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HABITAT ENGINEERING ROLE OF THE INVASIVE BIVALVE
DREISSENA POLYMORPHA (PALLAS, 1771) IN THE BOREAL
LAGOON ECOSYSTEM

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DVIGELDŽIO INVAZINIO MOLIUSKO DREISSENA POLYMORPHA (PALLAS, 1771) FUNKCINIS VAIDMUO FORMUOJANT DUGNO BUVEINES BOREALINĖS LAGŪNOS EKOSISTEMOJE

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“Nothing, nothing at all is born, dies, the shell says again and again...”

Shinkichi Takahashi
INTRODUCTION

Scope of the study. Deliberate or accidental human-mediated transfer of non-native species beyond the range of their natural occurrence is a very old phenomena dating back to pre-historical time (Leppäkoski et al. 2002). These species (also termed as non-indigenous, alien, exotic), once established in a new environment may multiply, spread over large areas, compete with native organisms, modify local habitats and effect ecosystem functioning. In other words, they may cause biological invasions which now are recognized as one of the major elements of the global change (Occhipinti-Ambrogi 2007). Although the problem of biological invasions became a rapidly growing research area in recent decades, there are still large gaps, both geographically and thematically, to be filled in the near future (Leppäkoski et al. 2002). While the gap in knowledge of bioinvasions geography is being rapidly filled in due to intensive collaborative research effort in several recent EU funded projects (DAISIE, ALARM, IMPASSE), the impacts of alien species, especially in aquatic environment, remain largely unknown.

The Baltic Sea is presently hosting nearly 110 alien species of plants and animals, yet less than one third of them have been scrutinized in order to assess at least some of their impacts on local biodiversity (Baltic Sea Alien Species Database 2009). The largest estuarine lagoon of the Baltic Sea, the Curonian Lagoon, is known to host at least 25 successful established invaders. This water body has been studied for more than seven decades (Zettler and Daunys 2007; Gasiūnaitė et al. 2008 and references therein); it was used as a model for a comparative study on the ecological role of the alien species in benthic habitats (Olenin and Leppäkoski 1999) and some aspects of the invasion impact on the ecosystem functioning have been studied here in detail (Daunys 2001; Jankauskienė 2003; Daunys et al. 2006). Nevertheless, a comprehensive view on the functional role of an invasive species at different levels, from a community to a habitat and an ecosystem is still lacking at this time. This is true not only for the Curonian Lagoon but
also for many other coastal areas in Europe and overseas (Leppäkoski et al. 2002; Grosholz 2002; Olenin et al. 2008).

In this study, the zebra mussel *Dreissena polymorpha* (Pallas, 1771) is being used as a model species. In the Curonian Lagoon it is known since early 1800s, being among the first reported non-native species there (Leppäkoski and Olenin 2000). The species is well-known as one of the most successful aquatic invaders worldwide. The zebra mussels have been reported to alter benthic habitats (Nalepa and Fahnenstiel 1995; Olenin 1997a; Stewart et al. 1998; Karatayev et al. 2002; Minchin et al. 2002; Vanderploeg et al. 2002), cause considerable shift in benthos and plankton community properties (Griffiths 1993; Heath et al. 1995; Lowe and Pillsbury 1995; Karatayev et al. 1997; Haynes et al. 1999; Bially and MacIsaac 2000; Karatayev et al. 2002), induce biogeochemical changes in the benthic and pelagic environments (James et al. 1997; Makarewicz et al. 2000; Hecky et al. 2004).

This study is the first attempt to provide a comprehensive view on zebra mussel engineering impact on benthic habitats in the boreal estuarine lagoon, showing its multiple outcomes at different levels of an ecosystem.

**Aim and objectives of the study.** The aim of the study was to assess habitat engineering role of zebra mussel *Dreissena polymorpha* in the Curonian Lagoon ecosystem.

The main objectives were:
1. To quantify and describe distribution of the zebra mussels and zebra mussel shell deposits in the Curonian Lagoon;
2. To assess the impact of *D. polymorpha* on structure and distribution of benthic macrofauna;
3. To assess the effect of the zebra mussel filtration and biodeposition on the benthic-pelagic linkage in the ecosystem;
4. To estimate the impact of zebra mussel on biogeochemical features of the bottom sediments;
5. To assess the xenodiversity in the habitats modified by *D. polymorpha* comparing to other habitats in the Curonian Lagoon and SE Baltic Sea

**Novelty of the study.** This study is the first attempt to provide a comprehensive view on zebra mussel habitat engineering impacts in the estuarine coastal lagoon ecosystem, showing their multiple effects on different levels of an ecosystem. The importance and effect of zebra mussel’s habitat engineering function was evaluated at the scale of benthic communities and entire ecosystem. The impacts of zebra mussel shell deposits have been described and quantified for the first time. The biogeochemical alterations of benthic habitats induced by zebra mussel were investigated *in situ* and linked to the macrozoobenthos (benthic macrofauna) structure. The comparative analysis of xenodiversity in different benthic habitats was applied in this work for the first time.

**Scientific and practical significance of the results.** This study assess the significance of different zebra mussel impacts in the Curonian Lagoon ecosystem. The data obtained during field and laboratory work may be further used for the modeling of biological, biogeochemical processes in the Curonian Lagoon, planning future monitoring of benthic communities. One of the most important results achieved in the current study is determination of the thresholds for distinction of natural habitats modified either by live zebra mussels or their shell deposits. This approach may be applied for benthic habitat studies in the Curonian Lagoon and other water bodies, where bottom has been altered essentially after the *D. polymorpha* invasion. A tool for comparison of ecosystems in respect of zebra mussel impact magnitude was demonstrated in this work.

**Defensive statements**

1. Zebra mussels and their shell deposits are capable of modifying bottom sediments and redistributing benthic macrofauna in the Curonian Lagoon.
2. Filtration and biodeposition by zebra mussels affect the deposition rates in the Curonian Lagoon ecosystem.
3. Presence of zebra mussels and their vital activity alter biogeochemical properties of the sediments and affect benthic biogeochemical processes and functioning of benthic macrofauna.
4. Habitats modified by zebra mussels have favorable conditions to sustain diverse and abundant alien macrofauna.
5. Zebra mussel has strong impact on different components of the Curonian Lagoon ecosystem in terms of biopollution assessment method.

Scientific approval. The results of this study were presented at 13 international conferences and seminars:
1. International Symposium „Functional Role of Invasive Species in European Coastal Waters“. Sylt, Germany, January 2005
2. MARBEF (“Marine Biodiversity and Ecosystem Functioning”) workshop. Yerseke, Netherlands, January 2006
3. ALARM (“Assessing Large-scale environmental risks with tested methods”) General Meeting. Lisboa, Portugal, February 2006
4. International Symposium “Research and management of eutrophication in coastal ecosystems” Nyborg, Denmark, June 2006
5. Seminar given at NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, MI, USA, July 2006
6. Seminar given at Lake Erie Centre, Toledo, MI, USA, July 2006
7. Seminar given at Great Lakes Commission, Ann Arbor, MI, USA, July 2006
8. Seminar given at US EPA Great Lakes National Program Office, Chicago, IL, USA, July 2006
9. 2\textsuperscript{nd} Regional Student Conference “Biodiversity and functioning of aquatic ecosystems”, Klaipėda, Lithuania, October 2006
10. MARBEF (“Marine Biodiversity and Ecosystem Functioning”) workshop “The role of native and/or invasive ecosystem engineers in explaining biodiversity”. Klaipėda, Lithuania, April 2007
11. ICAIS (International Conference on Aquatic Invasive Species). Nijmegen, Netherlands, September 2007

The material of this dissertation was presented in 5 original publications, 4 of them published in peer-reviewed scientific journals.

Volume and structure of the dissertation

The dissertation is presented in the following chapters: Introduction, Literature review, Materials and methods, Results, Discussion, Conclusions, References and Annex. The volume of the dissertation is 135 pages. References include 176 sources; the list of the author’s publications includes 5 entries. The body of the dissertation is written in English with Lithuanian summary. It contains 13 tables and 25 figures.
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DEFINITIONS

*Alien species* (also exotic, non-indigenous) - A species or organism that is not native to a locality, having been moved there from its natural range by humans or other agents. An alien that establishes a self sustaining wild population is described as naturalized, whereas one that depends on continual introduction is termed as casual (Martin & Hines 2000).

*Community* is any assemblage of populations living in a prescribed area or physical habitat; it is a loosely organized unit to the extent that it has characteristics additional to the individual and population components (Odum and Odum 1953).

*Ecosystem (habitat) engineers* are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In doing so, they modify, maintain and create habitats. Autogenic engineers change the environment via their own physical structures (*i.e.* their living and dead tissues). Allogenic engineers change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means (Jones *et al.* 1994).

*Ecosystem functioning, or function* – this term refers variously to the habitat, biological or system properties or processes of ecosystem and includes nearly everything that goes on in an ecosystem that is mediated by the inhabiting organisms in concert with the physical environment (Costanza *et al.* 1997).

*Habitat* here is defined as the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism (Hall *et al.* 1997).

*Invasibility* (susceptibility to invasion) can be defined as an emergent property of an environment, influenced by the interaction of biological and physical processes operating at the local scale (Lonsdale 1999; Davis *et al.* 2000). Physical factors include the region's climate, nutrient levels, and disturbance regime as defined by the frequency of
episodic events (Moyle & Light, 1996; Rejmanek 2000). Main biotic factors include native species richness or diversity, vacant niches, absence of enemies, and competitive abilities of resident species (Elton 1958; Herbolt & Moyle 1986; Mack et al. 2000).

Invasive species – an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health (Clinton 1999).

Xenodiversity – diversity caused by non-indigenous, invasive species (Leppäkoski and Olenin 2000).
1. LITERATURE REVIEW: CURONIAN LAGOON AS AN ENVIRONMENT FOR *DREISSENA POLYMORPHA*

1.1. Ecological overview of the Curonian Lagoon

The Curonian Lagoon is the largest lagoons in the Baltic Sea, separated from the latter by a narrow (0.5-4 km) sandy spit. Its area is about 1584 km², length – almost 93 km, volume – 6 km³ (Galkus and Jokšas 1997). The lagoon is rather shallow - its mean depth is only 3.8 m, maximal depth is 5 m and 3 m isobath circumscribes more than 2/3 of the lagoon (Rainys 1978).

According to different ecological features the Curonian Lagoon is traditionally divided into three parts: the northern, central and southern parts (Fig. 1). The southern part or *Buduma* is characterized by flat bottom topography and maximum depths (up to 5.8 m) for the entire lagoon. The most complex bottom landscape is in the central part. Numerous sandbanks and depth not exceeding 3-4 m are the main features of this area. The northern part of the lagoon is a large underwater plain with depths less than 2 m along the eastern side (mainland shore) and a narrow depression (3-4 m depth) along the Curonian Spit coast (Gudelis 1959; Kunskas 1978).

In its northernmost part, the narrow (width 400-600 m) Klaipėda strait connects the Curonian Lagoon to the Baltic Sea. It is characterized by the variety of bottom substrates: fine and coarse sand, gravel and pebble bottoms, moraine-clay and stones, and patches of mud as well as artificial substrates such as concrete embankments, submerged wood, *etc.* (Gasiūnaitė *et al.* 2008). This area is artificially deepened up to maximum depth of 14 meters. It is oligohaline with irregular salinity fluctuations from 0.5 to 8 PSU (Olenin and Daunys 2004).
Figure 1: Location and physiogeographic zonation of the Curonian Lagoon (dashed lines separate northern, central and southern parts of the lagoon).

The lagoon itself is predominantly freshwater (<0.03 PSU), due to discharge from Nemunas and other smaller rivers. However, depending on wind direction, affecting brackish water inflow from the Baltic Sea, the salinity in the central and northern parts may episodically increase.
up to 5-6 PSU (Dailidienė and Davulienė 2007). Brackish water intrusions are most common during August to October when 70% of the total annual input occurs (Pustelnikovas 1994). The usual duration of such inflows is 1-6 days (Gasiūnaitė et al. 2008) (Fig. 2).

**Figure 2:** Simulated average number of days per year with salinity higher than 2 PSU (Ferrarin et al. 2008).

The Nemunas River brings 98% of the total freshwater runoff (23 km$^3$) and enters the lagoon in its central area, dividing the water body into two different hydrological zones (Jurevičius 1959; Razinkovas et al.)
The zone northward from the mouth is a transitory river-like system transporting freshwater into the sea and receiving seawater during wind driven short-term inflow events. Due to Nemunas water input and water level differences between the sea and lagoon, a northward current is the predominant one and is usually more evident during the spring flood period, when Klaipėda strait is characterized by a unidirectional flow of fresh water from the lagoon to the Baltic Sea with a current speed of 1.5-2 m s⁻¹ (Pustelnikovas 1998; Gasiūnaitė et al. 2008).

The lacustrine southern part is characterised by a relatively closed water circulation and lower current velocities (Galkus and Jokšas 1997; Daunys et al. 2006). The current regime there is driven mainly by the wind which, depending on its direction and speed creates different circulation sub-systems. In most cases the system evolves a dominant gyre, with anti-clock-wise (wind from west) or clockwise (wind from south-east) direction, and some smaller gyres. In the case of south-western wind, the circulation pattern is characterised by a two-gyre system (Razinkovas et al. 2005).

Due to Nemunas River runoff and water exchange with the Baltic Sea, the northern part and Klaipėda strait are characterized by the shortest water residence time (10-40 days), while in the southern part water renewal may take more than 100 days (Ferrarin et al. 2008) (Fig. 3).

A very small depth, an active water dynamics and intensive sedimentation in the lagoon considerably affects the sediment distribution patterns and their changes over the time. The dominant bottom substrates are sand, silt, and shell deposits. Mud only prevails in the southern part of the Curonian Lagoon, i.e. in the zone of intensive sedimentation (Trimonis et al. 2003).

The seasonal water temperature dynamics are typical of shallow temperate water bodies, with annual amplitude of up to 25-29°C (Žaromskis 1996). Temperature stratification of the water column is weak and unstable. The temperature of the near-bottom water layer is lower than that in the upper layer by 1-2°C. The Klaipėda strait is
always ice free, while in the rest of the lagoon ice cover is present for 110 days on average (Pustelnikovas 1998; Gasiūnaitė et al. 2008).

Figure 3: Modeled average residence time distribution of the Curonian Lagoon (Ferrarin et al. 2008).
The oxygen concentration fluctuates spatially and temporally (both diurnally and seasonally) (Jurevičius 1959). Low concentrations down to 1.8 ml l⁻¹ were found during the ice cover period; local anoxia may take place in summer at night.

Other ecological characteristics of the Curonian Lagoon are presented in Table 1.

**Table 1.** Ecological characteristics of the Curonian Lagoon (based on Jurevičius 1959; Galkus and Jokšas 1997; Gasiūnaitė *et al.* 2008). *DW* dry weight, *WW* wet weight, *Chl a* chlorophyll *a*, *POC* particulate organic carbon, *TPM* total particulate matter.

<table>
<thead>
<tr>
<th>Latitudes, N</th>
<th>55°52'-55°42'</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic level</td>
<td>Eutrophic</td>
</tr>
<tr>
<td>Organic matter content in sediments (%DW)</td>
<td>&lt;1% in fine sand, &gt;5-15% in accumulation areas</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>0.3-2.2</td>
</tr>
<tr>
<td>pH</td>
<td>7.2-9.2</td>
</tr>
<tr>
<td>Oxygen saturation (%)</td>
<td>20-115</td>
</tr>
<tr>
<td>Ca²⁺ (mg/l)</td>
<td>34.5-108.4</td>
</tr>
<tr>
<td>POC (mg C l⁻¹)</td>
<td>0.4-2.4</td>
</tr>
<tr>
<td>TPM (mg l⁻¹)</td>
<td>1-88</td>
</tr>
<tr>
<td>Bacteria abundance (10⁶ ml⁻¹)</td>
<td>0.8-39.3</td>
</tr>
<tr>
<td>Chlorophyll concentration (μg Chl a l⁻¹)</td>
<td>Mean: 45, spring max: 302, autumn max: 458</td>
</tr>
<tr>
<td>Mesozoooplankton biomass</td>
<td>&lt;8</td>
</tr>
<tr>
<td>WW (mg l⁻¹)</td>
<td></td>
</tr>
</tbody>
</table>

1.2. Diversity of benthic macrofauna

Due to the high substrate variability and the high freshwater input from the Nemunas River, the Curonian Lagoon belongs to one of the most macrozoobenthos diverse estuarian areas of the Baltic Sea (e.g. in comparison with Vistula Lagoon, Stettin Lagoon, Boddens of Darß-Zingst) (Zettler and Daunys 2007 and references therein). The resent macrofauna inventory compiled for the littoral zone of the lagoon includes approximately 280 benthic species (Zettler and Daunys 2007).
Salinity is the main factor determining benthic species distribution in the Curonian Lagoon (Daunys 2001). Benthic fauna in the strait area is a mixture of freshwater and euryhaline organisms, with a total of 49 benthic and nektobenthic species identified (Bubinas and Vaitonis 2005). The western side of the Klaipėda strait is inhabited by a rather diverse benthic fauna that is able to withstand rapid environmental fluctuations and essential anthropogenic pressure. The number of species, abundance and biomass vary within a wide range and are subject to rapid changes. Communities are dominated by *Nereis diversicolor*, *Marenzelleria neglecta*, oligochaets and chironomids, *Balanus improvisus*, *Cordylophora caspia*, *Mya arenaria*, *Macoma balthica* and *Mytilus edulis* (Gasiūnaitė et al. 2008).

The eastern side of the Klaipėda strait is highly affected by port industry. The muddy sediments here are polluted with organic material, solid litter, heavy metals and oil products. Only the most tolerant species can survive in this heavily disturbed biotope; oligochaets and chironomids are the main forms, while *Nereis diversicolor* and *Marenzelleria neglecta* may be found in comparatively less polluted locations. Benthic macrofauna is absent in enclosed bays with restricted water exchange (Olenin and Daunys 2004; Gasiūnaitė et al. 2008).

In the northern part of the Curonian Lagoon, two main zones can be distinguished with respect to bottom macrofauna communities: a large eastern shallow (depth <1.5m) area with fine sand as the prevailing bottom substrate, and the deeper (depth between 1.5 and 4m) western area along the Curonian spit covered mainly with muddy sediment (Gasiūnaitė et al. 2008).

The sandy bottoms on the eastern side of the lagoon may be subdivided into a variety of biotopes: fine sand with macrophytes (e.g. *Potamogeton* species); fine sand with large native unionids (*Unio tumidus*); fine sand and silt with oligochaets and chironomids as well as biotopes by the alien invasive species *Dreissena polymorpha*, *Marenzelleria neglecta* and Ponto-Caspian and North American amphipods (mainly *Obessogammarus crassus*, but also *Pontogammarus robustoides* and *Gammarus tigrinus*). The biotope occupied by large numbers of mobile amphipods is present in the very narrow (<20m)
uppermost part of the underwater slope (depth <0.5m) and may be distinguished only during the warm period of the year when dense communities of gammarids develop (Daunys and Olenin 1999). All other biotopes alternate with each other on a scale of 10-100m. Invasive benthic macrofauna constitutes an important part of the biotope-forming species, contributing up to 95% of total community biomass. Even in locations where unionids are the predominant species, approximately 65% of them are fouled by zebra mussels (Gasiūnaitė et al. 2008).

The main community of the muddy bottom biotope is dominated by oligochaets and chironomids. A comparatively large part of the muddy bottoms is covered by shell deposits formed mainly by *Valvata* species with an admixture of *Bithynia* spp., *Radix* spp., *D. polymorpha* and *Potamopyrgus antipodarum*. In areas less exposed to saline water inflows, clumps of living zebra mussels may also be found (Gasiūnaitė et al. 2008).

In the central part of the lagoon, there are two principal most abundant communities – one is dominated by the zebra mussel *D. polymorpha*; another is dominated by a variety of oligochaets and chironomids (Daunys 2001; Olenin and Daunys 2004). Due to the habitat engineering activity of *D. polymorpha*, the community of co-occurring species is rich in species number (up to 29 per sample, and about 50 in total). The total biomass (up to 11 kg m\(^{-2}\)) and abundance (up to \(10^5\) ind. m\(^{-2}\)) are the highest for the entire Curonian Lagoon (Olenin and Daunys 2004).

