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Vulnerability of benthic habitats to the aquatic invasive species

**Anastasija Zaiko · Sergej Olenin ·
Darius Daunys · Tomas Nalepa**

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Abstract A comparative vulnerability analysis of 16 selected benthic habitat types in the SE Baltic Sea waters and the Curonian lagoon, including Klaipeda strait, was performed using long-term monitoring datasets (1980–2003) and results of several other surveys in the lagoon and the sea. Results indicated that invasive species richness (number of alien species per habitat) in lagoon habitats was significantly higher than in the sea. Habitats formed by artificial rock and stone, sand, mud, and habitats modified by zebra mussel shell deposits appeared to be the most invaded. Highest invasive species richness occurred in habitats with high native species richness indicating that the main factors driving native species distribution (such as favourable physical conditions, habitat alterations generated by human or/and biotic activities) are also driving aquatic invaders. Physical factors distinguished to be the most important for native and invasive species distribution were salinity, depth range (expressed by the maximal and minimal depths difference within a habitat), shallowness of a habitat (expressed by a minimal depth), and availability of a hard substrate.

Keywords Invasibility, Invasive species · Vacant niches · Species richness · Benthic macrofauna · Baltic Sea · Zebra mussel

Introduction

Accidental or human-mediated introductions of invasive species have occurred in most European seas and inland waters for the past several centuries. Recently, the brackish seas of Europe (e.g. Baltic Sea) have been subjected to particularly intense invasion of non-indigenous species (Paavola et al. 2005). Since the early 1980s, over 103 invasives have been recorded in the Baltic Sea (the Kattegat included) most of them being introduced by shipping (ballast water or hull fouling), or spread from their primary sites of introduction in adjacent freshwater bodies. It is assumed that some 70 species have been able to establish and maintain self-sustaining populations (Leppäkoski et al. 2002b).

The spread of invasive species has been the centre of scientific interest for the last few

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A. Zaiko (✉) · S. Olenin · D. Daunys
Coastal Research and Planning Institute, Klaipeda University, H. Manto 84, Klaipeda LT-92294, Lithuania
e-mail: anastasija@corpi.ku.lt

T. Nalepa
Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, 2205 Commonwealth Blvd, Ann Arbor, MI 48105-2945, USA

decades (Leppäkoski et al. 2002a, and references therein). This interest has been mostly driven by the serious ecological and economical consequences of bioinvasions. Much of this effort has been directed at identifying the risks of future introductions and the establishment of effective preventive techniques (Gollasch 2002; Hewitt and Hayes 2002). One of the central questions in the modern invasive ecology is: *What makes the ecosystem susceptible to invasion?* (Holdgate 1986; Li et al. 2000).

An ecosystem's susceptibility to invasion (invasibility) 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 and 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 and Moyle 1986; Mack et al. 2000).

Of the above factors, diversity and the effects of diversity on resource use are generally considered to play the primary role in the susceptibility of a community to invasion (Elton 1958; Levine 2000). On the other hand, abiotic factors such as climate, salinity, presence or absence of a necessary substrate, external disturbances etc., limit both indigenous biodiversity and invasibility of an ecosystem (e.g. With 2004, Romanuk and Kolasa 2005; Paavola et al. 2005).

The aim of our study was to identify the main driving factors affecting aquatic invasive species distributions, and to determine what makes a habitat susceptible to invasion.

The ability to forecast a system's vulnerability and response to species invasions is extremely important for successful ecosystem management. One of the possible approaches for such a prediction is empirical study. The accuracy of estimates of an organism's ability to invade a particular system is enhanced by knowledge of the organism's biology and the system's structure (Fuller and Drake 2000). In spite of the fact that our study was rather site-specific, the detailed analysis of successful invaders and their habitats offered insights into general invasibility patterns.

Study area

The area of this study includes the Lithuanian waters of the Baltic Sea (down to the 40 m depth), the Curonian Lagoon, and the Klaipeda strait areas (Fig. 1).

