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**Invasion history of the amphipods *Orchestia
cavimana* and *Gammarus tigrinus* in the
Estonian coastal sea**

MSc thesis

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1. INTRODUCTION

The dispersal of species, which may be either natural or human mediated, has an impact on local ecosystems (e.g. Parker et al. 1999; Carlton 2002; Streftaris et al. 2005). As increasing globalization is removing the physical barriers between regions, introduction of nonindigenous species has become one of the most serious threats to the biological diversity and have caused comparably big economical damage (Carlton and Geller 1993; Carlton 1999; Weidema 2000; Leppäkoski et al. 2002a). A nonindigenous (also known as alien, exotic, introduced, invasive, non-native) species is any species intentionally or accidentally transported and released by man into an environment outside its native geographical range of habitat (Gollasch and Leppäkoski 1999; IUCN 2000). New species entering ecosystems may dramatically change the species diversity, trophic structure, structure and dynamics of populations, nutrients availability and flow, and primary production of the local ecosystem (Carlton 1996). Successful invasive species may render previously stable systems unbalanced and unpredictable (Carlton and Geller 1993; Carlton 1996; Ruiz et al. 1999).

The Baltic Sea is a young, and in historical perspective, environmentally unstable sea. After the latest glaciation, freshwater periods alternated with conditions slightly more marine than what is prevailing today. Owing to short developing time, unstable environmental conditions and low salinity, only a limited number of species have been able to adapt to the local conditions. The communities are characterized by a mixture of marine and freshwater species. Specific brackish-water or endemic forms are nearly absent (Hällfors et al. 1981). In the species poor Baltic Sea ecosystem each function is often represented by a single species. Thus, a loss or addition of a species may correspond to a loss or addition of ecosystem function.

Due to the unstable environment, low number of species and intense anthropogenic impact, the Baltic Sea may be regarded as highly susceptible to biological invasions (Levine and D'Antonio 1999; Stachovicz et al. 1999; Leppäkoski and Olenin 2001). The Baltic has a long history of human mediated invasions. The bivalve *Mya arenaria* probably appeared already in the 12-13th centuries in Danish waters. Since the early 1800s, more than 100 nonindigenous species 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 (Leppäkoski et al. 2002b; Baltic Sea Alien Species Database, <http://www.ku.lt/nemo/index.html>). In recent decades the number of nonindigenous species has exponentially risen and the ranges of existing exotics have expanded in the Baltic Sea area (Gruszka, 1999; Leppäkoski and Olenin 2001; Kotta et al. 2006). The amphipods *Gammarus tigrinus* Sexton and *Chelicorophium curvispinum* Sars are among the most recent newcomers in the Northern Baltic Sea (Kotta et al. 2006).

The talitrid amphipod *Orchestia cavimana* Heller is a semi-terrestrial species found in moist habitats under stones or amongst damp vegetation, usually close to fresh or brackish water. The species has a relatively wide distribution area including Mediterranean, Black Sea, Red Sea, Atlantic coast of North Africa and of Europe up to the southern North Sea (Lincoln 1979). In the Baltic Sea the species has been previously found only in a few southern coastal sites in Poland and Germany (Żmudziński 1974; Järvekülg 1979). In the northern Baltic Sea *Orchestia cavimana* was found for the first time on the coast of northern Saaremaa Island in 1999 (Kotta 2000). During next three years the species considerably expanded its range.

North-American *Gammarus tigrinus* Sexton was introduced to Europe probably in ballast water and was first recorded in England in 1931 (Chambers 1977). In the Baltic Sea *G. tigrinus* was found already in 1975 (Bulnheim 1976), but the significant range expansion started in the 1990s (Jazdzewski et al. 2002; Szaniawska et al. 2003). In the Estonian coastal sea *G. tigrinus* was first found in Kõiguste Bay, northern Gulf of Riga in 2003. The invasion of *G. tigrinus* was extremely rapid and during two years the species became established and even dominant gammarid, in many locations throughout the northern Gulf of Riga. Concurrent with the invasion of *G. tigrinus* both the density and diversity of native gammarids have declined.

The aims of the master thesis are (1) to follow the establishment and range expansions of *O. cavimana* and *G. tigrinus* in relation to environmental conditions in the northern Baltic Sea and (2) to clarify the interactions between *G. tigrinus* and the native gammarid amphipods.

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2. MATERIALS AND METHODS

2.1. *Orchestia cavimana*

Wrack fauna was sampled annually at 79 sites of the Estonian coastal sea during the last week of September or the first week of October 1998, 1999, 2002 and 2004 (Fig. 1). One sample was taken in each station except for a site in the northern Saaremaa Island (first location of *O. cavimana* in Estonia) where three replicate samples were taken annually in 1998–2004. Sites were selected to cover maximum salinity range, different sediment and wrack types. Shores, which were overgrown with reeds, were excluded. At every site exposure (an estimate how much a site is exposed to open sea in degrees), steepness of coastal slope (a distance between shoreline and 5 m depth isoline), number, width and height of wrack belts, total coverage of wrack within a belt, dominant plant species, level of decomposition and humidity, type and granulometry of sediment particles were estimated. The sites were classified as dry, moist and wet. Where talitrid amphipods were found a biomass sample was taken using 20 × 20 cm metal frame. The material inside the frame was quickly removed and packed into a plastic bag. Samples were kept deep-frozen until analyzing in the laboratory.

Talitrid amphipods were picked up from the sample under a stereomicroscope. Animals were counted and divided into the following groups: adult males, adult females and juveniles (according to Lincoln 1979). The length of all individuals was measured to the nearest 0.1 mm. Dry weight of individuals was measured to the nearest 0.1 mg after drying at 60 °C for 48 h. Plants were separated by species and dry weight (60 °C, 336 h) of each species was measured. For each plant species the level of decomposition was estimated on three-stage scale: fresh, semi-decayed and highly decayed.

For univariate analyses the statistical programme "Statistica" was used (StatSoft, Inc. 2004). Multivariate data analyses were performed using the package "PRIMER" (Clarke and Warwick 2001). See Appendix I for more details.

2.2. *Gammarus tigrinus*

2.2.1. Field sampling

Benthos samples were collected from 23 stations in Kõiguste Bay, northern Gulf of Riga, in spring, summer and autumn 2003–2005. Additionally, the benthos samples were collected from about 200 stations in the bays of northern Gulf of Riga in summer 2005 (Fig. 4). The prevailing sediment types were sand and clay mixed with pebbles, gravel or boulders. The depths of the stations were between 0.5 and 10 m. An Ekman type bottom grab (0.02 m²) was used for the sampling of benthic invertebrates. Sediment samples were washed through a 0.25 mm mesh and residuals were stored in a deep freezer at –20 °C. Sorting, counting and determination of biomass of invertebrate (dry weight g m⁻², 60°C at 48h) and plant (dry weight g m⁻², 60°C at 336 h) species were performed in the laboratory using a stereomicroscope. In autumn the majority of gammarids can be determined to the species level whereas in other seasons juvenile gammarids prevail making the species determination difficult. Thus, in order to avoid the taxonomic uncertainties the multivariate statistics (ANOSIM and SIMPER) involved only autumn samples.