In the bottoms dominated by oligochaets and chironomids approximately half of the lagoon bottom macrofauna are found; however none of them is constant. The species number varies from 2 to 16 per sample, and total biomass from 10 to 40 g m\(^{-2}\) (Daunys 2001).

The muddy bottom of the southern Curonian Lagoon has the least diverse species composition. This community is dominated by the unevenly distributed chironomids. Higher abundances are found in the accumulation zone along the eastern coast of the lagoon. Other organisms typical for this community are oligochaets, *Valvata* and *Pisidium* species (Gasiūnas 1959). Few local patches of zebra mussel population are also found in the southern part of the lagoon (e.g. near

1.3. Aquatic invasions in the Curonian Lagoon: introduction pathways

Species become spread by a wide range of pathways either deliberately or inadvertently. Depending on the researcher and identification methods the number of possible pathways categories may vary from five to fifteen or even more (Carlton 1988; Minchin, 2001).

Among the possible unintentional aquatic introduction pathways, the movement of ballast water by ships is the largest single source of aliens’ transfer throughout the world today (Gollasch and Leppäkoski 1999). From this point of view, Klaipėda must be considered as a potential “hot spot” for ballast mediated introductions, since it is the only commercial sea port in Lithuania. It is the third largest port in the Baltic States and the most northern ice-free seaport in the Baltic Sea. Water in the harbour area does not freeze even at air temperature -25°C. The annual port cargo handling capacity is up to 40 million tons. The shortest distances connect the port with the most important industrial regions of eastern hinterland (Russia, Byelorussia, the Ukraine, etc.). The main shipping lines to the ports of Western Europe, South-East Asia and the continent of America pass through Klaipėda port (Klaipėda seaport 2008). Every year, about 7000 ships call the port. They release from 2 to 4 M tonnes of ballast water annually. However, yet no one primarily ballast water related introduction was detected in Klaipėda port. All invasive species of “ballast water origin” appeared in the Lithuanian coastal waters due to semi-natural secondary spread from other, previously inoculated parts of the Baltic Sea (Olenin et al. 1999a).

A number of aquatic alien species have been imported to the Curonian Lagoon through the system of canals, the so-called ‘Central European invasion corridor’ (Olenin 2002). Canals enabled species to enter previously uncolonized areas through corridors linking separate seas and river basins either aided by the movement of vessels, by natural expansion or both. European canals for navigation, since the late 1700s,
were built connecting Eastern Europe to the North Sea, The Mediterranean Sea and the Atlantic Ocean (Minchin et al. 2008).

The Lithuanian inland waters were connected by canals with the Black Sea drainage basin. The first canal, which linked the rivers of the Baltic and Black Seas watersheds, was the Dnieper-Neman (Oginsky) Canal. Its construction was initiated and originally funded by Polish hetman, composer and poet Michael Kasimir Oginsky. The canal itself is 54 km long, connecting the lake Vygonovskoje with Jaselda, an affluent of the Pripiat river, which in turn is the major tributary of the river Dnieper. On another side, the river Shchara springing from that small (max length 7 km) lake flows into the river Nemunas (Neman) (Fig. 4) (Kolupaila 1953). The construction of the canal lasted from 1770 to 1784, and then several repeated reconstructions were performed during 1866–1868. The canal was mostly used to export Russian timber by rafts. However, it was also used to transport grain, fur, linen, honey etc. by ships and steamships to the ports in the south-eastern Baltic Memel (now Klaipėda) and Königsberg (now Kaliningrad). The peak of cargo transportation was reached in 1847–1848. Heavily damaged during World War I, the canal was almost completely restored in 1924–1939 (Karatayev et al. 2008).

There are several invertebrate species which most likely have invaded the Curonian Lagoon, during the 19th century and early 1900s, through the above mentioned invasion corridors. The hydrozoan *Cordylophora caspia* dwelling on hard substrates, the corophiid amphipod *Chelicorophium (Corophium) curvispinum* attaching its tubes to hard surfaces (including mussel shells) and the snail *Litoglyphus naticoides* usually inhabiting zebra mussel aggregates in the Curonian Lagoon (Jazdzewski and Konopacka 2002; Olenin 2002). All these species could use drifts, jetsam or boats for their traveling along canals and rivers.
Ponto-Caspian crustaceans were transplanted as food to stimulate fish production in European lakes and reservoirs during the 20\textsuperscript{th} century. Within the immense former USSR program of transplantations of Peracarida, more than 30 amphipod species from the “Caspian complex” were used for acclimatization purposes. In 1960-1961 several species of Ponto-Caspian amphipods and mysids were imported to the Kaunas water reservoir located on Nemunas river to improve the fish forage base. During a few years these crustaceans have established sustainable populations and spread over the Lithuanian inland waters and the Curonian Lagoon (Gasiūnas 1972; Arbačiauskas 2002).
1.4. Invasive benthic species in the Curonian Lagoon: xenodiversity and impacts

There are 17 non-indigenous aquatic species that known to occur in the Curonian Lagoon. Most of them (11 species) originate from the Ponto-Caspian region, 4 – from the North America, 1 – from the China Sea, and 1 – from the South Pacific (Table 2) (Baltic Sea Alien Species Database 2009).

Table 2: Aquatic alien species in the Curonian Lagoon (based on Baltic Sea Alien Species Database 2009 and references therein).

<table>
<thead>
<tr>
<th>Species name</th>
<th>First observed</th>
<th>Ecofunctional group</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Balanus improvisus</em></td>
<td>1844</td>
<td>Benthic suspension feeder</td>
<td>North America</td>
</tr>
<tr>
<td><em>Cercopagis pengoi</em></td>
<td>1992</td>
<td>Zooplankton predator</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Chaetogammarus warpacowskiiyi</em></td>
<td>1964</td>
<td>Nekto-benthic omnivore</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Chelicorphium curvispinum</em></td>
<td>1920s</td>
<td>Benthic deposit feeder</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Cordylophora caspia</em></td>
<td>1800s</td>
<td>Benthic suspension feeder</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Dreissena polymorpha</em></td>
<td>1800s</td>
<td>Benthic suspension feeder</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Eriocheir sinensis</em></td>
<td>1926</td>
<td>Benthic omnivore</td>
<td>China Sea</td>
</tr>
<tr>
<td><em>Gammarus tigrinus</em></td>
<td>2004</td>
<td>Nekto-benthic omnivore</td>
<td>North Sea</td>
</tr>
<tr>
<td><em>Hemimysis anomala</em></td>
<td>1962</td>
<td>Nekto-benthic omnivore</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Limnomysis benedeni</em></td>
<td>1962</td>
<td>Nekto-benthic omnivore</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Lithoglyphus naticoides</em></td>
<td>1900s</td>
<td>Benthic deposit feeder</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Marenzelleria neglecta</em></td>
<td>1985</td>
<td>Benthic suspension feeder</td>
<td>North America</td>
</tr>
<tr>
<td><em>Mya arenaria</em></td>
<td>1200s</td>
<td>Benthic suspension feeder</td>
<td>North America</td>
</tr>
<tr>
<td><em>Obessogammarus crassus</em></td>
<td>1962</td>
<td>Nekto-benthic omnivore</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Paramysis lacustris</em></td>
<td>1962</td>
<td>Nekto-benthic omnivore</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Pontogammarus robustoides</em></td>
<td>1962</td>
<td>Nekto-benthic omnivore</td>
<td>Ponto-Caspian</td>
</tr>
<tr>
<td><em>Potamopyrgus antipodarum</em></td>
<td>1887</td>
<td>Benthic deposit feeder</td>
<td>South Pacific</td>
</tr>
</tbody>
</table>

The bivalve *D. polymorpha* dominates the benthic communities in the freshwater central and southern parts of the lagoon. Within the
northern oligohaline part the abundance of *Dreissena* declines towards the Sea and it does not occur in high densities closer than 8 km from the outlet. The colonial hydroid *Cordylophora caspia*, the polychaete *M. neglecta*, the barnacle *Balanus improvisus* and Ponto-Caspian gammarids predominate in different bottom habitats of the northern part (Fig. 5) (Olenin and Leppäkoski 1999).

*C. caspia* and *B. improvisus* densely foul firm substrates (single boulders, submerged trees, wrecks, hydrotechnical constructions, etc.) on a soft bottom of the littoral and sublittoral zone within the strait area. The Ponto-Caspian gammarids (*Pontogammarus robustoides, Obessogammarus crassus* and *Chaetogammarus warpachowskyi*) are dominant in the littoral zone. They inhabit floating mats of filamentous green algae in the Curonian Lagoon, reaching biomass of 120 g m\(^{-2}\) vs 10 g m\(^{-2}\) of native species. The bivalve *Mya arenaria* occurs predominantly close to the outlet in the soft bottom sediments together with other invasive euryhaline species, like *Chelicorophium curvispinum, Gammarus tigrinus* and *M. neglecta*. The nekto-benthic Ponto-Caspian mysids *Paramysis lacustris* and *Limnomysis benedeni* form dense populations in the central part of the Curonian Lagoon, where native marine mysids are absent. The surface deposit-feeder gastropod *Potamopyrgus antipodarum* inhabits the extremely soft bottoms in the central and northern parts of the lagoon (Olenin and Leppäkoski 1999; Daunys 2001).

All of the alien species in the Curonian Lagoon effect the functioning of the ecosystem to some extent. The alien species present in the Curonian Lagoon (e.g. *M. neglecta*, all the mysids and amphipods, *C. pengoi*) are known to regulate the trophic chain being a valuable food source for native fish (Gasiūnas 1964; Winkler and Debus 1997; Ložys 2003). Mysids, *C. pengoi* and *E.sinensis* are capable of regulating the zooplankton populations, preying on them (Ketelaars et al. 1999; Ojaveer et al. 2004; Grabowski et al. 2005; Lesutienė et al. 2008).
Since the niches of the newcomers and native species usually overlap (partly or fully), the competition for food and/or space is the most frequent impact reported (Baltic Sea Alien Species Database 2009). Although some of the aliens have caused an essential re-distribution of the native communities (*e.g.* *D. polymorpha*, *C. caspia*,

**Figure 5:** Distribution of alien species in the Curonian Lagoon: (dark) area dominated, (grey) area invaded (Olenin and Leppäkoski 1999).
amphipods), no extinctions caused by introduced species have been reported in the Curonian Lagoon yet.

The most successful alien species tend to markedly alter the habitats they invaded or were introduced to. They increase the three-dimensionality of the benthic habitats, link benthic and pelagic subsystems, create new microhabitats for associated fauna (Olenin and Leppäkoski 1999). Some functions of the non-native organisms are unique (new for the ecosystem), whereas some of them are already present (indigenous species have performed this activity earlier). Examples of novelty in functions are: *M. neglecta* – deep bioturbation of the sediments in the central part of the lagoon; *E. sinensis* – predation and scavenging in the northern part of the lagoon and strait area; *D. polymorpha* – active filtration and forming of beds and hard substrates for associated fauna on the soft bottom of the lagoon; etc. (Daunys 2001; Olenin and Leppäkoski 1999).

### 1.5. An ecological portrait of the zebra mussel

According to Orlova 2002, the recent taxonomic position of *Dreissena polymorpha* (Pallas, 1771) is identified as: Type: Mollusca; Class: Bivalvia; Order: Cardiida Ferussac, 1822; Family: Dreissenidae (Andrusov, 1897); Genus: *Dreissena* Van Beneden; Subgenus: *Dreissena s. str.* (Synonyms: *Mytilus polymorpha* Pallas, 1771; *Dreissensia polymorpha* (Pall.) Andrusov, 1897).

The zebra mussel gets its name from the distinctive, striped dark and pale shell colouration, although this is not seen on all specimens, especially older individuals (Minchin *et al.* 2002). It is a byssate epifouling bivalve, attaching by means of proteinaceous byssal threads to any different submerged substrates (Kilgour and Mackie 1993). It occurs usually on hard and mixed bottoms. On the soft sandy and silty bottoms it can foul the empty shells and live molluscs of the same and other species, as well as pieces and debris of different hard substrata. The mussels are met from the upper littoral down to tens of meters if ice abrasion is absent. Its maximal depth of occurrence registered in European waters is 60 m (Grim 1971). Maximum abundance is at 1-5 m depth. As a rule, lakes occupied by *Dreissena* are mesotrophic with
relatively high pH (7.4-8.5), moderate alkalinity (30-50 mg l\(^{-1}\) CaCO\(_3\)), and moderate amounts of dissolved mineral salts in the water (optimal conductivity >110 \(\mu\text{mhos cm}^{-1}\)) (Lyakhnovich et al. 1994; Orlova 2002).

Although zebra mussels have well defined environmental preferences, they are capable of tolerating a wide range of conditions outside the typical tolerance range. They can tolerate starvation for extended periods, desiccation, extremes of high and low temperatures, and highly variable dissolved oxygen levels. The mussels appear capable of adapting to a variety of temperature regimes, being found from Sweden to Italy. They have been found in lakes with highly variable acidity and calcium content. Large numbers have been reported growing in the static conditions of lakes and reservoirs and in the swift currents of pipes and rivers. They can be found in nutrient poor (oligotrophic) and nutrient rich (eutrophic) lakes. While normally considered as freshwater species, the zebra mussels can adapt and inhabit brackish areas. They are capable of tolerating a certain degree of pollution, although absent in heavily polluted waters. When exposed to acute, adverse conditions, the animal will close its shell and remain closed up to 2 weeks before reopening (Claudi and Mackie 1993).

Zebra mussels are filter feeders having both inhalant and exhalant siphons. They feed by filtering microscopic plankton organisms < 53 \(\mu\text{m}\) and organic particles from the water. Primarily, zebra mussels feed on algae and suspended detritus, and eventually – tiny free-floating zooplankton organisms might be captured (Mikheev 1994; Olenin et al. 1999b). Higher filtration activity of \(D.\) polymorpha population coincides with the location of higher biomasses. Maximum grazing rates can reach 234 ml h\(^{-1}\) ind\(^{-1}\) (Kryger J and Riisgård), the lowest values reported were around 0.11 ml h\(^{-1}\) ind\(^{-1}\) (Kotta et al. 1998).

The zebra mussel produces veliger larvae which remain within the plankton for some weeks and become concentrated by wind and water currents in embayments along rivers or in lakes producing high settling numbers. Mortalities during their free-living stage and metamorphosis are high and they may perish when carried downstream in rivers or estuaries (Minchin et al. 2002). The zebra mussel in Europe is characterized by annual reproduction, except for the most northern
populations. The species is an r-strategist; female zebra mussels can spawn more than a million eggs, and males up to nearly 10 billion sperm, each contributing to more than 30 percent of their body weight prior to spawning (Sprung 1991). Temperature and salinity are the most important environmental abiotic factors limiting the recruitment and development of *D. polymorpha*. The spawning period lasts from the late spring to the early autumn if the temperature is above 12°C (Orlova 2002).

According to the recent literature review (Molloy *et al.* 1997), there are approximately 200 species that may be considered predators or parasites of zebra mussels. These are birds and fishes that feed on attached mussels and larval stages, as well as copepods, coelenterates, leeches, crabs, crayfishes and rodents. Among organisms that compete with mussels for hard substrates are sponges, coelenterates, amphipods, bryozoans and other mussel species with the same life-style. In Europe, the most common parasite is *Bucephalus polymorphus* (Baer 1827) (Plathelmintes,Trematoda). The frequency of occurrence usually does not exceed 10-20% of the Dreissenid population (Zdun *et al.* 1994).

The round goby, *Neogobius melanostomus*, native to the Black and Caspian Seas and also introduced into many other regions via ship ballast waters, feeds preferentially on zebra mussels. Gobies 6 to 10 cm in standard length consume mussels up to 7 x 13 mm, with 4-13 mm mussels being taken under experimental conditions at an average of 36 to 47 mussels per day (Ghedotti *et al.* 1995).

In the Curonian Lagoon, the benthophagous fish (*e.g.* roach and bream) are capable of feeding on *Dreissena* mussels up to 12 mm length (Gasiūnas 1959).

### 1.6. Impacts of the zebra mussel – lessons learned in other ecosystems

To date, *Dreissena polymorpha* has been the most aggressive freshwater invader worldwide. Its life history facilitates its abilities as invader, and allows it to become enormously abundant when introduced into a new water body. Once introduced, its population can grow rapidly, and the total biomass can exceed 10 times that of all other
native benthic invertebrates. The zebra mussel is frequently competitively dominant over native benthic fauna, and can impact all components of the freshwater ecosystem, especially benthic animals. Most of the impacts of zebra mussels in freshwater systems are a direct result of their functioning as ecosystem (habitat) engineers (Karatayev et al. 2002 and references therein).

Zebra mussel is acknowledged by many authors as a powerful ecosystem engineer species in the most aquatic ecosystems it has invaded (Nalepa and Fahnenstiel 1995; Olenin 1997a; Stewart et al. 1998; Karatayev et al. 2002; Minchin et al. 2002; Vanderploeg et al. 2002). It alters habitats in both autogenic and allogenic way (sensu Jones et al. 1994), modifying the morphological and physical properties of sediments, extensively filtering suspended material and thereby affecting the availability of resources in ecosystem (Karatayev et al. 1997; Bially and MacIsaac 2000; Beekey et al. 2004; Hecky et al. 2004). Zebra mussel clumps (druses) are capable of increasing the colonisable benthic surface area (Botts et al. 1996; Stewart et al. 1998; Bially and MacIsaac 2000; Karatayev et al. 2002), providing the enemy- or stress-free space (Gutierrez et al. 2003; Beekey et al. 2004), controlling the transport of particles and solutes in the near-bottom environment (Gutierrez et al. 2003), altering boundary layer characteristics (Karatayev et al. 1994; Gutierrez et al. 2003), increasing the amount of organic material in the sediment by depositing feces and pseudofeces (Karatayev et al. 1994; Botts et al. 1996; Stewart et al. 1998; Karatayev et al. 2005), increasing water clarity via removing inorganic particulates and plankton from the water column, increasing dissolved nutrients concentrations via excretion or removing seston from the water column (Stewart et al. 1998; Karatayev et al. 2002; Rosemond and Anderson 2003). In addition, water flow induced by zebra mussel filtering activity enhances oxygenation of the benthic habitat (Karatayev et al. 1997). The later three impacts can be classified as allogenic and are subsistent only to live mussels, whereas the others (autogenic) might be induced by spent shells as well.

The principal and the most extensively studied zebra mussel impacts are presented in the Table 3. Yet, in addition to these direct impacts on
environment and/or biotic communities, the activities of zebra mussels can have many indirect impacts on an ecosystem (Karatayev et al. 2002).

Zebra mussels are functionally different than most benthic invertebrates in freshwater. Although they have large impacts on the structure and function of the benthos, they also have a large direct impact on the planktonic community. Via filtering large volumes of water and transporting the removed material to the bottom, they provide a direct link between processes in the plankton and those in the benthos (Karatayev et al. 2002). Therefore, zebra mussels, differently from the other aquatic invaders, are capable of unifying the remote parts of the freshwater ecosystem and inducing system wide effects. Still, it is quite tricky to overview and assess the whole spectrum of zebra mussel impacts, since these impacts are not strictly linear and the mechanisms by which zebra mussel causes such impacts sometimes are not very clear.
Table 3: Impacts of the zebra mussel reported from different ecosystems (based on Berkman et al. 1994; Bruner et al. 1994; Strayer and Smith 1996; Effler et al. 1997; Burlakova et al. 1999; Gollach and Leppäkoski 1999; Claudi and Leach 2000; Karatayev et al. 2002; Minchin et al. 2002; Lucy et al. 2005)

<table>
<thead>
<tr>
<th>Type of impact</th>
<th>Where reported</th>
<th>Impact outcomes</th>
</tr>
</thead>
</table>
| Fouling        | Baltic Sea region (inland waters), Belarus (lakes), Ireland (lakes), Spain (inland waters), USA (the Great Lakes) | - The overgrowth of native bivalves (predominantly unionids) by zebra mussels results in dramatic decline of their population  
- Navigational and recreational boating is affected by increased drag due to attached mussels  
- Small mussels can get into engine cooling systems causing overheating and damage  
- Fishing gear is being fouled if left in the water for long periods  
- Continued attachment of zebra mussel can cause corrosion of steel and concrete affecting its structural integrity |
| Filtration     | Belarus (lakes), Europe (inland waters), Ireland (lakes), USA (the Great Lakes) | - Active filtration by zebra mussels causes the decline in phytoplankton biomass  
- The efficient filtering by large numbers of zebra mussels greatly increases water clarity  
- The seston is transported from the plankton to the benthos via the biodeposition by zebra mussels  
- The zebra mussel may influence contaminant cycling by bioaccumulating high levels of hydrophobic contaminants in its tissue  
- The filtering activity of zebra mussels has the direct effect of reducing nutrients, which are associated with particles and plankton  
- Zebra mussels can mobilize substantial quantities of ammonia and phosphorus (via filtering and biodeposition activity) |
Native unionids may be affected by zebra mussels by competition for food as well as by fouling.

