kröncke 1996; Ragueneau *et al.* 2005; Kooijman 2006). The ensuing effects involve epi- and infaunal attraction to, as well as their facilitation and enhancement in, the suspension feeder's settlement sites (e.g. Krantz 1973; Radziejewska 1986; Jacobi 1987a,b; Commito & Boncavage 1989; Svane & Setyobudiandi 1996; Crooks 1998; Thiel & Ulrich 2002; Tsuchiya 2002; Duarte *et al.* 2006; Vaughn & Spooner 2006). However, biotic effects of sessile suspension feeders are not always clearly identifiable, and multiple and divergent results in complex systems have been observed (Cummins *et al.* 2001; Spooner & Vaughn 2006).

The zebra mussel (*Dreissena polymorpha*) is a sessile suspension feeding bivalve that has attracted immense attention as an invader in various aquatic ecosystems of the Northern hemisphere (Minchin *et al.* 2002), but also as a keystone species involved in benthic-pelagic couplings (Fréchette & Bourget 1985; Ackerman *et al.* 2001; Daunys *et al.* 2006) that exerts multiple effects in the reservoirs it inhabits. Zebra mussels have been reported to affect aquatic ecosystem energy budgets and food-web structure (e.g. Hamburger *et al.* 1990; MacIsaac *et al.* 1991, 1995; Richardson & Bartsch 1997; Thayer *et al.* 1997) by, among others, interaction with microorganisms (Frischer *et al.* 2000) as well as with bacterio-, phyto-, and zooplankton (e.g. Cotner *et al.* 1995; Lavrentyev *et al.* 1995; MacIsaac *et al.* 1995; Bastviken *et al.* 1998), by affecting fish predation and spawning (Prejs *et al.* 1990; Gonzalez & Downing 1999; Marsden & Chotkowski 2001; McCabe *et al.* 2006), and by augment-

ing food resources available to waterfowl, e.g. the coot (*Fulica atra*) (Piesik 1983). The major effects, however, involve – as in other sessile suspension feeder bivalves – an increase in architectural complexity of the bottom as well as energy transfer to the bottom via biofiltration of water, biodeposition, and organic enrichment of the sediment, and the resultant facilitation and enhancement of invertebrate communities (recently summarised by Ward & Ricciardi 2007).

The biofiltering capacity of the zebra mussel (Horgan & Mills 1997; Orlova *et al.* 2004) has rendered the species attractive as a potential tool for water quality management (Piesik 1983; Smit *et al.* 1993; Mackie & Wright 1994; Fenske 2002, 2005; Gulati *et al.* 2008). For this potential to be taken advantage of in a given water body, it is necessary to have information on the *Dreissena* distribution and the role it plays in the reservoir to be managed. With this general objective in mind, a research programme aimed at mapping *Dreissena* distribution and the bivalve's potential for affecting the local benthic communities was launched in June 2007 in the Kleines Haff, the western part of the Szczecin Lagoon (a Southern Baltic coastal water body; Radziejewska & Schernewski 2008). We asked whether, and to what extent, the presence of *Dreissena* aggregations on the bottom could be important in structuring assemblages of meio- and macrobenthos in the Kleines Haff, and whether the effects observed would conform to the universality of interactions between sessile suspension feeders and other invertebrates, proposed by Ward & Ricciardi (2007) (but see Buschbaum *et al.* 2009, who found exceptions to the seemingly universal pattern).

To summarise, the structural complexity of a *Dreissena* bed or a druse offers a variety of refuges and microhabitats to small invertebrates (Botts *et al.* 1996). In addition, as a result of the zebra mussel feeding mode involving ingestion of suspended particulates and release of faeces and pseudofaeces, the presence of the bivalve on the bottom results in organic enrichment of the sediment surrounding the aggregation (Griffiths 1993). In this way, *D. polymorpha* acts as a habitat modifier that facilitates and enhances the development of benthic invertebrate communities (Ward & Ricciardi 2007). This line of reasoning led us to expect that:

- 1 The sediment near a *Dreissena* bed will support meio- and macrobenthic assemblages more abundant than those living away from the bed, as a result of facilitation and enhancement rendered by organic enrichment produced by *Dreissena*;
- 2 The meio- and macrobenthic assemblages in the sediment adjacent to the *Dreissena* bed will show a stronger dominance of those taxa relying on the organic enrich-

ment, primarily nematodes among the permanent meiofauna, and oligochaetes and chironomids among the macrobenthos.

In addition, our study was meant to provide qualitative and quantitative data on the Kleines Haff benthos; such data, particularly with respect to the meiobenthos, are scarce, while being urgently needed for a comprehensive assessment of the Haff's biota.

Material and Methods

Area of study

The Kleines Haff (Fig. 1) is the western part of the Szczecin Lagoon (German: Oderhaff), a coastal Southern Baltic water body with a long history of pollution and eutrophication (Radziejewska & Schernewski 2008). The Kleines Haff is shallow (average depth of 4.4 m), its average salinity being 1 ppt. The bottom in the nearshore zone is sandy and becomes more and more fine-grained towards the central part where muddy sediment (<0.063 mm grain size fraction accounting for $>80\%$) prevails (Osadczuk 2004). Data on hydrographical parameters measured during the sampling campaign are summarised in Table 1.

Several areas supporting zebra mussel aggregations were revealed during the June 2007 campaign (*Dreissena* areas MB1–MB12; Fig. 2). The zebra mussels were estimated to cover a total of 6.56 km^2 of the Kleines Haff bottom (*i.e.* 2.4% of the bottom area). The *Dreissena* biomass was estimated at $8812.65 \times 10^3 \text{ kg}$, with abundances ranging from 864 to $10,444 \text{ ind} \cdot \text{m}^{-2}$.