2.2.2. Experiments

Mesocosm experiment

An *in situ* factorial field mesocosm experiment was carried out in Kõiguste Bay, northern Gulf of Riga during June–July 2003. In the experiment the relative effect of physical disturbance, isolation and macrofaunal feeding guild diversity on community development and sedimentation processes were studied. Experimental design included 96 sand-filled plastic cages attached to two floating rafts. The following factors were included: exposure (rafts in sheltered and exposed site; distance between rafts was 200 m), isolation (cages with and without 0.25 mm mesh screen) and initial feeding guild diversity. The suspension feeder *Cerastoderma glaucum* Bruguière, the deposit feeder *Macoma balthica* L. and the herbivore *Theodoxus fluviatilis* (L.) were deployed in the experiment. After the incubation period the sediment in the cages were sampled for the content of organic matter, chlorophyll *a*, macrophytobenthos and macrozoobenthos. During the early stages of the experiment we observed the presence of *G. tigrinus* in many mesocosms. This observation

corresponded to the first finding of *G. tigrinus* in the Estonian coastal sea. Consequently, in parallel with our initial hypothesis we estimated whether the effect of exposure, isolation and the initial feeding guild diversity had an effect on the invasion success of *G. tigrinus*. See Appendix II for details.

Physical disturbance experiment

In 2005 an in situ experiment was performed in Kõiguste Bay to study the effects of physical disturbance (mimicking ice scraping or dredging activity) and timing of disturbance on the development of benthic communities including gammarid amphipods. The experiment was carried out in shallow water (1 m) area where the bottom sediment was characterized by a layer of sand mixed with few pebbles on hard clay. The physical disturbance was effected as a removal of the upper sediment layer (ca. 3 cm) including vegetation and animals. Sediment was removed from 1 × 1 m quadrates with sharp-edged handnet. The quadrates were marked with numbered stones. Excavated material was discarded at a distance of at least 25 m shoreward from the experimental area. This disturbance was performed three times: in May, July and September. In concurrent with the removal of sediment both disturbed and undisturbed quadrats were sampled in triplicate. The sampling was done immediately after the removal of sediments and also in July and September for those quadrats established in May and in September for those quadrats established in July. Within each quadrat one sample was taken. Ekman type bottom grab (0.02 m²) was used for sampling. Further treatment of samples was the same as described in *Field sampling*.

Habitat choice and grazing experiments

Habitat choice and grazing experiments were performed in Kõiguste Bay in May, July and September 2005. Depending on the natural occurrence of the macrophytes in the field different species were deployed in the experiment. Nine different macrophyte species and/or forms were used: the brown algae *F. vesiculosus* L. and *Pylaiella littoralis* (L.) Kjellm., the red alga *Ceramium tenuicorne* (Kütz.) Waern and *Furcellaria lumbricalis* (Huds.), the green algae *Cladophora glomerata* (L.) Kütz. and *Enteromorpha intestinalis* (L.) Nees. and the higher plant *Myriophyllum spicatum* L. Besides the typical *F. vesiculosus*, the dwarf form, nowadays recognized as *F. radicans* sp. nov. (Bergström et al.

2005), and both attached and free-floating forms of *F. lumbricalis* were deployed. *Gammarus* spp. were collected from shallow water either under the stones by means of handnet or within the stands of *F. vesiculosus* by shaking the algae. Only adult specimens were used in the experiment.

Grazing was studied in $5 \times 5 \times 20$ cm nylon netbags of 1 mm mesh size. Each macroalgal treatment was added either six specimens of *G. tigrinus*, six specimens of native *Gammarus* spp. or three specimens of *G. tigrinus* and native *Gammarus* spp. Three replicates of each treatment were used. Additionally, three control netbags contained algae relevant to each algal treatment and no amphipods. The wet weight of algae was determined prior to the experiment to the nearest of 0.01 g. Before weighing the algae were gently dried on plotting paper until the paper did not become wet any more. Additional three replicates of each macroalgal treatment served as control to obtain the ratio of wet to dry weight. The algae were dried at 60 °C during 48 h. On average 0.2 g dw of algae was deployed in each netbag. The netbags were placed at 2 m depth about 0.5 m above the bottom. Each series of the experiment lasted 15–20 days. At the end of the experiment the test animals were counted and the dry weights of macroalgae were determined. The changes in the dry weight of algae per individual of invertebrates in the nylon mesocosms served as the estimates of invertebrate grazing in the field. These values were corrected to the weight increment due to the photosynthetic activity of the algae i.e. control values.

The habitat choice of *Gammarus* spp. was studied in 3 replicate 100 l aquaria with a light regime similar to the field conditions. The aquaria received running seawater at a flow rate of 3 l h^{-1} . The water was taken from 2 m depth nearby Kõiguste Marine Biological Laboratory. Each aquarium were added available macrophyte in field and either ten native gammarids, ten *G. tigrinus* or the mixture of five specimens of native gammarids and five specimens of *G. tigrinus*. The algae were attached to the aquarium floor by pebbles. Additionally a few pebbles without macroalgae were added. The coverage of algae, pebbles and the area without vegetation in the aquaria was 20%, 10% and 70%, respectively. The number of *Gammarus* spp. on different macroalgae, under pebbles and those swimming freely were recorded every hour for 30 h. The survival of *Gammarus* spp. in the habitat choice experiment was 100%. More details on grazing and habitat choice experiments are available in Appendix III.

3. RESULTS

3.1. *Orchestia cavimana*

Despite of intensive field sampling in 1998 the talitrid amphipods were not found within the wrack fauna. *Orchestia cavimana* was found for the first time on the coast of northern Saaremaa Island in 1999 (Fig. 1). *O. cavimana* inhabited damp wrack cast up on shore. The species was restricted within 200 m shore area. The average abundance and biomass were 22,400 ind m⁻² and 14 g dw m⁻², respectively. In 2000 the species expanded its range to a few kilometres but the average abundance and biomass decreased down to 2,433 ind m⁻² and 2 g dw m⁻², respectively.

In 2002 *O. cavimana* was found in nine areas (Fig. 1.). In 2004 the distribution of *O. cavimana* had remained the same as in 2002. However, the abundance of the species had decreased considerably in the majority of stations. Only three locations had sufficiently high abundances for capturing animals into the sampling frame.

