Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonisation and sedimentation processes*

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Abstract

The relative effect of physical disturbance, isolation and key macrozoobenthic species on community development and sedimentation processes were studied in an in situ factorial field mesocosm experiment in the northern Baltic Sea. Differences in abundance and biomass structure of recolonising invertebrates were due to exposure and isolation. The initial invertebrate communities had a negligible effect on the final communities. However, the organic matter content of the sediment in isolated cages increased with the initial number of invertebrate species. The main conclusion of the study: physically driven fluxes override the effects of biological interactions in shallow water systems of the northern Baltic Sea.

The complete text of the paper is available at http://www.iopan.gda.pl/oceanologia/

1. Introduction

Biodiversity is decreasing globally at an unprecedented rate. The causes of this reduction are crucial to any ecosystem processes – see e.g. Vitousek et al. (1997), Loreau (2000), Loreau et al. (2001), Biles et al. (2003), Giller et al. (2004), Solan et al. (2004) and Mermillod-Blondin et al. (2005). These recent studies have focused on resolving the question whether ecosystems with decreasing diversity would be able to continue functioning in a way that is comparable to unaffected systems (Loreau 2000, Loreau et al. 2001, Giller et al. 2004). The majority of experimental studies of the relationships between biodiversity and ecosystem functioning have been carried out in terrestrial ecosystems (e.g. Naeem et al. 1994, Tilman et al. 1997, Hector 1998, Hector et al. 1999, Tilman et al. 2001, Wardle & Zackrisson 2005); only recently has the topic become the central issue in freshwater and marine ecosystems (Duffy et al. 2001, Emmerson et al. 2001, Bolam et al. 2002, Downing & Leibold 2002, Biles et al. 2003, O'Connor & Crowe 2005).

The impact of functions on ecosystem processes appears to be controversial. The extent to which ecosystems are controlled by the type and number of functions in them is not clear (Tilman et al. 1997 and the references therein, Loreau et al. 2001). The presence of certain functional groups appears to have a great impact on ecosystem processes in terrestrial habitats, whereas biological control is often less important in abiotic driven freshwater and marine systems. On smaller spatial scales, however, ecosystem processes may still be affected by biotic controls in abiotic controlled systems (Tilman et al. 1997, Loreau et al. 2001). It has been concluded that there are mutual interactions among biodiversity changes, ecosystem functioning and abiotic factors. In disturbance driven systems it is the colonisation ability of individual species rather than biotic interactions that might be driving ecosystem processes (Loreau et al. 2001).

Current knowledge of the relationships between functions and ecosystem processes tends to be qualitative rather than quantitative (Hector et al. 2001). Experimental studies manipulating key functional species and the abiotic environment are needed to quantify how environmental variability modifies the relationships between communities and ecosystem processes (Loreau et al. 2001).

In the Baltic Sea the number of benthic invertebrate species is low, and often each function is represented by a single species. Thus, the loss of a species may correspond to the loss of ecosystem function. The shallow water ecosystems of the northern Baltic Sea are very dynamic, characterised by substantial physical and biological disturbances (e.g. Hällfors et al. 1981). Wave-induced currents are the prevailing physical disturbance and

eutrophication-induced blooms of macroalgae and their decomposition are ranked among the most severe biological disturbances (Norkko & Bonsdorff 1996a,b, Kotta et al. 1999, Paalme et al. 2002).

In this study the relationships between the key macrozoobenthic species, community development and ecosystem processes were investigated at two levels of exposure and isolation in a shallow water ecosystem of the northern Baltic Sea. The following aspects were tested: (1) whether ecosystem functioning is positively correlated with the initial number of invertebrate species, (2) whether the systems with relatively few functions are less stable and have a higher recolonisation rate than more diverse communities, and (3) whether the physically driven fluxes in more exposed systems override the effects of biological interactions. It is likely that ecologically different species lead to greater resource utilisation, and that declining functional diversity can result in a reduction in positive mutualistic interactions or complementary diversity effects (Emmerson & Raffaelli 2000, Loreau et al. 2001). If this is true, then functionally rich communities are expected to reduce the probability of invasion and/or recolonisation through increased competition for space and food (e.g. Stachowicz et al. 1999). Strong fluctuations in abiotic factors such as the oxygen concentration or wave-induced disturbance are expected to reduce the importance of biotic interactions within communities (Laine et al. 1997, Kotta et al. 1999, Worm et al. 2002), and physical control of ecosystem processes is more commonplace (Flöder & Sommer 1999, Buckling et al. 2000). The objective of this experiment was to clarify the influence of the key functional species on the stability of the simple benthic communities in the northern Baltic Sea in order to understand better the role these processes play in more complex ecosystems.