<table>
<thead>
<tr>
<th>Aggregation</th>
<th>Belarus (lakes), Lithuania (Curonian Lagoon), USA (the Great Lakes)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>- Aggregating in large densities, <em>D. polymorpha</em> creates new two- and three-dimensional habitats for different organisms, radically changing bottom substrates.</td>
</tr>
<tr>
<td></td>
<td>- Shell deposits of zebra mussels change soft bottoms (sand or silt) into shell gravel, and create patches of hard substrate for sessile species on uniform soft bottom sites.</td>
</tr>
<tr>
<td></td>
<td>- The occurrence of zebra mussels in shallow areas where bathing occurs has resulted in an increase in foot lacerations with possible consequences of infection from a number of freshwater organisms.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Transfer of parasites</th>
<th>Belarus (lakes), USA (the Great Lakes)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>- <em>Dreissena</em> is known to be a host of 34 parasites and commensals. At least some of these are host specific and several of these invade new habitats with <em>Dreissena</em>.</td>
</tr>
</tbody>
</table>
1.7. Zebra mussel in the Curonian Lagoon: introduction, distribution, research history

The native range of the zebra mussel includes Danube, Dniestr, Berezan, Southern Bug, Dniepr, Molochnaya, Don, Kuban, Kamchia, and Veleca river basins; isolated and semi-isolated relic estuarian reservoirs along the Bulgarian, Romanian, Ukrainian, and Russian Black and Azov seas coasts (Son 2007). It was formerly present in the Aral Sea, but due to increasing salinities and reduced lake area it no longer exists there (Karatayev et al. 1998).

Without the vagaries of human interference, the zebra mussel would most likely have remained for a long time within its native range (Minchin et al. 2002). It is most likely, that the introduction of the zebra mussel Dreissena polymorpha into the Vistula and Curonian coastal lagoons happened in the early 1800s, due to the transportation of timber rafts with attached molluscs via the Central European invasion corridor. The interesting fact is that the next “destination point” of the species in Western Europe was London (1824) and Amsterdam (1826), the principal recipient ports for the Baltic timber trade at that time (Olenin et al. 1999b). From there zebra mussel started its spread over the Western and Central Europe.

However, there is a point of view that zebra mussel spread could happen much earlier. According to the palaeontological data Dreissena could exist in the Baltic Sea drainage area during the interglacial time, but later became extinct and was re-introduced in the early 1800s (Starobogatov and Andreyeva 1994).

To date, zebra mussels are very abundant in the Curonian Lagoon. They can be found from the upper littoral down to 3-4 m depth, on hard substrates (boulders, embankments, hydrotechnical constructions) and soft bottoms (sand, silt or mud) (Zemlys et al. 2001). The largest area occupied by zebra mussel community is located in the central part of the water body (Gasiūnas 1959; Aristova 1965; Bubinas 1983; Olenin 1987; Olenin 1988; Olenin 1997b; Daunys 2001). On the bottom dominated by Dreissena, the sediment is formed mainly by zebra mussel shell deposits and zebra mussel clumps. The largest ever found zebra mussel biomass (up to 11 kg m\(^{-2}\)) and abundance (up to 38000 ind. m\(^{-2}\)) were obtained
from this part of the lagoon (Galko 2003; Gasiūnaitė et al. 2008). Few local patches of zebra mussel population are also found in the southern part of the lagoon, yet no quantitative data are available for these sites. Therefore in the current study predominantly zebra mussel community from the central part of the Curonian Lagoon was considered.

Studies on bottom macrofauna diversity and biology in the Curonian Lagoon started in the early 1920s (Szidat 1926; Willer 1931; Lundbeck 1935). The most comprehensive inventory of the Curonian Lagoon bottom macrofauna was carried out in 1950s (Gasiūnas 1959). Several later studies focused on the ecology of introduced species (Daunys 2001; Olenin and Leppäkoski 1999). Although *D. polymorpha* was not the direct subject of all the mentioned researches, it was addressed to some extent in each of them. Later on, some of the impacts of zebra mussel were modeled and quantitatively evaluated (Zemlys et al. 2001; Daunys et al. 2006). Some aspects of zebra mussel functioning have been studied within the framework of student research program at Klaipėda University. However, there is still a lack of any holistic insight of zebra mussel impacts on the lagoon’s ecosystem, and no comprehensive overview of its ecosystem engineering effects on different levels of the ecosystem.
2. MATERIALS AND METHODS

2.1. Peculiarities of the zebra mussel studies in the Curonian Lagoon

The direct pre- and post-invasion comparisons could not be applied in the Curonian Lagoon, since zebra mussel invasion in the lagoon happened long before ecological research commenced. Therefore in the current study the habitat engineering impact of *D. polymorpha* were assessed referring to the control bottom sites, free from live mussels and their shell deposits. All the control sites were situated within the distribution area of zebra mussel in the Curonian Lagoon.

The major obstacle that have been confronted with was the impossibility of applying the traditional techniques of underwater observations commonly used for benthic research (e.g. remote underwater video or SCUBA diving) in the Curonian Lagoon, because of very low visibility (the Secchi depth is less than 0.5 m). Due to the complexity of the bottom landscape, this part of the lagoon is characterized by the high patchiness in species distribution. For instance, three replicates taken from the same sampling site may show an extremely high data spread in species abundance (e.g. 790, 3520 and 4030 ind m⁻² (Solovjova 2001)) and biomass (1, 24 and 50 g m⁻² (Solovjova 2001). It was impossible to make any *a priori* choice of the accurate positions for sampling sites, so stratified sampling design, which would give the best fit to the study and ensure that the major habitat types are included in the sample could not be applied. Therefore the systematic sampling was considered to be the best (and likely the only appropriate) option for the benthic habitat studies in this ecosystem. Yet such a “blind” sampling method forced me to apply an *a posteriori* habitat classification, based on the results of quantitative analysis of samples. This has brought a certain extent of circularity into the applied approach. The only possible way to overcome this problem under the given circumstances was to plan some kind of field experiment with bottom areas chosen in advance and manipulated by a researcher by removing or adding mussels and shells accordingly. Still the aim of the current study was to gain some insight into the natural
benthic habitats and communities, so the experimental approach was not accepted as appropriate in this case.

2.2. Research methods applied for zebra mussel bed and shell deposits

The quantitative characteristics of *D. polymorpha* population and macrozoobenthic communities were obtained from the results of two surveys performed in 1999 and 2006, using different sampling strategies (Fig.6).

In 1999, sampling stations were distributed evenly in the northern and central parts of the lagoon, in order to estimate the distribution patterns and the size of the area colonized by the zebra mussel community. In total, 27 sites were sampled with one replicate in each.

In 2006, the sampling was performed along the transect crossing the area occupied by zebra mussel population (Fig.6) in order to obtain data along the shell deposits and zebra mussel biomass gradients and assess the small-scale habitat patchiness. In total, 10 stations with 3 replicates in each were sampled.

All the samples were obtained from the sites with resembling depths (2.6 ±1 m) and hydrodynamic conditions.

A Van-Veen type grab (catch area 0.1 m²) was used for macrofauna sampling. Each sample was sieved (0.5 mm mesh size) and preserved (4% formaldehyde solution) on board. Once in the laboratory, the macrozoobenthic species were sorted out, 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, taxonomic identification of shell deposits (up to genus or species level if possible) was carried out. Then shell deposits of different taxonomic groups were dried and weighed separately.
2.2.1. Classification of habitats

Since the *a priori* identification of habitat type or its localization under existing conditions in the studied ecosystem could not be performed, therefore the preliminary differentiation of habitats into ‘bare sediments’, ‘zebra mussel shell deposits’ and ‘zebra mussel bed’ was possible only after the onboard visual inspection of sampled material during the field sampling campaign, and more precisely – after the quantitative treatment of samples. Gradient analysis was performed in order to determine essential changes in species composition along the habitat gradient. For that purpose all species presence/absence data were
set up according to the dry weight of shell deposits and log-transformed zebra mussel biomass. The thresholds for occurrence of species that have been observed only in live zebra mussel clusters or its shell deposits were analyzed.

2.3. Experimental study of zebra mussel filtration and biodeposition

The experiment was conducted in a 300 l laboratory flume (Table 4).

Table 4: Main geometrical and hydrological characteristics of the experimental flume.

<p>| | |</p>
<table>
<thead>
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</thead>
<tbody>
<tr>
<td>Length, m</td>
<td>2.3</td>
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<tr>
<td>Width, m</td>
<td>0.48</td>
</tr>
<tr>
<td>Height, m</td>
<td>0.61</td>
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<tr>
<td>Maximal water level, m</td>
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</tr>
<tr>
<td>Maximal current velocity, m s⁻¹</td>
<td>0.22</td>
</tr>
<tr>
<td>Reynolds number</td>
<td>11875</td>
</tr>
</tbody>
</table>

Two electric pumps generated a flow typical for the central part of the lagoon (5-10 cm s⁻¹). The flume was equipped with a double bottom to enable water circulation and a set of laminators to decrease turbulence in the experimental area. The experimental area (61x48 cm) was situated about 45 cm down-stream from the laminators (Fig. 8).

The experimental design was based on assumption, that zebra mussels are non-selective filter-feeders, although they do ingest particles selectively. While algae and other organic particles can be digested, assimilated and excreted, the inorganic fraction of the seston is not absorbed, but is expelled in the form of faeces or pseudofaeces. Knowing the amount of inorganic matter (ash weight) which has been settled by mussels over a time period and the concentration of particulate inorganic matter (PIM) in the water adjacent to the mussels, the volume of water cleared by the mussels can be calculated (Yu and Culver 1999).
Figure 8: The conceptual scheme of the experimental flume and its equipment.
Also, knowing the total particulate matter (TPM) and PIM concentrations in the adjacent water it is easy to calculate the concentration of the particulate organic matter (POM), and consequently – the PIM/POM ratio. Similarly, this ratio may be calculated for the deposited matter. Thus, the one can assess the transportation of seston from plankton to benthos by zebra mussels via filtration and biodeposition.

2.3.1. Experimental set-up

Plastic 0.5 l vessels (with a bottom area of 0.01 m² and a height of 5 cm) were used to collect the faeces and pseudofaeces of zebra mussels. A total of 16 experimental vessels were used for experimental treatments, 3 replicates for each zebra mussel density: D1, D2 and D3, and 4 control vessels with a zero-density – C0. The vessels were arranged in the experimental area following the Latin squares design and put in the sampling area. Mussel clumps with different densities were chosen to evaluate the “refiltration” effect described by Yu and Culver in 1999. The applied mussel densities were close to those found in the Curonian Lagoon: 1) 15 ± 3 ind. vessel⁻¹, 2) 35 ± 8 ind. vessel⁻¹, 3) 60 ± 15 ind. vessel⁻¹ (equivalent to 1300 ± 249, 3000 ± 684 and 5100 ± 1282 ind. m⁻², respectively). The zero-density vessels were used to measure the background (physical) sedimentation rate.

The first experimental factor was the density of a clump (druse), with 4 treatments and 4 replicates in each. To fix the other two random factors – the so-called ‘wall effect’ (the decline of current velocity from the center towards the walls of the flume) and ‘laminator effect’ (the decline of current velocity when receding from the laminators) – the Latin square layout was applied. This layout consisted of arranging four replicates of each treatment so that every treatment was equally represented in the two directions of the grid that may have gradients of variability running across them (the ‘wall effect’ in the horizontal direction and the ‘laminator effect’ in the vertical direction). The scheme of the arrangement is shown in Fig. 9.
Three replicates of the experiment were conducted in time. Due to the natural fluctuations, the concentration and composition of the seston was not constant. Thus, the TPM concentration was considered as another fixed factor of the experiment. The ANOVA model of the experiment could be presented as following:

$$X_{ijkm} = \mu + C_i + D_j + CD_{ij} + Vert_k + Hor_l + e,$$

where: $\mu$ is the overall mean, $X_{ijkl}$ is the biodeposition, $C_i$ is the TPM concentration, $D_j$ is the density of a druse, $Vert_k$ is the ‘laminator effect’, $Hor_l$ is the ‘wall effect’, $e$ is the residual. Here, it is assumed that factors $C_i$ and $D_j$ are orthogonal to each other, so there is potentially an interaction between them $(CD_{ij})$. The interactions with/between random factors $Vert_k$ and $Hor_l$ are assumed to be zero.

Zebra mussels for the experiment were collected from the upper littoral in the central part of the Curonian Lagoon, near the mouth of the Nemunas river (see Fig. 1), 10 days prior to the experiment, and were acclimated in the laboratory, in 60 l aquaria, in permanently aerated
lagoon water, at a temperature of $16 \pm 0.5{}^\circ C$. The water for acclimation was taken from the same site and was renewed twice per acclimation period.

250 litters of water from the littoral in the central part of the lagoon, preliminarily sieved through 0.5 mm mesh to remove coarse debris, were poured into the flume and laid off for at least 60 h (to omit the most intensive physical sedimentation). After that the 16 experimental vessels were inserted. Before the experiment, mussels were sorted by size and only small druses with medium-sized individuals ($10 – 20$ mm) were selected. To form an aggregate of a wanted density, several druses were placed into a vessel. Each experiment lasted for 72 hours (3 days). Then, all the vessels were carefully closed under the water (to avoid resuspension of the deposited material) and removed from the flume. The water with deposits and supernatant siphoned from the druses was collected for the analysis.

The experimental mussels were separated from the druses, counted, weighed and measured. The shell free dry weight (SFDW) of the each druse was measured after drying the soft tissue of mussels at $105{}^\circ C$ to constant weight.

To measure TPM, PIM and POM concentrations in the ambient water, 0.5 l of flume water was collected once per day and also in the very beginning (when the water was poured into the flume). Three replicates of the water sample were taken at a time. The results of the replicates were averaged for the further analysis.

2.3.2. Sample analysis and calculation

The TPM and PIM concentrations in experimental vessels and in the flume were determined by filtering up to 500 ml of each water sample through a pre-dried and weighed Fisherbrand general filtration membrane filter (pore size = 0.45 μm, diameter = 47 mm). Filters were dried at $105{}^\circ C$ to a constant weight, and weighed. The TPM concentration ($C_{TPM}$) was calculated as:

$$C_{TPM} = \frac{(mg l^{-1})}{(m_2 - m_1)} V^{-1},$$
where \( m_1 \) is the weight of the pre-dried filter (mg), \( m_2 \) is the weight of the filter with the filtered and dried seston (mg), \( V \) is the volume of the filtered water (l).

Further, the filters were ignited in a furnace at 500 °C for one hour to ash the seston samples. The residual was then weighed. The POM concentration (\( C_{POM} \)) was calculated as:

\[
C_{POM} = \left( \frac{mg}{l} \right) = (m_3 - m_2) \frac{mg}{V},
\]

where \( m_3 \) is the weight of the ignited filter. The PIM concentration was assessed as a difference between \( C_{TPM} \) and \( C_{POM} \).

The effective clearance rate (\( ECR \)) – the actual ability of zebra mussels to clear particulate matter under given hydrodynamic conditions (Yu and Culver 1999) – for a given density treatment was calculated as:

\[
ECR = (l \ h^{-1} \ ind^{-1}) = (W - W_0) \frac{(C_{PIM} \ N \ T)^{-1}}{T},
\]

where \( W \) is the total sediment ash weight from the experimental vessel with zebra mussels (mg), \( W_0 \) is the average ash weight in the zero-density control vessels (mg), which represents the background sedimentation, \( C_{PIM} \) is the PIM concentration in the ambient flume water (mg l\(^{-1}\)) averaged from samples collected during the experiment, \( T \) is the duration of incubation (h), and \( N \) is the number of mussels in that experimental vessel. Later on, the ECR was recalculated into l day\(^{-1}\) gSFDW\(^{-1}\), to verify the results of the 0-dimentional clearance rate model for zebra mussel population (Zemlys et al. 2001) and zebra mussel seasonal clearance rates estimated from the TPM budget of the Curonian Lagoon (Daunys et al. 2006).

The biodeposition rate (\( BDEP \)) – the amount of TPM, sedimented by zebra mussels under given hydrodynamic conditions, for a given density treatment, was calculated as:

\[
BDEP = (mgTPM \ h^{-1} \ ind^{-1}) = (U - U_0) \frac{(N \ T)^{-1}}{T},
\]

where \( U \) is the amount of sedimented TPM in the experimental vessel with zebra mussels (mg), \( U_0 \) is the average amount of sedimented TPM in the zero-density control vessels (mg), \( T \) is the duration of
incubation (h), and \( N \) is the number of mussels in that experimental vessel.

The background sedimentation rate (\( SED \)) reflecting both the level of sediment input due to the physical precipitation and sediment resuspension in the control vessels due to the flow, and thus, representing an integrated sediment load for the whole experiment (Yu and Culver 1999), was calculated as:

\[
SED = (gTPM \ h^{-1} \ m^{-2}) = U_0 (a \ T)^{-1},
\]

where \( a \) is the bottom area of the experimental/control vessels.

### 2.4. Evaluation of the biogeochemical parameters in the benthic habitats modified by zebra mussels

This research was performed as a pilot study of the basic biogeochemical properties of sediments modified by zebra mussel (zebra mussel bed and zebra mussel shell deposits), referring to the unmodified (bare) soft bottom.

Three sampling sites, each corresponding to the one of the three specified habitat types, were selected. The main requirements for the appropriate sampling sites were defined as follows: all of them must be located within the distribution area of the \( Dreissena polymorpha \) in the Curonian Lagoon, with resembling depth, sediment grain size and hydrodynamic conditions. Each of the chosen sites should represent the averaged habitat of the corresponding type (‘zebra mussel bed’, ‘zebra mussel shell deposits’ and ‘bare sediments’) (as it was classified in section 2.2.1.).

Based on the data received from the earlier surveys and preliminary sampling in the area, the sites were empirically selected as presented in Fig.10.
Figure 10: Three sampling sites in the central part of the Curonian Lagoon.

2.4.1. Sampling design
In 2006 three sampling surveys (in May, August and October) were accomplished in the central part of the Curonian Lagoon, at the three earlier defined sites, corresponding to different bottom types. Parameters 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 sediments layer: medium grain size, organic carbon, total nitrogen and phosphorus concentrations, oxygen consumption, anaerobic organic matter mineralization, redox conditions.
A Van-Veen type grab (catch area 0.1 m²) was used for macrozoobenthos and sediment sampling. Samples were collected and treated following standard guidelines for bottom macrofauna sampling (HELCOM 1988). Surface and near-bottom water was sampled using 2 l Ruttner type sampler.

2.4.2. Treatment procedures for hydro- and geo-chemical samples

The hydrochemical parameters (temperature, pH, red-ox potential (Eh) and salinity) in the upper and near-bottom water layers were measured in situ with a portable universal meter MultiLine F/Set-3 (WTW). Dissolved oxygen concentration was measured using Winkler’s method. Dissolved organic carbon (DOC) was measured using the dichromate oxidation method. Nutrients concentrations were measured as defined by Merkienė and Čeponytė (1994). Phosphate-phosphorus compound was assessed via molybdate ascorbic acid method after digestion with sulphuric acid. The total phosphorus (TP) concentration was measured using persulphate-H₂SO₄ digestion and molybdate ascorbic acid methods. Nitrate nitrogen compound was determined using potassium persulfate-K₂S₂O₈ with following Cd reduction to NO₂. Total N (TN) was analysed by the Kjeldahl method (Jirka et al. 1976).

