

**Biogeochemical
alteration of the benthic
environment by the zebra
mussel *Dreissena polymorpha*
(Pallas)***

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Abstract

The aim of this study was to verify whether the biogeochemical features (e.g. concentration of nutrients, oxygen consumption, mineralization rate, Eh) of sediments changed by the zebra mussel or its shell deposits differ from those in the ambient soft bottom, and how these differences are related to the structure of benthic macroinvertebrates. In 2006 three sampling sessions were carried out in the Curonian Lagoon, SE Baltic Sea, at three pre-defined sites, corresponding

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to different bottom types: zebra mussel bed, zebra mussel shell deposits and bare soft sediments. Similarity analysis of biogeochemical parameters indicated that bottom sediments covered with zebra mussel shell deposits were rather distinct from the other bottom types because of the lowest total organic matter mineralization rate and highest organic carbon, total phosphorus and total nitrogen content. The parameters measured in the zebra mussel bed did not deviate conspicuously from the values observed in bare bottoms, except for the higher rate of oxygen consumption in the upper sediment layer. Unsuitable anoxic conditions on the one hand and the 'attractive' shelters provided by zebra mussels on the other hand may promote the epifaunal life style in the habitats formed by dense zebra mussel clumps.

1. Introduction

Many recent studies have indicated that zebra mussels may cause considerable shifts in the community properties of an invaded ecosystem (Griffiths 1993, Karatayev et al. 1997, 2002, Haynes et al. 1999, Bially & MacIsaac 2000, Zaiko et al. 2009). Less attention has been paid to the physical and biogeochemical changes to the benthic habitats induced by the presence and functioning of the zebra mussel. The observed changes are probably linked to, or partly caused by, changes in the structure of the macrozoobenthos community (Thayer et al. 1997, Strayer et al. 1998).

Earlier studies reported some biogeochemical changes in the benthic and pelagic environments induced by zebra mussels, including nutrients and water quality (Karatayev et al. 1994, 2005, Johengen et al. 1995, Fahnenstiel et al. 1995, Heath et al. 1995, Botts et al. 1996, James et al. 1997, Stewart et al. 1998, Makarewicz et al. 2000, Lucy et al. 2005), reduction of suspended particulate matter (MacIsaac et al. 1991, Holland 1993), the increased nutritional value of surficial sediments (Thayer et al. 1997) and the alteration of the oxygenation regime and redirection of nutrient flow in the benthic environment (Karatayev et al. 1997, Hecky et al. 2004). It has also been reported that a number of different taxa (predominantly benthic macroinvertebrates) respond to the presence of zebra mussels by either reducing or increasing their abundance and biomass (Dusoge 1966, Dermott et al. 1993, Griffiths 1993, Slepnev et al. 1994, Nalepa 1994, Schloesser & Nalepa 1994, Stewart & Haynes 1994, Strayer & Smith 1996, Minchin et al. 2002). Our recent research in the Curonian Lagoon has indicated that a zebra mussel bed is distinguished from other habitat types not only by higher benthic invertebrate biomass, abundance and species richness, but also that habitats formed by live zebra mussels and zebra mussel shell deposits maintain benthic communities structurally different from those common in soft, bare sediments (Zaiko et al. 2009). However, there is still not sufficient understanding of the biogeochemical

aspects of the zebra mussel habitat engineering impact to show its multiple effects at different levels of an ecosystem.

At least two mechanisms of sediment property change by zebra mussels have been identified. One is that surface sediments become nutrient-enriched because of the extensive biodeposition of seston by zebra mussels in the form of faeces and pseudofaeces (Karatayev et al. 1994, 2005, Botts et al. 1996, Stewart et al. 1998, Daunys et al. 2006, Zaiko 2009). Secondly, the development of dense aggregations of zebra mussels with a multitude of interstices provides an enemy- or stress-free space for macrozoobenthos (Botts et al. 1996, Stewart et al. 1998, Bially & MacIsaac 2000, Karatayev et al. 2002, Gutierrez et al. 2003, Beekey et al. 2004, and others). These beds physically modify the bottom surface and control the transport of particles and solutes in the near-bottom environment (Gutierrez et al. 2003), thus altering the boundary layer characteristics (Karatayev et al. 1994, Gutierrez et al. 2003). We suspect that the biogeochemical processes involved are also altered and differ in habitats modified by live zebra mussels and their empty shells (shell deposits).