2. Material and methods

The it in situ factorial field mesocosm experiment was carried out in Kõiguste Bay (58°22.10′N 22°58.69′E), northern Baltic Sea during June–July 2003. The experiment ran for 38 days. The experimental design involved 96 plastic cages (11 cm diameter, 10 cm deep) attached to two floating rafts. One raft was placed in a moderately sheltered part and another in an exposed part of the bay. The rafts were 10 m long and placed 200 m apart, i.e. the distance between rafts was small relative to their dimensions. It is likely that hydrodynamic conditions varied within a raft. Assuming a randomised experimental design, it may be argued that the samples within a raft are not pseudoreplicates, at least in ecological terms.

The following factors were included: exposure (rafts in sheltered and exposed sites), isolation (cages with and without a 0.25 mm mesh screen)

and initial invertebrate communities. The experiment was set up with 3 replicates of each exposure × isolation × community combination, including control treatments of each factor.

The 'isolation' factor involved both physical (i.e. high and low water exchange rate) and biological terms (i.e. high and low recolonisation level). Screening partly reduced the sedimentation rate. Comparison between the control cages showed that screening decreased the organic matter content of the sediment regardless of exposure (two-way ANOVA, $F_{1,8} = 24.956$, $p = 0.001$). On the other hand, screening had no effect on sediment chlorophyll a content (two-way ANOVA, $F_{1,8} = 0.938$, $p = 0.361$). Screening did have an effect on the abundance structure of the recolonising benthic invertebrates (ANOSIM, $r = 0.283$, $p = 0.039$). The screened cages were characterised by lower densities of dominant macroinvertebrate species. There was no significant difference in the biomass structure of the recolonising benthic animals in the control cages because of screening (ANOSIM, $r = 0.128$, $p = 0.11$). The number of recolonising invertebrate species was significantly lower in the screened cages (two-way ANOVA, $F_{1,8} = 10.125$, $p = 0.013$).

The suspension feeder *Cerastoderma glaucum* Bruguière, the deposit feeder *Macoma balthica* L. and the herbivore *Theodoxus fluviatilis* (L.) were deployed in the experiment. These three species were selected because they are the prevalent representatives of the above-mentioned functions in the study area. All possible combinations of *C. glaucum*, *M. balthica* and *T. fluviatilis* and additional controls without animals served as the treatment of the initial invertebrate community.

The cages were 2/3 filled with sand from the nearby seafloor. Before the experiment, the sediment was sieved through a 1 mm mesh and sun-dried for several days to ensure that it was free of living benthic invertebrates. In order to obtain similar starting conditions, the sediment was homogenised before use. The test animals were collected from Kõiguste Bay. Prior to the experiment, shell length was measured to the nearest 0.1 mm with dial callipers. The assembled species had similar biomasses at the beginning of the experiment since the individuals of modal class only were used. The average length of *C. glaucum*, *M. balthica* and *T. fluviatilis* individuals deployed in the experiment were 9.7 mm, 11.0 mm and 5.2 mm, respectively. Two individuals of *C. glaucum* and *M. balthica* and five individuals of *T. fluviatilis* were used per treatment, corresponding to densities of 228 indiv. m^{-2} for *C. glaucum* and *M. balthica* and 570 indiv. m^{-2} for *T. fluviatilis*. The selected densities of benthic invertebrates were similar to those found earlier in Kõiguste Bay (Kotta & Kotta 1997, Kotta et al.