Field work

Samples for the study of the zebra mussel-associated meiobenthos were collected from two localities (*Dreissena* areas MB4 and MB5, *cf.* Fig. 2), two sites being sampled in each. The idea was to sample the sediment as close as possible to a *Dreissena* bed and away from it, and to compare the composition and abundance of meiobenthic assemblages from the two sites.

At MB4 (Fig. 2), located at the depth of about 3 m and about 150 m away from the shore, *Dreissena* occurred in scattered clumps (druses) anchored in the bottom rather than forming a distinct bed. Consequently, the two sites sampled in the locality (denoted A and B) could not be sharply contrasted for the *Dreissena*-close *versus* *Dreissena*-away effect, although an effort was made to collect the sediment close to the druses (site A) and, as much as possible, away from any druse (site B). Visual observations of the sediment in samples from the two sites showed hardly any difference between them; the sediment consisted of sand, abundant shell debris, and coarse and fine detritus.

Dreissena area MB5 supported a distinct zebra mussel bed, and was sampled at sites denoted R (sediment cores collected close to the mussel bed) and O (about 10 m away from the bed). Visual observations of the sediment in samples showed fairly distinct differences between the two sites: whereas the site O sediment consisted of sand, shell debris, and rather fine detritus, the site R samples contained sediment with a clearly higher amount of shell debris and detritus. In addition, the site R cores showed a characteristic sediment composition whereby about 1 cm of heavily organically enriched sand mixed with shell debris.

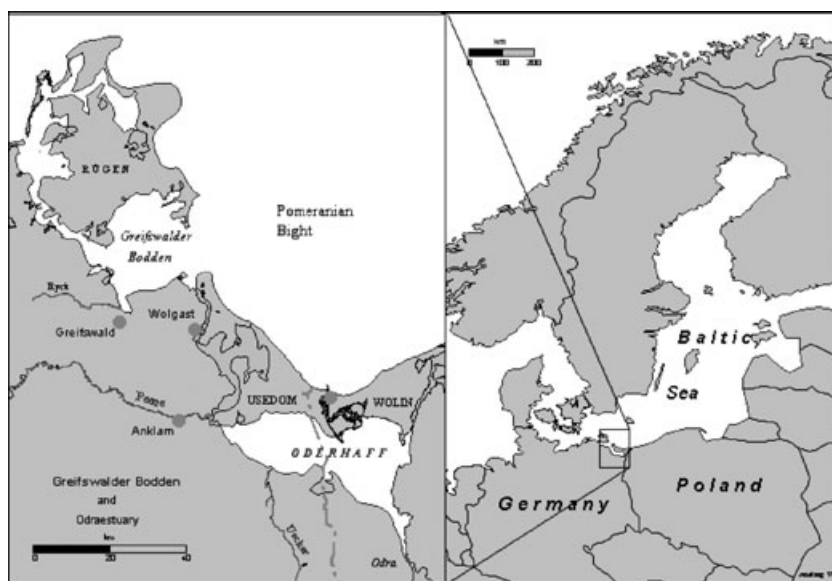


Fig. 1. The Szczecin Lagoon (Oderhaff): general location; the Kleines Haff occupies the western part of the Szczecin Lagoon.

Table 1. Hydrographic parameters measured at the sites sampled during the June 2007 sampling campaign in the Kleines Haff.

parameter	average or mean (\pm SD) value (range)
Secchi depth (m)	0.57 (0.4–1.7)
dissolved oxygen content ($\text{mg}\cdot\text{dm}^{-3}$)	10.12 ± 1.72 (1 m below surface), 8.71 ± 2.19 (0.4 m above bottom)
$\text{PO}_4\text{-P}$ content ($\text{mg}\cdot\text{dm}^{-3}$)	0.1 (0.03–0.2)
total P ($\text{mg}\cdot\text{dm}^{-3}$)	0.2 (0.16–0.32)
total N ($\text{mg}\cdot\text{dm}^{-3}$)	1.21 (0.9–1.9)
BOD_5 ($\text{mg}\cdot\text{dm}^{-3}$)	3.72 (2.6–5.39)
suspended particulates concentration ($\text{mg}\cdot\text{dm}^{-3}$)	13.7 (9.5–18.1)
chlorophyll <i>a</i> content ($\mu\text{g}\cdot\text{dm}^{-3}$)	61.3 ± 9.5

ris overlay a peat-like deposit consisting of tightly packed large plant remains interspersed by shell fragments and sand grains.

Meiobenthos sampling

Sediment samples for the study of meiobenthos were collected by divers using hand-held corers (22 mm inner diameter) consisting of transparent polycarbonate tubes. At each site, five sediment cores were retrieved. The tubes were inserted into the sediment to the depth of about 10 cm. When in the sediment, the tube was closed from above with a rubber stopper and was carefully pulled out; once out of the sediment, the lower end of the tube was closed with a rubber stopper to prevent sample loss. Following retrieval, the near-bottom water overlying the sediment was siphoned off into a container, and the entire core was pushed up, from below, by a piston. The

uppermost 1-cm-thick layer was cut off to form the ‘upper sediment’ sample and transferred to a container, and the remainder of the core (the ‘lower sediment’ sample) was placed in another container. The water and sediment samples were preserved with 10% buffered formalin and stained with Rose Bengal. At each station, five sediment cores were collected.