Our research was a pilot study of the basic biogeochemical properties (e.g. concentration of nutrients, oxygen consumption, mineralization rate, Eh) of sediments modified by zebra mussels (zebra mussel bed and zebra mussel shell deposits) in a boreal estuarine lagoon, with reference to the properties of the unmodified (bare) soft bottom. The objective of this study was to verify whether the sediments, changed either by live zebra mussels or shell deposits, differ in their biogeochemical character from the ambient soft bottom, and how these differences are related to the structure and functioning of the benthic macroinvertebrate community in the different habitats.

2. Methods

2.1. Study area

The Curonian Lagoon is a large (1584 km²), shallow (mean depth 3.8 m) and mainly freshwater body connected to the south-eastern part of the Baltic Sea by the narrow Klaipeda Strait (Figure 1). The River Nemunas carries 98% of the total freshwater input and enters the lagoon in its central area, dividing the water body into two different parts (Jurevicius 1959). The northern part is a transitory river-like system transporting freshwater into the sea, where salinity may episodically increase up to 5–6 PSU during short-term wind-driven inflows of Baltic Sea water. The southern part is fresher and characterized by a relatively closed water circulation and lower

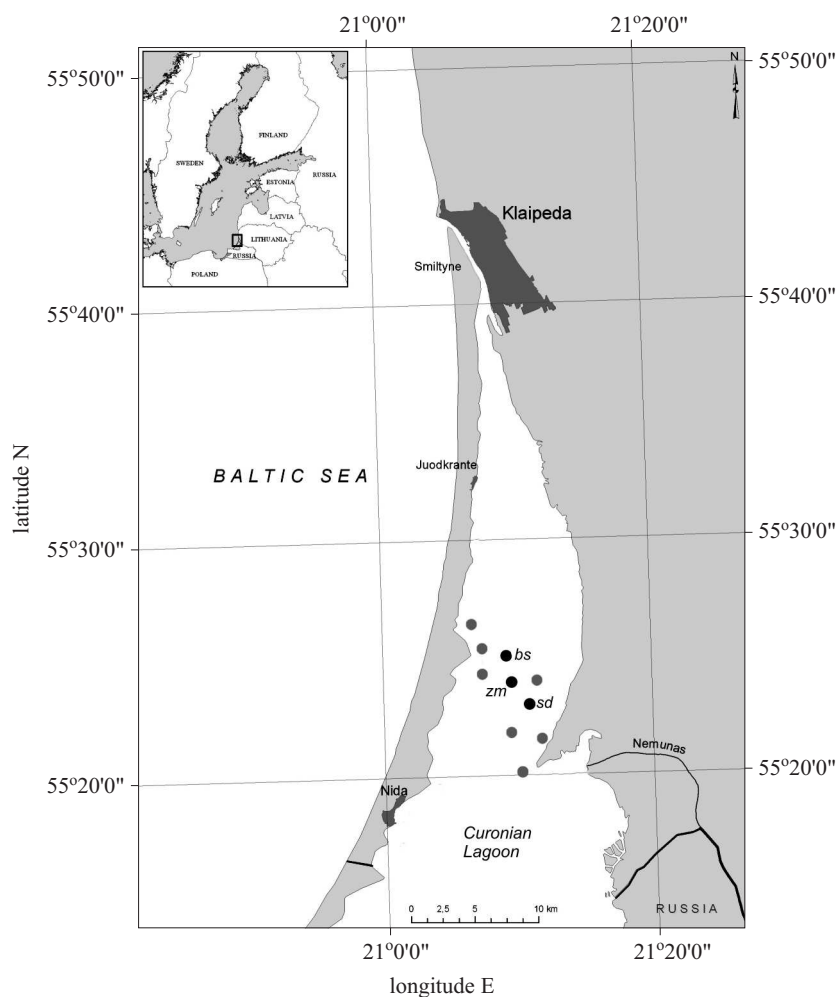


Figure 1. Sampling stations of the preliminary survey in the central part of the Curonian Lagoon. The sites selected for the current study are indicated in black: *bs* – bare sediments, *zm* – zebra mussel bed, *sd* – shell deposits

current velocities; this, therefore serves as the main depositional area of the lagoon (Pustelnikov 1983, Galkus & Jokšas 1997, Daunys et al. 2006).

Shallowness, water dynamics and intensive sedimentation in the lagoon considerably affect the sediment distribution patterns and their changes over time. The dominant bottom substrates are sand, silt and shell deposits. Mud prevails only in the southern part of the lagoon, i.e. in the zone of intensive sedimentation (Trimonis et al. 2003).