2000, Lauringson & Kotta 2006). The cages were attached to the floating rafts at 0.5 m depth and the rafts were anchored at 2 m depth.

After the incubation period the sediment in the cages was sampled for organic matter and chlorophyll a content with a 20 mm diameter metal tube. Care was taken that only samples devoid of macrofauna were further analysed. Samples for organic matter content were deep-frozen and samples for chlorophyll a were extracted in 96% ethanol overnight. The organic matter content was measured as the percentage loss of ignition (3 h, 500°C). Chlorophyll a was quantified fluorometrically with a correction for phaeopigments (Strickland & Parsons 1972).

The remaining sediment was sieved through 0.25 mm mesh and the residuals were placed in plastic bags. The samples were kept deep-frozen until analysis. In the laboratory all samples were sorted under a binocular microscope (20–40 × magnification). All species were determined to the species level, except for oligochaetes, chironomids and juveniles of gammarid amphipods. Individuals of all taxa were counted and weighed. Prior to weighing, the animals and plants were dried at 60°C for 48 hours and two weeks respectively. The length of each assembled individual was measured to the nearest 0.1 mm.

Three-way ANOVA with exposure level, isolation level and initial invertebrate community as factors was used for describing differences in the growth and mortality of the assembled animals, the total abundance and the biomass of the recolonising species. The effect of exposure, isolation and the initial invertebrate community on the abundance or biomass structure of the invertebrate communities was analysed using the PRIMER statistical program (Clarke & Warwick 2001). Non-metric multidimensional scaling analysis (MDS) of invertebrate abundance or biomass was used to quantify the dissimilarities between the invertebrate communities. The Bray-Curtis similarity measure was used to construct the similarity matrices (Bray & Curtis 1957). The statistical differences in the invertebrate assemblages between the factor levels were obtained using the ANOSIM permutation test. The contribution of different taxa in the differences was calculated by the SIMPER procedure (Clarke 1993).

3. Results

T. fluviatilis had significantly higher growth rates with the highest initial invertebrate diversity as compared to the other invertebrate communities but only in the sheltered site and at low isolation (three-way ANOVA, $F_{3,31} = 3.33$, $p = 0.032$). No significant differences in growth rates were found in *C. glaucum* and *M. balthica*.

No significant differences in the mortality of the three key species were due to the initial invertebrate communities (three-way ANOVA, $p > 0.05$). However, in the sheltered site the mortality of *C. glaucum* (three-way ANOVA, $F_{1,30} = 13.68$, $p < 0.001$) and *T. fluviatilis* (three-way ANOVA, $F_{1,31} = 89.85$, $p < 0.001$) was higher at low isolation, whereas in the exposed site the mortality of *T. fluviatilis* was higher at high isolation (three-way ANOVA, $F_{1,31} = 89.85$, $p < 0.001$). The mortality of *M. balthica* was higher at high isolation regardless of exposure level (three-way ANOVA, $F_{1,30} = 4.71$, $p = 0.038$).

The mesocosms were colonised by a limited number of species. The most frequent taxa were *Cerastoderma glaucum*, Chironomidae larvae, *Gammarus* juv., *Corophium volutator* and *Hediste diversicolor*. These taxa were also the dominant macroinvertebrates in the study area.

The initial invertebrate communities had no effect on the abundance and biomass structure of the recolonising macrofauna (ANOSIM, $p > 0.05$), but the levels of exposure (ANOSIM, $r = 0.504$, $p = 0.001$) and isolation (ANOSIM, $r = 0.112$, $p = 0.001$) did significantly affect the abundance structure of the recolonising macrofauna (Fig. 1). The total abundance of recolonising invertebrates was significantly higher at low isolation than at high isolation (three-way ANOVA, $F_{1,62} = 5.6706$, $p = 0.020$). The total number of recolonising animal species was significantly higher in the sheltered site at low isolation, whereas there were no differences due to exposure at high isolation (three-way ANOVA, $F_{1,62} = 11.62$, $p = 0.001$). Differences in abundance structure due to exposure were related to the higher abundance of *Cerastoderma glaucum* and Chironomidae larvae in the exposed site and the higher abundance of *Gammarus* juv. in the sheltered site (SIMPER). The abundance of *Cerastoderma glaucum*, Chironomidae larvae and *Gammarus* juv. was higher at low than at high isolation (SIMPER).