Macrobenthos sampling

Macrobenthos was sampled at five stations representative of various sedimentary habitats in the Lagoon. Four of the sites were close to the meiobenthos sampling stations (near MB5; Fig. 2), one being located in the western part of the Kleines Haff (near MB10; Fig. 2). At three sampling stations (P16S3, P6S1, P6S2; Fig. 2), macrobenthos was collected away from *Dreissena* aggregations; the sediment at those stations was silt, silty sand and sand, respectively. The two remaining stations (P13S3, P18S1; Fig. 2) supported *Dreissena* druses or a *Dreissena* bed, the underlying sediment containing a high proportion of shell debris and detritus. The samples were collected from RV *Bornhöft* with Günther box corers (10 cm \times 10 cm or 10 \times 6 cm surface area, both penetrating about 20 cm into the sediment). At each site, three sediment samples were collected. The samples were sieved through an 0.5-mm sieve and the sieving residue was fixed in 10% buffered formalin.

Laboratory procedures

In the laboratory, the content of each meiobenthos sample container was wet-sieved on a series of sieves (mesh sizes used: 1.00 and 0.500 mm to separate the macrobenthic animals; 0.180; 0.090 and 0.032 mm). The residues from the two coarsest sieves were retained for

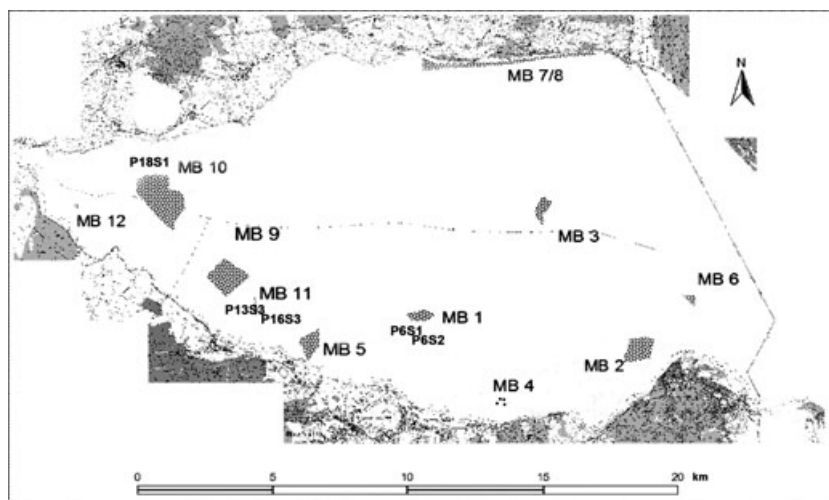


Fig. 2. Zebra mussel beds in the Kleines Haff and location of macrobenthos sampling stations.

identification of any macrobenthic animals present (see below). The residues from the 0.032–0.500-mm sieves were transferred, in portions, onto ruled Petri dishes and examined under a stereomicroscope. Meiobenthic organisms were identified to the lowest taxon possible and enumerated.

Macrobenthic animals were removed from the sieving residue, rinsed with tap water (on a 0.5-mm sieve), examined under a stereomicroscope, identified to the lowest taxon possible, and enumerated.

Statistical treatment

Significance of differences between mean abundances and mean relative abundances of the benthic assemblages was tested by means of non-parametric Kruskal–Wallis test (Sokal & Rohlf 1995).

Results

Meiobenthos

The number of meiobenthic taxa present in the sediment (Table 2) was found to depend on both the site and the core section, the uppermost sediment layer usually supporting more diverse meiofauna. In terms of the total number of taxa found in the core, meiobenthic assemblages at sites A and B proved more diverse than those at the other pair of sites, Site R showing the widest within-site variability in the number of taxa.

The meiobenthic assemblages were found to be dominated by nematodes (Fig. 3A,B). In terms of the entire core (Fig. 3B), the mean percent contribution of nematodes to the entire assemblage ranged from about 35% at site B to about 85% at site O, the nematode domination at the MB5 sites, particularly at site O, being much stronger than at the MB4 sites. Other taxa of importance were ostracods, oligochaetes, chironomid larvae, and harpacticoid copepods (cf. Fig. 3).

The total meiobenthos abundance was found to range from a minimum of $255.11 \text{ ind} \cdot (10 \text{ cm}^2)^{-1}$ to a maximum of $3084.99 \text{ ind} \cdot (10 \text{ cm}^2)^{-1}$. Generally, the MB4 sites supported meiobenthic communities that were signifi-

cantly ($P < 0.05$) less abundant than those at MB5 (Fig. 3A). The whole-core meiobenthos abundances at the MB4 sites were very similar; on the other hand, at MB5, the meiobenthos at site O (away from the *Dreissena* bed) was much more abundant than that at site R, although the difference was not significant ($P > 0.05$) due to the high within-site variability.

At all sites, the top centimetre of the sediment was inhabited by most of the meiobenthic animals found in the entire core (Table 3). This trend was at its weakest at site O where more than half of the meiobenthic animals (about 56%) dwelt below the uppermost sediment layer. At MB4, there were no significant between-sites differences ($P > 0.05$) in the partitioning of the meiobenthic assemblages between sediment layers; conversely, the two MB5 sites differed significantly in this respect ($P < 0.05$), the site located next to the *Dreissena* bed (R) showing a marked aggregation of the meiobenthos (about 86% of the total abundance) in the uppermost sediment layer.

Meiobenthic abundances in the uppermost sediment layer (Fig. 3C) repeated some of the pattern evidenced by the total abundances, namely significantly lower ($P < 0.05$) abundances at MB4 than at MB5 and no significant between-site differences ($P > 0.05$) at either of the site pairs. At MB5, however, the meiobenthos was much more abundant in the uppermost sediment layer of site R than of site O, although the difference was not significant ($P > 0.05$) due to the high within-site variability.

Macrobenthos

The number of macrobenthic taxa per sample varied from 2 to 8. Although we found a total of 27 macrobenthic taxa, the maximum taxon richness per sample was rather low, even at the zebra mussel bed stations. Oligochaetes and chironomid larvae were the dominant taxa at most stations (Fig. 4A), except for one mussel bed station dominated by *D. polymorpha*, abundant also at the other *Dreissena* bed sampling site (Fig. 4A).