The lagoon has a diverse benthic macrofaunal community with approximately 280 species recorded in the littoral zone. The soft bottoms of its

northern part are characterized by communities of oligochaetes, chironomids and the invasive spionid *Marenzelleria neglecta* (Zettler & Daunys 2007).

Most likely, the zebra mussel *Dreissena polymorpha* was introduced into the Curonian Lagoon in the early 1800s. The molluscs would have been attached to timber rafts transported via the Central European invasion corridor (Olenin et al. 1999). However, it may have spread much earlier. According to palaeontological data, *Dreissena* could have existed in the Baltic Sea area during the last interglacial, later becoming extinct, before being re-introduced in the early 1800s (Starobogatov & Andreyeva 1994).

Zebra mussels are now very abundant in the Curonian Lagoon. They occupy the upper littoral down to 3–4 m depth and occur on hard substrates (boulders, embankments, hydrotechnical structures) and soft bottoms (sand, silt or mud) (Zemlys et al. 2001). The largest area occupied by a zebra mussel community is located in the central part of the lagoon (Gasiūnas 1959, Aristova 1965, Bubinas 1983, Olenin 1987, 1988, 1997, Daunys 2001, Zaiko 2009). On *Dreissena*-dominated bottoms, the sediment is formed mainly by zebra mussel shell deposits and zebra mussel clumps. The largest zebra mussel biomass ever found (up to 11 kg m⁻²) and abundance (up to 38 000 indiv. m⁻²) were obtained from this part of the lagoon (Gasiūnaitė et al. 2008).

2.2. Selection of representative sampling sites

A preliminary survey was performed in order to locate appropriate sampling sites corresponding to the three pre-specified habitat types (zebra mussel bed – *zm*, zebra mussel shell deposits – *sd* and bare soft sediments – *bs*). A number of benthic samples were taken along a transect crossing the area occupied by the zebra mussel colony in the central (Lithuanian) part of the lagoon (Figure 1). In total, 10 stations with 3 replicates each were sampled. All the samples were obtained from sites with similar depths (2.6 ± 1 m) and hydrodynamic conditions.

A Van Veen grab (catch area 0.1 m²) was used for sampling the macrofauna. Each sample was sieved (0.5 mm mesh size) and preserved (4% formaldehyde solution) on board. Once in the laboratory, the macro-zoobenthic species were sorted, identified and counted using a binocular microscope at 15x magnification. Wet weight was determined to within 0.001g. Samples were collected and treated following standard guidelines for bottom macrofauna sampling (HELCOM 1988). Along with the standard treatment procedure of benthic samples, the shell deposits were identified taxonomically, to the genus or species level if possible. The shell deposits of the different taxonomic groups were then dried and weighed separately.

Since the habitat type or its localization under existing conditions in the ecosystem under study could not be identified a priori, preliminary differentiation of habitats into *bs*, *sd* and *zm* was possible only after an onboard visual inspection of the sampled material during the field sampling campaign. The habitats were then defined more precisely following quantitative treatment of samples, according to Zaiko et al. (2009).

Three representative sampling sites for biogeochemical measurements were chosen in accordance with the following requirements: all of them should be located within the distribution area of the *Dreissena polymorpha* community in the Curonian Lagoon, with similar depth, sediment grain size and hydrodynamic conditions. Each site was chosen to represent one of the following types: in the *zm* habitat the biomass of live mussels should exceed 200 WWg m⁻²; in the *sd* habitat the amount of empty shells should be 1000 DWg m⁻² or more, with very few (< 200 WWg m⁻²) or no live zebra mussels present; in the *bs* habitat the amount of live zebra mussels should be < 200 WWg m⁻² or zero and the amount of empty shells should be < 1000 DWg m⁻² or zero (Zaiko et al. 2009).

3. Sampling and analytical methods

Three sampling surveys (in May, August and October 2006) were performed in the central part of the Curonian Lagoon at the three pre-defined sampling sites; these were relocated using onboard GPS equipment. The following parameters were measured in the upper and near-bottom water layers: pH, oxygen concentration, salinity, dissolved inorganic nitrogen (DIN) and total nitrogen concentration, phosphate and total phosphorus concentration. In the upper sediment layer, median grain size, concentrations of organic carbon, total nitrogen and phosphorus, oxygen consumption rates, organic matter mineralization rates and redox conditions (Eh) were also determined.

A Van Veen grab (catch area 0.1 m²) was used for sediment sampling. Surface and near-bottom water was sampled using a 2 L Ruttner sampler.