The levels of exposure (ANOSIM, $r = 0.333$, $p = 0.001$) and isolation (ANOSIM, $r = 0.119$, $p = 0.001$) significantly affected the biomass structure of the recolonising benthic animals (Fig. 2). At low isolation the total invertebrate biomass was higher in the sheltered site than in the exposed site, whereas at high isolation the biomass was higher in the exposed site than in the sheltered site (three-way ANOVA, $F_{1,62} = 15.810$, $p < 0.001$). Differences in biomass structure due to exposure were related to the higher biomass of *Saduria entomon* (L.) in the exposed site and the higher biomass of *Cerastoderma glaucum* and *Hydrobia ulvae* (Pennant) in the sheltered site (SIMPER). The biomass of *Cerastoderma glaucum* increased (SIMPER) with decreasing level of isolation.
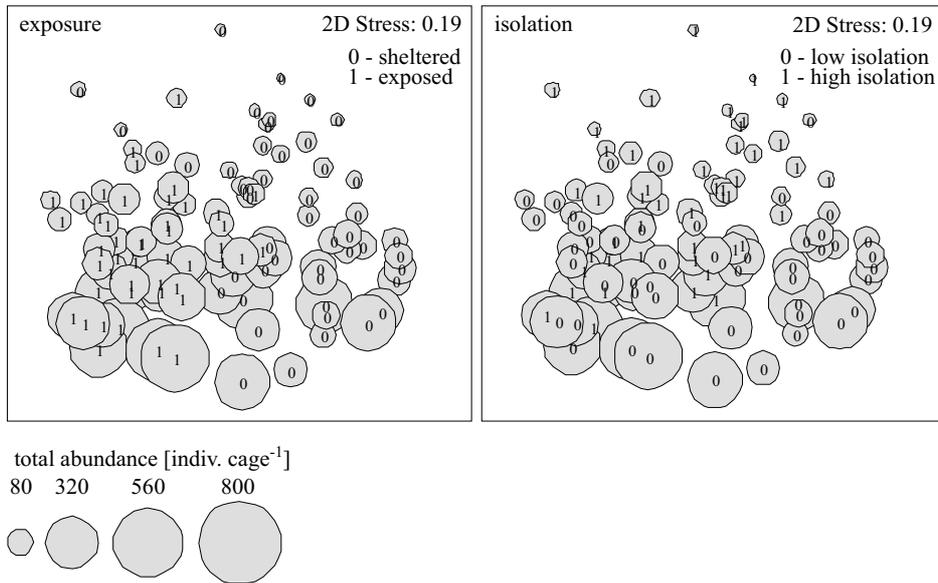
Fig. 1. nMDS ordination of abundance structure of recolonised macroinvertebrates. The number shows the factor level, and the relative size of the bubbles indicates the total abundance of recolonised macroinvertebrates in a cage
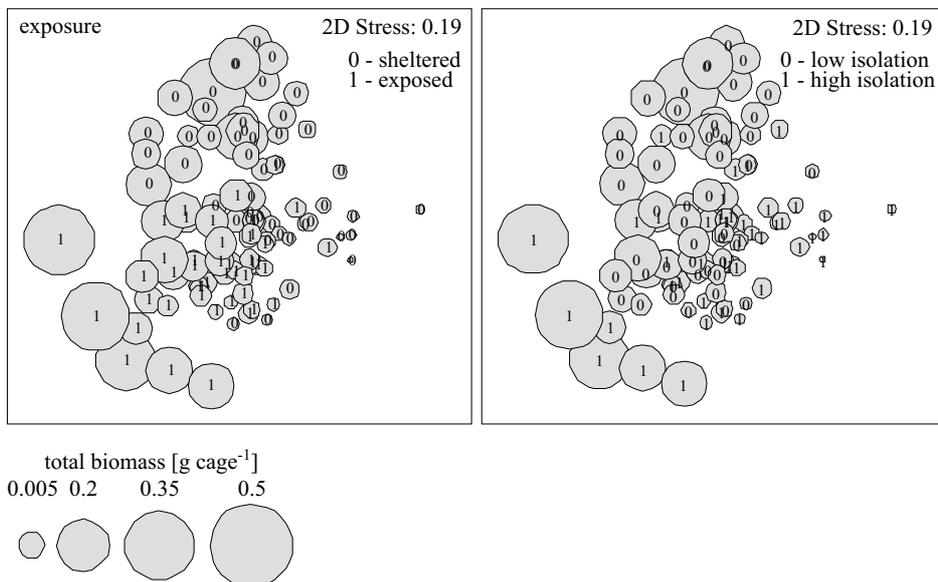

