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

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Alien species; Baltic Sea; *Dreissena polymorpha*; macrobenthos; meiobenthos; organic enrichment; Szczecin Lagoon.

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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 *Dreissena* druses and the other (MB5) supporting a distinct zebra mussel bed. The two localities differed in their meio-benthic communities: whereas no difference in abundance and composition was observed between the sets of samples collected at MB4, MB5 showed a distinctly more abundant meio-benthos 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 meio-benthic 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 meio-benthos. 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.
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**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 (Cinar *et al.* 2008), but their major role is perhaps in 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 epis- 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; Committ & Boncavage 1989; Svane & Sæto (2001); 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 (Cummings *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.* 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 (Cinar *et al.* 2008), but their major role is perhaps in 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 epis- 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; Committ & Boncavage 1989; Svane & Sæto (2001); 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 (Cummings *et al.* 2001; Spooner & Vaughn 2006).

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-
iment, 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 & Scherniewski 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 (Osa-dczuk 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 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 deb-
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 Bornhøft with Günther box corers (10 cm × 10 cm or 10 × 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
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. Meiofaunal 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 meiofaunal 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, meiofaunal 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 meiofaunal 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 meiofaunal abundance was found to range from a minimum of 255.11 ind·(10 cm$^2$)$^{-1}$ to a maximum of 3084.99 ind·(10 cm$^2$)$^{-1}$. Generally, the MB4 sites supported meiofaunal communities that were significantly (P < 0.05) less abundant than those at MB5 (Fig. 3A). The whole-core meiofauna abundances at the MB4 sites were very similar; on the other hand, at MB5, the meiofauna 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 meiofauna animals found in the entire core (Table 3). This trend was at its weakest at site O where more than half of the meiofauna 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 meiofaunal 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 meiofauna (about 86% of the total abundance) in the uppermost sediment layer.

Meiofauna 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 meiofauna 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 macrofaunal taxa per sample varied from 2 to 8. Although we found a total of 27 macrofaunal 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 macrofaunal abundance varied greatly over the area sampled: the mean total abundances ranged from 3367 to 18,333 ind·m$^{-2}$ (Table 3; 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 macrofauna 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 meiofaunal samples (Table 5) represented six major taxa (Oligochaeta, Hirudinea, Gastropoda, Bivalvia, Crustacea, and Dip-
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* aggregations) 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 meiobenthos.
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Benthic assemblages inhabiting those areas. The meio-benthic 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 meiofaunal 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 meio-benthic 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 meio-benthic 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 & Woźniaczka 2008). Coupled with high

Fig. 4. Macrobenthos in the Kleines Haff. (A) Relative abundance of macrobenthic taxa. (B) Mean abundances (ind·m⁻² ± SD) of macrobenthos.
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 & Drzymciski 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 4. Mean (± SD) macrobenthic abundances (ind.m⁻²) at the Kleines Haff sites sampled for the macrobenthos during the June 2007 campaign.

<table>
<thead>
<tr>
<th>sampling site</th>
<th>P16S3</th>
<th>P6S1</th>
<th>P68S2</th>
<th>P13S3</th>
<th>P18S1</th>
</tr>
</thead>
<tbody>
<tr>
<td>sediment type</td>
<td>silt</td>
<td>silty sand</td>
<td>sand</td>
<td>shells, Dreissena clumps</td>
<td>silt, Dreissena bed</td>
</tr>
<tr>
<td>taxon</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dendrocoelum lacteum</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>166.67 ± 288.68</td>
</tr>
<tr>
<td>Pisidium spp.</td>
<td>0</td>
<td>33.33 ± 57.74</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dreissena polymorpha</td>
<td>0</td>
<td>0</td>
<td>10.388.9 ± 7874.8</td>
<td>3833.33 ± 2020.77</td>
<td></td>
</tr>
<tr>
<td>Bithynia tentaculata</td>
<td>66.67 ± 57.74</td>
<td>100.0 ± 100.0</td>
<td>111.11 ± 96.23</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Potamopyrgus antipodarum</td>
<td>0</td>
<td>33.33 ± 57.74</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Theodoxus fluviatilis</td>
<td>0</td>
<td>0</td>
<td>55.56 ± 96.23</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Valvata piscinalis</td>
<td>111.11 ± 96.23</td>
<td>233.33 ± 251.66</td>
<td>200.0 ± 100.0</td>
<td>55.56 ± 96.23</td>
<td>0</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>2333.33 ± 0</td>
<td>3000.0 ± 1664.3</td>
<td>4833.33 ± 1026.3</td>
<td>3944.44 ± 1512.3</td>
<td>6611.11 ± 4715.12</td>
</tr>
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<td>Cricodrilus lacuum</td>
<td>0</td>
<td>0</td>
<td>66.67 ± 57.74</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Marenzelleria neglecta</td>
<td>0</td>
<td>0</td>
<td>444.44 ± 384.91</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Erpobdella octoculata</td>
<td>0</td>
<td>0</td>
<td>166.67 ± 166.67</td>
<td>55.56 ± 96.3</td>
<td></td>
</tr>
<tr>
<td>Glossiphonia sp.</td>
<td>0</td>
<td>0</td>
<td>388.89 ± 254.59</td>
<td>944.44 ± 693.90</td>
<td></td>
</tr>
<tr>
<td>Helobdella stagnalis</td>
<td>0</td>
<td>0</td>
<td>222.22 ± 192.45</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Hirudinea juv.</td>
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<td>0</td>
<td>111.11 ± 96.23</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Gordius aquaticus</td>
<td>0</td>
<td>0</td>
<td>33.33 ± 57.74</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Gammarus spp.</td>
<td>0</td>
<td>466.67 ± 230.94</td>
<td>199.99 ± 346.41</td>
<td>0</td>
<td>1222.22 ± 2116.99</td>
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<tr>
<td>G. zaddachi</td>
<td>0</td>
<td>166.67 ± 288.68</td>
<td>2388.89 ± 1170.7</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>G. tigrinus</td>
<td>55.56 ± 96.23</td>
<td>0</td>
<td>0</td>
<td>166.67 ± 166.7</td>
<td></td>
</tr>
<tr>
<td>Trichoptera</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>55.56 ± 96.23</td>
<td></td>
</tr>
<tr>
<td>Chironomidae</td>
<td>1166.67 ± 166.67</td>
<td>2336.67 ± 603.68</td>
<td>1933.33 ± 608.49</td>
<td>0</td>
<td>3666.67 ± 3355.18</td>
</tr>
<tr>
<td>total</td>
<td>3666.67 ± 333.34</td>
<td>6466.67 ± 1680.3</td>
<td>7566.67 ± 1721.4</td>
<td>18,333.3 ± 10,332.2</td>
<td>16,722.2 ± 12,549.41</td>
</tr>
<tr>
<td>no. of taxa per sample</td>
<td>2–4</td>
<td>4–6</td>
<td>4–7</td>
<td>6–8</td>
<td>5–7</td>
</tr>
</tbody>
</table>
The zebra mussel (*Dreissena polymorpha*) and the benthic community in a coastal Baltic lagoon