Temperature, pH, redox potential (Eh) and salinity in the sampled upper and near-bottom water layers were measured onboard with a portable universal MultiLine F/Set-3 meter (WTW). Dissolved oxygen concentration was determined by Winkler's method. Dissolved nutrient (phosphate and nitrate) analyses were performed according to Merkienė & Čeponytė (1994): phosphate-P was assessed by the molybdate ascorbic acid method after digestion with sulphuric acid. The total phosphorus (TP) concentration was measured using persulphate-H₂SO₄ digestion and the molybdate ascorbic

acid method. Nitrate-N was determined using potassium persulphate- $\text{K}_2\text{S}_2\text{O}_8$ followed by Cd reduction to NO_2 and photometric analysis. Total nitrogen (TN) was analysed by the Kjeldahl method (Jirka et al. 1976).

TN and TP concentrations in the upper sediment samples were estimated using the spectrophotometric phenol-hypochlorite method. For TN analysis the organic and inorganic nitrogen was converted into ammonium by digestion with concentrated sulphuric acid, followed by treatment with sodium salicylate and hypochlorite. TP was measured after perchlorate- H_2SO_4 digestion with analysis as above. Organic carbon (C_{org}) was measured by the dichromate oxidation method (Potapova 1980).

The rate of aerobic and total (aerobic + anaerobic) organic matter mineralization was determined by the isolated columns method (Kuznecov & Dubinina 1980). Undisturbed bottom sediment cores (5 cm diameter) were taken using glass cores. Live zebra mussels (if there were any) were carefully eliminated from the cores, after which these and the control (without bottom sediments) were carefully filled with near-bottom water and incubated in situ for 24 hours. The oxygen consumption ($\text{mgO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and inorganic carbon flux ($\text{mgC m}^{-2} \text{ d}^{-1}$) were estimated after incubation by the differences between sample and control.

4. Data analysis

In order to minimize the possible influence of data variation in time, and to emphasize the site (habitat type) effect, the data from the three sampling sessions were treated as replicates.

The similarity of the biogeochemical sediment properties at the three sampling sites was assessed using a non-metric multidimensional scaling (NMDS) procedure. The Wilcoxon signed rank test was applied to verify whether there was a statistically significant difference in physicochemical parameters between the surface and near-bottom water layers.

5. Results

5.1. Basic ecological conditions in the habitats sampled

The three sites were situated in the central part of the lagoon, to the north of the mouth of the Nemunas, within the bottom area modified by the zebra mussel (Figure 1). All three sites were relatively close to each other, so the hydrodynamic conditions and water residence times were assumed to be similar. The main geo- and biological characteristics of the habitats and the physicochemical parameters of the water at the sampling sites are presented in Tables 1, 2 and 3.

Table 1. Ecological characteristics of the sampling sites

	Zebra mussel bed	Shell deposits	Bare sediments
depth	3 m	2.6 m	2.2 m
sediment type	fine sand	fine sand	fine sand
sediment grain size (Md)	0.195 mm	0.198 mm	0.165 mm
zebra mussel shells DW	884 g m ⁻²	1041 g m ⁻²	0 g m ⁻²

Table 2. Physicochemical water parameters at the sampling sites (averages for 3 sampling sessions, SD in parentheses)

	Zebra mussel bed	Shell deposits	Bare sediments
Secchi depth	0.7(0.2) m	0.9(0.7) m	0.7(0.1) m
temperature	16.7(4.3)°C	16.5(4.3)°C	16.9(5.2)°C
salinity	0.1(0.1) PSU	0.1(0.1) PSU	0.1(0.1) PSU
pH (surface)	8.9(0.3)	8.8(0.6)	9.0(0.3)
pH (near-bottom)	8.9(0.4)	8.8(0.7)	9.0(0.3)
O ₂ (surface)	9.6(1.4) mg dm ⁻³	9.4(0.7) mg dm ⁻³	12.2(0.7) mg dm ⁻³
O ₂ (near-bottom)	9.4(0.9) mg dm ⁻³	9.2(0.3) mg dm ⁻³	10.2(0.7) mg dm ⁻³
N(NH ₄)	0.011(0.006) mgN dm ⁻³	0.019(0.006) mgN dm ⁻³	0.021(0.017) mgN dm ⁻³
N(NO _x)	0.079(0.107) mgN dm ⁻³	0.315(0.433) mgN dm ⁻³	0.024(0.021) mgN dm ⁻³
dissolved N total	0.92(0.14) mgN dm ⁻³	1.21(0.43) mgN dm ⁻³	0.87(0.17) mgN dm ⁻³
P(PO ₄)	0.033(0.006) mgP dm ⁻³	0.046(0.011) mgP dm ⁻³	0.043(0.045) mgP dm ⁻³
dissolved P total	0.051(0.022) mgP dm ⁻³	0.068(0.006) mgP dm ⁻³	0.062(0.046) mgP dm ⁻³