Fig. 2. nMDS ordination of biomass structure of recolonised macroinvertebrates. The number shows the factor level, and the relative size of the bubbles indicates the total biomass of recolonised macroinvertebrates in a cage

The level of isolation had a significant effect on the biomass structure of the macrophytes (ANOSIM, $r = 0.077$, $p = 0.003$). No significant differences in the macrophyte community structure were due to exposure or the initial invertebrate communities. At high isolation the total biomass of macrophytes was significantly higher in the exposed site than in the sheltered site, whereas at low isolation the biomass was higher in the sheltered site than in the exposed site (three-way ANOVA, $F_{1,62} = 38.267$, $p < 0.001$). At high isolation the number of macrophyte species was significantly higher in the exposed site than in the sheltered site, whereas at low isolation, exposure had no effect on the number of macrophyte species (three-way ANOVA, $F_{1,62} = 17.518$, $p < 0.001$). The biomass of annual filamentous algae and Cyanophyta was higher at low than at high isolation (SIMPER).

In the control treatments (no added animals) the content of organic matter in sediment was significantly higher without mesh than with mesh. However, in the other treatments (involving the key invertebrate species), screening did not reduce the sedimentation of organic matter (three-way ANOVA, $F_{7,62} = 2.970$, $p = 0.009$). The organic matter content significantly increased with the number of invertebrate species in cages covered by mesh (i.e. high isolation), whereas such a relationship was not found for cages without mesh (i.e. low isolation) (three-way ANOVA, $F_{3,78} = 4.910$, $p = 0.004$, Fig. 3).

The content of sediment chlorophyll a was significantly higher in the exposed site than in the sheltered site (three-way ANOVA, $F_{1,62} = 14.821$, $p < 0.001$) and at high isolation (with mesh) than at low isolation (without mesh) (three-way ANOVA, $F_{1,62} = 4.0426$, $p = 0.049$). No significant differences in the content of chlorophyll a were due to the initial invertebrate communities. However, the content of chlorophyll a did correlate positively with the number of recolonising animal species at low isolation (linear regression analysis, $r = 0.32$, $p < 0.05$).