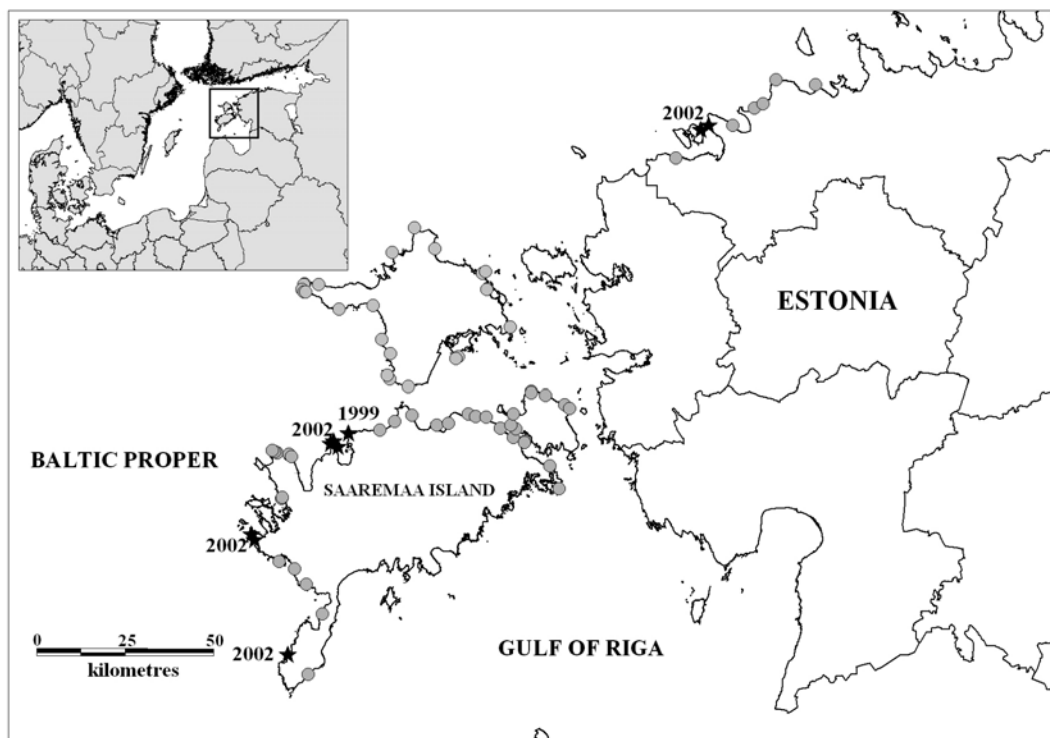


Fig. 1. Study area. Filled circles indicate the sampling sites of talitrid amphipods and stars the locations where *O. cavimana* were found. Years show the time of first record of *O. cavimana* in a site.

O. cavimana inhabited very exposed shores except for a partly sheltered site on the western coast of Saaremaa Island. However, there was no statistically significant difference in exposure between the sites with and without *O. cavimana*. Similarly, there were no statistical differences in the sediment characteristics regardless of the presence of *O. cavimana*. In the presence of *O. cavimana* the wrack coverage varied between 40–100 % with an average at 73 % and the wrack biomass varied between 1224–4924 g dw m⁻² with an average at 2712 g dw m⁻². In the absence of *O. cavimana* the average coverage and biomass were lower, 54 % and 1820 g dw m⁻², respectively. *F. vesiculosus* prevailed in the wrack in seven areas and *Polysiphonia fucoides* (Huds.) Grev. in the other two areas. *Pilayella littoralis* (L.), *Zostera marina* and *Ruppia maritima* L. were the second dominant plant species within the wrack.

The biomasses and abundances of *O. cavimana* ranged between 0.6–29.0 g dw m⁻² and 50–6275 ind m⁻², respectively. The average biomass was 9.1 g dw m⁻² and the average abundance was 1975 ind m⁻². The amphipod length varied between 3–20 mm with an average at 9.9 mm. The 9–10 mm size class formed nearly 40 % of the population density and biomass. The amphipod dry weight varied between 0.0001–0.0201 g with an average at 0.005 g. Males had significantly greater average length than females (11.4 vs 10.4 mm, one-way ANOVA, $p < 0.001$). The differences in the weights were not statistically significant (one-way ANOVA, $p = 0.22$). The average sex ratio was female-biased (1:0.83, chi-square test, $p < 0.05$).

BIOENV analysis suggested that wrack biomass, humidity and interaction between wrack biomass and exposure were the best predictor of the abundances of *O. cavimana* whereas wrack biomass and interaction between wrack biomass and exposure explained the variability in biomasses. The size structure of the population of *O. cavimana* was mostly related to humidity and wrack biomass (Table 1).

Table 1. The combination of the best environmental variables that predicts abundance, biomass and biomass size structure of *O. cavimana* in the study area.

Similarity matrix	Significant environmental variables	Spearman ρ
Abundance	humidity of wrack wrack biomass wrack biomass \times exposure	0.676
Biomass	wrack biomass wrack biomass \times exposure	0.600
Abundance size structure	humidity of wrack wrack biomass	0.623
Biomass size structure	humidity of wrack wrack biomass	0.609

The biomass of *O. cavimana* increased with the wrack biomass (Fig. 2). However, there was no significant relationship between the biomass of wrack and the abundance of *O. cavimana*. The abundance of *O. cavimana* correlated positively with the biomass of higher plants in the wrack (linear regression analysis, $r^2 = 0.52$, $p < 0.05$). The variability in juvenile dry weight correlated with average size of sediment particles (linear regression analysis, $r^2 = 0.83$, $p < 0.05$). The humidity of wrack was significantly related to the abundance of *O. cavimana*. The amphipod abundances were highest in moist, intermediate in wet and lowest in dry wrack, respectively. However, only dry and moist wrack were significantly different in terms of amphipod abundances (233 vs 4000 ind m⁻², ANOSIM, $p = 0.042$).

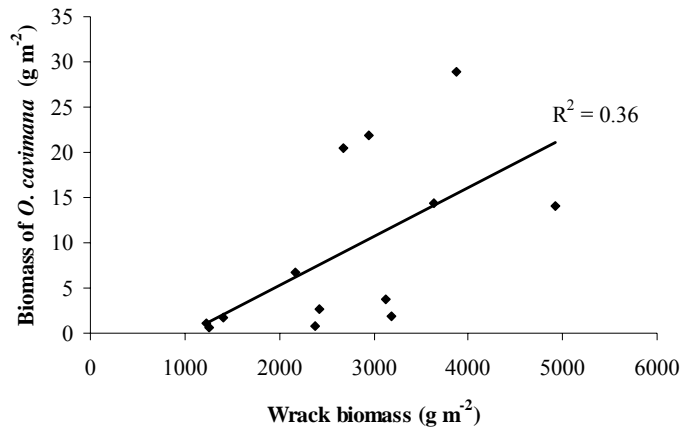


Fig. 2. Relationship between the biomass of wrack and the amphipod *O. cavimana* in the study area.

In the station of the first record of *O. cavimana* (northern coast of Saaremaa Island) the highest abundance and biomass of the talitrids were found in 1999. In the following years the abundance and biomass have stabilized on remarkably lower levels with a slight increase in 2004 (Fig. 3).

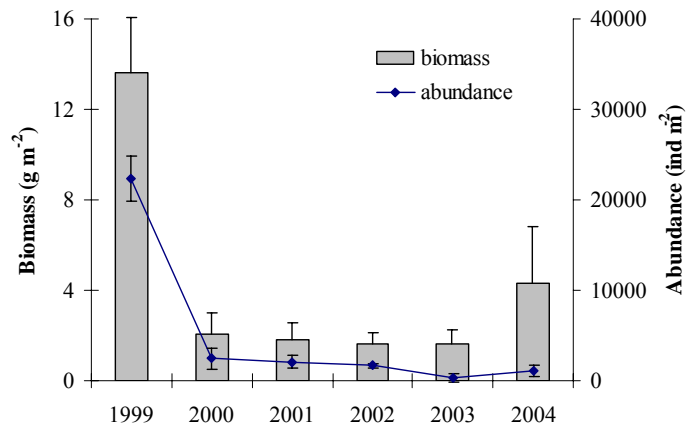


Fig. 3. Interannual variation in the abundance and biomass of *O. cavimana* (\pm S.E.) at the station of the first record of the species (northern coast of Saaremaa Island).