The macrobenthic abundance varied greatly over the area sampled: the mean total abundances ranged from 3367 to $18,333 \text{ ind} \cdot \text{m}^{-2}$ (Table 4; Fig. 4B). Higher abundances were found at the station in the *Dreissena* area MB10 (P13S3), with live *Dreissena* and empty shells (Fig. 4B). The mean total abundances of the macrobenthos sampled in the vicinity of the *Dreissena* beds were much higher than away from the beds; however, due to the high within-site variability (cf. high standard deviations in Table 4 and Fig. 4B), the difference between the two groups of stations was not significant ($P > 0.05$).

Macrobenthic animals retrieved from the meiobenthic samples (Table 5) represented six major taxa (Oligochaeta, Hirudinea, Gastropoda, Bivalvia, Crustacea, and Dip-

Table 2. Taxon richness of meiobenthic assemblages at sites sampled: ranges of the number of taxa.

locality	MB4		MB5	
	site A	site B	site O	site R
core part				
uppermost	11–13	9–12	7–9	6–12
lower sediment	6–9	7–10	5–8	3–9
total	11–14	9–13	8–10	6–13

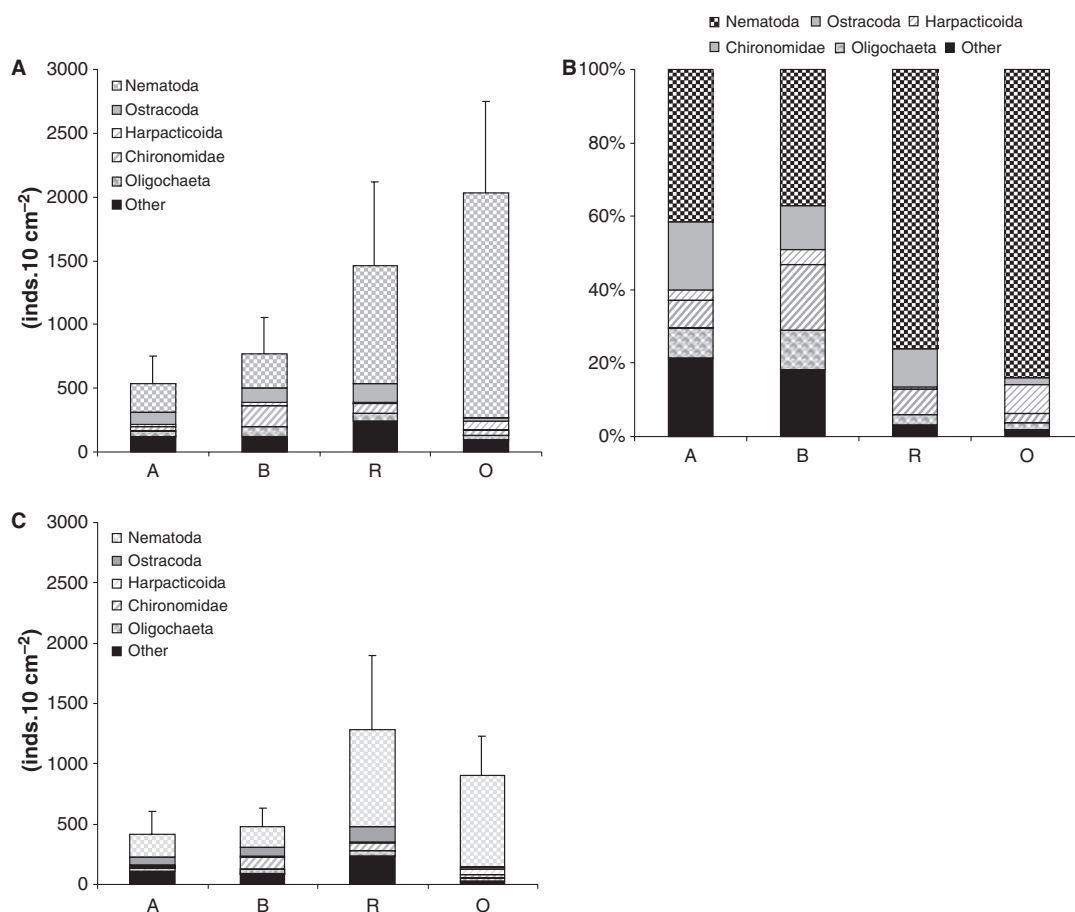


Fig. 3. Meiobenthos in the Kleines Haff. (A) Total meiobenthos abundance. (B) Composition of the Kleines Haff meiobenthos (total core). (C) Meiobenthos abundance in top sediment layer.

Table 3. Partitioning of meiobenthic abundance between the core parts examined: mean (\pm SD) percentages of total abundance at the core parts.

locality	site	U upper core part	Lower sediment part	significance of within-locality difference
MB4	A	74.79 \pm 5.56	25.21 \pm 5.57	not significant ($P > 0.05$)
	B	62.67 \pm 4.85	37.33 \pm 4.85	
MB5	R	88.76 \pm 12.98	11.24 \pm 12.98	significant ($P < 0.05$)
	O	44.16 \pm 6.36	55.83 \pm 6.36	

tera). Generally, a higher taxon richness was evident at sites A and R (closest to *Dreissena* druses or beds). The macrobenthos was dominated by chironomid larvae and oligochaetes, except for site A showing a high proportion of *Gammarus tigrinus* (prominent also at site R) and small specimens of *Dreissena polymorpha* (Fig. 5A). The mean total abundances varied from 64,924 to 87,273 ind·m⁻² (Table 5; Fig. 5B). Although the total abundances at sites A and R (closest to *Dreissena* aggrega-

tions) tended to be higher than elsewhere, the high within-site variability precluded statistical significance of the differences.