During this experiment *Gammarus tigrinus* Sexton was found for the first time in the northern Baltic Sea. The species was only found in the sheltered site. Significant differences in the abundance (ANOSIM, $r = 0.274$, $p = 0.001$) and biomass structure (ANOSIM, $r = 0.415$, $p = 0.001$) of the recolonising macrofauna were found between treatments with and without *G. tigrinus*. The cages with *G. tigrinus* were characterised by a lower abundance of *Cerastoderma glaucum* and Chironomidae larvae, and a higher abundance of juvenile gammarid amphipods (SIMPER). Differences in biomass structure were related to the higher biomass of *Cerastoderma glaucum* and *Hydrobia ulvae* in the cages with *G. tigrinus* than in the cages without the nonindigenous species. Both the number
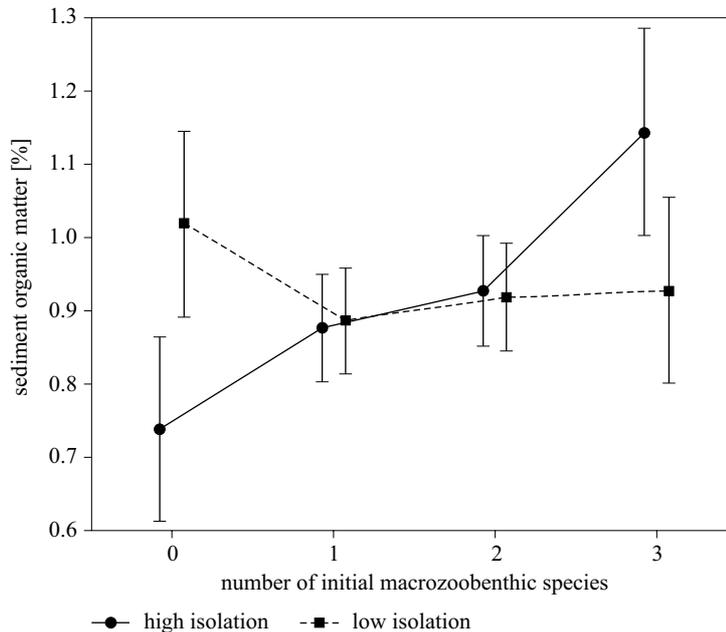
Fig. 3. Effects of isolation level and number of initial macrozoobenthic species on the sediment organic matter content in cages. Vertical lines indicate 95% confidence intervals

of recolonising macrozoobenthic species (one-way ANOVA, $F_{1,92} = 16.856$, $p < 0.001$) and the number of feeding guilds these species represented (one-way ANOVA, $F_{1,92} = 4.697$, $p = 0.033$) were significantly higher in the presence of *G. tigrinus*.

4. Discussion

Physical disturbance overrode the effect of biotic interactions in terms of community development in the northern Baltic Sea. No effect was observed of the initial invertebrate communities on the mortality of the assembled animals, the abundance and biomass structure of the recolonised communities, or the chlorophyll *a* content in the sediment. The number of recolonising macrofauna significantly decreased with rising exposure. This is in accordance with earlier observations that exposed areas with high sediment mobility are known to be an inhospitable habitat for biota as compared to sheltered areas hosting diverse benthic invertebrate communities (Gray 2002).

Relationships between the number of functions and processes tend to be weak in species-poor ecosystems such as the northern Baltic Sea. Many species-poor ecosystems are dominated by resource generalists, and the

addition of new species may add no new function (Parker et al. 2001). Both *M. balthica* and *C. glaucum* can potentially switch between suspension and deposit feeding modes (Brafield & Newell 1961, Ólafsson 1986, Hawkins et al. 1990, Kang et al. 1999, Herman et al. 2000, personal observations of the authors of this study), which may partly explain the paucity of biotic interactions in this study.

All initially seeded macrozoobenthic species increased the organic content of the sediment, and the combination of all the species studied resulted in a higher organic matter content than in treatments with just one or two initial species. However, this pattern only appeared in treatments with a high level of isolation (screened cages): the screening of cages may reduce wave-induced water movement (i.e. physical disturbance) in the cages and therefore enhance the importance of biotic factors in ecosystem functioning. The chlorophyll *a* content in the sediment was also related to biodiversity, as chlorophyll *a* correlated positively with the number of recolonising macrozoobenthic species in the cages at the low isolation level.

The elevated content of organic matter/chlorophyll *a* due to the higher number of key invertebrate species may result from the complementary effect of functional diversity or positive mutualistic interactions between guilds, since ecologically different species lead to greater resource utilisation (Emmerson & Raffaelli 2000). Alternatively, increasing functional richness has been found to increase nutrient release from the marine soft sediments (Biles et al. 2003), leading to higher local primary production (Heip et al. 1995). Besides, changes in diversity at one trophic level may generate important feedback at others (Worm et al. 2000, Emmerson et al. 2001, Hector et al. 2001), e.g. the increase in the organic matter content of the sediment through the biodeposition of suspension feeders would increase the biomass of microalgae, deposit feeders and microherbivores (Kotta 2000, Rossi & Underwood 2002).