3.2. *Gammarus tigrinus*

3.2.1. Field sampling

In 2003 *G. tigrinus* was found in several experimental mesocosms in Kõiguste Bay but the species was not observed in regular monitoring stations in Kõiguste Bay. Since 2004 *G. tigrinus* was common all over the Kõiguste Bay area. The species occupied the same areas as compared to the native gammarid species, though, being more abundant in less exposed areas. The average abundance of *G. tigrinus* in the inner bay was 162 and in the outer bay 8 ind. m⁻². The maximum density and biomass in the inner bay reached 4700 ind m⁻² and 12.22 g m⁻², respectively. The share of *G. tigrinus* usually reached to 25% in total gammarid abundances, with maximum values above 75% in the inner part of Kõiguste Bay. The invasive species had higher abundances in autumn than in spring and summer.

In 2005 the alien amphipod was found all over the northern Gulf of Riga – throughout the southern coast of Saaremaa Island and in Rame Bay, western mainland (Fig. 4).

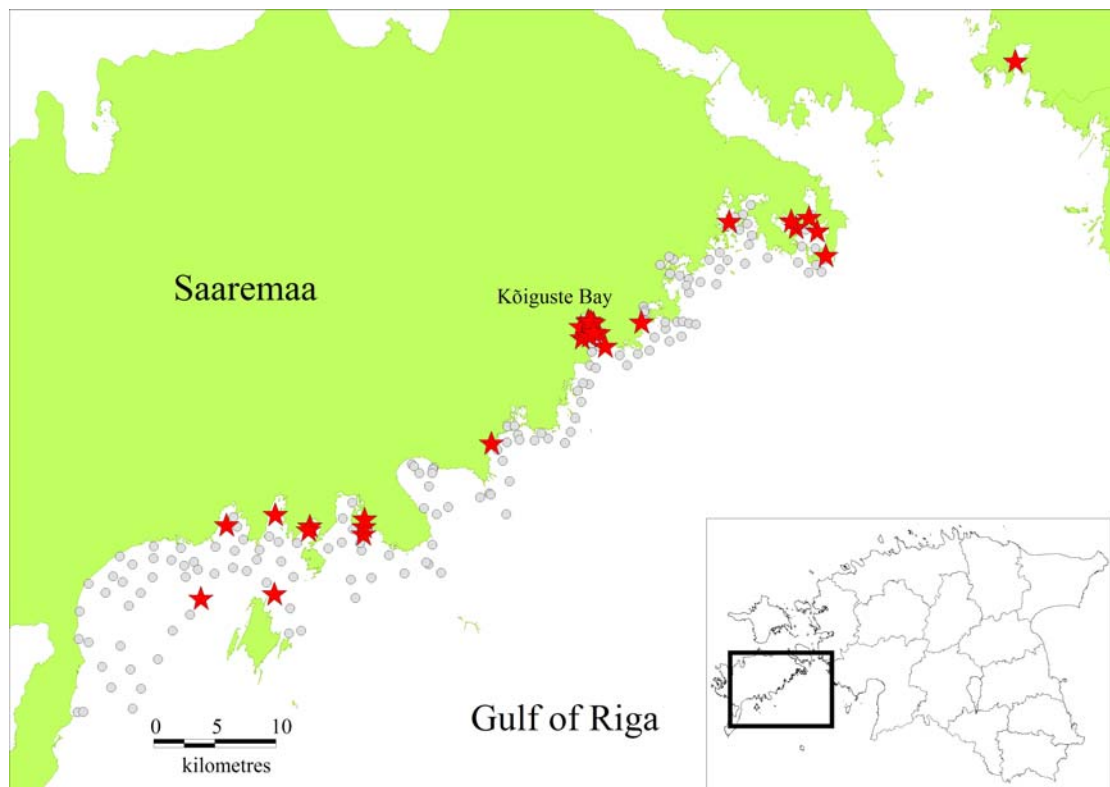


Fig. 4. Study area. Circles indicate sampling stations and stars the locations where *Gammarus tigrinus* was found.

In Kõiguste Bay the samples with and without *G. tigrinus* had significantly different biomass structure of phytobenthos (ANOSIM, $r = 0.23$, $p = 0.003$) and zoobenthos (ANOSIM, $r = 0.265$, $p = 0.002$) and abundance structure of zoobenthos (ANOSIM, $r = 0.322$, $p = 0.001$). The samples with the invasive amphipod were characterised by higher biomass of *Chara aspera*, *Enteromorpha intestinalis* and *Ruppia maritima* and lower biomass of *Fucus vesiculosus* and *Furcellaria lumbricalis* (SIMPER). *F. vesiculosus* and *F. lumbricalis* were loose lying and *E. intestinalis* was either loose lying or attached to macrophytes. The abundance and biomass of *Cerastoderma glaucum* and *Theodoxus fluviatilis* were higher and the abundance and biomass of *Macoma balthica* was lower in samples with *G. tigrinus* (SIMPER).

Concurrent with the invasion of *G. tigrinus* the total abundance of native gammarid species (*G. oceanicus*, *G. salinus*, *G. zaddachi*) significantly declined (one-way ANOVA, $p < 0.001$) whereas the overall abundance of gammarids did not change in 2003–2005 (one-way ANOVA, $p = 0.87$, Fig. 5). The abundance of the dominating *G. oceanicus* and *G. salinus* significantly decreased whereas the densities of less abundant *G. zaddachi* did not significantly change after the invasion of *G. tigrinus*. On the other hand the addition of *G. tigrinus* reduced both overall and native gammarid diversity (Shannon H' , \log_e , one-way ANOVA, $p < 0.001$) in the study area (Fig. 6).

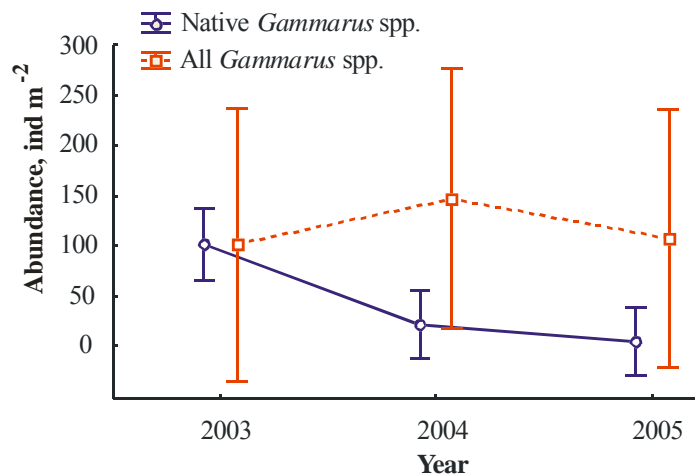


Fig. 5. Mean abundance (\pm 95% C.I.) of native (ANOVA, $p < 0.001$) and all gammarids (ANOVA, $p = 0.87$) in Kõiguste Bay in 2003-2005.