The sites sampled for macrobenthos revealed the presence of some non-indigenous taxa. Among those, the amphipod *G. tigrinus* was found at two of the five stations sampled, with the maximum abundance of 167 ind·m⁻² (cf. Table 4). Other invaders included *Obesogammarus crassus* and *Pontogammarus robustoides*, both found in an ancillary sample collected for the concurrent study of macrophytes at MB4; and the polychaete *Marenzelleria neglecta*. The latter occurred only at the sandy stations (P6S2) and was not very abundant (67 ind·m⁻²).

Discussion

Meiobenthos

Examination of cores collected within areas supporting *Dreissena* beds and druses in the Kleines Haff provided information on the composition and abundance of meio-

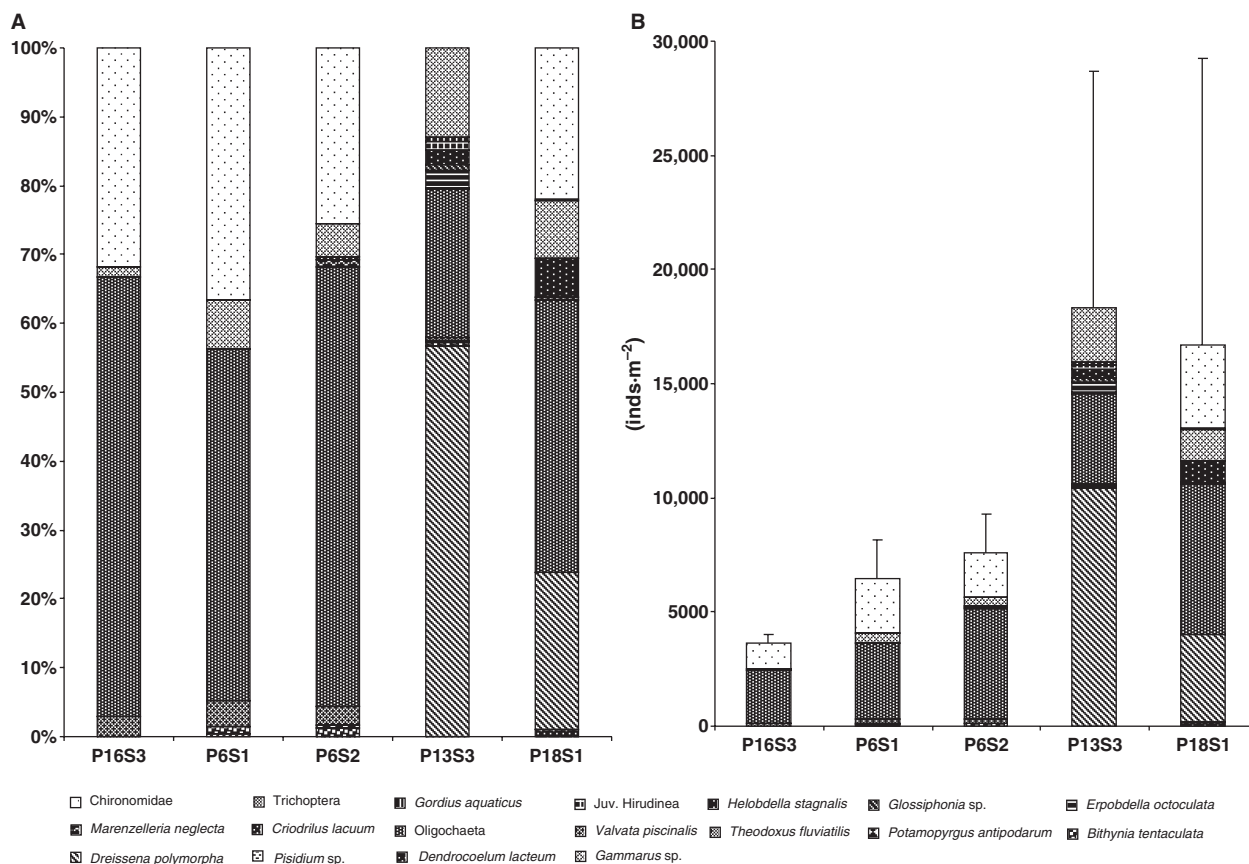


Fig. 4. Macrobenthos in the Kleines Haff. (A) Relative abundance of macrobenthic taxa. (B) Mean abundances (ind·m⁻² ± SD) of macrobenthos.

benthic assemblages inhabiting those areas. The meiobenthic aspect of *Dreissena*–benthos interactions has been largely ignored so far. It was only Dermott & Kerec (1997) who reported increased abundances of meiofauna, notably ostracods, nematodes, and harpacticoids following *Dreissena* settlement in the Eastern Lake Erie. They attributed the very highly significant increase in mean densities of those meiobenthic taxa to an increase in the amount of organic matter and associated bacteria in the faeces and pseudofaeces being deposited onto the sediment surface by *Dreissena*. In the present study, the abundance of meiobenthic assemblages, estimated from the total core data (Fig. 3A), only partially conformed to the expected pattern, in that the mean abundances at the *Dreissena* bed-supporting locality (MB5) were significantly higher than those at the locality with scattered zebra mussel druses (MB4). However, no significant difference in the mean total abundance was found between the two sites sampled within MB5, although a strong tendency towards higher abundances at the site away from the *Dreissena* bed was observed (cf. Fig. 3A). The effect could have been partially a result of sediment differences between the two sites:

whereas at site R the underlying sediment was very consolidated, peaty, and thus hardly penetrable by the fauna, site O supported sediment that was mostly sandy and thus amenable to colonisation by interstitial fauna throughout the entire depth sampled. On the other hand, had we considered the uppermost sediment layer only, the enhancement hypothesis (higher abundance near the *Dreissena* bed than away from it, i.e. at site R versus site O; cf. Fig. 3C) would have been borne out by the data from MB5. The results for the whole core, however, weaken the actual support for the hypothesis. It seems that the result observed could have been caused by a combination of factors: *Dreissena* facilitation (increased organic matter content in the sediment) on the one hand and purely physical effect (more available space in the penetrable uppermost sediment layer) on the other.