The salinity of the open sea waters varies between 6 and 8 PSU. In the area north of Klaipeda, major hydrological features are determined by the interaction between the south-eastern Baltic offshore waters and the runoff of the mostly freshwater Curonian Lagoon. Southward of the Klaipeda strait, there are typical Baltic Proper waters. Benthic macrofauna numbers about 60 species. Benthic communities on the hard bottom are dominated by the blue mussel *Mytilus edulis* and invasive barnacle *Balanus improvisus*. Sandy bottoms at a depth of 5–10 m are dominated by polychaetes, and at a the depths of 20 m and downward—by the bivalve *Macoma baltica* (Olenin 1994; Bubinas and Vaitonis 2003; Olenin and Daunys 2004).

The narrow (width 400–600 m) Klaipeda strait area connects the Curonian lagoon and the south-eastern part of the Baltic Sea. This area is artificially deepened and its maximum depth is about 14 m. It is oligohaline with irregular salinity fluctuations from 0.5 to 8 PSU (Olenin and Daunys 2004). 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). Soft bottom communities in this area are dominated by polychaetes, whereas littoral hard substrates (mostly artificial) are characterized by a seasonal vegetation and domination of nekto-benthic crustaceans (Zettler and Daunys submitted).

The Curonian Lagoon is a large shallow (total area 1584 km^2, mean depth 3.8 m; maximum depth 5 m) water body with low salinity (0–3 PSU) due to discharge mainly from the Nemunas river (98% of total freshwater input). The lagoon has a diverse benthic macrofaunal

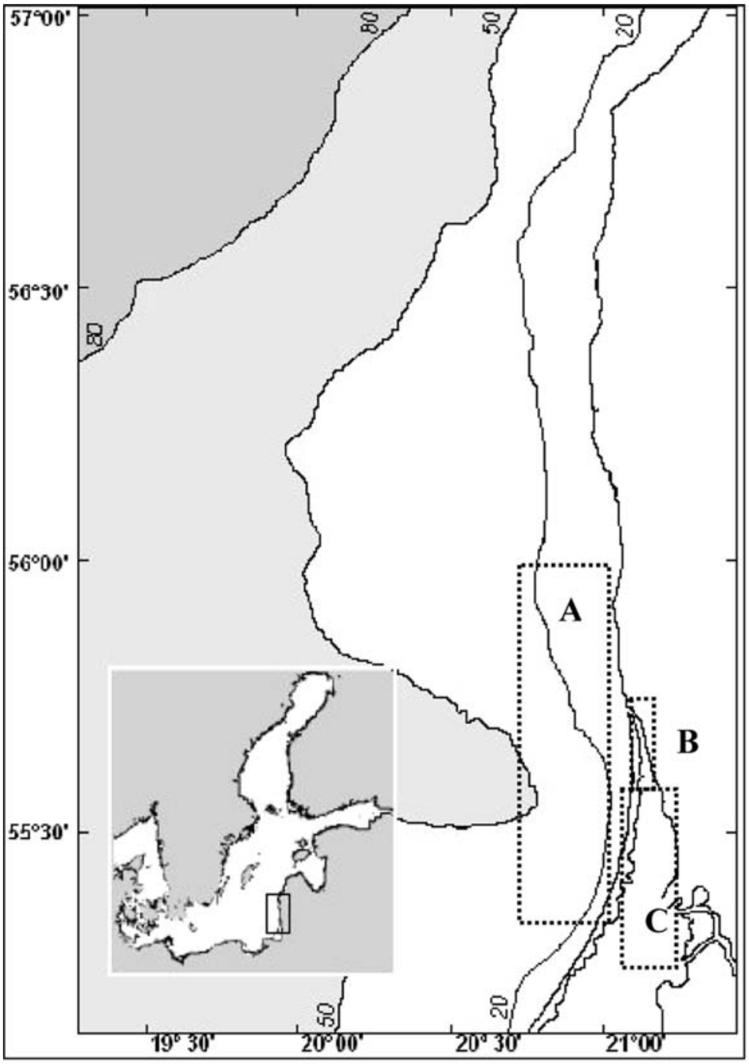

Fig. 1 Study area in the southeastern part of the Baltic Sea: A, Baltic Sea; B, Klaipeda strait; C, Curonian lagoon

community with approximately 280 species recorded in the littoral zone. Soft bottom of the northern part of the lagoon is characterized by oligochaetes, chironomids and the invasive spionid *Marenzelleria neglecta* communities. Bottom sediments in the central part are modified by the invasive zebra mussels and their shell deposits (Zettler and Daunys submitted).