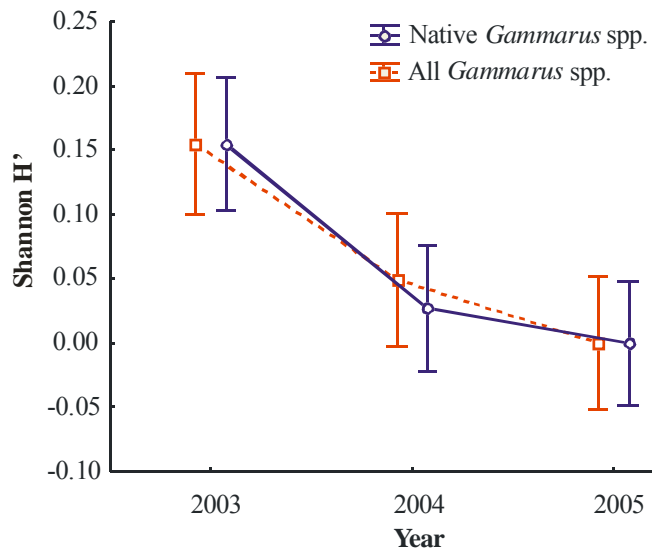


Fig. 6. Shannon diversity index (\log_e) (\pm 95% C.I.) of native (ANOVA, $p < 0.001$) and all gammarid fauna (ANOVA, $p < 0.001$) in Kõiguste Bay in 2003-2005.

3.2.2. Experiments

Mesocosm experiment

In the experimental cages the abundance and biomass of *G. tigrinus* ranged between 100–800 ind m^{-2} and 0.2–2.3 g m^{-2} , respectively. The invasive amphipod was only found in cages of 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 recolonized macrofauna were found between treatments with and without *G. tigrinus*. The cages with *G. tigrinus* were characterized by lower abundance of *Cerastoderma glaucum* and Chironomidae larvae, and higher abundance of juvenile gammarid amphipod (SIMPER). Differences in the biomass structure were related to the higher biomass of *Cerastoderma glaucum* and *Hydrobia ulvae*, and lower biomass of *Gasterosteus aculeatus* in the cages with *G. tigrinus* than in the cages without the nonindigenous species. Both the number of recolonized macrozoobenthic species (one-way ANOVA, $p < 0.001$) and the number of invertebrate feeding guilds (one-way ANOVA, $p = 0.033$) were significantly higher in the presence of

G. tigrinus. The abundance and biomass of *G. tigrinus* did not differ due to initial feeding guild diversity and isolation ($p > 0.05$).

Physical disturbance experiment

Amongst gammarids *G. tigrinus* had the highest average abundance and biomass. The abundance of *G. tigrinus* was significantly higher on the quadrates that were disturbed in July and sampled in September as compared to the undisturbed quadrats in the same period (two-way ANOVA, $p = 0.007$, Fig. 7). Disturbance had no effect on the abundance of native gammarid species ($p > 0.05$). Additionally, disturbance had no effect on the overall abundance (ANOSIM, $r = -0.202$, $p = 0.9$) and biomass (ANOSIM, $r = -0.115$, $p = 0.72$) structure of zoobenthos and biomass structure of phytobenthos (ANOSIM, $r = 0.464$, $p = 0.19$) on the quadrates disturbed in July and sampled in September.

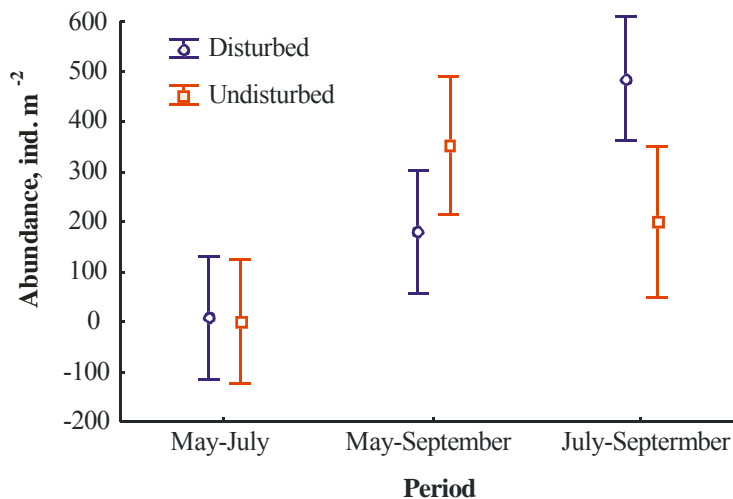


Fig. 7. Abundance of *Gammarus tigrinus* (\pm 95% C.I.) in physical disturbance experiment.

Habitat choice and grazing experiments

Habitat selection experiments showed that the majority of studied gammarids hid under the stones regardless of macrophyte community. Amongst nine most abundant macrophyte species and/or forms the gammarids had no clear preference. The presence of *G. tigrinus* reduced the affinity of native gammarids towards the brown alga *Pylaiella littoralis* (two-way ANOVA, $p < 0.001$) whereas other differences were not statistically significant ($p >$

0.05). Based on the visual observations *G. tigrinus* had substantially higher swimming speed as compared to the native gammarids.

Feeding choice experiments indicated that *P. littoralis* was the most preferred macrophyte species followed by the green alga *E. intestinalis*. Grazing was lower in spring than in other seasons (one-way ANOVA, $p < 0.001$). Macrophyte species had no effect on the survival of gammarids ($p > 0.05$). The presence of native gammarids had no impact on the survival of *G. tigrinus*. The presence of *G. tigrinus* reduced the survival of the native gammarids within *P. littoralis* (two-way ANOVA, $p = 0.03$).

4. DISCUSSION

4.1. *Orchestia cavimana*

In the northeastern Baltic Sea *O. cavimana* inhabits damp wracks cast up on shore and the upper layer of sediment. The habitat corresponds to the previous records in the Baltic and other seas (Den Hartog 1965; Lincoln 1979; Źmudziński 1974; Curry et al. 1972). The amphipod reaches its maximum length (Lincoln 1979) in the Estonian coastal sea suggesting that environmental conditions during summer are favourable in the area.

The studied environmental factors did not predict the presence of *O. cavimana* in a site. As the amphipod is a recent immigrant, it is likely that the species has not yet colonized all suitable habitats in the northeastern Baltic Sea due to the stochastic nature of invasion process.

Population characteristics varied considerably between and within sites. Most of the variability was explained by quantity and quality of wrack. Quantity, composition and other properties of wrack are important for aspects of foraging and habitat suitability (Backlund 1945; Persson 1999). In our study area the biomass of *O. cavimana* was higher in areas of more intensive accumulation of wrack whereas the abundances increased only with the biomass of higher plants.

The type and granulometry of sediment are also important habitat qualities of *O. cavimana*. The variability in juvenile weight increased with the average size of sediment particles indicating that juvenile amphipods are more associated with sediment than adults. Juveniles may require better protection in the exposed environments. Alternatively they may actively search for more decayed plant debris that can be found in the upper layer of sediment.

O. cavimana was found for the first time on the coasts of northern Saaremaa Island, the northeastern Baltic Sea in 1999 corresponding to the extension of its Baltic distribution of some 400 km. The species was observed only in a single site and the amphipod densities were very high. The exact time of the first inoculation of *O. cavimana* remains uncertain.

Considering the high densities of the amphipod in 1999, it is likely that the species arrived on the Estonian shore either late 1998 or early 1999. Alternatively, the species may have arrived even earlier providing that the amphipods had densities below detection limits. However, this seems very unlikely as the site has been regularly surveyed since 1994 (database of the Estonian Coastal Sea Monitoring Program, available at Estonian Marine Institute).