The lack of a clear-cut pattern in the meiobenthic assemblage response could also have been associated with seasonal effects. Aggregations of suspension feeders, including *Dreissena polymorpha*, were reported to exhibit seasonal variability (e.g. Cummings *et al.* 2001; Wolnomiejski & Woźniczka 2008). Coupled with high

Table 4. Mean (\pm SD) macrobenthic abundances (ind·m⁻²) at the Kleines Haff sites sampled for the macrobenthos during the June 2007 campaign.

	sampling site				
	P16S3	P6S1	P6S2	P13S3	P18S1
sediment type	silt	silty sand	sand	shells, <i>Dreissena</i> clumps	silt, <i>Dreissena</i> bed
taxon					
<i>Dendrocoelum lacteum</i>	0	0	0	0	166.67 \pm 288.68
<i>Pisidium</i> spp.	0	33.33 \pm 57.74	0	0	0
<i>Dreissena polymorpha</i>	0	0	0	10,388.9 \pm 7874.8	3833.33 \pm 2020.77
<i>Bithynia tentaculata</i>	0	66.67 \pm 57.74	100.0 \pm 100.0	111.11 \pm 96.23	0
<i>Potamopyrgus antipodarum</i>	0	0	33.33 \pm 57.74	0	0
<i>Theodoxus fluviatilis</i>	0	0	0	55.56 \pm 96.23	0
<i>Valvata piscinalis</i>	111.11 \pm 96.23	233.33 \pm 251.66	200.0 \pm 100.0	55.56 \pm 96.23	0
Oligochaeta	2333.33 \pm 0	3300.0 \pm 1664.3	4833.33 \pm 1026.3	3944.44 \pm 1512.3	6611.11 \pm 4715.12
<i>Criodrilus lacuum</i>	0	0	0	55.56 \pm 96.23	0
<i>Marenzelleria neglecta</i>	0	0	66.67 \pm 57.74	0	0
<i>Erpobdella octoculata</i>	0	0	0	444.44 \pm 384.91	0
<i>Glossiphonia</i> sp.	0	0	0	166.67 \pm 166.67	55.56 \pm 96.3
<i>Helobdella stagnalis</i>	0	0	0	388.89 \pm 254.59	944.44 \pm 693.90
Hirudinea juv.	0	0	0	222.22 \pm 192.45	0
<i>Gordius aquaticus</i>	0	0	33.33 \pm 57.74	111.11 \pm 192.45	0
<i>Gammarus</i> spp.	0	466.67 \pm 230.94	199.99 \pm 346.41	0	1222.22 \pm 2116.99
<i>G. zaddachi</i>	0	0	166.67 \pm 288.68	2388.89 \pm 1170.7	0
<i>G. tigrinus</i>	55.56 \pm 96.23	0	0	0	166.67 \pm 166.67
Trichoptera	0	0	0	0	55.56 \pm 96.23
Chironomidae	1166.67 \pm 166.67	2366.67 \pm 603.68	1933.33 \pm 608.49	0	3666.67 \pm 3355.18
total	3666.67 \pm 333.34	6466.67 \pm 1680.3	7566.67 \pm 1721.4	18,333.3 \pm 10,332.2	16,722.22 \pm 12,549.41
no. of taxa per sample	2–4	4–6	4–7	6–8	5–7

susceptibility of meiobenthic assemblages to temporal variability (Radziejewska & Chabior 2004), the seasonal effect could have masked or obliterated the responses expected, had they occurred.

The meiobenthos at all sites was strongly dominated by the taxa relying on the organic enrichment, *i.e.* nematodes, chironomids, and ostracods. The Kleines Haff, like the entire Szczecin Lagoon, has been heavily eutrophic for decades (Radziejewska & Schernewski 2008), hence the sediment is highly organically enriched as a result of background sedimentation. Nematodes, chironomids, and ostracods have been reported as absolute dominants of the Lagoon meiobenthos (Radziejewska & Drzycimski 1988, 1990; T. Radziejewska, unpublished observations). It seems then that the enhancement hypothesis is only partially borne out by the meiobenthos data, and that site-specific effects could play an important role in shaping the meiobenthic assemblages associated with *Dreissena* aggregations in the Kleines Haff. In a different setting, Norkko *et al.* (2001) pointed out the importance of site-specific effects, related to a sedimentation gradient, leading to changes in interactions between the suspension-feeding bivalve *Atrina zelandica* and the benthos in a coastal ecosystem.

It is noteworthy that the maximum meiobenthic mean total abundance recorded in this study, 3084.99 ind·(10 cm²)⁻¹, proved higher than any meiobenthic abundance reported so far from the entire Szczecin Lagoon (Radziejewska & Drzycimski 1988, 1990; Radziejewska & Schernewski 2008). The only other set of Kleines Haff meiobenthos abundance data on hand (T. Radziejewska, unpublished observations) originated from research carried out in the early 1990s, based on samples collected in the central part of the area (muddy bottom). The maximum abundance recorded then was about 380 ind·(10 cm²)⁻¹ and the meiobenthic assemblages were strongly dominated by ostracods.