5.2. Biogeochemical features of the three habitats sampled

According to the NMDS results, the properties of the *sd* habitat differed from those measured in the two other habitat types (Figure 2). This distinction was due to the lowest total organic matter mineralization rates (195 ± 52 mgC m⁻² day⁻¹ versus 955 ± 22 and 597 ± 271 mgC m⁻² day⁻¹ in *zm* and *bs* respectively) and the highest concentrations of organic carbon (3.75% versus 0.95 and 1.25% in *zm* and *bs* respectively) in the *sd* habitat during all three surveys. Bottom sediments in *sd* were also characterized by the highest total TP and TN concentrations (Figure 3). The relatively low organic matter mineralization rates in *sd* were predominantly the result of aerobic processes in May and August.

Table 3. Macrofauna: mean abundances (indiv. m⁻²; SD in parentheses) and total biomass of different trophic functional groups (g m⁻²; SD in parentheses) in the 3 habitat types analysed (based on the classifications by Olenin (1996) and Monakov (1998))

Trophic functional group	Taxon	Habitat type		
		Bare sediments	Zebra mussel bed	Shell deposits
suspension feeders and/or grazers	<i>Bithynia tentaculata</i>	5(9)	25(45)	–
	<i>Dreissena polymorpha</i>	85(93)	1456(1639)	114(140)
	<i>Pisidium</i> spp.	13(17)	82(130)	8(20)
	<i>Sphaerium</i> spp.	4(12)	1(3)	7(12)
	Unionidae	–	1(3)	–
	<i>Valvata piscinalis</i>	–	8(13)	25(55)
	<i>V. pulchella</i>	3(6)	1(3)	–
total biomass		38.2(33.9)	958.0(1026.5)	51.6(76.3)
deposit feeders and/or grazers	<i>Asellus aquaticus</i>	–	4(7)	1(2)
	<i>Chelicorophium curvispinum</i>	2(4)	–	–
	<i>Corophium volutator</i>	–	6(14)	1(3)
	<i>Eiseniella tetraedra</i>	4(12)	14(24)	12(23)
	<i>Lithoglyphus naticoides</i>	–	3(4)	1(3)
	<i>Marenzelleria neglecta</i>	1(3)	–	–
	Ostracoda	8(18)	948(1524)	75(92)
	<i>Radix ovata</i>	–	–	1(2)
	<i>Theodoxus fluviatilis</i>	–	3(11)	–
	<i>Viviparus viviparus</i>	1(3)	5 (7)	1(3)
	total biomass	8.7(13.6)	24.4(21.9)	15.7(15.1)
predators and/or omnivores	<i>Chaetogammarus warpachowskyi</i>	1(3)	4(12)	3(11)
	Chironomidae	721(592)	1487(1084)	220(192)
	<i>Erpobdella octoculata</i>	22(33)	396(292)	31(39)
	<i>Glossiphonia complanata</i>	1(3)	14(23)	6(10)
	<i>G. heteroclita</i>	–	16(10)	3(8)
	<i>Helobdella stagnalis</i>	1(3)	58(67)	15(26)
	<i>Hydra vulgaris</i>	–	1(3)	–
	Hydrachnellae	1(3)	3(7)	1(2)
	Nematoda	–	10(24)	5(10)
	<i>Obessogammarus crassus</i>	1(3)	4(14)	1(3)
	Oligochaeta	983(619)	2366(1432)	1232(1383)
	<i>Planaria torva</i>	1(3)	1(3)	–
	<i>Pontogammarus robustoides</i>	4(7)	8(24)	7(11)
	Trichoptera	8(11)	23(27)	4(8)
	Turbellaria undet.	3(8)	11(9)	3(7)
	total biomass	5.5(4.3)	17.7(8.8)	6.3(6.3)