TN and TP concentrations in the upper sediment layer were analysed using spectrophotometric phenol-hypochlorite method. The organic and other compounds of nitrogen were converted into ammonium by digestion with concentrated sulphuric acid. The concentration of organic carbon (Corg) in the bottom sediments was determined using the dichromat oxidation method (Potapova 1980).

The intensity of aerobic and total (aerobic + anaerobic) organic matter mineralization was determined using the isolated columns (Kuznecov & Dubinina 1980). Undisturbed bottom sediment columns (5 cm diameter) were taken using glass cores. Then the cores and the control (without bottom sediments) were carefully filled with near-bottom water and incubated in situ for 24 hours. The oxygen consumption (mg O₂ m⁻² d⁻¹) and inorganic carbon flux (mg C m⁻² d⁻¹)
were estimated after incubation correspondingly to the differences between sample and control.

2.5. Comparative analysis of xenodiversity in different benthic habitats

The analysis was performed using data collected as part of a long-term monitoring program (1980 – 2003), and also data from several episodic surveys in the Curonian Lagoon, Baltic Sea and Klaipeda strait area (Table 5).

2.5.1. Selection of habitats and alien species for the comparative study

For the analysis, six main sediment types were delineated (artificial hard bottom, hard bottom, gravel, sand, mud, and zebra mussel shell deposits) based on the literature data (Galkus and Jokšas 1997; Pustelnikovas 1998; Olenin and Daunys 2004) and own observations during the benthic surveys. Besides the sediment type a habitat was also characterized by its location within a certain vertical zone: littoral, euphotic sublittoral, aphotic sublittoral, or simply sublittoral (where the boundary between euphotic and aphotic zones was not distinguishable). Thus a total of 16 habitats were defined for the analysis. The identification of habitats generally corresponded to the classification approach at the second level of the European Nature Information System (EUNIS 2005).

Total number of benthic samples used for the analysis exceeded 500 (Table 5). Generally sampling effort adequately represented species richness in the habitats under consideration. Three habitats had rather small datasets available (<10 samples), however due to their distribution in the aphotic layer, variation in species composition and biomass was also considerably lower (Olenin 1997b).

A total of 16 benthic alien species were selected for the analysis (Table 6). These species were listed in the Baltic Sea Alien Species Database (Olenin et al. 2002; Olenin 2004). Only established benthic macrofaunal species (as the mostly linked to the occupied habitat) were chosen. The benthic crustacean Eriocheir sinensis was excluded from
the analysis since the standard methods used in monitoring routines did not provide reliable quantitative population estimates.

**2.5.2. Invasibility assessment method**

The invasibility of a given habitat was defined by two variables: a) the total number of alien species (alien species richness), and b) structural change in the community as measured by the ‘relative amount of alien species biomass’. An additional variable used in the analysis was the number of native species (native species richness) in a habitat.

The influence of physical factors on the distribution of native and alien species was also examined. These factors were the availability of hard and/or soft substrate nominally identified at a presence/absence level, minimal annual salinity (PSU), salinity range (PSU), depth range (expressed by the maximal and minimal depths difference within the habitat), and shallowness of a habitat (expressed by a minimal depth in meters). The relative biomass of the zebra mussel was also included as a factor in the analysis.
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<th>Habitat specification</th>
<th>Short name</th>
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<th>n</th>
<th>Sampling methods</th>
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<td>34</td>
<td>frame sampling</td>
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<td>benthic grab, SCUBA diving, frame sampling</td>
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<td>benthic grab</td>
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<td>Grav Eu</td>
<td>6-8</td>
<td>11</td>
<td>benthic grab</td>
<td>Olenin, Daunys 2004</td>
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**Table 6:** Alien species distribution, native and alien species richness in the analyzed habitats.

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<tr>
<td>Orconectes limosus</td>
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<tr>
<td>Paramysis lacustris</td>
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<tr>
<td>Pontogammarus robustoides</td>
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<tr>
<td>Potamopyrgus antipodarum</td>
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<td></td>
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<tr>
<td>Alien species richness</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>5</td>
<td>7</td>
<td>4</td>
<td>11</td>
<td>8</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Native species richness</td>
<td>9</td>
<td>6</td>
<td>18</td>
<td>27</td>
<td>39</td>
<td>17</td>
<td>18</td>
<td>24</td>
<td>12</td>
<td>15</td>
<td>15</td>
<td>8</td>
<td>4</td>
<td>6</td>
<td>10</td>
<td></td>
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</tr>
</tbody>
</table>
2.6. Statistical methods used for data analysis

The impact of *D. polymorpha* on macrozoobenthos biodiversity was assessed comparing species richness, abundances and biomass in two habitats modified by zebra mussel (zebra mussel bed and zebra mussel shell deposits) and control bottom sites (bare sediments). Therefore, species abundance and biomass were converted to m² bottom surface area and treated as the response variables. Prior to the analysis, the abundance and biomass data were log-transformed to meet normality and homogeneity assumptions. Zebra mussel biomass was used as an explanatory variable and therefore was excluded from the total macrozoobenthos biomass.

The comparison of macrofauna abundances in three analyzed habitat types – zebra mussel bed, shell deposits and bare sediments – was accomplished using two-tailed non-parametric Kruskal-Wallis test, followed by a multiple rank test.

The macrofauna community structure in the modified and unmodified habitats was compared using a non-metric multidimensional scaling (NMDS) procedure. To assess the benthic communities’ differences relative to the habitat patchiness, and to find any patterns of macrofauna distribution concerned with engineering impact of zebra mussel, only 2006 data were used, since the sampling strategy was assumed to be more appropriate for this analysis.

Abundance of associated macrofauna species was related to zebra mussel biomass, amount of shell deposits and environmental variables – depth, distance to the sea and medium sediment grain size, using redundancy analysis (RDA). In this case RDA was considered to be more appropriate than canonical correspondence analysis (CCA) since the most relationships between response and explanatory variables were approximately linear. Since the data from both (1999 and 2006) surveys were pooled together for this analysis, sampling year was included as an explanatory nominal variable.

Linear regression model was used to relate macrofauna abundance to the living zebra mussel biomass and the amount of its shell deposits. All response variables were log-transformed to meet the normality assumption.
For the analysis of results from zebra mussel filtration and biodeposition experiment, the effective clearance rate (ECR) and biodeposition (BDEP) variables were calculated as described in 2.3.2. section, and log-transformed to meet the normality and homogeneity assumptions. Factorial analysis of variance (ANOVA) (after Cochran’s C test of homogeneity of variances) was used to test for effects of two fixed factors - zebra mussel density and initial total particulate matter (TPM) concentration - on ECR. Additionally, two random factors – the ‘wall effect’ and ‘laminator effect’ were also included into the analysis. Since in the analysis, the additional sums of squares for each factor were computed, the contribution of each factor was measured having removed the effects of all other factors. This let to block the potential impact of random factors on the data variation.

Forasmuch as three zebra mussel density treatments have been applied, and the experiment was repeated three times with different seston concentrations, each of the density and TPM factors has three levels. Two levels of ‘wall effect’ factor were applied, dependently whether a vessel was placed near the wall or in the center. Accordingly, four levels of ‘laminator effect’ factor were distinguished due to the distance to the laminators.

The non-parametric two-tailed Kruskal-Wallis test was applied to compare the medians of particulate organic matter (POM) content in the zebra mussel biodeposits and physically sedimented material in the zero-density controls.

For the analysis of zebra mussel impact on biogeochemical characteristics of the benthic environment, the similarity of the biogeochemical sediment properties in three sampled (modified and unmodified by zebra mussel) habitats was assessed using the NMDS procedure.

For the vulnerability analysis of benthic habitats, the comparison of invasive species richness in three studied areas – lagoon, strait and the sea - was accomplished via two-tailed non-parametric Kruskal-Wallis test. The alternative parametric tests were considered to be unsuitable in this case due to the low number of habitats in the lagoon and strait area (4 habitats at each).
The relation of invasive and native species richness was assessed using linear regression model, with invasive species richness as a dependent variable.

The similarity analysis of the invasive species composition in selected habitats was performed using the similarity index of Jaccard, for SIMPER analysis. Only presence-absence of species was considered in the analysis. The Jaccard index here was the most appropriative measure of association since it considers the data as presence-absence, and does not take into account joint absence (Zuur et al. 2007).

Species richness was related to the environmental variables using RDA (since there were many double-zeros values and the most relationships between species and explanatory variables were approximately linear).

The invasive species composition, and invasive species relative biomass distribution in the analyzed habitats was compared using NMDS procedure.

Confidence level of 0.05 was accepted for statistical tests to differentiate between statistically significant and random effects.

The statistical analyses were performed using Statgraphics Plus for Windows® (Statistical Graphics Corp. 1996), Primer 5 for Windows® (Clarke and Warwick 1994), Brodgar (Highland Statistics Ltd.) and Statistica 6.0™ (StatSoft) software.
3. RESULTS

3.1. Identification and quantitative description of habitats modified by zebra mussel

After the quantitative treatment of samples, it was ascertained that there was a number of species that tend to appear only in habitats modified either by live zebra mussels or its shells. Those benthic invertebrates were not found in bare sediments (or only single specimens were observed). 13 species or higher taxons were subsistent for zebra mussel druses: *Hydra vulgaris*, *Turbellaria*, *Erpobdella octoculata*, *Glossiphonia complanata*, *G. concolor*, *G. heteroclita*, *Helobdella stagnalis*, *Eiseniella tetraedra*, *Viviparus viviparus*, *Asselus aquaticus*, *Corophidae*, *Pontogammarus spp.*, and Trichoptera. The same species, except for *G. complanata* have been found in shell deposits as well. The presence/absence analysis of these species along zebra mussel biomass gradient has shown that they started to appear when zebra mussel biomass reached ca. 30 g m\(^{-2}\) (Fig.7). This corresponded to one medium-sized druse. All 13 species appear at 209 g m\(^{-2}\) of zebra mussel biomass (and are present at higher zebra mussel biomass). Considering shell deposits gradient, the typical for this habitat type benthic community forms in the range from 179 to 1111 g m\(^{-2}\) shells dry weight.

Therefore, ‘zebra mussel bed’ was distinguished by the biomass of mussels exceeding 200 WW g m\(^{-2}\). ‘Zebra mussel shell deposits’ were characterized by the presence of spent shells in the amount of 1000 DW g m\(^{-2}\) or more, with either no or very few (less than 200 WW g m\(^{-2}\)) live zebra mussel therein. Finally, sites where live mussel biomass was less than 200 WW g m\(^{-2}\) and the amount of empty shells was less than 1000 DW g m\(^{-2}\), were defined as ‘bare sediments’ and treated as a control (Table 7).

Since in natural environment a certain amount of empty shells is always found together with live mussels, in the case of the ‘zebra mussel bed’ it was considered zebra mussel biomass as a main determinative factor and did not take into account the shell deposits found therein.
**Figure 7:** Appearance of subsistent species in accordance with the zebra mussel biomass (upper graph) and zebra mussel shells DW (lower graph).
Table 7: Classification of habitat types according to live zebra mussel biomass and dry weight of shell deposits.

<table>
<thead>
<tr>
<th>Shell deposits, DW g m(^{-2})</th>
<th>Zebra mussel biomass, WW g m(^{-2})</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-200</td>
</tr>
<tr>
<td>0-1000</td>
<td>Bare sediments</td>
</tr>
<tr>
<td>&gt; 1000</td>
<td>Shell deposits</td>
</tr>
</tbody>
</table>

According to the composition and amount of shell deposits as well as the biomass of zebra mussels, amongst the overall 57 benthic samples taken during the surveys in 1999 and 2006, 11 were identified as taken from the live zebra mussel bed, 17 – from the zebra mussel shell deposits, 19 – from the bare sediments. Other 10 samples, predominantly taken from the western near-shore of the Curonian Lagoon, were differentiated into a separate group as belonging to “Valvata shell deposits”, due to their specific substrate formed by shells of tiny *Valvata* spp. gastropods (mainly *V. piscinalis* and *V. pulchella*), aggregated on the soft bottom (>10\(^3\) gDW/m\(^2\) *Valvata* shells) (Fig. 8).

The median sediment grain size in all sampling sites was analogous: 0.15 ± 0.04 in the bare sediments, 0.17 ± 0.03 in the zebra mussel bed, 0.16 ± 0.05 in the zebra mussel shell deposits and 0.15 ± 0.07 in the *Valvata* shell deposits.

The maximal amount of empty shells found in zebra mussel bed was 2.73 \(10^3\) g DW m\(^{-2}\) (average 1.37 \(10^3\) ± 0.83 \(10^3\) g DW m\(^{-2}\)), in zebra mussel shell deposits - 11.72 \(10^3\) g DW m\(^{-2}\) (average 2.56 \(10^3\) ± 2.54 \(10^3\) g DW m\(^{-2}\)). Zebra mussel biomass ranged from 0 to 3.8 \(10^3\) g m\(^{-2}\) (average 0.62 \(10^3\) ± 2.25 \(10^3\) g m\(^{-2}\)).

The estimated bottom area where zebra mussel shell deposits (>\(10^3\) g m\(^{-2}\)) could be observed was *ca.* 400 km\(^2\). Area of the potential zebra mussel bed distribution (>200 g m\(^{-2}\)) was *ca.* 300 km\(^2\) (Fig.8). Both areas were overlapping with a patchy structure within. The polygons shown on the Figure 8 indicate the most probable whereabouts of a certain habitat type. However one could obtain local sites of zebra mussel shells accumulation or live zebra mussel druses almost all over the central part of the lagoon. As it was estimated, habitats formed by zebra mussel bed or zebra mussel shell deposits may potentially extend in \(\frac{1}{4}\) of the Curonian Lagoon.
3.1.1. Benthic macrofauna structure in the zebra mussel engineered versus control sites

There was about 40 species or higher taxa observed in the habitats modified by living zebra mussels or its empty shells (Table 8). The most species found in the habitats altered by zebra mussels were present also in the bare sediments, but in lower abundances. However, there were a number of organisms, like *Hydra vulgaris*, *Nematoda*, *Planaria torva*, *Glossiphonia concolor*, *Lithoglyphus naticoides*, *Radix ovata*, *Theodoxus fluviatilis*, *Viviparus viviparus*, *Argyroneta aquatic*ica, *Chelicorophium curvispinum*, *Ch. multisetosum*, *Ch. volutator*,...
Corixidae, *Argulus foliceus*, Musidae, and Corixidae observed exceptionally in the habitats modified by zebra mussel. On the other hand, there were only few species (e.g. *Chaetogammarus warpachowskyi*, *Pisidium spp.*, *Valvata piscinalis*, chironomids) which reached higher abundances in bare sediments, when compared to the modified ones. However, no statistically significant difference from other groups was obtained for these invertebrates (Table 8). None of the species unique for bare sediments were found.

**Table 8:** Macrofauna mean abundances (ind/m²; SD in parentheses) in 3 analyzed habitat types. * denotes a statistically significant difference from one or both other groups, revealed from the Kruskal-Wallis and multiple rank tests.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Bare sediments</th>
<th>Zebra mussel bed</th>
<th>Shell deposits</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hydra vulgaris</em></td>
<td>-</td>
<td>30(74) *</td>
<td>-</td>
</tr>
<tr>
<td>Nematoda</td>
<td>-</td>
<td>5(18)</td>
<td>3(8)</td>
</tr>
<tr>
<td>Turbellaria undet.</td>
<td>15(26)</td>
<td>78(105) *</td>
<td>6(12)</td>
</tr>
<tr>
<td><em>Planaria torva</em></td>
<td>-</td>
<td>1(3)</td>
<td>1(2)</td>
</tr>
<tr>
<td><em>Erpobdella octoculata</em></td>
<td>117(169)</td>
<td>242(276)</td>
<td>357(1117)</td>
</tr>
<tr>
<td><em>Glossiphonia complanata</em></td>
<td>8(20)</td>
<td>212(456) *</td>
<td>6(12)</td>
</tr>
<tr>
<td><em>G. concolor</em></td>
<td>-</td>
<td>65(167) *</td>
<td>-</td>
</tr>
<tr>
<td><em>G. heteroclita</em></td>
<td>58(143)</td>
<td>459(1206) *</td>
<td>18(43)</td>
</tr>
<tr>
<td><em>Helobdella stagnalis</em></td>
<td>111(140)</td>
<td>49(59)</td>
<td>630(2361)</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>3382(2914)</td>
<td>3516(3566)</td>
<td>2790(3749)</td>
</tr>
<tr>
<td><em>Eiseniella tetraedra</em></td>
<td>13(30)</td>
<td>31(42)</td>
<td>11(27)</td>
</tr>
<tr>
<td><em>Marenzelleria neglecta</em></td>
<td>5(17)</td>
<td>-</td>
<td>2(6)</td>
</tr>
<tr>
<td><em>Dreissena polymorpha</em></td>
<td>87(134)</td>
<td>2741(4537) *</td>
<td>98(139)</td>
</tr>
<tr>
<td><em>Pisidium spp.</em></td>
<td>356(437)</td>
<td>103(128)</td>
<td>151(328)</td>
</tr>
<tr>
<td><em>Sphaerium spp.</em></td>
<td>9(15)</td>
<td>8(24)</td>
<td>6(12)</td>
</tr>
<tr>
<td>Unionidae</td>
<td>5(7)</td>
<td>8(24)</td>
<td>3(7)</td>
</tr>
<tr>
<td><em>Bithynia tentaculata</em></td>
<td>5(10)</td>
<td>1(3)</td>
<td>12(32)</td>
</tr>
<tr>
<td><em>Lithoglyphus naticoides</em></td>
<td>-</td>
<td>2(3)</td>
<td>1(3)</td>
</tr>
<tr>
<td><em>Radix ovata</em></td>
<td>-</td>
<td>-</td>
<td>1(2)</td>
</tr>
<tr>
<td><em>Theodoxus fluviatilis</em></td>
<td>-</td>
<td>7(24)</td>
<td>1(7)</td>
</tr>
<tr>
<td><em>Valvata piscinalis</em></td>
<td>157(289)</td>
<td>10(19)</td>
<td>103(236)</td>
</tr>
<tr>
<td><em>V. pulchella</em></td>
<td>2(6)</td>
<td>1(3)</td>
<td>1(4)</td>
</tr>
<tr>
<td><em>Viviparus viviparus</em></td>
<td>-</td>
<td>10(24)</td>
<td>3(5)</td>
</tr>
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</table>
The redundancy analysis showed that there was a number of species positively correlated with zebra mussel biomass (e.g. Hydroidea, Turbellaria, Glossiphonia spp., Erpobdella octoculata, Eiseniella tetraedra, Viviparus viviparus, Lithoglyphus naticoides, Asselus aquaticus, etc.) (Fig. 12). Helobdella stagnalis, unionids, oligochaets and chironomids were related to the depth variable and, consequently to the salinity gradient (expressed as a distance to the sea) and the amount of zebra mussel shell deposits, since these three variables indicated a positive correlation. Two taxa (Bithynia and Nematoda) were positively related to the sediment medium grain size and the year of sampling. Pisidium, Valvata and Gammaridae species were mostly related to the amount of shell deposits.
Figure 12: RDA biplot for log-transformed species abundances with shell dry weight (zm_shells), zebra mussel biomass (zebra_biomass), depth, median sediment grain size (Md), distance to the sea (distance_to_sea) and year of sampling (year) as explanatory variables. For the better perception, only species revealing any relation to the analyzed factors are shown.
Larger amount of zebra mussel shells tend to occur at higher depths and finer sediments. Zebra mussel biomass and amount of empty shells in the sediments has not shown any association on the presented RDA biplot. The sampling year positively correlated with sediment grain size and negatively – with depth and distance to the sea. This might be the result that in 2006 samples were taken further north than during the 1999 survey. The correlations of the year factor with other response or explanatory variables were not considerable.