Macrobenthos

Compared to the meiobenthos, the macrobenthic assemblages sampled in this study showed a more pronounced abundance pattern supporting the facilitation and enhancement hypothesis, and conforming to situations reported in other studies (*e.g.* Beekey *et al.* 2004). The macrobenthic abundances near the zebra mussel bed were substantially higher than the abundances recorded at the bottom away from the *Dreissena* bed (*cf.* Fig. 5). It is worth mentioning

Table 5. Mean (\pm SD) total macrobenthic abundances (ind·m⁻²) at the Kleines Haff sites sampled for the meiobenthos during the June 2007 campaign.

taxon (% frequency)	sampling locality/site			
	MB4/A	MB4/B	MB5/R	MB5/O
Oligochaeta (12.1)	22,727.3 \pm 28,747.98	19,090.9 \pm 8743.36	38,181.8 \pm 25,430.18	6818.2 \pm 5868.16
Hirudinea (9.1)	3636.4 \pm 5926.55	0.0	2272.7 \pm 0.00	3030.3 \pm 2624.32
<i>Valvata piscinalis</i> (6.1)	909.1 \pm 2032.79	0.0	6818.2 \pm 3214.12	0.0
<i>Valvata pulchella</i> (3.0)	0.0	0.0	4545.5 \pm 0.00	0.0
<i>Pisidium nitidum</i> (6.1)	909.1 \pm 2032.79	3409.1 \pm 4351.94	0.0	0.0
<i>Dreissena polymorpha</i> (6.1)	17,272.7 \pm 22,590.50	0.0	4545.5 \pm 0.00	0.0
<i>Gammarus tigrinus</i> (6.1)	24,545.5 \pm 47412.38	0.0	4545.5 \pm 0.00	0.0
<i>Procladius</i> sp. (3.0)	0.0	2272.7 \pm 0.00	0.0	0.0
<i>Chironomus</i> sp. (12.1)	11,818.2 \pm 14766.48	25,000.0 \pm 15414.39	4545.5 \pm 0.00	3030.3 \pm 2624.32
<i>Glyptotendipes</i> sp. (12.1)	2727.3 \pm 4065.58	1515.2 \pm 0.00	12,727.3 \pm 7468.94	4545.5 \pm 0.00
<i>Tanytarsus</i> sp.(9.1)	0.0	5681.8 \pm 0.00	6818.2 \pm 0.00	30,303.0 \pm 31,926.22
Chironomidae indet. (9.1)	0.0	6818.2 \pm 0.00	2272.7 \pm 0.00	34,090.9 \pm 0.00
Chironomidae pupae (6.1)	0.0	1136.4 \pm 0.00	0.0	2272.7 \pm 0.00
total	84,545.5 \pm 102,982.4	64,924.2 \pm 20,680.6	87,272.7 \pm 28,640.0	84,090.91 \pm 40,092.9
total number of taxa (range)	8.0 (4–6)	8.0 (2–7)	10.0 (2–6)	7.0 (0–5)

that under conditions of the highly polluted Rhine-Meuse estuary, the only site among those sampled by Smit *et al.* (1995) that showed elevated abundances of the macrobenthos was the locality supporting a *Dreissena* bed.

On the other hand, the macrobenthos data provided by the small meiobenthos sediment cores failed to reveal any pattern, perhaps due to too small sediment volume being available for projecting the macrobenthic abundance.

The most abundant macrobenthic assemblages differed in their composition and domination structure (*cf.* Fig. 4), but did show domination of the taxa known to be associated with organically enriched sediment (oligochaetes and chironomid species typical of muddy habitats). However, those taxa were prominent at other sites as well, for reasons already discussed above.

On the other hand, the sites supporting the highest macrobenthic abundance were not particularly taxa-rich. The station with the highest abundance (P13S3) supported 18,333 ind·m⁻², but only 10 taxa. This finding lends support to the conclusion of Buschbaum *et al.* (2009) who, having analysed diversity of mussel bed-associated fauna in different parts of the world, contended that mussel beds themselves were hardly universal centres of biodiversity, and that their effects on associated species were site-specific. The macrobenthic community at the highest-abundance station showed the presence of chironomid [*Glyptotendipes* sp., *Polypedilum (nubeculosum)* group], *Tanytarsus* sp.] and mollusc (*Valvata piscinalis*) species known for their association with sandy rather than muddy sediment.

It has to be remembered that facilitation and enhancement of macrobenthos by an aggregation of a suspension-

feeding bivalve are not absolute. Species that produce planktonic larvae, *e.g.* polychaetes, will not be enhanced, and may even be inhibited by a suspension feeder, as demonstrated by Duarte *et al.* (2006) for *Mytilus chilensis*, Ragnarsson & Raffaelli (1999) for *Mytilus edulis*, Crooks & Khim (1999) for *Musculista senhousia*, and Dermott & Kerec (1997) for *Dreissena polymorpha*. In the latter case, the detrimental effects were shown by the burrowing amphipod *Diporeia hoyi* and by fingernail clams (Sphaeriidae) (see also Lauer & McComish 2001). In contrast, non-planktonic developers (*e.g.* chironomid larvae, oligochaetes, amphipods) showed positive responses to the mussels, and might have even be favoured in the presence of suspension feeders such as *Dreissena* or *M. edulis* (see *e.g.* Commito & Boncavage 1989 for discussion of facilitative effects in the oligochaete *Tubificoides benedeni*).