Physical disturbance due to the sedimentation of macroalgal debris at the end of the experiment may partly explain why strong biotic control of the ecosystem processes in the study area was not detected. The eutrophication-induced proliferation of annual filamentous algae and the formation of drifting algal mats have increased the organic matter content of the sediment and the occurrence of short-term hypoxia practically throughout the coastal range of the Baltic Sea (Kiirikki & Blomster 1996, Norkko & Bonsdorff 1996a,b, Bäck et al. 2000, Vahteri et al. 2000, Lehvo & Bäck 2001, Paalme et al. 2004). No clear indication of hypoxia was found in the present treatments, because the mortality of benthic invertebrates was low and not significantly higher in the screened cages, as would be expected from their lower water exchange. However, owing to high sedimentation rates, the

sediment was relatively rich in organic material, and no food limitation occurred in the cages.

The initial invertebrate diversity of the assembled communities did not affect the subsequent recolonisation of mesocosms, indicating that the colonisation is driven mainly by physical factors.

During this experiment *G. tigrinus* was found for the first time in the northern Baltic Sea. The number of recolonising macrozoobenthic species and feeding guilds was significantly higher in the cages with *G. tigrinus* than those without this invasive amphipod. With its high number of functions, the benthic community seems to provide more resources for newcomers, whose food and habitat choices probably differ from those of native species. Following physical disturbance, dominant/opportunistic species recolonise the sediment quickly, whereas rare species do not (Kenny & Rees 1996). Similarly, in our experiment the cages were colonised mainly by species dominating in the adjacent sea area. In that respect, an opportunistic species like *G. tigrinus* has an advantage over many native species, since it is highly mobile, tolerates wide ranges of environmental conditions and has high rates of reproduction (Dorgelo 1977, MacNeil & Prenter 2000, Wijnhoven et al. 2003).

It has been suggested that the resistance of a community to biological invasions is related to its diversity (Stachowicz et al. 1999, Levine & D'Antonio 1999). The complexity of ecosystems may both stabilise communities on a local scale (by dampening oscillations), and increase landscape-scale diversity (by promoting variability in time and space). Reduced diversity may destabilise ecosystem functioning by rendering these communities more vulnerable to invasion (Stachowicz et al. 1999). Hence, a low species diversity, together with the extensive anthropogenic impact in the Baltic Sea (Rosenberg 1985, Bonsdorff et al. 1997), may make the region susceptible to invasion (Stachowicz et al. 1999). However, the opposite relationship between community diversity and the occurrence of invasive species has also been demonstrated (Kaufman 1992, Lodge 1993, Cohen & Carlton 1998, Levine & D'Antonio 1999). In the present study, too, a significant positive correlation was found between the number of macrozoobenthic species and the abundance of *G. tigrinus* in the mesocosms. It may be that the communities of the Baltic Sea are not saturated in complete post-glacial recolonisation. To date, about one hundred non-native species have been reported in the Baltic Sea. Increasing invasion rates in the past decades (Leppäkoski & Olenin 2001) suggest that the invasional meltdown model, in which a group of nonindigenous species facilitate one another's invasion (Simberloff & Von Holle 1999), may be a more likely model for the Baltic Sea.

The loss or addition of species and function is expected to reduce the performance of an ecosystem and alter the fluxes of energy and matter (e.g. Loreau at al. 2001, Solan et al. 2004). This study has indicated that the physical factors controlling the ecosystem processes and biotic interactions are weak in the shallow water habitat of the northern Baltic Sea. In a fluctuating environment, the physically driven fluxes are likely to override the effects of biological interactions when the relative importance of feeding functions and interactions between functions and processes are highly variable. However, while the loss or addition of any one feeding guild may have little impact on a particular ecosystem process, the presence of such a feeding guild may have a great impact on others, not involved in this study (Tilman et al. 1997). The present experiment lasted for only 38 days, and it is possible that the role of biotic interactions may become more important on longer time scales.

Acknowledgements

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