Table 9: Conditional effects for the invasive and native species richness data. The total sum of all eigenvalues is 0.31 and the total inertia is 1. The second column shows the increase in explained variation due to adding an extra explanatory variable. The third column shows an eigenvalue as % using only one explanatory variable

<table>
<thead>
<tr>
<th>Variable</th>
<th>Cond. effects</th>
<th>Eigenvalue as %</th>
<th>F-statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>zebra mussel biomass</td>
<td>0.1</td>
<td>32.19</td>
<td>6.540</td>
<td>0.001</td>
</tr>
<tr>
<td>depth</td>
<td>0.09</td>
<td>31.55</td>
<td>6.562</td>
<td>0.001</td>
</tr>
<tr>
<td>medium sediment grain size</td>
<td>0.05</td>
<td>29.16</td>
<td>3.318</td>
<td>0.001</td>
</tr>
<tr>
<td>distance to the sea</td>
<td>0.03</td>
<td>12.31</td>
<td>2.293</td>
<td>0.007</td>
</tr>
<tr>
<td>year</td>
<td>0.03</td>
<td>26.37</td>
<td>1.931</td>
<td>0.032</td>
</tr>
<tr>
<td>shell dry weight</td>
<td>0.02</td>
<td>8.62</td>
<td>1.548</td>
<td>0.090</td>
</tr>
</tbody>
</table>

Three physical variables, zebra mussel biomass and amount of zebra mussel shell deposits explained 31% of the variation in invertebrate abundances. The 2-dimentional approximation explained 70% of this (52.7% on axis 1 and 17.3% on axis 2). The results of a forward selection and permutation tests (Table 9) indicated that the contribution of the explanatory variables (except for the shell dry weight) to the variation of data is significant.

Analysis of data obtained in 2006 revealed a smooth shift in benthic community structure caused by alteration of a habitat type (Fig. 13). Six samples distinct from all others referred to the sediments modified by the small snail *Valvata* shell deposits (average dry weight $4.6 \cdot 10^3 \pm 0.3 \cdot 10^3$ g m$^{-2}$). The samples from bare sediments, zebra mussel
shell deposits and zebra mussel bed formed a blend with shell deposits in intermediate position.

The differentiation of the habitats is rather clear, yet several samples (3/3_s, 4/3_s, 7/1_s), taken in the habitat defined as zebra mussel shell deposits, pooled into zebra mussel bed. All these samples are characterized by comparatively high amount of empty shells (ca. 2000 g m⁻²) and absence of live zebra mussels.

**Figure 13:** Similarity in macrozoobenthos structure in different habitats. The arrow shows the shift from bare sediments to zebra mussel bed. The figures indicate sample code (station number/replicate number_abreviated habitat type (see legend)).
The linear regression model distinguished species having statistically significant positive correlation with zebra mussel biomass. This let to define the specific “zebra mussel bed community”. Such community is formed in the benthic habitat when live zebra mussel biomass attained ca. 200 g m^-2 (i.e. the assumption made in the above definition of “zebra mussel bed” is true) (Fig. 14). Still the “shell deposits” factor could not be ignored while assessing the macrozoobenthos distribution. As it followed from the analysis, the macrofauna community, typical to zebra mussel bed, tended to appear even devoid of live *D. polymorpha* druses, when there was a sufficient amount of empty shells on the bottom (10^3 g m^-2) (Fig. 14). The two leeches *Erpobdella octoculata* and *Helobdella stagnalis* were subsistent for the “zebra mussel shell deposits community” as their abundances had statistically significant positive correlation with the dry weight of shell deposits on the bottom.
Figure 14: The distribution range of species, typical for zebra mussel bed or shell deposits, corresponding to the zebra mussel biomass (on the right) and amount of shell deposits (on the left). For shell deposits only samples devoid of live mussels were analyzed. Only species with statistically significant correlation of abundance with either zebra mussel biomass or dry weight of shell deposits are presented (correlation coefficients are shown next to genus name).
3.2. Zebra mussel filtration and biodeposition rates

The average length of the experimental mussels, measured at the end of the incubation period, was 15 ± 6 mm, average wet weight – 0.9 ± 0.7 g. Several dead mussels were retrieved from the experimental vessels in the end of each experiment, therefore assuming mortality at the beginning of the installation due to handling stress, these mussels were excluded from the further calculations.

During three 3-day experiments, the seston (dry weight) concentrations, organic and inorganic content in the ambient flume water ranged as presented in the Table 10.

The calculated biodeposition rate of zebra mussels ranged from 0.35 to 540 mgTPM h⁻¹ ind⁻¹ (70.8 ± 109.5 mgTPM h⁻¹ ind⁻¹ in average). The background sedimentation rate varied from 24.3 gTPM h⁻¹ m⁻² during the second experiment to 91.5 and 80.9 gTPM h⁻¹ m⁻² during the first and third experiments respectively.

**Table 10:** The average amounts (SD) of the total particulate matter (TPM), particulate organic matter (POM) and particulate inorganic matter (PIM) concentrations in the ambient flume water, at the beginning and in the end of each experiment.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Start</th>
<th>End</th>
<th>Start</th>
<th>End</th>
<th>Start</th>
<th>End</th>
</tr>
</thead>
<tbody>
<tr>
<td>TPM, mg l⁻¹</td>
<td>15.4(5.2)</td>
<td>0.5(0.1)</td>
<td>19.1(11.6)</td>
<td>1.3(0.5)</td>
<td>16.6(4.7)</td>
<td>0.5(0.1)</td>
</tr>
<tr>
<td>POM, mg l⁻¹</td>
<td>11.1(1.2)</td>
<td>0.4(0.1)</td>
<td>9.2(4.9)</td>
<td>0.4(0.3)</td>
<td>12.6(0.4)</td>
<td>0.4(0.1)</td>
</tr>
<tr>
<td>PIM, mg l⁻¹</td>
<td>4.3(4.2)</td>
<td>0.1</td>
<td>9.9(6.9)</td>
<td>0.9(0.3)</td>
<td>4.0(2.9)</td>
<td>0.1</td>
</tr>
</tbody>
</table>

After the incubation period, the amounts of biodeposited matter in experimental vessels with mussels in average 1,5-10 times exceeded physically deposited matter in the control ones (Fig. 15).
The organic content of physically precipitated sediments tended to be greater than in the biodeposited matter (Fig. 16). The applied Kruskal-Wallis test indicated significant difference (P<0.001) between the control and density treatments.

The effective clearance rate of the zebra mussels during the experiments ranged between 0.4 and 434.4 ml h⁻¹ ind⁻¹ (or from 0.3 to 227.6 l day⁻¹ gSFDW⁻¹ respectively). The average ECR value estimated from three experiments was 77.1±106.2 ml h⁻¹ ind⁻¹ (or 33.2±46.7 l day⁻¹ gSFDW⁻¹).

As it followed from the ANOVA results, both fixed factors – mussel density and initial TPM concentration showed significant impact on the effective clearance rate of the experimental zebra mussels (F = 6.06; d.f. = 2; P < 0.05 and F = 134.07; d.f. = 2; P < 0.001, respectively) (Fig. 17). Concerning the random factors, the ‘wall effect’ had no significant effect on ECR. On the contrary, the ‘laminator effect’ appeared to have significant impact (F = 13.3; d.f. = 3; P < 0.001). No significant two-factor interactions were observed.
**Figure 16:** Partitioning of organic and inorganic matter deposited in the experimental vessels with different mussels’ densities: 0 (control); 1) 15 ± 3, 2) 35 ± 8, 3) 60 ± 15 mussels per vessel), at the end of the experiments.
Figure 17: Means’ plots for log-transformed effective clearance rate (ECR) of zebra mussels versus mussel density (top) and initial TPM concentration (bottom). The applied mussel densities: 1) 15 ± 3, 2) 35 ± 8, 3) 60 ± 15 mussels per vessel; TPM concentrations: 1) 15, 4, 2) 19, 1 3) 16, 6 mg/l. Vertical bars denote 0.95 confidence intervals.

The budget of total particulate matter calculated for the flume, indicated that due to zebra mussel filtration/biodeposition activity, the amount of the TPM in the system was reduced by 70% on average during an experiment (approximately 20% was biodeposited in a form of faeces and pseudofaeces and 50% was assimilated by mussels). For
reference, about 25% of the TPM is physically deposited in the flume during an experiment.

3.3. Biogeochemical sediment properties in the habitats modified by zebra mussels

A number of biogeochemical parameters were measured in three pre-defined habitat types: zebra mussel bed, shell deposits and bare soft bottom. The basic ecological conditions in the sampled habitats corresponded to the common requirements defined above (see section 2.4). All of them were situated in the central part of the lagoon, to the north of the Nemunas river mouth, within the bottom area modified by zebra mussel (Fig.6). All three sites were relatively close to each other, so it was assumed that hydrodynamic conditions and water residence time were analogous. The main geo- and biological characteristics of the studied habitats are presented in the Table 11.

<table>
<thead>
<tr>
<th>Table 11: Ecological characteristics of the sampling sites.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zebra mussel bed</td>
</tr>
<tr>
<td>Depth</td>
</tr>
<tr>
<td>Sediment type</td>
</tr>
<tr>
<td>Sediment grain size (Md)</td>
</tr>
<tr>
<td>Shells DW</td>
</tr>
<tr>
<td>Zebra mussel biomass WW</td>
</tr>
<tr>
<td>Zoobenthos biomass WW</td>
</tr>
<tr>
<td>Species richness</td>
</tr>
</tbody>
</table>

According to the NMDS results, the parameters obtained from the bottom covered by zebra mussel shell deposits were different from those measured in other habitat types (Fig.18). This distinction resulted from 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 zebra mussel bed and bare sediments respectively). The highest values of organic carbon (3.75% versus 0.95 and 1.25% in zebra mussel bed and bare sediments respectively) observed in the upper layer of sediments formed by shell deposits (Fig. 19) during all three surveys. The highest value of oxidized
form of dissolved inorganic nitrogen (DIN) (0.621 mgN l\(^{-1}\) versus 0.154 and 0.024 mgN l\(^{-1}\) in zebra mussel bed and bare sediments respectively) observed in the near-bottom water layer above the shell deposits, during the October sampling. The relatively low organic matter mineralization rates were determined mostly by aerobic processes both in the middle and at the end of active vegetation period.

**Figure 18:** NMDS plot of similarities between three sampled habitats (shell deposits – ‘shells’, bare sediments – ‘bare_sed’ and zebra mussel bed – ‘mussels’) according to the biogeochemical properties of the sediments.

Bottom sediments in the shell deposits were also characterized by the highest total phosphorus and total nitrogen content (Fig. 18).
Figure 19: Average organic carbon (C$_{org}$), total nitrogen (TN) and total phosphorus (TP) content in different bottom sediments.

The highest redox values were obtained from the surface sediments formed by zebra mussel shell deposits. Although dissolved oxygen concentration in the near-bottom water layer was resembling in all three sediment types (9±1.8 mgO$_2$ l$^{-1}$), yet at the depth of 1 cm below the bottom surface, the Eh values have varied substantially among the sampling sites (Fig. 20). Due to the specific roughness of sediments sampled from the zebra mussel bed and shell deposits, it was impossible to measure the 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 zebra mussel bed was distinguished by the higher oxygen consumption in the upper sediment layer: 530±383 mgO$_2$ m$^{-2}$ day$^{-1}$ versus 228±180 and 444±18 mgO$_2$ m$^{-2}$ day$^{-1}$ in bare sediments and shell deposits respectively. The highest organic matter mineralization rate in this habitat type was determined basically by anaerobic processes (average anaerobic organic matter mineralization rate - 721±191 mgC m$^{-2}$).
3.4. Xenodiversity in the benthic habitats modified by zebra mussel vs. other habitats in the Curonian Lagoon and Lithuanian coastal zone

For the 16 species selected, relative invasion success was defined as the number of habitats in which an individual species was found. The North American polychaete *Marenzelleria neglecta* was the most successful invader, since it was found in 14 of 16 defined habitats (Table 6). The next 4 most successful aliens were *Balanus improvisus*, *Dreissena polymorpha*, *Chelicorophium curvispinum* and *Chaetogammarus warpachowskyi* (7, 6, 6 and 5 invaded habitats respectively). All other species were characterized by lower invasiveness (2-4 habitats invaded). The intentionally introduced mysid shrimps *Hemimysis anomala* and *Limnomysis benedeni* were each found in a single habitat.

Similarity analysis of the alien species composition showed that the level of similarity between the lagoon and sea habitats was rather
low, since only three species were common within both areas (hydroid *Cordylophora caspia*, barnacle *Balanus improvisus* and polychaete *Marenzelleria neglecta*). Species in the sea and strait habitats grouped distinctly from the lagoon habitats, including hard artificial structures in the strait area (Fig. 21). The average Jaccard index value for sea habitats was 0.28 ± 0.18 and the value for lagoon habitats was 0.42 ± 0.25. There was also a high dissimilarity between the strait area and both the sea and lagoon. The average dissimilarity for strait and sea habitats was 60.96%, and the dissimilarity for the strait and lagoon habitats was 62.32%. The species that contributed mostly to these distinctions were *Balanus improvisus* (13.04% for strait and sea habitats, 18.54% for strait and lagoon habitats), *Chelicorophium curvispinum* (10.29% and 13.81% respectively) and *Gammarus tigrinus* (9.23% and 11.41% respectively).

Sand, mud and shell deposits habitats within the Curonian Lagoon and in the presence of the zebra mussel had the greatest numbers of invasive species (8-12 species per habitat). The next most invaded habitats were artificial rock and stone structures in the Klaipeda strait and the Curonian Lagoon (4-5 species per habitat). Sea habitats appeared to be the least invaded (only 1-3 species per habitat) (Table 6). Species richness in the lagoon habitats was significantly higher than in the sea and strait habitats (Kruskal-Wallis test, P < 0.001).

The highest native species richness was found in those habitats modified by zebra mussels – up to 39 species per habitat (mainly due to high diversity of freshwater bivalves and gastropods). Also having a high native species richness were those sea habitats with available hard substrate within the euphotic zone – up to 26 species per habitat (due to presence of the small benthic and nekto-benthic crustaceans). The highest proportion (33%) of alien species occurred in two sandy sea habitats: littoral and euphotic zone. There was a significant positive correlation between native and alien species richness in the various habitats (r=0.55, P=0.02).
3.4.1. Physical factors influencing the distribution of alien species

The redundancy analysis showed that alien species richness was higher in the soft bottom habitats within the Curonian Lagoon, but negatively associated with both salinity and depth factors (Fig. 22). Native species richness was positively associated with zebra mussel biomass and habitats modified by zebra mussel shell deposits.

Six physical variables and zebra mussel biomass explained 73% of the variation in alien and native species richness, completely defined by the 2-dimensional approximation (62% on axis 1 and 11%
on axis 2). The results of a forward selection and permutation tests (Table 12) indicated that native and alien species richness were significantly related to minimal salinity ($P=0.004$), salinity range ($P=0.012$) and availability of hard substrate ($P=0.015$).

**Figure 22:** Triplot obtained by Redundancy Analysis. Response variables: native and invasive species richness (‘Native’ and ‘Invasive’ respectively); explanatory variables: availability of hard and/or soft substrate (‘Hard_sub’ and ‘Soft_sub’ respectively), salinity minimum (‘Sal_min’), salinity range (‘Sal_range’), depth minimum (‘Depth_min’),
*depth range* (‘Depth_range’), *zebra mussel relative biomass* (‘ZM_biomass’) in a habitat.

**Table 12:** Conditional effects for the alien and native species richness data. The total sum of all eigenvalues is 0.73 and the total inertia is 1. The second column shows the increase in explained variation due to adding an extra explanatory variable. The third column shows an eigenvalue as % using only one explanatory variable.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Cond. effects</th>
<th>Eigenvalue as %</th>
<th>F-statistic</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>minimal salinity</td>
<td>0.31</td>
<td>42.63</td>
<td>6.268</td>
<td>0.004</td>
</tr>
<tr>
<td>salinity range</td>
<td>0.21</td>
<td>0.67</td>
<td>5.538</td>
<td>0.012</td>
</tr>
<tr>
<td>availability of hard substrate</td>
<td>0.14</td>
<td>10.39</td>
<td>4.842</td>
<td>0.015</td>
</tr>
<tr>
<td>depth range</td>
<td>0.03</td>
<td>25.91</td>
<td>0.951</td>
<td>0.404</td>
</tr>
<tr>
<td>minimal depth</td>
<td>0.03</td>
<td>18.16</td>
<td>0.896</td>
<td>0.427</td>
</tr>
<tr>
<td>zebra mussel relative biomass</td>
<td>0.01</td>
<td>29.09</td>
<td>0.444</td>
<td>0.653</td>
</tr>
<tr>
<td>availability of soft substrate</td>
<td>0.00</td>
<td>2.56</td>
<td>0.094</td>
<td>0.916</td>
</tr>
</tbody>
</table>

The highest percentage of alien species biomass (relative to native species biomass) occurred in the artificial hard bottom habitat of the strait area (97.4%), in the sandy sea littoral (94.1%) and in the zebra mussel shell deposits habitat in the lagoon (76.3%) (Fig. 23). Three most successful aliens – *M. neglecta, D. polymorpha* and *B. improvisus* dominated biomass (>50%) in most of invaded habitats. Other species had rather tenuous impact on the community structure of an invaded habitat.

The prevalence of *M. neglecta* in sea habitats with sandy and gravel bottom determined the structural affinity of these areas (Fig. 24). The similar assimilation was apparent in lagoon habitats dominated by zebra mussel (Zebra Shell LAG; Mud LAG; Art-Hard Li STRAIT). Hard bottom habitats of the sea also formed a certain cluster due to the high abundance of *B. improvisus*. The muddy habitat of the strait area with the least invasive biomass showed a clear dissimilarity from other habitats.
Figure 23: Percentage of alien species biomass relative to total biomass.
Figure 24: The Multidimensional Scaling plot based on alien species relative biomass distribution over the analyzed habitat types.
4. DISCUSSION

Whatever impact of the zebra mussels on a freshwater ecosystem one may consider, it will most likely be a direct result of their functioning as an ecosystem engineer. Whether they filter the water, or form a ‘reef’, or ‘leave’ empty shells on the soft bottom of the lagoon, such activity will undoubtedly lead to the alterations in availability of resources for different biotic components of the ecosystem or modification of its physical – chemical conditions. In order to summarise the habitat engineering impact of zebra mussels on the ecosystem, it seems to be logical to determine its major outcomes revealed in the present study.

4.1. Benthic macrofauna in the habitats modified by zebra mussels

Generally, in an estuarine lagoon ecosystem with a heterogeneous benthic environment it is hard to obtain any valid arguments to distinguish among different habitat types (Elliott and Quintino 2007). In the Curonian Lagoon, the composition of benthic species has proved to be a distinctive factor, sufficient to differentiate the thresholds between zebra mussel bed, zebra mussel shell deposits and bare sediments. Such distinction of natural habitats modified either by live zebra mussels or by their shell deposits, determined in this study, is an important stepping stone for the further analysis of the functional role of *D. polymorpha*.

The NMDS analysis of the macrozoobenthos community structure in different habitats (zebra mussel bed, shell deposits and bare sediments) indicated that habitat formed by zebra mussel shell deposits maintain benthic communities different from those common in bare sediments. Although this difference is not as pronounced as between the bare sediments community and living zebra mussel bed (Fig. 13).

The main argument for the importance of empty shells as an ecosystem engineering agent is the fact that a typical “zebra mussel bed community” in the lagoon is being formed even devoid of living
zebra mussel druses, if a certain amount of empty shells persists on the bottom.

As it has been reported earlier (Karatayev et al. 1997, 2002; Bially and MacIsaac 2000; Reed et al. 2004), zebra mussels in soft-bottom environments provide substrata for the epifaunal invertebrates that are normally unable to attach to bare sediments. On the other hand, mussel beds on the soft bottom should not have much impact on the infaunal species, because these organisms are capable to survive and shelter in the ambient sediments (Gutierrez et al. 2003). The results of the present study support this statement, since invertebrates correlated with zebra mussel biomass were predominantly the epifaunal organisms (Hydroidea, Glossiphonia spp., Viviparus viviparus, Lithoglyphus naticoides, Asselus aquaticus), which likely take advantage of both structural complexity and resources provided by zebra mussel druses.