In the following years the amphipod abundances stabilized on remarkably lower levels. This is in agreement with earlier observations that in many cases invading species attain a peak of population density and then decline due to interactions between the invader and its resources or enemies (Carlton 1996; Williamson and Fitter 1996). In 2002 eight additional locations of *O. cavimana* were found in Saaremaa Island and northwestern Estonia corresponding to the additional extension of its Baltic distribution of some 150 km. The distribution of *O. cavimana* remained the same in 2004, indicating that the amphipod can survive extremely severe winters (e.g. 2002/2003) and therefore the species has a potential for invading coastal areas further north. However, the densities were extremely low in 2004 at most stations. In Britain a severe winter did not affect the populations of *O. cavimana* and the colonies of amphipod remained active beneath snow (Curry et al. 1972). The winter temperature, however, might become a regulating factor of the range expansion of *O. cavimana* in colder climate. In the Baltic Sea area the high temperature in the wrack banks through autumn to spring is an ecological factor which positively influences the populations of the talitrid amphipod *Orchestia gammarellus* (Backlund 1945).

The timing of the range expansion of *O. cavimana* may be connected with climate warming. Shorter period of ice cover and strong storms in autumn and winter may favour the transport of wrack over large distances. As the climate warming in northern Europe has been primarily expressed as warmer winters (Ottersen et al. 2001), it is likely that the hibernating conditions for the species have become more favourable.

The southern coast of the Baltic Sea may be regarded as the initial donor region for the Estonian populations of *O. cavimana*. It remains unknown whether *O. cavimana* first colonized northern coasts of Saaremaa Island and then dispersed to the other sites in the northeastern Baltic Sea or there have been several secondary introductions from the southern Baltic Sea to the northern Baltic Sea.

The vector of this invasion is unknown but most likely it is related to the natural dispersal of the drifting algae. However, as the northern Saaremaa Island is an important recreational area unintentional introduction can not be excluded. Wildish (1970) showed that talitrid amphipods survived at least 14 days of submersion. In another experiment (Persson 2001) the mortality of submerged *O. gammarellus* and *Platorchestia platensis* was very low during first two weeks but some individuals of both species survived more than three months of submersion. The results suggest that long dispersal episodes are possible even entirely submerged. Animals may survive even longer episodes of dispersion when attached to material drifting on the surface of water. In the Baltic Sea dispersion probably takes place in late autumn when the water level is high and storms are frequent (Persson 2001).

Prior to 1999 the northernmost distribution limit of the amphipod was located at the southern coasts of the North and Baltic Seas (Żmudziński 1974; Lincoln 1979). To date *O. cavimana* is found as north as in Estonia. The incredible speed of the invasion of *O. cavimana* and its high biomasses indicate that the species has formed permanent populations and will very likely extend its distribution on the coasts of Estonia in the following years.

4.2. *Gammarus tigrinus*

The North-American amphipod *Gammarus tigrinus* was observed for the first time in the northern Baltic Sea in summer 2003 in connection to in situ mesocosm experiment performed in Kõiguste Bay, northern Gulf of Riga. Despite intensive sampling throughout ice-free season in 2003, the species was not observed in regular monitoring stations in Kõiguste Bay. The species has, therefore, most probably arrived in 2003. There is a possibility that *G. tigrinus* may have arrived even earlier providing that the animals had densities below detection limits. However, as thorough samplings as well as experimental studies have been carried out throughout the bay in previous years, earlier arrival of *G. tigrinus* is very unlikely. Similarly to previous records in the southern Baltic Sea (Grabowski et al. 2006; Jazdzewski et al. 2002), the further invasion of *G. tigrinus* was extremely rapid in the northern Gulf of Riga.

Already in 2003 in the experimental mesocosms, the abundance and biomass of *G. tigrinus* was relatively high exceeding those of the most abundant native species *G. salinus*. As the incubation in mesocosm experiment started with bare sand (control treatments) or with only a few added animals (initial community treatments), opportunistic *G. tigrinus*, may have taken advantage of the available free space in the beginning of the experiment. However, in the end of the experiment the number of recolonized macrozoobenthic species and feeding guilds was significantly higher in the cages with *G. tigrinus* than those without the invasive amphipod. While established higher functional trait richness of benthic community may provide more resources for newcomers and contribute to the persistence of the invasive species. This is in agreement with the earlier observations that the invasion rate of nonindigenous species increases with community species diversity (Levine 2000).

In the mesocosm experiment *G. tigrinus* occupied only cages of the sheltered site. In field the abundance and biomass of the species was higher in the inner part of the Kõiguste Bay also indicating the species' preference to lower exposure. Additionally, the samples where *G. tigrinus* was present, were characterized by higher biomass of shallow and/or less exposed water macrophytes like *Chara aspera* and *Enteromorpha intestinalis* and lower biomass of plants characteristic to deeper and more exposed areas (*Fucus vesiculosus*, *Furcellaria lumbricalis*). Similarly to plant communities, the macrozoobenthic abundance and biomass structure in samples with *G. tigrinus* was characteristic to shallow water habitats. Preference towards less exposed areas is in agreement with earlier studies from other Baltic Sea areas (Jazdzewski et al. 2002; Szaniawska et al. 2003).

G. tigrinus has caused a dramatic decline of native gammarid fauna in the southern Baltic Sea area (Grabowski et al. 2006; Jazdzewski et al. 2004; Szaniawska et al. 2003). Decrease in native gammarid density and diversity has also been observed in the Estonian coastal sea. The total abundance of *Gammarus* spp has remained the same during 2003-2005 (Fig. 5), whereas the abundance of native gammarids has decreased considerably. This indicates that habitat and/or food is limiting gammarid densities in the area and there is a competition between native gammarids and *G. tigrinus*. The habitat choice and grazing experiments supported the field observation as there were no substantial differences in the microhabitat and grazing preferences between native gammarids and *G. tigrinus*. When *G. tigrinus* was present then the native gammarids avoided *P. littoralis* i.e. the prime diet of

the invasive species. Besides, the presence of *G. tigrinus* induced higher mortality of native gammarids within *P. littoralis*.

Experimental removal of the upper layer of seabed sediment seemed to favour *G. tigrinus*. However, the positive effect of disturbance on the abundance of *G. tigrinus* emerged only in autumn and on the patches that were disturbed in summer. The possible reasons for this pattern are many-fold. As only grown-up gammarid amphipods can be identified to the species level, the number of adults in the field was very low during summer sampling, thus, making the statistical distinction between treatments unlikely. Based on its life history *G. tigrinus* is likely more successful in colonizing newly disturbed areas than the native species and outcompetes native gammarids in the beginning of succession process. Thus, the period from May to September might be too long for the effect of disturbance to emerge as compared to the period from July to September. The winter 2002/2003 was extremely severe in the northern Baltic area and extensive ice scraping was observed in the shallow coastal sea. The results from the disturbance experiment support the idea that the extensive ice scraping may have facilitated the establishment of *G. tigrinus* in the Estonian coastal sea in 2003. As a euryhaline (Bousfield 1973), pollution tolerant (Savage 1996), and highly reproductive (Chambers 1977) species, *G. tigrinus* has a potential to invade the whole Estonian coastal sea and reduce the native biological diversity.