Materials and methods

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 1).

Selection of habitats and availability of benthic data

For analysis, six main sediment types were delineated: *artificial hard bottom, hard bottom, gravel, sand, mud, and zebra mussel shell deposits.* Besides sediment type, the other defined feature of a habitat was its location within a certain vertical zone: *littoral*, *euphotic sublittoral*, *aphotic sublittoral*, or simply *sublittoral* (where euphotic and aphotic zones could not be defined). Thus a total of 16 habitats were distinguished. The

Table 1 Specifications, abbreviations, salinity ranges, number of samples, sampling methods, and data sources for each identified habitat

Habitat specification	Short name	Salinity, PSU	*n*	Sampling methods	Data Source
Artificial hard bottom substrate in the littoral of Klaipeda strait area	Art-Hard Li STRAIT	0–8	34	rame sampling	Česnauskas unpublished
Hard bottom substrate in the littoral of the Baltic Sea	Hard Li	6–8	12	benthic grab, SCUBA diving, frame sampling	Olenin 1994
Hard bottom substrate in the euphotic layer of the Baltic Sea	Hard Eu	6–8	69	SCUBA diving, frame sampling	Olenin, Daunys 2004; 1980–2003 monitoring data, unpublished
Hard bottom substrate in the aphotic layer of the Baltic Sea	Hard Ap	6–8	8	benthic grab	Olenin, Daunys 2004
Gravel bottoms in the euphotic layer of the Baltic Sea	Grav Eu	6–8	11	benthic grab	Olenin, Daunys 2004
Gravel bottoms in the aphotic layer of the Baltic Sea	Grav Ap	6–8	9	benthic grab	Olenin, Daunys 2004
Sand in the littoral of the Curonian Lagoon	Sand Li LAG	0–3	83	pneumatic grab, core sampler	Razinkovas 1996; Daunys, Olenin 1999; Poškys unpublished
Sand in the littoral of the Baltic Sea	Sand Li	6–8	17	benthic grab, dredge	Olenin 1994
Sand in the sublittoral (euphotic + aphotic layer) the Curonian Lagoon	Sand LAG	0–3	28	benthic grab	1999 survey data, unpublished
Sand in the sublittoral of Klaipeda strait	Sand STRAIT	0–8	24	benthic grab	2002–2004 harbour monitoring data, unpublished
Sand in the euphotic layer in the Baltic Sea	Sand Eu	6–8	13	benthic grab	Olenin, Daunys 2004
Sand in the aphotic layer in the Baltic Sea	Sand Ap	6–8	7	benthic grab	Olenin, Daunys 2004
Zebra mussel shell deposits in the fine sand and muddy (soft bottom) sediments in the sublittoral of the Curonian Lagoon	Zebra Shell LAG	0–3	20	benthic grab	Razinkovas 1996; 1999 survey data, unpublished
Muddy bottoms in sublittoral of Klaipeda strait	Mud STRAIT	0–8	10	benthic grab	2002 – 2004 harbour monitoring data, unpublished
Muddy bottoms in the sublittoral of the Curonian lagoon	Mud LAG	0–3	33	benthic grab	1999 survey data, unpublished; 1980–2003 monitoring data, unpublished
Mixed bottom in the sublittoral of Klaipeda strait	Mixed STRAIT	0–8	56	benthic grab	1980–2003 monitoring data, unpublished

identification of habitats corresponded to the European University Information System (EUNIS 2005) benthic habitat classification approach at a level two.

Total number of benthic samples used for the analysis exceeded 500 (Table 1). 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 1997).

Selection of invasive species

A total of 17 benthic invasive species were selected for the analysis (Table 2). These invasive species are 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. Three benthic crustacean species (*Eriocheir sinensis, Orconectes limosus, Rhithropanopeus harrisii*) were excluded from the analysis since the standard methods used in monitoring routines did not provide reliable quantitative population estimates.