The carnivorous species (e.g. leeches) also benefit from the resource availability enhanced by zebra mussel (easily accessible preys sheltered in druses or empty shells), as it was verified by RDA and Pearson’s R (see section 3.1.1.).

Abundances of chironomids and oligochaets (common infaunal invertebrates on the soft bottom of the Curonian Lagoon) did not differ much between the bare soft bottom and sediments modified by zebra mussel. Yet the reported numbers of these organisms in the samples from zebra mussel bed were not obtained from the soft bottom sediments but rather from the druses, covering the bottom. It means that in this case the infaunal organisms were functioning as epifaunal ones at a certain extent. This might be also a result of the biogeochemical alteration of benthic environment induced by zebra mussels.

The typical calcium carbonate production rates for Dreissena polymorpha ranges from 10 to 10,000 gDW m$^{-2}$ year, depending on the population size (Strayer and Malcom 2007). Based on this, the density of calcite and aragonite, assuming shells have a calcite/aragonite ratio of 1:1 (Gutierrez et al. 2003), zebra mussels may deposit 0.035 – 3.5 mm of CaCO$_3$ per year. This is rather high,
given that resent annual sedimentation rate in the Curonian Lagoon is about 3.2 mm (Pustelnikovas 1995). The shell material can persist for a long time after mussel dies. The durability of shells and their occurrence at high densities are characteristics that increase the likelihood of important engineering effects over large temporal and spatial scales (Kidwell 1985; Gutierrez et al. 2003). Thus zebra mussel is capable of maintaining its autogenic engineering impact even if complete extinction of the population occurs in an ecosystem.

The redundancy analysis (Fig. 12) revealed a positive correlation between the depth and the amount of empty shells therein. It means that shell deposits not necessarily accumulate in the areas occupied by living zebra mussel bed, but transported with hydraulic flows towards the bottom depressions. This might be confirmed also by the fact that both depth and shell deposits factors in RDA showed negative correlation with sediment grain size variable, i.e. fine sedimentary particles also tend to sink in these bottom cavities, where favourable hydrodynamic conditions for sedimentation occur. It is likely that increased roughness of the bottom, induced by protruding shell aggregations, may locally promote sedimentation process in these areas (the particle trapping effect). Yet, in the context of the Curonian Lagoon depth should not be considered as a driving factor in distribution of benthic communities, as soon as there are no substantial depth differences, at least in the northern part of the water body. The impact that has been obtained most probably refers to a local bottom depressions or eminences with depths deviating from the average not more than by 1.5 m.

Still it is rather complicated to quantify the system wide effect of zebra mussel’s habitat provider’s function in the Curonian Lagoon. The distribution of the described habitats is very patchy and abundance of zebra mussels and shell deposits within these patches is very uneven.

The replicate samples taken at each station in 2006 survey have represented the bottom patchiness within the area of ca. 50 square meters. The replicates from the station 3, 7 and 8 exemplified the patchiness of the bottom within the zebra mussel distribution area
(Fig. 13). These samples were assigned to different habitat types according to the amount of shells and zebra mussel biomass. Moreover, they were distinct by their benthic fauna composition and abundances, what was clearly reflected in MDS results.

Jones et al. (1997) emphasized the importance of spatial scale in predicting the effects of ecosystem engineers on biodiversity. According to this hypothesis at the patch level, i.e. comparing species richness in individual engineered patches and individual unmodified patches, the obtained engineering impact might be tenuous. In the current study species richness was not treated as the main index of engineering effect, but the complex of variables (species composition and abundances). Thus it let us to obtain the differences among individual patches as well, and to show the propriety of the applied ‘patch-to-patch’ analysis. This approach has also revealed the ability of zebra mussel to affect the distribution of species by changing the resource availability at a site of its direct occurrence (not necessarily at a large ‘Dreissena reef’), and form some sort of “oases” of structural and biological diversity in the benthic environment of the Curonian Lagoon.

4.2. Benthic-pelagic linkage caused by zebra mussel filtration and biodeposition

Dreissena polymorpha, because of its high filter area per unit mass (Kryger and Riisgård 1988) and small size, has an intrinsically high filtering (clearance) rate that is ~10 times that of other freshwater filter-feeding bivalves (Vanderploeg et al. 2002). The composition and quantity of pseudofaeces and faeces produced by zebra mussels may have important ecosystem consequences. Basing on the results of the performed filtration and biodeposition experiments, the contribution of zebra mussel population to sedimentation process in the Curonian Lagoon might be rather substantial. Thus, even the lowest biodeposition rate revealed from the experiments (0.35 mgTPM h⁻¹ ind⁻¹), multiplied by the average density of zebra mussels (2.7x10³ ind m⁻²) and assuming a filtering activity of 16 h day⁻¹ (Morton 1969; Walz 1978; Horgan and Mills 1997), will result in
essential redistribution of TPM between the water column and benthos with the annual biodeposition of 5.5 kg m\(^{-2}\). Yet, the pathway of these deposits does not end up in the bottom sediments. Faeces and pseudofaeces in shallow systems (like Curonian Lagoon is) or nearshore habitats represent also an energy flux to the benthos, especially for deposit-feeding benthos that are associated with zebra mussels and can utilize faeces (Karatayev et al. 1994; Vanderploeg et al. 2002; Hecky et al. 2004). Sorting of unwanted particles into pseudofaeces is far from perfect, especially in the case of suspended sediment, and some of these particles are ingested and end up in faeces (Roditi et al. 1997). Pseudofaeces containing clay or algae can be quite fragile. They are easily resuspended, like feces, especially under turbulent mixing that occurs in estuaries (Roditi et al. 1997; Vanderploeg et al. 2001). Because mussels do not assimilate clay and other inorganic particles, these particles can be returned to the water column; thus, in systems dominated by inorganic particles (in the Curonian Lagoon it is common for autumn and winter seasons), zebra mussels may only have a modest impact on water clarity and seston concentration (Vanderploeg et al. 2002). The data from the earlier study on zebra mussel impact on the budget of suspended material in the Curonian Lagoon (Daunys et al. 2006) perfectly supported this notion. As it was concluded by the authors, the zebra mussel is not capable of controlling the TPM transport in this ecosystem. That is primarily determined by natural ecosystem peculiarities such as hydrologic regime and hydrographical conditions. Although the zebra mussel clearance rate obtained by the applied in that study seasonal TPM budget and modelling approaches most likely was underestimated (7.4 ± 2.3 l day\(^{-1}\) gSFDW\(^{-1}\)), these values were relatively consistent with the ones revealed from the current experimental results (33.2 ± 46.7 l day\(^{-1}\) gSFDW\(^{-1}\)) in the context of the high variability of clearance rates mentioned in different literature sources (Karatayev and Burlakova 1994; Kryger and Riisgård 1998; Yu and Culver 1999). Still the obtained results should not be considered as an absolute value, due to the numerous environmental
factors that may have influence on the filtration activity of the mussels.

Seston depletion by benthic suspension feeders is known to be density dependent when the delivery of food particles from the water column to the benthic boundary is limited (Yu and Culver 1999). The presented experimental data indicated that effectiveness of particle removal by zebra mussels is influenced by the density of mussel clumps as well. However, unlike the results, presented earlier by Yu and Culver (1999), the mean ECR value was significantly higher in the clumps with higher mussel density. Nevertheless, this does not deny the existence of refiltration phenomenon, described by the aforementioned authors. According to Mikheev (1966), the filtering activity of zebra mussel is highly dependant on the TPM concentration and content. As a rule the filtration rate is reducing when seston concentration increases. The natural TPM concentration in the lagoon water, used for experiment, was twice as much as the seston concentrations in ambient lake water during the experiment conducted by Yu and Culver (1999). In the dense aggregates only mussels from the top are exposed to the natural seston concentrations and may response by reducing their filtration efficiency. The mussels in the center of a druse receive water filtered by the upper individuals, with the real TPM concentration much lower than the initial one. Subsequently, assuming that there is a refiltration effect, it may be concluded that net clearance rate of mussels in a dense clump under relatively high TPM concentration will be higher than that of the mussels in a loose druse.

The experiments presented here have also revealed a significant negative impact of TPM concentration on the clearance rate of zebra mussels. That is consistent with the common hypothesis mentioned above. Likely, the high seston concentration inhibits the filtering activity of the mussels due to the mechanical plugging of their inhaling siphons with suspended particles (Karatayev and Burlakova 1994).
4.3. Biogeochemical properties of habitats engineered by zebra mussels

Comparing to the bottoms formed by zebra mussel shell deposits and bare sediments, sediments covered by dense layer of mussel clumps are physically isolated from the near-bottom water layer. Beside this, zebra mussels exert changes in sediment composition that likely cascade to affect the sediment redox conditions and biogeochemical cycles of nitrogen, phosphorus and carbon (Bruesewitz et al. 2006). The respiration-based oxygen demand exerted by dense populations of zebra mussels usually is much greater than the bare sediment oxygen demand associated with highly enriched organic deposits (Effler et al. 1996). Thus, severe oxygen depletion due to respiration demands of dense zebra mussel population in addition to the physical ‘isolation’ of sediments by zebra mussel clumps result in the facilitation of anaerobic mineralization processes in the benthic environment.

Some resent researches have indicated zebra mussel can mobilize substantial quantities of ammonia and phosphorus (Effler et al. 1997). Of the particulate nutrients contained in the natural seston and inhaled by mussels, a proportion is invested in new mussel biomass, but a large proportion is excreted as solutes (e.g. ammonium NH$_4^+$) or released in particulate form as either faeces or pseudofaeces and is a subject for the further mineralization processes (Hecky et al. 2004). Further, because of anaerobic conditions and accumulation of C-rich biodeposits underlying zebra mussel bed, it is likely that denitrification (microbial reduction of NO$_3^-$ to gaseous nitrous oxide (N$_2$O) and dinitrogen (N$_2$)) occurs at rates higher than in unmodified bare sediments (Seitzinger 1988). The results of the current study support these general findings, since the highest anaerobic mineralization rate was revealed from the zebra mussel bed. The comparatively low amount of organic carbon, total phosphorus and total nitrogen in this bottom type, despite the high biosedimentation induced by mussels, is likely the result of the lower proportion of organic matter in the biodeposits comparing to the naturally sedimneted material (what is also indicated by the experimental
results, see Fig. 16) on the one hand, and extensive anaerobic mineralization of organic matter besides the utilization of biodeposits by the dense associated benthic fauna on the other hand.

Bottoms modified by zebra mussel shell deposits are more favorable for accumulation of sediments comparing to the bare soft bottoms (due to physical particle trapping). Yet, in comparison to the zebra mussel bed, low organic matter mineralization and no anaerobic mineralization were obtained there. It is likely caused by the better aeration in this type of sediments brought on by its specific roughness. This and lower abundances of benthic organisms, associated with this habitat type, result in the highest concentrations of organic C, TP and TN there.

4.4. Xenodiversity in the habitats modified by zebra mussel

Vitousek (1990) noted that invasive engineer species have much larger effects on their new community than non-engineer species, since both biological and physical characteristics of the environment will be altered. On the other hand, the combination of invasive species and habitat modification is often considered as a presage for new invasions (Cuddington and Hastings 2004). Thus the comparative analysis of different habitats of the SE Baltic Sea region has revealed in particular, that habitats altered by zebra mussel were distinguished by the highest relative biomass of the alien species comparing to other habitats in the Curonian Lagoon. In this sense the significance of zebra mussel engineering impact becomes even more apparent and relevant for the future research.

There are two major hypotheses concerning the relationship between species diversity and invasibility of a given habitat. One hypothesis can be termed the ‘diversity resistance hypothesis’ and argues that diverse communities are highly competitive and therefore should be resistant to invasions (Elton 1958; Stachowicz et al. 1999; Levine 2000). The other hypothesis, termed the ‘biodiversity increasing invasibility hypothesis’, suggests that communities rich in species may be more invasible because of the facilitative effect of
previously introduced species (Cohen and Carlton 1998; Stohlgren et al. 1999).

Recent studies have indicated that spatial scale likely plays an important role in the diversity-invasibility relationship (Stohlgren et al. 1999; Levine 2000; Kennedy et al. 2002). Thus these two hypotheses do not necessarily need to be mutually exclusive. Diverse communities can be more resistant to alien species invasion at a relatively small spatial scale but, measured at a regional scale, the relationship between diversity of native and alien species is more likely to be positive.

A paradox was revealed, however, in the current comparatively small scale study. Higher alien species richness occurred in habitats with higher native species richness. It is hard to conclude unambiguously whether these results disprove the common theory, or whether the results were unique to the studied region. Based on these results, I would rather agree that abiotic factors play a leading role in defining the vulnerability of a given habitat to invasives (at least in the Baltic Sea ecosystem). The classical hypothesis that diversity is the independent variable and invasibility is the dependent variable (Davis et al. 2000) seems to be inappropriate in this case. It would be more correct to state that both native and alien species diversity depends on the ecosystem’s physical factors, which may promote invasibility or inhibit it. This assumption is supported by not only this study but also other studies in brackish water ecosystems. For instance, the negative correlation of species richness and depth range corresponds to the depth distribution pattern of invasive and native species caused by decline in oxygen content (Leppäkoski and Olenin 2000).

Higher alien species richness occurred in the nearly limnetic lagoon ecosystem. This is consistent with the classical Remane (1934) curve which shows minimum native species number in salinities between 5 and 8 PSU. So the common pattern derived for native fauna is fairly suitable for invasive species as well. As noted earlier, the majority of established aliens in the Baltic Sea occur in the coastal inlets, lagoons and gulfs (Paavola et al. 2005). Thus these areas should
be considered as “hot spots” for the introduction of aliens and should be the focus of the corresponding monitoring programs.

Finally, another important factor when considering invasibility of a given system is the level of anthropogenic or/and invasive disturbance. This study indicated that the most invaded habitats were those modified either by man (breakwaters, embankments, piers in Klaipeda strait and in the Curonian Lagoon), or by invasive species (e.g. zebra mussel community). The facilitative effect of such modifications may be asserted through physical or biological mechanisms. Hydrotechnical harbour constructions in the Klaipeda strait provide hard substrates which were naturally absent in this area. Consequently there were almost no competitors for alien sessile organisms associated with this type of habitat. Clusters of living zebra mussels and shells present on muddy bottom provide habitats unusual for this bottom type, and offer native and alien invertebrates opportunities for food and shelter. As proposed by Simberloff and Von Holle (1999), once established, some invaders may alter habitat conditions in favour of other invaders, thereby creating a positive feedback system that accelerates the accumulation of invading species. Thus there might be a synergetic impact of favourable physical conditions and facilitative effect of human and zebra mussel mediated habitat alterations, causing significantly higher invasive species richness in the lagoon compared to sea habitats.

It would be rather unfair, however, to evaluate the invasibility of a habitat solely on alien species richness, since there is at least one more determinative feature: the propensity of a habitat to sustain a demographically successful aliens’ population (Davis et al. 2000). If a habitat has a small number of alien species, it does not necessarily follow that the same habitat has a high resistance to invasions. Some habitats (like ArtHardLi STRAIT, Sand Li, etc.) are not able to sustain a diverse community (does not matter invasive or native) due to their physical properties (discussed above). The percentage of invasive species biomass may show that aliens are much more successful though. Alien species may form up to 90% of total community biomass (Fig. 23), despite there being only a few present. Even a
single invader in such a species-poor community may cause drastic structural changes and even a loss of native diversity.

Species with high ecological plasticity (M. neglecta, B. improvisus, D. polymorpha) appeared to be more successful in becoming established in a variety of different habitats, tending to dominate the biomass of the occupied community. This likely causes a certain biological affinity of different habitat types that are often rather remote from each other (like Sand Ap, Sand STRAIT and Sand Li, dominated by M. neglecta, see Fig. 24) and, consequently, the loss of β-diversity. Based on these results, I would recommend to use the percentage of alien species biomass (relative to native species biomass), instead of (or along with) alien species richness, as an appropriate invasibility measure for habitats with naturally low diversity.

Summarizing the results of the study and the results of an extensive literature analysis (Nilsson 1985; Herbold and Moyle 1986; Vitousek et al. 1997; Brooks 1999; Simberloff and Von Holle 1999; Davis et al. 2000; Ruiz et al. 1999, Hewitt and Hayes 2002; Nehring 2002; Van der Velde et al. 2002), the generalized verbal model of an ‘invader-friendly’ habitat could be briefly defined by the following features:

- the habitat has favourable physical conditions for maintaining diverse communities (in this case high native species richness might be considered as an indicator of habitat’s invasibility);
- the habitat lacks certain species which should to be present under normal conditions (there are “vacant niches”);
- the habitat is disturbed due to natural or anthropogenic factors, e.g. big storm, bottom dredging (every new disturbance event may promote a new surge of invasions);
- ecosystem properties are altered due to previous introductions, creating unstable conditions (successfully established habitat engineering species should be considered as a powerful facilitative factor for further invasions); the habitat is a subject to increased amounts of utilized resources, such as from eutrophication (the abrupt
increase of nutrient loads should be considered as an invasibility stimulating factor).

4.5. Impacts of the zebra mussels on native communities, habitats and ecosystem functioning: an interregional context

Although many generalizations can be made about the functioning of zebra mussels and their impacts on the Curonian Lagoon ecosystem, it is important to recognize that impacts will not be uniform across the given water body, and are likely to change over the time (Karatayev et al. 2002). The quantification of the zebra mussel impacts is a great challenge for researches unless there is no universal assessment tool in use. The biopollution assessment method proposed by Olenin and co-authors in 2007, should be one of the most comprehensive approaches appropriate for this purpose by now. This method was applied here to estimate the magnitude of zebra mussel impact on the Curonian Lagoon ecosystem.

To determine the biopollution level the abundance and distribution range of alien species is assessed, then the magnitude of impacts of the species on community, habitat and ecosystem functioning are considered. The estimated biopollution level is a net result of a combination of abundance and distribution range (ADR) class and of impact of alien species on communities (C), invaded habitat (H) and ecosystem functioning (E) (the particular description of the method and all the classifications are given in Olenin et al. 2007). According to this approach, the Curonian Lagoon should be asserted class D of abundance and distribution range, since zebra mussel occurs there in high numbers in many localities. The impact of zebra mussel on communities is strong (C3) – the alien species is dominant, former community dominant species still present but their relative abundance is severely reduced. The impact on habitats also may be defined as strong (H3) – alteration of a key habitat, severe reduction of spatial extent of habitats; loss of habitats within a small area of the lagoon. The impact on ecosystem functioning is classified as moderate (E2) – moderate modification of ecosystem performance and addition of a new functional group in part of the lagoon. Hence, the magnitude of zebra mussel impact in the Curonian Lagoon is defined as strong
(BPL = 3). It is notable, that zebra mussel is one of the three species causing strong biopollution level of the Curonian Lagoon (Daunys 2008). Other two species are also the Ponto-Caspian aliens, gammarids *Obesogammarus crassus* and *Pontogammarus robustoides*. It is notable, that these crustaceans are also capable of modifying the habitats they invaded, although not so crucially as zebra mussel does. Hence, the experiments conducted in 2002 revealed that the burrowing activity of the non-indigenous amphipods can modify the structure of the sediment surface and cause the resuspension of sedimented material (Zaiko and Olenin 2003).

The biopollution assessment method may be also applied to compare the invasiveness of the zebra mussel in the different ecosystems or evaluation of impact dynamics caused by the species over time (Table 13).

**Table 13**: Comparison of zebra mussel invasiveness using biopollution assessment method (based on Daunys 2008; Mastitsky 2008; Minchin 2008; Semenchenco 2008).