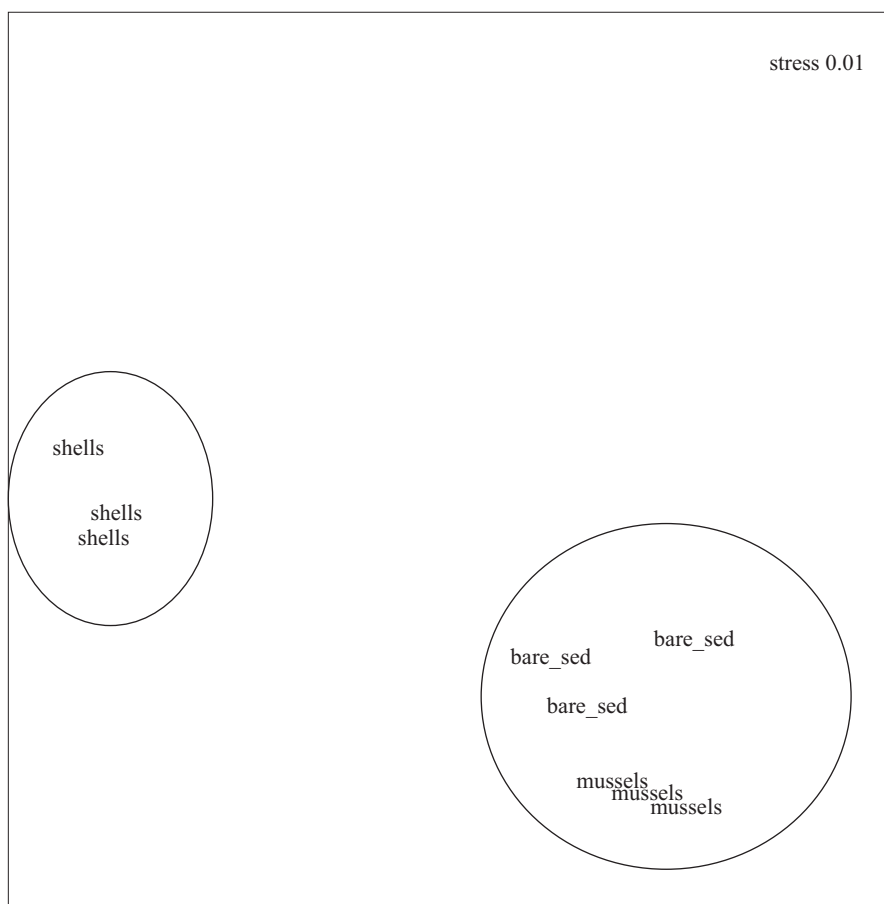


Figure 2. NMDS plot of similarities between the three habitats sampled (shell deposits – ‘shells’, bare sediments – ‘bare_sed’ and zebra mussel bed – ‘mussels’) according to the biogeochemical properties of the sediments

The highest concentration of the oxidized form of dissolved inorganic nitrogen ($\text{N}(\text{NO}_x)$) ($0.621 \text{ mgN dm}^{-3}$ versus 0.154 and $0.024 \text{ mgN dm}^{-3}$ in *zm* and *bs* respectively) was recorded in *sd* during the October sampling. The other parameters of the upper and near-bottom water measured in the three habitat types did not display any statistically significant differences (Wilcoxon signed rank test $p = 0.43$).

The highest redox potential was also measured in the surface sediments in the *sd* habitat. Although the dissolved oxygen concentration in the near-bottom water layer was similar in all three habitat types ($9 \pm 1.8 \text{ mgO}_2 \text{ dm}^{-3}$), the Eh values varied substantially among the sampling sites at a depth of 1 cm below the bottom surface (Figure 4). Owing to

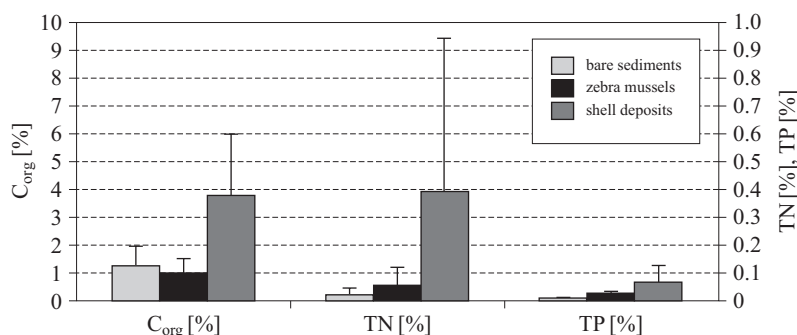


Figure 3. Average organic carbon (C_{org}), total nitrogen (TN) and total phosphorus (TP) content in different bottom sediments