Invasibility assessment of the habitats

The invasibility of a given habitat was defined by two variables: (a) the total number of invasive species (invasive species richness), and (b) structural change in the community as measured by the ‘relative amount of invasive 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 invasive 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). As a measure of the influence of another invasive, also included as a factor in the analysis was the relative biomass of the zebra mussel, *Dreissena polymorpha*, in the Curonian lagoon habitats.

Data analysis

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 in Statgraphics Plus for Windows® (Statistical Graphics Corp. 1996). 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 via a 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 in Primer 5 for Windows® (Plymouth Marine Laboratory, Clarke and Warwick 1994). Only presence/absence was considered in the analysis.

Species richness was related to the environmental variables using redundancy analysis (RDA). In this case, RDA was considered to be more appropriate than CCA (canonical correspondence analysis) since there were many double-zeros values and the most relationships between species and explanatory variables were approximately linear. The analysis performed in Brodgar software (Highland Statistics Ltd.).

The invasive species composition, and invasive species relative biomass distribution in the analyzed habitats was compared using multidimensional scaling (MDS) procedure in Primer software.

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

Table 2 Invasive species distribution, native and invasive species richness in the analyzed habitats

Species	Art-Hard Li STRAIT	Mud STRAIT	Sand STRAIT	MixedSTRAIT	ZebraShell LAG	Mud LAG	Sand Li LAG	Sand LAG	Hard Li	Hard Eu	Hard Ap	Grav Eu	Grav Ap	Sand Li	Sand Eu	Sand Ap
Balanus improvisus			X	X			X		X	X	X	X				
Cordylophora caspia	X		X	X				X								
Chaetogammarus ischnus			X		X		X	X								
Ch. warpachowskyi					X	X	X	X								
Chelicorophium curvispinum				X	X		X		X					X	X	
Dreissena polymorpha	X			X	X	X	X	X								
Gammarus tigrinus		X	X			X										
Hemimysis anomala									X							
Limnomysis benedeni							X									
Lithoglyphus naticoides							X	X								
Marenzelleria cf. viridis		X	X	X	X	X	X	X		X		X	X	X	X	X
Mya arenaria										X					X	
Obessogammarus crassus	X				X		X	X								
Orconectes limosus																
Paramysis lacustris					X		X	X								
Pontogammarus robustoides	X				X		X	X								
Potamopyrgus antipodarum							X									
Invasive species richness	4	2	5	5	8	4	12	9	3	3	1	2	1	2	3	1
Native species richness	9	6	18	27	39	17	18	24	12	26	15	15	8	4	6	10

Results

Distribution of invasives in the selected habitats

For the 17 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 2). The next 4 most successful invasives were *Balanus improvisus, Dreissena polymorpha, Chelicorophium curvispinum* and *Ch. 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.

Patterns of habitat invasibility

Similarity analysis of the invasive 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. 2). 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).

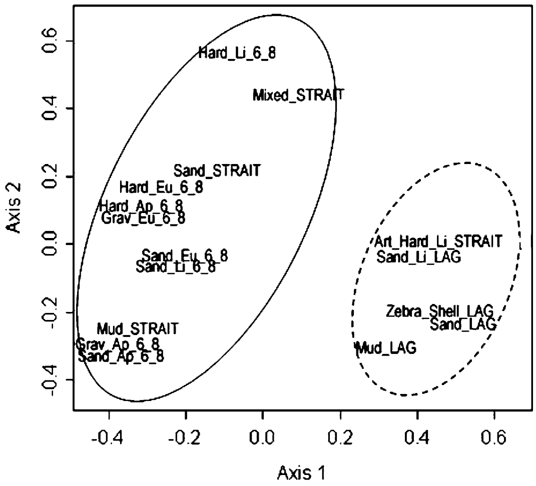

Fig. 2 The ordination plot for similarity analysis of invasive species composition in the selected habitats (sea and strait habitats within the solid line, lagoon habitats including artificial within the dashed line)

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 2). Species richness in the lagoon habitats was significantly higher than in the sea and strait habitats (Kruskal–Wallis test, $P < 0.001$).