<table>
<thead>
<tr>
<th>Assessment unit (assessment period)</th>
<th>ADR</th>
<th>Impact on communities</th>
<th>Impact on habitats</th>
<th>Impact on ecosystem</th>
<th>BPL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pripiat river &amp; Dnieper-Bug canal (2007)</td>
<td>C</td>
<td>C1</td>
<td>H1</td>
<td>E1</td>
<td>2</td>
</tr>
</tbody>
</table>

Zebra mussel has arrived to these four ecosystems at different times: in 1770s – to the Dnieper-Bug canal and Pripiat river; in 1800s – to the Curonian Lagoon; in 1990s – to the Lough Derg (Minchin and Moriarty 1998; Minchin *et al.* 2002). Although the abundance and distribution range differs among the assessment units (D – in the Curonian Lagoon and Lough Derg, C – in Pripiat river and Dnieper-Bug canal), most likely it has reached there the same introduction phase – adjustment (the fourth phase of introduction, following the arrival, establishment and
expansion) (Reise et al. 2006), by now. Also varies the strength of the species impact on different parts of the ecosystems, and consequently, the biopollution level induced by *Dreissena polymorpha* in the presented assessment units. The highest BPL (3) obtained for the Curonian Lagoon, since the strong impact on habitats and communities reported there.

The differences in invasiveness of zebra mussel may also ride on the specific features of an ecosystem. Applying the biopollution assessment method, it is possible to evaluate the significance of different impacts and basic functions of a species in a context of a certain ecosystem. For instance, the physical presence of zebra mussel is causing a strong impact on native communities (C3), strong impact on habitats (H3) and moderate impact on ecosystem functioning (E2). Consequently, this zebra mussel function causes BPL=3. Similarly, the filtration activity of zebra mussel would result in weak impact on communities (C1), weak impact on habitats (H1), moderate impact on ecosystem functioning (E2), and BPL=2; growth and reproduction, respectively, - C2, H2, E2, and BPL=2; metabolism – C0 (impact unknown), H1, E1, BPL=2. Thus, we can see that the strong invasiveness of zebra mussel in the Curonian Lagoon is largely conditioned by the physical presence of the species.

Since the Curonian Lagoon has predominantly soft bottom, expectedly any species able to form hard reef-like structures would have a crucial impact here. Meanwhile in an ecosystem with variability of available hard substrates (e.g. in the Great Lakes, USA), relatively high water residence time and sparse native filtrators’ population, zebra mussel likely would have high impact on water clarity and phytoplankton reduction due to its filtering activity (Hebert et al. 1991; Leach 1993; Fahnenstiel et al. 1995).

Using this approach one could compare the ecosystems in respect of zebra mussel (or other common invader) invasiveness and determine which properties of an ecosystem cause the significance of a certain impact. It would be extremely helpful to have a uniform tool for assessment of ecosystem sensitivity to alien species invasion, taking into account the specific features of an ecosystem.
4.6. General overview of the zebra mussel functioning as habitat engineer in the Curonian Lagoon ecosystem

The specific distribution of zebra mussels in the Curonian Lagoon (Fig. 8) is likely conditioned by several environmental gradients common for this ecosystem. Thus in the north, zebra mussel population is limited by the rapid salinity changes caused by episodic inflows of brackish water from the Baltic Sea (see Fig. 2). Besides, northward from the main zebra mussel distribution area, there is a transitional river-like part of the lagoon with the least residence time of water and strong currents (see Fig. 3). Current velocities are known to affect the rate of settlement of zebra mussel post-veligers. Settlement cannot normally occur at flow velocities above 2 m s\(^{-1}\) (Lyakhov 1968). The critical for zebra mussel current velocities (1.5 – 2 m s\(^{-1}\)) are prevalent in the northern part of the lagoon (from the Nemunas delta towards the Klaipėda strait) (Pustelnikovas 1998; Ferrarin et al. 2008). On the other hand, the whole southern part of the lagoon, which is limnic and characterized by fine sediments, is classified as a stagnant (Ferrarin et al. 2008) and might be unsuitable for colonization by zebra mussel. Thus the most appropriate area for zebra mussel population is an “intermediate zone” of the Curonian Lagoon – the central part, westward from the Nemunas delta, with the optimal environmental characteristics for the species (sufficiently coarse sediments, current velocity below 2 m s\(^{-1}\), no or little salinity fluctuations, permanent input of fresh seston from the Nemunas river, etc.).

Since the heterogeneity of the bottom habitats in the study area was extremely high (see Fig. 13 and section 4.1), the performed sampling results were applied only for estimation of the bottom area where modified habitats may potentially occur (Fig. 8). The confines of the defined distribution area seemed to be rather constant (Daunys 2001), still the size and location of the bottom patches modified by zebra mussels or shell deposits may vary significantly over time.

Since the species is quite aggressive and very abundant invader, each of its activity potentially may cause a kind of a ‘chain reaction’ in an ecosystem. For instance, due to the extensive filtering, the clarity
of water increases → increases light penetration → changes in species composition and community structure → alteration of the food web and energy flow → impact on the diversity and stability of the entire ecosystem. One can draw a number of variations of similar logical series with the same initial function of zebra mussel in the beginning and different outcomes at the end.

Based on the results revealed in this study and all the assumptions presented above, the conceptual scheme of zebra mussel engineering impact on benthic environment may look as presented in Fig. 25.

The soft bottom devoid of the live zebra mussel druses or shell deposits in the turbulent environment of the lagoon is characterized by a rather poor macrozoobenthic community with dominating common infaunal species (like oligochaets and chironomids), concentrated in the upper (aerated) sediment layer.

Specific roughness of the bottom covered by zebra mussel empty shells promotes the microcirculation flows in the benthic boundary layer and enhances the aeration of sediments. This and burrowing activity of the more abundant infaunal organisms result in a thicker oxidized layer of the sediments. A few epifaunal organisms may be observed in this habitat. Empty shells are also capable of trapping the suspended particles thus accumulating temperate amounts of organic matter on the bottom.

Live zebra mussel druses besides the physical trapping actively deposit a lot of particulate matter, which is partly utilized by the numerous detritovores and decomposed via intensive anaerobic processes, facilitated by the anoxic conditions just under the mussel bed. Large epibenthic organisms are abundant in this habitat type. The infaunal species are abundant here too, yet they are shifted to a kind of epifaunal life style, since are found above the real sediment layer, inside the zebra mussel clumps. This phenomenon is conditioned by the unsuitable anoxic conditions on the one hand and ‘attractive’ shelters provided by zebra mussels on the other hand.
Figure 25: Habitat changes and functioning of macrozoobenthic community induced by the engineering impact of zebra mussel. The model represents 3 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).
The attempt to summarize and visualize schematically the most important functions of the zebra mussel in the Curonian Lagoon, and several levels of possible (and reported in the present study) impacts, resulting from these functions, is presented in Fig. 26.

**Figure 26:** Zebra mussel basic functions (inner circle), impacts on habitat (second circle from the center), impacts on communities (third circle from the center) and impacts on ecosystem (outer circle). The cells are ordered correspondingly with impact interactions.
The scheme is based on the results obtained from the present study in the Curonian Lagoon. Still this does not disclaim the possibility of other impacts, did not broached in this work. It can be assumed, that zebra mussel is capable of affecting the abundance of benthopagous and/or planktonophagous fish via sheltering benthic invertebrates and competing for food with zooplankton, thus decrease the availability of the potential fish preys. The species may promote periphyton production, bacterial activity; influence the near-bottom hydrodynamics; accumulate and transfer toxic substances through the food web. It is also known that zebra mussels are consumed by vimba (Vimba vimba), white bream (Blicca bjorkna), roach (Rutilus rutilus), invasive round gobies (Neogobius melanostomus) and some other benthophagous fish (Kublickas 1959). Yet, the mussels less than 10 mm length are usually preferred (Nagelkerke and Sibbing 1995; Ray and Corkum 1997). The large mussels with their hard calcareous shells are consumable neither by fish, nor by diving birds preying on them. Hence, zebra mussels are largely an energy ‘dead end’ in the ecosystem (Cooley 1991).

Taken together, the results of this study indicate a major shift in ecosystem functioning pattern caused by the zebra mussel. An extent of such a shift is so fundamental that all levels of the ecosystem are likely affected either directly or indirectly. Nevertheless, zebra mussels are present in the Curonian Lagoon long enough to become an integral part of its community, having a multiple (and sometimes rather sophisticated) linkages with every component of the ecosystem.
5. CONCLUSIONS

1. The thresholds for distinction of natural habitats modified either by live zebra mussels or their shell deposits, based on composition of benthic species, were determined: ‘zebra mussel bed’ was distinguished by the biomass of live mussels exceeding 200 WWg/m²; ‘zebra mussel shell deposits’ – by the presence of spent shells in the amount of 1000 DWg/m² or more, with either no or very few (less than 200 WWg/m²) live zebra mussel therein; sites where live mussel biomass was less than 200 WW g/m² and the amount of empty shells was less than 1000 DWg/m² were defined as ‘bare sediments’.

2. Habitats formed by zebra mussel bed or zebra mussel shell deposits may potentially extend in ¼ of the Curonian Lagoon and maintain benthic communities different from those common in bare sediments. The typical “zebra mussel bed community” in the lagoon occur even devoid of zebra mussel clumps, if a certain amount of empty shells (>10³ g m⁻²) persists on the bottom.

3. Macrozoobenthos in habitats modified by zebra mussels is distinguished by higher abundances of epifaunal organisms (e.g. Glossiphonia spp., Viviparus viviparus, Lithoglyphus naticoides, Asselus aquaticus) comparing to bare soft sediments, and shift of infaunal biota to epifaunal lifestyle.

4. The estimated annual biodeposition by zebra mussels is approximately equal to 5.5 kg m⁻². Together with the calcium carbonate production rate (0.01 to 10 kg m⁻²) it is an essential annual increase of bottom sediments (comparing to the physical sedimentation rate in the Curonian Lagoon). The effectiveness of particle removal by zebra mussels is influenced by the density of mussel clumps and total particulate matter concentration in the water.

5. The extensive anaerobic mineralization processes in the zebra mussel bed are facilitated by the anoxic conditions under the dense layer of zebra mussel clumps. The bottom formed by zebra mussel shells is characterized by the thicker layer of oxidized sediments and higher amounts of organic carbon, total phosphorus and total nitrogen.

6. Zebra mussel appeared to be among the 3 most successful invaders in the SE Baltic and abundant in 6 of 16 analysed benthic
habitat types. Habitats modified by zebra mussels are distinguished by the highest xenodiversity and highest relative biomass of invasive species in the Curonian Lagoon. The magnitude of zebra mussel impact in the Curonian Lagoon is defined as strong (BPL = 3) and is largely determined by the physical presence of the species.
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LIST OF PUBLICATIONS

The dissertation is based on 5 publications (4 of them in peer-reviewed scientific journals) listed below:


SUMMARY

ĮVADAS


Šis darbas – tai pirmas bandymas pateikti apibendrintą dreisenos, kaip buveines formuojančios rūšies, vaidmens borealinės estuarinės lagūnos ekosistemoje analizę, parodant jos daugialypį poveikį visiems ekosistemos elementams.

**Darbo tikslas ir uždaviniai.** Pagrindinis šio darbo tikslas – įvertinti invazinio moliusko Dreissena polymorpha funkcinį vaidmenį formuojant dugno buveines Kuršių marių ekosistemoje.

Darbo tikslui pasiekti buvo iškelti šie uždaviniai:
1. Įvertinti ir aprašyti D. polymorpha populiacijos ir jų kriauklių sankaupų pasiskirstymą Kuršių mariose.
2. Įvertinti dreisenų poveikį dugno makrofaunos struktūrai ir pasiskirstymui.
3. Įvertinti dreisenų filtracijos ir biosedimentacijos įtaką pelaginei ir bentosinėi Kuršių marių ekosistemos dalims.
4. Įvertinti dreisenų poveikį Kuršių marių dugno nuosėdų biogeocheminiams rodikliams ir procesams.
5. Įvertinti introdukuotų rūšių įvairovę ir pasiskirstymą D. polymorpha suformuotose buveinėse, lyginant su kitomis Kuršių marių ir pietryčių Baltijos jūros dugno buveinėmis.


Ginamieji teiginiai
1. *Dreissena polymorpha* ir jos kriaulės keičia dugno nuosėdas ir sąlygoja dugno makrofaunos pasiskirstymo pokyčius Kuršių mariose.
2. Dreisenų filtracija ir biosedimentacija keičia suspenzijų medžiagos nusėdimą greičius Kuršių mariose.
3. Dėl dreisenų buvimo ir gyvybinės veiklos keičiasi biogeocheminės nuosėdų savybės ir įtako žemės dugno biogeocheminių procesų bei bentosinių organizmų funkcijas.
4. Dreisenų suformuotoms dugno buveinėms būdingi didesnis introdukuotų rūšių gausumas ir įvairovė lyginant su kitomis Kuršių marių ir pietryčių Baltijos dugno buveinėmis.
5. Remiantis biologinio užterštumo vertinimo metodika, dreisena turi stiprų poveikį įvairiems Kuršių marių ekosistemose komponentams.

Šios disertacijos rezultatai buvo paskelbti 5 mokslinėse publikacijose, 4 iš jų – recenzuojamuose moksliniuose leidiniuose.

**Padėkos.** Nuoširdžiai dėkoju šio darbo vadovui Sergejui Oleninui ir moksliniam konsultantui Dariui Dauniui už rūpinimąsi, vertingus patarimus, teigiamą nuostatą ir teisėtą kritiką; Sauliui Gulbinskui - už suteiktą pagalbą geologinėje dugno nuosėdų analizėje; Petruui Zemliui - už konsultacijas Kuršių marių hidrologijos klausimais; Ričardui Paškauskui - už kritišką disertacijos juodraščio skaitmą ir esmines pastabas; Zitai Gasiuńaitę, Renatai Pilkaitytę ir Artūrii Razinkovui - už vertingus patarimus ir palaikymą rengiant disertaciją; mano kolegoms doktorantams Klaipėdos universiteto Pajūrio tyrimų ir planavimo institute: Jūratei Lesutienėi, Aurelijai Samuilovienėi, Aistei Paldavicienei, Evelinai Grinienei, Loretai Kelpšai, Rasai Bukonai, Dianai Vaičiūtei, Martynui Bučiui, Tomui Ruginiui, Nerijui Nikai, Mindaugui Žiliui, Viktorui Didžiuliui, Andriui Šiauliui, Aleksui Narščiui ir Alekseju Šaškovui - už jų draugiškumą, įkvėpiančias diskusijas, draugišką kritiką doktorantų seminariuose ir visokeriopą pagalbą ekspedicijose ir laboratorijoje; Simonai Mačiukaitei ir Alinai Mockutei - už jų geranoriškumą ir vertingą administracinę pagalbą. Dėkoju Klaipėdos universiteto leidyklai ir Mokslo skyriui už jų administracinę pagalbą ir disertacijos santraukos leidybą.

Ypač dėkoju savo šeimai: mamai ir tėčiui bei uošviui už jų kantrybę ir palaikymą, raginimą ir neįkainuojamą pagalbą priziūrint vaikus disertacijos rengimo metu; seseriai Jekaterina ir jos vyri Džonui Fogui - už lingvistinę pagalbą ir gerus palinkėjimus; dukterėčioms Eleonorai ir Anais už jų meilę ir dėmesingumą. Pagaliau dėkoju savo vyri Arturui už supratimą, visokeriopą pagalbą, dalykiškus patarimus, kantrybę ir rūpestingumą; taip pat savo mylimoms dukrėms Neli ir Sofijai už jų šviesias šypsenas ir nuolatinį įkvėpimą!
Nėra abejonių, kad prie šio darbo prisidėjo, buvo palankūs ir daugelis kitų, čia nepaminėtų kolegų ir artimujų. Visiems Jiems nuoširdus mano ačiū!


MEDŽIAGA IR METODAI
Dugno nuosėdų su dreisenomis ir dreisenų kriaulėmis tyrimo metodai


Analizuojant biogeocheminius pokyčius dreisenos suformuotose buveinėse, 3-se skirtinėse buveinėse (smulkiai smėlyje, dugne su dreisenomis ir dugne su dreisenų kriaulėmis) (10 pav.) buvo įvertinti šie biogeocheminiai parametrai: paviršiniame ir išdugniniame vandens sluoksniuose buvo nustatyta pH, ištirpusios deguonies koncentracija, druskingumas, ištirpusio neorganinio azoto ir bendro ištirpusio azoto
koncentracijos, fosfatų ir bendro ištimpusio fosforo koncentracijos; viršutiniame nuosėdų sluoksnyje buvo matuotas nuosėdų granuliometrinė sudėtis, organinės anglies koncentracija, bendro azoto ir fosforo koncentracijos, deguonies suvartojimas, bendra bei anaerobinė organinės medžiagos destrukcija, Eh. Biogeocheminiai parametrai buvo matuojami tose pačiose vietose 3 kartus: 2006-ų gegužės, rugpjūčio ir spalio mėnesiais.

**Buveinių klasifikacija**

Dėl didelio vandens drumstumo ir dugno heterogeniškumo buvo sunku numatyti dugno buveinių įvairovę ir planuoti tikslų mėginių surinkimą. Todėl sąlyginis buveinių skirstymas į smulkiausius smulkius, organinęs anglies koncentracija, bendro azoto ir fosforo koncentracijos, deguonies suvartojimas, bendra bei anaerobinės medžiagos destrukcija, Eh. Biogeocheminiai parametrai buvo matuojami tose pačiose vietose 3 kartus: 2006-ų gegužės, rugpjūčio ir spalio mėnesiais.

Reikšmingi skirtumai rūšinėje bendrijos sudėties (buvimo/nebuvimo) duomenys buvo ranguojami dreisenos biomasės ir kriauklių svorio atžvilgiu. Buvo nustatytos slenkstinių dreisenos biomasės ir kriauklių svorio reikšmės, ties kuriomis sutinkamos visos šioms buveinėms būdingos rūšys.

**Eksperimentiniai dreisenos filtracijos ir biosedimentacijos tyrimai**

Eksperimentai atlikti 300 l laboratoriniame srovės kanale, kuriamo buvo įrengti du elektriniai siurbliai, sukuriantys ir palaikantys centrinei Kuršių marių daliai būdingą (5-10 cm s⁻¹) vandens srovę. Vandens cirkuliacijai užtikrinti ir tėkmės turbulencijai bandymų lauke mažinti srovės kanale buvo įrengti dvigubas dugnas ir laminatorius. Bandymų laukas (61x48 cm) nuo laminatoriaus buvo nutoleę 45 cm. Plastikiniai 0,5 l indai (indo dugno plotas - 0,01 m², aukštis - 5 cm) buvo naudojami dreisenų fekalijų ir pseudofekalijų surinkimui. Iš viso eksperimente buvo naudojama 16 indų: 3 pakartojimai kiekvienam moliuskų tankiui (1) 15 ± 3 ind. inde, (2) 35 ± 8 ind. inde, (3) 60 ± 15 ind. inde (1300 ± 249, 3000 ± 684 ir 5100 ± 1282 ind. m⁻², atitinkamai) ir 4 kontroliniai indai be moliuskų. Eksperimentinių moliuskų tankiai buvo parinkti atsižvelgiant į dreisenos populiacijos tyrimų Kuršių mariose duomenis. Kontroliniai indai buvo naudojami foniniam suspenduotos...
medžiagos sedimentacijos greičiui nustatyti. Indai bandymų lauke buvo išdėstyti taikant Lotynų kvadratų metodą. Eksperimentas buvo atliktas naudojant 3 skirtingas natūralaus sestono koncentracijas.

Eksperimente buvo taikomi 2 fiksuoti faktoriai – dreisenos moliuskų tankis ir bendros suspenduotos medžiagos (TPM, angl. total particulate matter) koncentracija srovės kanale; ir 2 atsitiktiniai faktoriai – šoninių srovės kanalo „sienelių efektas“ (srovės greičio mažėjimas kanalo sienelių link) ir „laminatoriaus efektas“ (srovės greičio mažėjimas tolstant nuo laminatoriaus).

TPM, suspenduotos neorganinės medžiagos (PIM, angl. particulate inorganic matter) ir suspenduotos organinės medžiagos (POM, angl. particulate organic matter) koncentracijos srovės kanale buvo nustatomos prieš eksperimentą bei kasdien eksperimento metu. TPM koncentracijai bei POM daliai sedimentacinėje medžiagoje ir vandenye nustatyti, iki 500 ml vandens mėginio buvo filtruojama per išdžiovintą ir pasvertą stiklo pluošto filtrą, vėliau juos pakartotinai džiovinant ir deginant.