The polychaete *Marenzelleria neglecta*, a non-indigenous species introduced in the 1980s, was very abundant on sandy sediments in the mid-1990s (averaging 8278 ind·m⁻² in 1996; Fenske 2003). In 2007, *M. neglecta* did occur, but in much lower abundances (67 ind·m⁻²). This is a phenomenon known from many biological invasions (Strayer *et al.* 2006): at first, the invader occurs at a very high abundance ('explosion'), but after a few years it becomes integrated in the existing community and its abundance becomes stabilised at a lower level on account of niche opportunity constraints (*sensu* Shea & Chesson 2002). Our study showed the *Dreissena* bed-associated macrobenthos to include another frequent and abundant non-indigenous species, the amphipod *Gammarus tigrinus*. It is also known to have been present in the Szczecin Lagoon since the late 1980s (Wawrzyniak-Wydrowska &

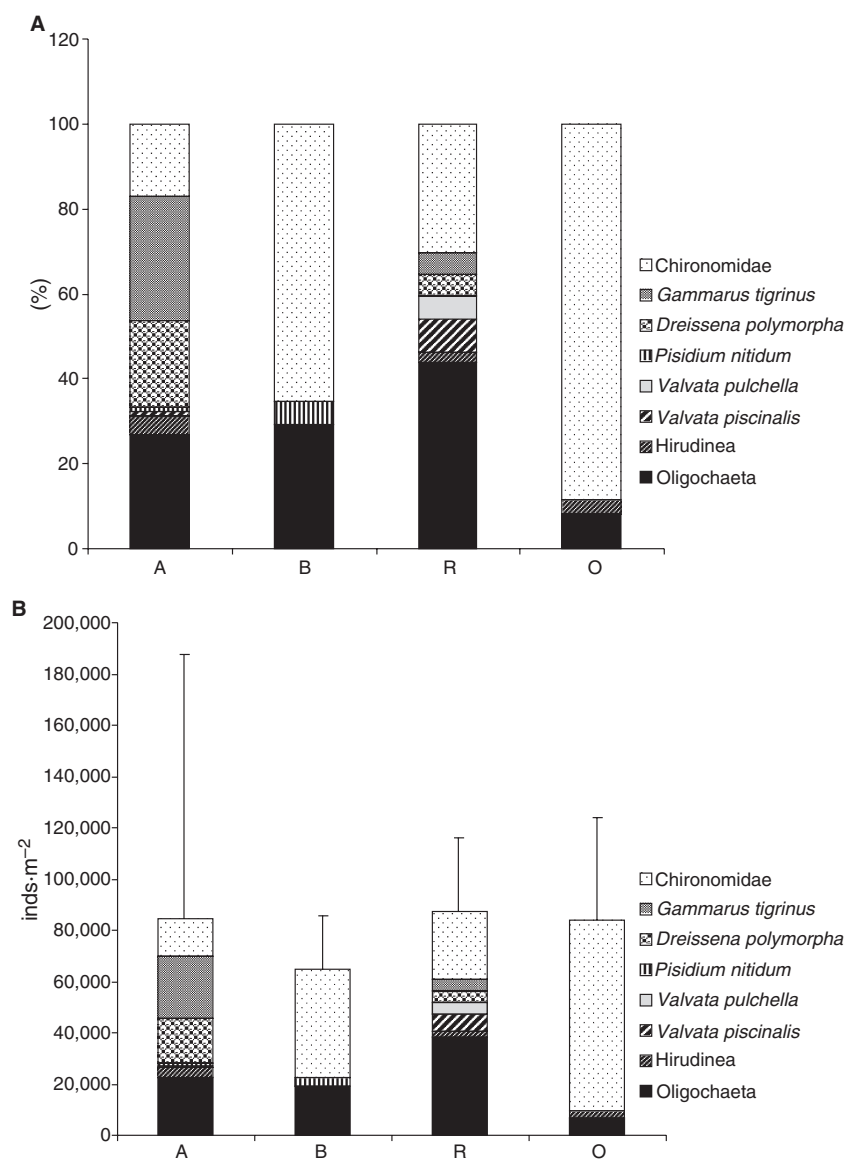


Fig. 5. Macrobenthos retrieved from meiobenthic samples. (A) Relative abundances of macrobenthic taxa. (B) Mean abundances (ind·m⁻² ± SD) of macrobenthos.

Gruszka 2005). *Gammarus tigrinus*, the commonest invader in the eastern part of the Lagoon (Wawrzyniak-Wydrowska & Gruszka 2005), was found at several stations sampled, including the sediment sampled for meiobenthos. The presence of this amphipod in the Kleines Haff is in line with two other interesting, interconnected findings reported in other accounts on research focusing on *Dreissena* bed-associated macrobenthos: a preference of amphipods for inhabiting *Dreissena* beds (e.g. Griffiths 1993; Dermott & Kerec 1997; Thayer *et al.* 1997; Gonzalez & Downing 1999) and facilitation of non-indigenous species' expansion in aquatic environments by *Dreissena* (e.g. Limén *et al.* 2005; Çinar *et al.* 2008). Positive amphipod response to *Dreissena* is thought to be a result of the amphipod's reliance on increased habitat complexity

(a physical effect; Botts *et al.* 1996) as a means to aiding the release from predation pressure exerted by, for example, fish (a biotic effect; Gonzalez & Downing 1999). Limén *et al.* (2005) used a stable isotope technique in an attempt to elucidate mechanisms of success of an invader amphipod, *Echinogammarus ischnus*, in replacing the native amphipod *Gammarus fasciatus*. Both species show positive responses to the presence of *Dreissena* beds (Palmer & Ricciardi 2004); exploitative competition for food (*Dreissena* faeces/pseudofaeces) was put forward by Limén *et al.* (2005) as an underlying cause for the *E. ischnus* success. However, evidence obtained showed that not to be the case. Palmer & Ricciardi (2004) postulated segregation of the two amphipod species along physicochemical gradients in the habitat, *E. ischnus* showing a stronger

preference towards coarse-grained sediment which *Dreissena* beds might resemble. By revealing the presence and abundance of the alien amphipods associated with the Kleines Haff *Dreissena* aggregations, our study contributes to the ongoing discussion on and concern about non-native species colonising the Southern Baltic coastal waters (Wawrzyniak-Wydrowska & Gruszka 2005).

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