Native versus invasive richness

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

The role of physical factors

The redundancy analysis showed that invasive species richness was positively associated with the

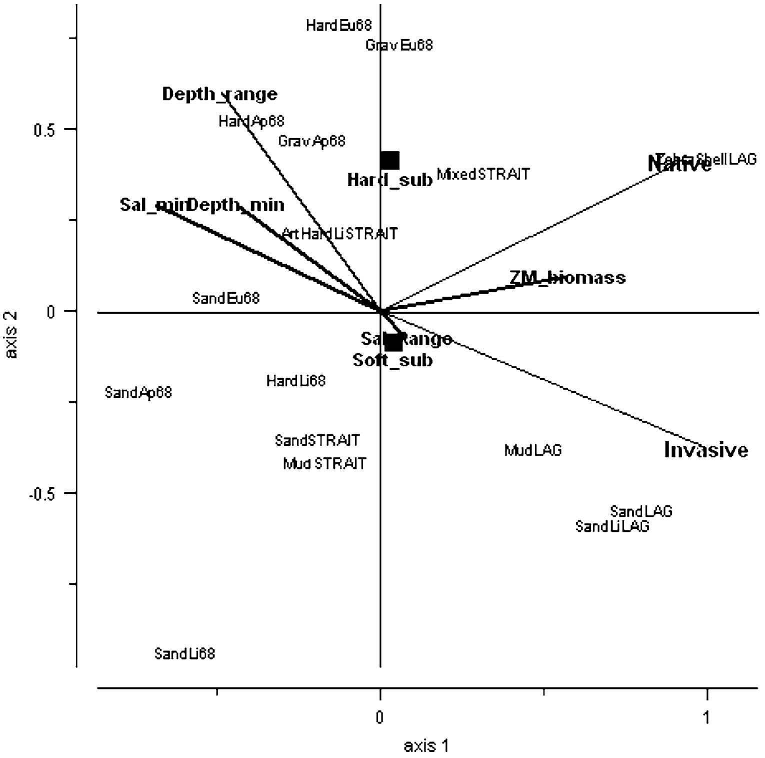

Fig. 3 Triplot obtained by Redundency Analysis. Response variables: native and invasive species richness; explanatory variables: availability of hard and/or soft substrate, salinity minimum, salinity range, depth minimum, depth range, zebra mussel relative biomass in a habitat

soft bottom habitats within the Curonian lagoon, but negatively associated with both salinity and depth factors (Fig. 3). 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 invasive and native species richness, completely defined by the 2-dimentional approximation (62% on axis 1 and 11% on axis 2). The results of a forward selection and permutation tests, presented in Table 3, indicated that native and invasive species richness were significantly related to minimal salinity ($P = 0.004$), salinity range ($P = 0.012$) and availability of hard substrate ($P = 0.015$).

Structural changes in a habitat's community

The highest percentage of invasive 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. 4). Three most successful invasives—*M. neglecta, D. polymorpha* and *B. improvisus* dominated biomass (>50%) in most of invaded habitats. Other species had

Table 3 Conditional effects for the invasive 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

Variable	Cond. effects	Eigenvalue as %	F-statistic	p-value
Minimal salinity	0.31	42.63	6.268	0.004
Salinity range	0.21	0.67	5.538	0.012
Availability of hard substrate	0.14	10.39	4.842	0.015
Depth range	0.03	25.91	0.951	0.404
Minimal depth	0.03	18.16	0.896	0.427
Zebra mussel relative biomass	0.01	29.09	0.444	0.653
Availability of soft substrate	0.00	2.56	0.094	0.916