SUMMARY

In the northern Baltic Sea the semi-terrestrial talitrid amphipod *Orchestia cavimana* was found for the first time on the coast of northern Saaremaa Island in 1999. In the Baltic Sea the species has been previously found only on its southern coast. Six additional locations of *O. cavimana* were found in Saaremaa Island and two locations in the northwestern part of Estonia in 2002. *O. cavimana* inhabited damp wracks cast up on shore and the upper layer of sediment. Abundances and biomasses were highest in the first year of the invasion. Wrack biomass and interaction between wrack biomass and exposure were the best predictors of the abundances and biomasses of *O. cavimana*. The southern coast of the Baltic Sea may be regarded as the initial donor region for the Estonian populations of *O. cavimana*. The vector of this invasion is most likely related to the natural dispersal of the drifting algae but human activities as a transport vector can not be excluded.

The North-American amphipod *Gammarus tigrinus* was observed for the first time in the northern Baltic Sea in 2003. The species was found in Kõiguste Bay, northern Gulf of Riga, in connection with a mesocosm experiment. In 2003 *G. tigrinus* had colonized several experimental mesocosms, but the species was not found in the adjacent sea area. In 2004 *G. tigrinus* was found all over the Kõiguste Bay and by 2005 the species was found throughout the northern Gulf of Riga. *G. tigrinus* occupied the same areas as compared to the native gammarid species, though, being more abundant in less exposed areas. Concurrent with the invasion the density of native gammarids declined manifold whereas the overall density of gammarids did not change. This indicates that food and/or space is limiting the population growth of gammarids and there is a food and/or space competition between *G. tigrinus* and the native species. Experiments supported the field observation as there were no substantial differences in the microhabitat and grazing preferences of native gammarids and *G. tigrinus*. The addition of *G. tigrinus* reduced both overall and native gammarid diversity. Experimental disturbance to the seabed (removal of the upper layer of sediment) had a positive effect on the densities of *G. tigrinus*, indicating that the invasion of the gammarid to the Estonian coastal sea was related to the physical disturbance due to the extremely severe winter 2002/2003.

KOKKUVÕTE

Kristjan Herkül. Kirpvähiliste *Orchestia cavimana* ja *Gammarus tigrinus* invasiooniajalugu Eesti rannikumeres

Poolmaismaalise eluviisiga kirpvähiline *Orchestia cavimana* leiti Läänemere põhjaosas esmakordselt 1999. aastal Saaremaalt Küdema lahest. Varasemad kindlad andmed liigi esinemise kohta Läänemeres on Poola ja Saksamaa rannikult. 2002. aasta leiti liiki lisaks esmaleiukohale veel kuuest kohast Saaremaa põhja- ja läänerannikul ja kahest kohast Paldiski lahe ümbruses. *O. cavimana* asustab Eestis kirjanduses mainitule sarnaseid elupaikasid – rannale uhutud mereheidiseid ja heidisealuse pinnakatte ülemist kihti. Kirpvähilise arvukus ja biomass oli suurim esmaleiu aastal. Mereheidise biomass ja elupaiga merele avatus kirjeldasid kõige paremini *O. cavimana* arvukust ja biomassi. *O. cavimana* Eesti populatsioonide algseks doonorregiooniks on ilmselt Läänemere lõunaosa. Teadmata on, kas liik asustas Eestis algselt ühe koha ja levis sealt edasi teistesse 2002. aastal leitud leiukohtadesse või sattus liik Eesti levikupiirkondadesse otse algsest doonorregioonist. Levikuvektoriks on olnud ilmselt looduslik levimine meres triivivate mereheidistega või inimtegevuse vahendatud introduktsioon.

Läänemere põhjaosas leiti Põhja-Ameerikast pärit kirpvähiline *Gammarus tigrinus* esmakordselt Saaremaa lõunarannikult Kõiguste lahest 2003. aastal, kus liik oli asustanud *in situ* eksperimendi mesokosme. 2003. aastal ei leitud kirpvähki ümbritsevatelt merealadelt. 2004. aastal oli *G. tigrinus* levinud üle kogu Kõiguste lahe ja 2005. aastal leiti liiki kogu Liivi lahe põhjaosa ulatuses. *G. tigrinus*'e ja kohalike kirpvähkide (*Gammarus* spp.) elupaigad Kõiguste lahes olid sarnased, kuid võõrliigi arvukus oli mõnevõrra suurem madalaveelistel varjatud merealadel. *G. tigrinus*'e invasiooniga kaasnes oluline kohalike kirpvähkide arvukuse ja mitmekesisuse langus. Vaatamata kohalike liikide arvukuse langusele ei muutunud kirpvähiliste summaarne arvukus (kohalikud liigid ja *G. tigrinus*) aastatel 2003-2005. See võib näidata, et toit ja/või elupaigad limiteerivad kirpvähiliste asustustihedust ja esineb konkurents kohalike liikide ja *G. tigrinus*'e vahel. Kirpvähiliste toidu- ja elupaigavaliku katsed kinnitasid, et kohalike ja võõrliigi toidu ja elupaiga valik ei erine üksteisest oluliselt. Merepõhja eksperimentaalse füüsikalise häirimisega (ülemise settekihi eemaldamine) kaasnes *G. tigrinus*'e arvukuse kasv katselappidel, mis näitab, et kirpvähi invasioon Eesti rannikumerre võis olla seotud 2002/2003 a. erakordselt karmist talvest tingitud füüsikalise häiritusega.

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APPENDIXES

Appendix I. Herkül K, Kotta J, Kotta I (2006) Distribution and population characteristics of the alien talitrid amphipod *Orchestia cavimana* in relation to environmental conditions in the northeastern Baltic Sea. Helgol Mar Res 60:121–126

Appendix II. Herkül K, Kotta J, Kotta I, Orav-Kotta H. Effects of physical disturbance, isolation and macrofaunal feeding guild diversity on community development, recolonization and sedimentation process. Submitted to Oceanologia.

Appendix III. Orav-Kotta H, Kotta J, Herkül K, Kotta I. Habitat and feeding choice of the invasive gammarid *Gammarus tigrinus* explain the decline of native gammarid diversity in the northern Baltic Sea. Manuscript.

Appendix I

Distribution and population characteristics of the alien talitrid amphipod *Orchestia cavimana* in relation to environmental conditions in the northeastern Baltic Sea

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Abstract

The talitrid amphipods were found for the first time in the northeastern Baltic Sea in 1999. *Orchestia cavimana* inhabited damp wracks cast up on shore within a 200 m area of Saaremaa Island. In the following year the species expanded its range to a few kilometres. In 2002 six additional locations of *O. cavimana* were found in Saaremaa Island and two locations in the northwestern part of Estonia. Abundances and biomasses were highest in the first year of the invasion. In the following years the values stabilized on remarkably lower levels. Population characteristics of the species varied significantly between locations. The average biomass and abundance were 9 g dw m⁻² and 1975 ind m⁻², respectively. Wrack biomass and interaction between wrack biomass and exposure were the best predictors of the abundances and biomasses of *O. cavimana*. Humidity explained additional variability in biomasses. The size structure of the population of *O. cavimana* was mostly related to humidity and wrack biomass. The southern coast of the Baltic Sea may be regarded as the initial donor region for the Estonian populations of *O. cavimana*. The vector of this invasion is most likely related to the natural dispersal of the drifting algae but human activities as a transport vector can not be excluded. The incredible speed of the invasion of *O. cavimana* and its high biomasses indicate that the species will very likely extend its distribution along the coast of the northeastern Baltic Sea in the following years.