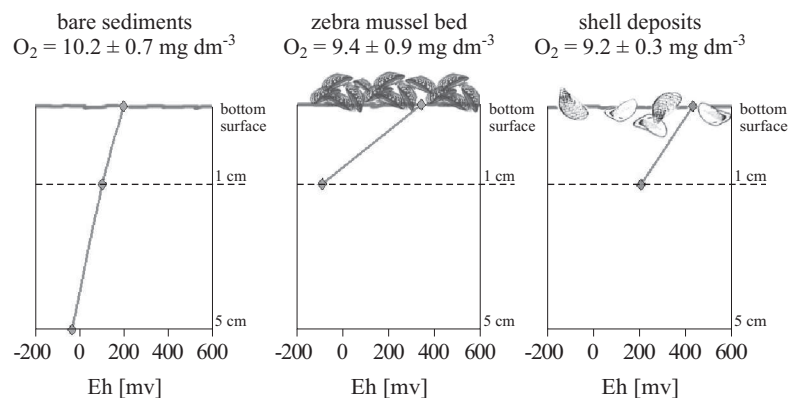


Figure 4. Redox conditions of sediments and near-bottom dissolved oxygen concentration in the three habitats sampled

the roughness, which is specific to the sediments sampled from the zebra mussel bed and shell deposits, it was impossible to measure Eh at the depth of 5 cm below the bottom surface. Thus, Eh values at 5 cm depth were obtained only for the bare sediments.

The *zm* habitat was distinguished by the highest oxygen consumption rate in the upper sediment layer: $530 \pm 383\ mgO_2\ m^{-2}\ day^{-1}$ versus 228 ± 180 and $444 \pm 18\ mgO_2\ m^{-2}\ day^{-1}$ in *bs* and *sd* respectively. The high organic matter mineralization rate in this habitat type was due basically to anaerobic processes and reached on average $721 \pm 191\ mgC\ m^{-2}$.

6. Discussion

It is often assumed that the zebra mussel is capable of altering boundary layer characteristics, increasing dissolved nutrient concentration through

excretion or by removing seston from the water column (Stewart et al. 1998, Karatayev et al. 2002, Rosemond & Anderson 2003). We did not find any evidence for such effects in the current study, probably because of the extensive water mixing in the shallow Curonian Lagoon. The biogeochemical parameters of the upper and near-bottom water measured in the three habitat types did not exhibit any statistically significant differences.

Compared to the bottoms formed by zebra mussel shell deposits and bare sediments (*sd* and *bs*), the sediments in *zm* are physically isolated from the near-bottom water layer by dense accumulations of mussel clumps. This may inhibit exchange processes across the sediment-water boundary layer. In addition, physiological processes within the zebra mussel colonies may give rise to changes in sediment composition that affect the sediment redox conditions and biogeochemical cycles of nitrogen, phosphorus and carbon (Bruesewitz et al. 2006). The respiration-based oxygen demand of the zebra mussels themselves and of other macrobenthic organisms associated with this habitat type (see Table 3) is usually much greater than that of the bare sediments (Effler et al. 1996). Thus, severe oxygen depletion due to respiration of the abundant zebra mussel community, in addition to the physical 'isolation' of the sediments by the zebra mussel clumps, facilitates anaerobic mineralization processes near the surface sediment-water interface.

Previous research has indicated that zebra mussels mobilize substantial quantities of ammonia and phosphorus (Effler et al. 1997). Some of the particulate nutrients contained in seston and inhaled by mussels is invested in new mussel biomass, but a large portion is excreted as solutes (e.g. ammonium NH_4^+), or released in particulate form in the form of faeces or pseudofaeces. This material then becomes subject to further mineralization (Hecky et al. 2004). Because of the anaerobic conditions and the accumulation of C-rich biodeposits underlying the zebra mussel beds, it is likely that denitrification (microbial reduction of NO_3^- to gaseous nitrous oxide (N_2O) and dinitrogen (N_2)) occurs at rates higher than those in unmodified bare sediments (Seitzinger 1988). To some extent, the findings of the current study endorse these general assumptions, since the highest anaerobic mineralization rate was recorded in the *zm* habitat. Yet comparatively low concentrations of organic carbon, total phosphorus and total nitrogen were found there, despite the substantial biosedimentation induced by *D. polymorpha* and the other suspension feeders abundant in *zm* (Table 3). This was probably caused by the lower relative organic matter content in the biodeposits compared to that in the naturally sedimented material, as also indicated by the experimental results (Zaiko

2009). Furthermore, the utilization of biodeposits by the dense deposit-feeding benthic fauna may result in reduced concentrations of organic carbon as well.