Efektyvus filtracijos greitis (ECR, angl. effective clearance rate) – faktinė dreisenės geba išvalyti tam tikrą vandens tūrį nuo suspenduotų dalelių, duotomis hidrodinaminėmis ir moliuskų tankio sąlygomis (Yu and Culver 1999) – buvo skaičiuojamas pagal formulę:

$$ECR = (l \text{val}^{-1} \text{ind}^{-1}) = (W - W_0) \frac{C_{PIM}}{N_T}$$

kur $W$ – iš eksperimentinio indo su dreisenomis surinktos neorganinės medžiagos svoris (mg), $W_0$ – iš kontrolinio indo surinktos neorganinės medžiagos svoris (mg), $C_{PIM}$ - vidutinė suspenduotos neorganinės medžiagos koncentracija srovės kanale (mg l$^{-1}$), $T$ – eksperimento trukmė (val), ir $N$ – moliuskų skaičius eksperimentiniame inde. Eksperimentinių moliuskų biodepozicijos greičių (BDEP) buvo apskaičiuojami pagal formulę:

$$BDEP = (mgTPM h^{-1} \text{ind}^{-1}) = (U - U_0) \frac{N_T}{T}$$

kur $U$ – iš eksperimentinio indo su dreisenomis surinktos sedimentacinės medžiagos svoris (mg), $U_0$ – iš kontrolinio indo surinktos sedimentacinės medžiagos svoris (mg).
Palyginamoji introdukuotų organizmų įvairovės analizė skirtingose buveinėse


Analizei buvo pasirinktos 16 bentosinių introdukuotų rūšių, kurios įtrauktos į Baltijos jūros svetimų rūšių duomenų bazę (Olenin et al. 2002; Olenin 2004) kaip regione įsitvirtinusios ir nuolatines populiacijas turinčios rūšys.

Buveinių imlumas invazijoms buvo charakterizuojamas dviem kintamaisiais: a) bendru invazinių rūšių skaičiumi ir b) struktūriniais pokyčiais dugno bendrijoje (santykine introdukuotų rūšių biomase). Kaip nepriklausomi kintamieji analizėje buvo panaudoti šie rodikliai: vietinių rūšių įvairovė buveinėje, kieto ir (arba) minkšto substrato buvimas, minimalus metinis druskingumas, druskingumo svyravimų intervalas, buveinės minimalus gylis ir gylių intervalas bei santykinė dreisenos biomase buveinėje.

Statistinių metodų taikymas
Duomenų analizei buvo taikomas neparametrinis Kruskal-Wallis testas, faktorinė dispersinė analizė (ANOVA), NMDS (angl. non-metric multidimensional scaling) metodas, RDA (angl. redundancy analysis) bei SIMPER (angl. similarity percentage) panašumo analizė.

REZULTATAI
Dreisenų suformuotų buveinių apibūdinimas
Remiantis dugno faunos rūšių įvairovės dreisenos kolonijose ir kriauklių liekanose analizės rezultatais, dugno nuosėdų su dreisenomis buveinei taikytina slenkstinė Dreissena polymorpha moliuskų biomasė
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yra 200 g m\(^{-2}\) šlapio svorio. Dugnas su dreisenų kriaulkėmis įgyja buveinės savybės esant 10\(^{3}\) g m\(^{-2}\) (arba didesniam) sauso dreisenos kriaulių svorio ir kai dreisenų biomasė mažesnė nei 200 g m\(^{-2}\). Dugnas, kuriam gryvų dreisenų biomasė buvo mažesnė nei 200 g m\(^{-2}\) ir dreisenos kriaulių mažiau nei 10\(^{3}\) g m\(^{-2}\) buvo apibūdintas kaip smėlėtas dugnas.

Dreisenų ir jų kriaulių užimamos teritorijos dydis nėra stabulis, ir atliktų tyrimų rezultatais galima vertinti tik teritorija, kurioje gali būti aptinkamos dreisenų suformuotos buveines (8 pav.). Apskaičiuotas Kuršių marių dugno plotas, kuriame potencialiai gali būti aptikta daugiau nei 10\(^{3}\) g m\(^{-2}\) dreisenos kriaulių yra apie 400 km\(^{2}\), tuo tarpu plotas, kuriam gali būti sutinkama 200 g m\(^{-2}\) ir daugiau dreisenų – apie 300 km\(^{2}\). Šie plotai persidengia ir pasižymi dideliu heterogeniškumu.

**Dugno makrofaunos struktūra dreisenų suformuotose buveinėse**


Duomenų, surinktų 2006 metų tyrimų metu, analizė parodė, kad dreisenų poveikis biojuvairovei yra labiau reikšmingas, nei dreisenų kriaulių. Dugne su dreisenomis dugno faunos gausumas ir rūšinė įvairovė didesnė, taip pat šioje buveinėje didesnė dugno bestuburių biomasė. NMDS analizės rezultatai rodo (13 pav.), kad dugno makrofaunos gausumas ir rūšinė struktūra taip pat skirtingas nuo smėlėto dugno, kuriam dreisenų arba jų kriaulių poveikio dugno faunai nėra. Analizuojaugant dugno bestuburių rūšinę sudėtį ir individų gausumą stebimas nuoseklus kiekvienių rodiklių didėjimas smėlėto dugno buveinė keičiant dugnus su dreisenų kriaulkėmis, o pastarają - dugnus su dreisenomis.

Šešiuose mėginiuose, kuriuose makrozoobentoso struktūra skyrėsi nuo rastos kituose mėginiuose, registruotos gausios *Valvata* genties pilvakojų moliuskų kriaulių liekanos (vidutinis sausas kriaulių svoris 4,6·10\(^{3}\) ± 0,3·10\(^{3}\) g m\(^{-2}\)). Tiesinės regresijos modeliu nustatytos rūšys, kurių gausumas ženkiai koreliuoja su dreisenų ar jų kriaulių kiekium. Tai leido apibūdinti savitą dugnus su dreisenomis būdingą makrozoobentoso bendriją. Ši bendrija formuojama dugno buveinėse, kur dreisenų biomasė
pasiekia apie 200 g m\(^{-2}\). Dugne su dreisenų kriaulkėmis, kur sausas kriauklių svoris viršija 10\(^3\) g m\(^{-2}\), bendrijos struktūra labai panaši į bendrijas, išikūrusias dugne su gyvomis dreisenomis.

**Dreisenų filtracijos ir biosedimentacijos greičiai**

Laboratorinių eksperimentų rezultatai parodė, kad biologiškai nusodintos medžiagos kiekis eksperimentiniuose induose su moliuskais vidutiniškai 1,5-10 kartų viršijo nusėdusios medžiagos kiekį kontroliniuose induose. Organikos dalis kontrolinių induų sedimentacinėje medžiagoje buvo ženkliai didesnė, nei induose su dreisenomis (Kruskal-Wallis testas, P<0,001). Remiantis ANOVA rezultatais, galima teigti, kad abu fiksuoti faktoriai – moliuskų tankis ir pradinė suspenduotos medžiagos koncentracija srovės kanale – turėjo reikšmingą poveikį moliuskų filtracijos greičiams (atitinkamai F = 6,06; d.f. = 2; P < 0,05 ir F = 134,07; d.f. = 2; P < 0,001). Iš atsitiktinių faktorių tik „laminatoriaus efektas“ turėjo reikšmingą poveikį (F = 13,3; d.f. = 3; P < 0,001). Efektyvus dreisenų filtracijos (ECR) greitis eksperimento metu kito nuo 0,4 iki 434,4 ml val\(^{-1}\) ind\(^{-1}\), vidutinė ECR reikšmė - 77,1 ± 106,2 ml val\(^{-1}\) ind\(^{-1}\).

**Biogeocheminės nuosėdų savybės dreisenų paveiktose buveinėse**

NMDS panašumo analizė parodė, kad pagal pasirinktus biogeocheminius parametrus dreisenų kriauklių suformuota buveinė skiriasi nuo kitų analizuotų buveinių (18 pav). Šioje buveinėje matuoti mažesni bendros organinės medžiagos destrukcijos greičiai (195 ± 52 mgC m\(^{-2}\) per parą dugne su dreisenų kriaulkėmis lyginant su 955 ± 22 dugne su dreisenomis ir 597 ± 271 mgC m\(^{-2}\) per parą smėlėtame dugne), rastas didžiausias organinės anglies kiekis paviršinėse nuosėdose (3,75% lyginant su 0,95% dugne su dreisenomis ir 1,25% smėlėtame dugne) bei didžiausia oksiduoto ištirpusio neorganinio azoto koncentracija (0,621 mgN l\(^{-1}\) lyginant su 0,154 dugne su dreisenomis ir 0,024 mgN l\(^{-1}\) smėlėtame dugne) spalio mėnesį. Santykinai nedidelė organinės medžiagos destrukcija dugne su dreisenos kriaulkėmis vyksta aerobiniu būdu tiek vegetacinio periodo viduryje, tiek pabaigoje.
Kriauklų suformuotoms nuosėdoms būdingos didžiausios bendro fosforo ir bendro azoto reikmės, taip pat buvo geriausios oksidacinės sąlygos paviršiniame sluoksnyje. Nors piedugnyje ištirpusios deguonies koncentracija visose buveinėse buvo panaši (9 ± 1,8 mgO₂ l⁻¹), tačiau 1 cm nuosėdų gylyje Eh reikmės ženkliniai skyrėsi (20 pav.).

Dugnas su dreisenu kolonijomis išskyrė didesniu deguonies suvartojimu viršutiniame nuosėdų sluoksnyje ir vyraujančia anaerobine organinės medžiagos destrukcija.

**Introdukuotų organizmų įvairovė dreisenų suformuotose buveinėse, lyginant su kitomis Kuršių marių ir pietryčių Baltijos buveinėmis**

Visų 16 analizuotų introdukuotų rūsių santykinių invazijos sėkmė buvo nustatoma pagal šiomis rūsimis kolonizuotų dugno buveinių skaičių. Nustatyta, jog *Dreissena polymorpha* paplitusi 6 iš 16 analizuotų buveinių ir yra viena iš trijų sėkmingiausių introdukuotų rūsių.

Rezultatai parodė, kad introdukuotų rūsių įvairovė Kuršių marių buveinėse ženkliniai didesnė nei jūrinėse arba sąsiaurio buveinėse (Kruskal-Wallis testas, P < 0,001). Didžiausia svetimų rūsių įvairove patirta kieto substrato buveinėse (8-12 rūsių buveinėje). Jūrinėse buveinėse aptinkamų introdukuotų rūsių skaičius buvo mažiausias (1-3 rūšys buveinėje). Didesnėmis santykiniomis introdukuotų rūsių biomasėmis patirta sąsiaurio dirbtinis kietas dugnas(97,4%), smėlėtas dugnas jūros litoralėje (94,1%) bei dreisenos suformuotos buveinės Kuršių mariose (76,3%).

Remiantis RDA rezultatais, vietinių ir svetimų rūsių pasiskirstymui analizuotose buveinėse reikšmės turėjo druskingumas, gylių diapazonas, minimalus gylis bei kieto substrato sutinkamumas.

**REZULTATŲ APTARIMAS**

**Dugno makrofauna dreisenų suformuotose buveinėse**

Rezultatai apie dugno faunos rūšinę sudėtį būtų panaudoti skiriant tris Kuršių marių buveines: dugną su dreisenomis, dugną su dreisenų kriauklėmis ir smėlėtą dugną. Makrozoobentoso struktūriniai rodikliai parodė, kad dreisenų kriauklių buveinės bendrija skiriasi nuo smėlėtame dugne randamos bendrijos, nors skirtumas ir nėra toks ženklus, kaip tarp
dugno su dreisenomis ir smėlėto dugno (13 pav.). Tai, jog dugnus su dreisenomis būdinga bendrija gali susiformuoti nuosėdose ir be gyvų moliuskų tik esant tam tikram kriauklių kiekui, išrodo dreisenų kriauklių, kaip buveines formuojančio faktoriaus, svarbą.


Įvertinus dreisenų kriauklių, susikaupusių Kuršių marių dugne, kiekį (apie 600 000 t), paaiškėja jų svarba ekosistemai. Priklausomai nuo populiacijos dydžio, D. polymorpha kalcio karbonato produkcija kinta nuo 10 iki 10000 g m⁻² sauso svorio per metus (Strayer and Malcom 2007). Remiantis šiais vertinimais, kalcito ir aragonito tankių bei jų santykių 1:1 (Gutierrez et al. 2003), galima apskaičiuoti, kad dugno nuosėdų paviršiuje dreisenos sugeba akumuliuoti nuo 0,035 iki 3,5 mm kalcio karbonato per metus kriauklių liekanų pavidalu. Įvertinus vidutinių 3,2 mm sedimentacijos greitį Kuršių mariose (Pustelnikovas 1995), toks sukaupiamas kriauklių kiekis gali būti reikšmingas nuosėdėnės medžiagos formavimuosi bei medžiagų transportui.
Ryšys tarp bentosinės ir pelaginės ekosistemos dalių dėl dreisenų filtracijos ir biosedimentacijos

Filtracijos ir biosedimentacijos eksperimentų rezultatai parodė, kad dreisenos gali ženkliai įtakoti sedimentacinius procesus Kuršių mariose. Net mažiausi eksperimentų metu matuoti biosedimentacijos greičiai (0,35 mgTPM val⁻¹ ind⁻¹), įvertinus vidutinį dreisenų gausumą (2,7x10³ ind m⁻²) bei 16 val. per parą filtracijos aktyvumą (Morton 1969; Walz 1978; Horgan and Mills 1997) rodo reikšmingą, iki 5,5 kg m⁻² per metus, suspenduotos medžiagos perskirstymą tarp vandens storymės ir dugno nuosėdų.

Pateiktı eksperimentų duomenys parodę reikšmingą neigiamą priklausomybę tarp filtracijos efektyvumo ir sestono koncentracijos srovės kanale. Tikėtina, kad didelė sestono koncentracija slopina moliuskų mitybinį aktyvumą, nes filtracinis aparatas yra mechaniskai užkemšamas pakibusiomis vandenyje dalelėmis (Karatayev and Burlakova 1994).

Biogeocheminė nuosėdų charakteristikos dreisenų suformuotose buveinėse

Lyginant su smėlėtu bei dreisenos kriaulkėmis padengtu dugnu, dugnas su tankiomis moliuskų kolonijomis yra fiziškai izoliuotas nuo priedugninių vandenų sluoksnių. Dėl aktyvių respiracijos deguonies suvartojimas dugne su dreisenomis būna ženkliniai didesnis nei kitose buveinėse (Effler et al. 1996). Tokiu būdu reikšmingas deguonies suvartojimas moliuskų respiracijos metu ir fizinė dugno nuosėdų izoliacija palengvina anaerobinės destrukcijos procesus ir skatina greitesnę organinės medžiagos mineralizaciją dugno nuosėdose.

Smėlėtame dugne, kur dėl aktyvių hidrodinamikos nėra sąlygų kauptis detritui, azoto ir fosforo koncentracijos buvo mažiausios. Dreisenų kriauklių suformuotose dugno nuosėdose sąlygos yra palankesnės organikos akumuliacijai. Tačiau, lyginant su dugnu padengtu dreisenu, suformuotose kolonijomis, mineralizacijos procesai čia yra lėtesni, o anaerobinė destrukcija visiškai nevyksta. Matyt, tai lemia geresnė tokių nuosėdų aeracija dėl jų specifinio šiurkštumo. Todėl dugne su dreisenos kriaulkėmis buvo aptiktos didžiausios organikos anglių, bendro azoto ir bendro fosforo reikšmės.

Introdukuotų rūšių įvairovė dreisenų suformuotose buveinėse

**Dreisenos poveikio vietinėms bendrijoms, buveinėms ir ekosistemos funkcionavimui lyginamasis vertinimas**


Šis metodas galėtų būti panaudotas dreisenos invaziškumui palyginti skirtingose vandens ekosistemose, arba jos poveikio stiprumo pokyčių laike vertinimui. Pavyzdžiui, lyginant tris skirtingus vandens telkinius: Kuršių marias, Lough Derg ežerą ir Priepetės upę – labiausiai dreisenos veikiamos yra Kuršių marios dėl stiprūs rūšies poveikio tiek bendrijoms (C3), tiek buveinėms (H3).
Dreisenų poveikio skirtumai įvairiuose vandens telkiniuose gali būti nulemti ekosistemų ypatumų. Taikant biologinės taršos vertinimo metodą galima nustatyti skirtingų invazinės rūšies poveikių svarbą visos ekosistemos kontekste. Pavyzdžiui, dreisenų formuojamos (kietam dugnui būdingos) erdvinės struktūros nuosėdų paviršiuje turi stiprų poveikį vietinėms bendrijoms (C3), stiprų poveikį buveinėms (H3) ir vidutinių – ekosistemai (E2). Tokiu būdu šios dreisenos funkcijos poveikio stiprumo lygis yra 3. Analogiškai dreisenų filtracija silpnai veikia bendrijas (C1) bei buveines (H1) ir vidutiniškai - ekosistemos funkcionavimą (E2), reiškia šios funkcijos BPL=2; atitinkamai dreisenų augimo ir reprodukcijos - C2, H2, E2, ir BPL=2; medžiagų apykaitos – C0 (poveikis nežinomas), H1, E1, BPL=2. Tokiu būdu stiprūs poveikiai Kuršių marioms sąlygoja dreisenos formuojamos erdvinės struktūros nuosėdų paviršiuje.

Kuršių mariose vyrauja minkštos dugno nuosėdos. Todėl bet kuri rūšis, formuojanti biogeniniams rifams būdingas struktūras ant tokio dugno, gali stipriai įtakoti visą ekosistemą keisdama epibiontinių ir endobiontinių rūšių santykį, kai kurių rūšių gyvensenos strategijas, dugno faunos struktūrinius rodiklius ir kitas charakteristikas. Tuo tarpu ekosistemose, pasižyminčiose didelė kietų substratų įvairove (pvz., Didieji ežerai, JAV), palyginus mažų vandens apykaitos greičių bei negausiais filtruojančiais organizmais, dreisenų vaidmuo keičiant vandens skaidrumą ir fitoplanktono skaitlingumą ypač ženklus (Hebert et al. 1991; Leach 1993; Fahnsteniel et al. 1995).

Pristatyto darbo rezultatai pažymi dreisenos daromos įtakos svarba formuojant dugno buveines Kuršių marių ekosistemoje. Ši įtaka pasireiškia skirtinguose ekosistemose lygmenyse ir tiesiogiai ar netiesiogiai veikia daugelį ekosistemos komponentų.

**IŠVADOS**

7. Pagal dugno makrofaunos rūšinę sudėtį nustatytos slenkstinės dreisenų suformuotų buveinių charakteristikos: dugnai su dreisenomis – gyvų moliuskų biomasė, viršijanti 200 g m⁻²; dugnai su dreisenų kriauklėmis – sausas kriauklių svoris viršijantis 10³ g m⁻² (ir gyvų dreisenų biomase mažesne nei 200 g m⁻²); smulkaus smėlio (dreisenų
nepaveiktam) dugnui – dreisenų biomasė, mažesnė nei 200 g m\(^{-2}\) ir sausas kriauklių svoris mažesnis nei 10\(^3\) g m\(^{-2}\).

8. Dreisenų arba jų kriauklių suformuotos buveinės gali būti aptinkamos ketvirtadalyje Kuršių marių dugno ploto. Šioms buveinėms būdinga dugno makrofaunos struktūra skiriasi nuo smėlėtame dugne be dreisenų randamos makrofaunos struktūros. *D. polymorpha* kriauklių suformuotoje buveinėje, kur sausas kriauklių svoris viršija 10\(^3\) g m\(^{-2}\), dugno faunos struktūra yra ypač panaši į randamą dugne su dreisenų kolonijomis.


10. Dėl dreisenų filtracijos ir biosedimentacijos Kuršių mariose per metus nusodinama iki 5,5 kg m\(^{-2}\) suspenduotos medžiagos. Kartu su kalcio karbonato produkcija (0,01-10 kg m\(^{-2}\)) ir įvertinus vidutinį sedimentacijos greitį, toks sukaupiamas medžiagos kiekis gali būti reikšmingas Kuršių marių nuosėdų formavimui.