Radziejewska, Fenske, Wawrzyniak-Wydrowska, Riel, Wozniczka & Grusza

**Table 5.** Mean (± SD) total macrobenthic abundances (ind·m⁻²) at the Kleines Haff sites sampled for the meio-benthos during the June 2007 campaign.

<table>
<thead>
<tr>
<th>taxon (%) frequency</th>
<th>MB4/A</th>
<th>MB4/B</th>
<th>MB5/R</th>
<th>MB5/O</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligochaeta (12.1)</td>
<td>22,727.3±7,477.98</td>
<td>19,090.9±7,843.36</td>
<td>38,181.8±25,430.18</td>
<td>6818.2±5,868.16</td>
</tr>
<tr>
<td>Hirudinea (9.1)</td>
<td>3636.4±5926.55</td>
<td>0.0</td>
<td>2272.7±0.00</td>
<td>3030.3±2624.32</td>
</tr>
<tr>
<td>Valvata piscinalis (6.1)</td>
<td>909.1±2032.79</td>
<td>0.0</td>
<td>6818.2±3214.12</td>
<td>0.0</td>
</tr>
<tr>
<td>Valvata pulchella (3.0)</td>
<td>0.0</td>
<td>0.0</td>
<td>4545.5±0.00</td>
<td>0.0</td>
</tr>
<tr>
<td>Pisidium nitidum (6.1)</td>
<td>909.1±2032.79</td>
<td>3409.1±4351.94</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Dreissena polymorpha (6.1)</td>
<td>17,272.7±22,590.50</td>
<td>0.0</td>
<td>4545.5±0.00</td>
<td>0.0</td>
</tr>
<tr>
<td>Gammarus tigrinus (6.1)</td>
<td>24,545.5±47412.38</td>
<td>0.0</td>
<td>4545.5±0.00</td>
<td>0.0</td>
</tr>
<tr>
<td>Procladius sp. (3.0)</td>
<td>0.0</td>
<td>2272.7±0.00</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Chironomus sp. (12.1)</td>
<td>11,818.2±14766.48</td>
<td>25,000.0±15414.39</td>
<td>4545.5±0.00</td>
<td>3030.3±2624.32</td>
</tr>
<tr>
<td>Glyptotendipes sp. (12.1)</td>
<td>2727.3±4065.58</td>
<td>1515.2±0.00</td>
<td>12,727.3±7468.94</td>
<td>4545.5±0.00</td>
</tr>
<tr>
<td>Tanytarsus sp. (9.1)</td>
<td>0.0</td>
<td>5681.8±0.00</td>
<td>6818.2±0.00</td>
<td>30,303.0±31,926.22</td>
</tr>
<tr>
<td>Chironomidae indet. (9.1)</td>
<td>0.0</td>
<td>6818.2±0.00</td>
<td>2272.7±0.00</td>
<td>34,090.9±0.00</td>
</tr>
<tr>
<td>Chironomidae pupae (6.1)</td>
<td>0.0</td>
<td>1136.4±0.00</td>
<td>0.0</td>
<td>2272.7±0.00</td>
</tr>
<tr>
<td>total</td>
<td>84,545.5±102,982.4</td>
<td>64,924.2±20,680.60</td>
<td>87,272.7±28,640.0</td>
<td>84,090.91±40,092.9</td>
</tr>
<tr>
<td>total number of taxa (range)</td>
<td>8.0 (4−6)</td>
<td>8.0 (2−7)</td>
<td>10.0 (2−6)</td>
<td>7.0 (0−5)</td>
</tr>
</tbody>
</table>

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 meio-benthos 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 dominance 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* (subglobulosum 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 (*Sphaerididae*) (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 been favoured in the presence of suspension feeders such as *Dreissena* or *M. edulis* (see e.g. Committ & 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 &
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

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

**Acknowledgements**

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**References**


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