Bottoms modified by zebra mussel shell deposits *sd* are potentially more favourable to the accumulation of sediments than the *bs* bottoms (due to the physical particle trapping effect). This could explain their higher C_{org} , TN and TP content. But in comparison to *zm*, organic matter mineralization rates were low and there was no anaerobic mineralization in *sd*. This was very likely caused by the better aeration in this type of sediments, resulting from its specific roughness (soft sediments mixed with the debris of shell deposits are more porous than those in the bare bottom) and bioturbation by abundant infaunal organisms.

Since *D. polymorpha* is quite an 'aggressive' and very abundant invader, each of its activities may potentially cause a cascade of effects in an ecosystem. For instance, because of the extensive filtering, the clarity of water increases → increases light penetration → species composition and community structure may change → alteration of the food web and energy flow occurs. All these causally related effects could lead to changes in the diversity and stability of the entire ecosystem. One can draw up several variants of such causal chains with the same initial function of the zebra mussel at the beginning but with different outcomes at the end.

On the basis of the results of this and earlier studies and also the assumptions presented above, the conceptual scheme of the impact of zebra mussel engineering on the benthic environment of the ecosystem studied can be visualized schematically (see Figure 5).

The soft bottom devoid of live zebra mussel clumps or shell deposits in the turbulent environment of the lagoon is characterized by a rather poor macrozoobenthic community with common infaunal species (like oligochaetes and chironomids) dominating in the upper (aerated) sediment layer. The sedimentation of organic matter in this habitat type is compensated in part by physical resuspension and in part by mild mineralization processes.

The bottom becomes rougher when it is covered by empty zebra mussel shells, which provides microhabitats and refuges for infaunal benthic organisms, promotes microcirculation flows in the benthic boundary layer and enhances the aeration of sediments. This and the burrowing activity of the abundant infauna result in a thicker oxidized layer of sediments. A few epifaunal organisms may be observed in this habitat. The empty shells building up on the surface of the soft bottom are also capable of trapping suspended particles, thus accumulating intermediate amounts of organic matter. This material is partly consumed by the deposit-feeding

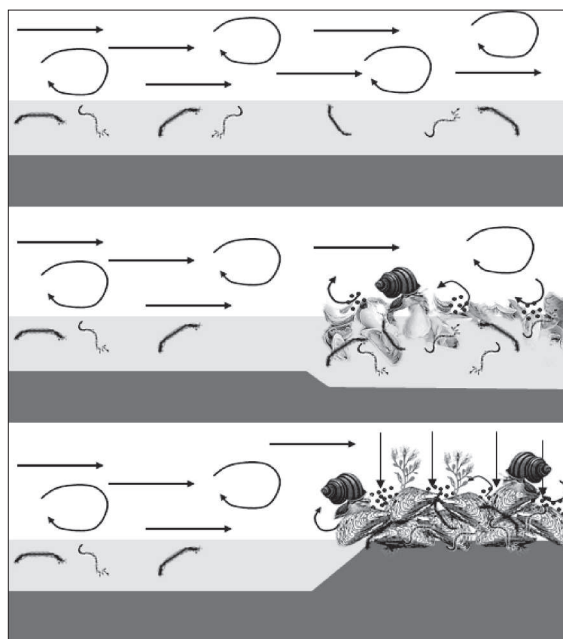


Figure 5. Habitat changes and functioning of the macrozoobenthic community induced by the engineering impact of the zebra mussel. The model represents three typical benthic habitats in the central part of the Curonian Lagoon: soft bare sediments (top), soft bottom with zebra mussel shell deposits (middle) and soft bottom with zebra mussel bed (bottom). See the text for a detailed description

macrofauna and is gradually mineralized in the aerated upper sediment layer.

Live zebra mussel clumps may actively deposit particulate matter as well as physically trap it. Part of this matter is utilized by the numerous deposit-feeders and decomposed during intensive anaerobic processes, facilitated by the anoxic conditions just below the mussel bed. Large epibenthic organisms are abundant in this habitat type. The infaunal species are abundant here as well, but they are forced to adopt a quasi-epifaunal life style, since they are found above the real sediment layer – inside the zebra mussel clumps. This phenomenon is caused by the unsuitable anoxic conditions in the sediments on the one hand, and the attractive shelter provided by zebra mussel aggregations on the other.

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