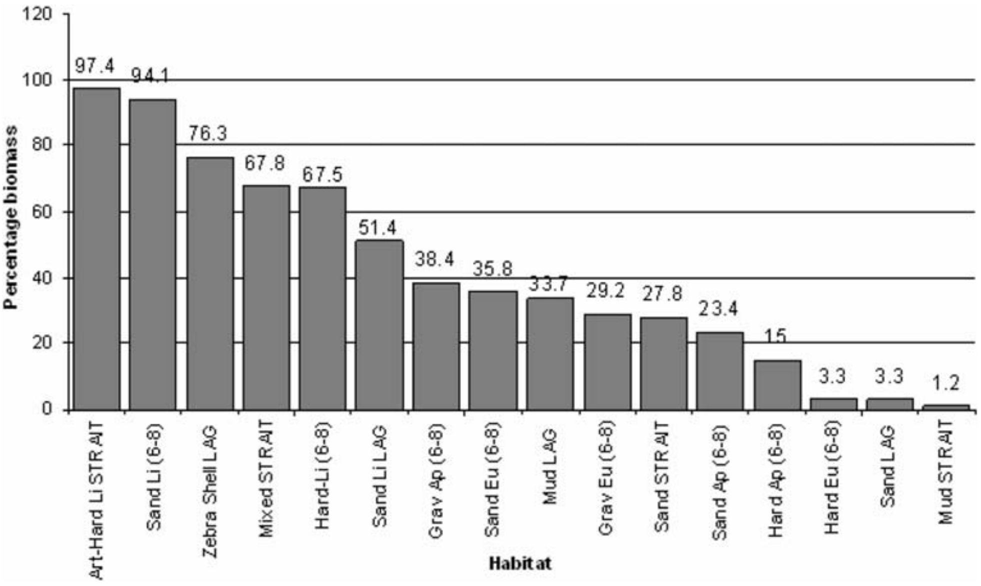

Fig. 4 Percentage of invasive species biomass relative to total biomass

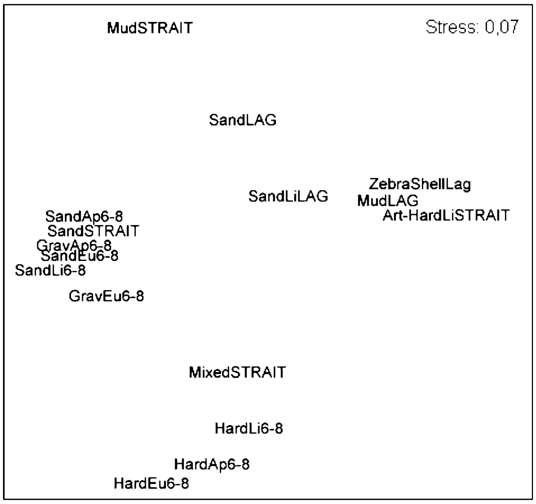

Fig. 5 The Multidimentional Scaling plot based on invasive species relative biomass distribution over the analyzed habitat types

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. 5). 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.

Discussion

There are two 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. 2003).

Recent studies have indicated that spatial scale likely plays an important role in the diversity-invasibility relationship (Stohlgren et al. 2003; 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 invasive species at a relatively small spatial scale but, measured at a regional scale, the relationship between diversity of native and invasive species is more likely to be positive.

A paradox was revealed, however, in our comparatively small scale study. Higher invasive species richness occurred in habitats with higher native species richness. It is hard to conclude unambiguously whether our results disprove the common theory, or whether results were unique to the studied region. Based on our results, we 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 our case. It would be more correct to state that both native and invasive species diversity depends on the ecosystem's physical factors, which may promote invasibility or inhibit it. This assumption is supported by not only our 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 invasive 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 invasives 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 invasives 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. Our 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 substrate which may not be naturally present in this area, so there are almost no competitors for invasive 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 invasive 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 invasive species richness, since there is at least one more determinative feature: the propensity of a habitat to sustain a demographically successful invasives' population (Davis et al. 2000). If a habitat has a small number of invasive 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 invaders are much more successful though. Invasive species may form up to 90% of total community biomass (Fig. 4), 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. 5) and, consequently, the loss of β-diversity. Based on our results, we recommend to use the percentage of invasive species biomass (relative to native species biomass), instead of (or along with) invasive species richness, as an appropriate invasibility measure for habitats with naturally low diversity.

Summarizing the results of our study and the results of an extensive literature analysis (Nilsson 1985; Herbold and Moyle 1986; Vitousek et al. 1997; Brooks 1999; Simberloff and VonHolle 1999; Davis et al. 2000; Ruiz et al. 1999, Nehring 2002; Van der Velde et al. 2002; Ruiz and Hewitt 2002), the generalized 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");

- 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 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).

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