Keywords: *Orchestia cavimana*, nonindigenous species, Amphipoda, Baltic Sea

Introduction

The dispersal of species to new areas has an impact on local ecosystems (Parker et al. 1999). New species entering ecosystems may dramatically change the species diversity, trophic structure, structure and dynamics of populations, nutrients availability and flow, and primary production of the local ecosystem (Carlton 1996). Successful invasive species may render previously stable systems unbalanced and unpredictable (Carlton and Geller 1993; Carlton 1996; Ruiz et al. 1999). Hence biological invasions may represent severe threats to the integrity of natural communities, endangered species and economy (Carlton and Geller 1993; Carlton 1999a, 1999b).

Owing to its low number of species and extensive anthropogenic impact, the ecosystem of the Baltic Sea is considered vulnerable to biological invasions (Stachovicz et al. 1999; Levine and D'Antonio 1999; Leppäkoski and Olenin, 2001). In recent decades the number of nonindigenous species has increased exponentially and the ranges of existing exotics have expanded rapidly in the Baltic Sea area (Gruszka 1999; Leppäkoski and Olenin 2001). Among most recent newcomers *Marenzelleria neglecta* (Sikorski and Bick sp. nov.) and *Cercopagis pengoi* (Ostroumov) have invaded practically all suitable biotopes in the Baltic Sea within a few years period (Kotta and Orav 2001; Zettler et al. 2002; Telesh and Ojaveer 2002). Well-established alien *Dreissena polymorpha* (Pallas) suddenly expanded its distribution area in the 1990 and 2000s (Kotta 2000b).

The Talitridae is the only family of amphipods which has truly terrestrial species, and although many are found close to the sea on the upper parts of the shore, some occur considerable distances inland (Lincoln 1979). It is a very large family that comprises five genera: *Talitrus* Latreille, *Orchestia* Leach, *Talorchestia* Dana, *Talitroides* Bonnier and *Brevitalitrus* Bousfield (Lincoln 1979). Talitrid amphipods are important members of the wrack fauna throughout the world (Persson 1999). *Orchestia* is a large cosmopolitan genus comprising more than 70 recognised species, which are semiterrestrial, typically living amongst intertidal stones and algae, although some are found inland and may occur several hundred meters above sea-level (Lincoln 1979).

In the Baltic Sea, five species of talitrid amphipods have been found. Two of these, *Talorchestia deshayesii* Audouin and *Talitrus saltator* (Montagu), live on sandy beaches, whereas *Platorchestia platensis* (Krøyer), *Orchestia gammarellus* (Pallas) and *O. cavimana* Heller are found in wrack beds on harder substrata, such as rocks, stones, gravel, and shore meadows (Persson 1999; Kotta 2000a). *O. gammarellus* has the widest distribution in the Baltic, and has been reported from the central parts of the Baltic proper (Persson 1999). Prior to 1999 there were no talitrid amphipod species found further north.

The talitrid amphipod *Orchestia cavimana* has a relatively wide distribution area inhabiting Mediterranean, Black Sea, Red Sea, Atlantic coast of North Africa and of Europe up to the southern North Sea (Lincoln 1979). In the Baltic Sea the species has been previously found only in a few southern coastal sites in Poland and Germany (Żmudziński 1974; Järvekülg 1979). The Ponto-Caspian region but likely Asia are suggested as its origin (Kinzelbach 1965, 1972; Belgian Biodiversity Platform 2004: www.biodiversity.be/bbpf/forum/invasion/invspecies.html). To date the information about arrival, invasion vector, range expansion, current distribution and possible impact of the species is extremely limited. The aims of this paper are (1) to follow the establishment and range expansion of *O. cavimana* in the Baltic Sea and (2) relate the biomass distribution and size structure of the populations to habitat characteristics.

Material and Methods

Wrack fauna was sampled annually at 79 sites of the Estonian coastal sea during the last week of September or the first week of October 1998, 1999, 2002 and 2004 (Fig. 1). One sample was taken in each station except for a site in the northern Saaremaa Island (first location of *O. cavimana* in Estonia) where three replicate samples were taken annually in 1998–2004. Sites were selected to cover maximum salinity range, different sediment and wrack types. Shores, which were overgrown with reeds, were excluded. At every site exposure (an estimate how much a site is exposed to open sea in degrees), steepness of coastal slope (a distance between shoreline and 5 m depth isoline), number, width and height of wrack belts, total coverage of wrack within a belt, dominant plant species, level of decomposition and humidity, type and granulometry of sediment particles were estimated. The sites were classified as dry, moist and wet. Where talitrid amphipods were found a biomass sample was taken using 20×20 cm metal frame. Typically, the algal belt was a few metres wide. Within the belt the densities of *O. cavimana* varied little whereas the densities varied highly at the edges of the belt. Therefore, the samples were taken within well developed and not fragmented parts of wrack belt. The material inside the frame was quickly removed and packed into a plastic bag. Samples were kept deep-frozen until analyzing in the laboratory.

Talitrid amphipods were picked up from the sample under a stereomicroscope. Animals were counted and divided into the following groups: adult males, adult females and juveniles (see Lincoln 1979). The smallest males with visible sexual characteristics were 9 mm long. Thus, all animals below 9 mm were considered juveniles. The length of all individuals was measured by camera lucida using a stereomicroscope to the nearest 0.1 mm. Dry weight of individuals was measured to the nearest 0.1 mg after drying at 60 °C for 48 h. Plants were separated by species and dry weight (60 °C, 336 h) of each species was measured. For each plant species the level of decomposition was estimated on three-stage scale: fresh, semi-decayed and highly decayed. In

some cases of very low amphipod densities no animals were captured inside the quadrat. These samples were excluded from the statistical analyses.

For univariate analyses the statistical programme "Statistica" was used (StatSoft, Inc. 2004). We employed analysis of variance (ANOVA) to describe differences between sexes and environmental conditions in stations with and without *O. cavimana*, chi-square test to analyse sex ratio, and linear regression to analyze relationships between population characteristics of *O. cavimana* and habitat characteristics. Prior to the analyses normality (Shapiro-Wilk W test) and homoscedasticity (Bartlett's test) of the data was checked. Multivariate data analyses were performed using the package "PRIMER" (Clarke and Warwick 2001). Double square root transformed data were used for Bray-Curtis similarity matrices. BIOENV analysis was used to explain the importance of habitat characteristics in determining the abundance, biomass, and size structure of *O. cavimana*. ANOSIM permutation test was performed to examine differences in abundance, biomass, and size structure due to habitat characteristics.

Results

The investigated habitats were mainly exposed shores. The steepness of coastal slope varied highly. The distances between shoreline and 5 m depth isoline ranged from 75 m to about 12 km with an average at 1518 m. Limestone sediments were predominant followed by granite boulders. The wrack coverage within a belt was on average 57 % varying between 5 and 100 %. Altogether 19 plant species were identified in the wrack. *Fucus vesiculosus* L. had highest biomasses followed by *Zostera marina* L. and *Furcellaria lumbricalis* (Huds.) J. V. Lamour. The plant species were mainly fresh to semi-decayed and the wrack beds were predominantly moist to wet.

Despite of intensive field sampling in 1998 the talitrid amphipods were not found within the wrack fauna. *Orchestia cavimana* was found for the first time on the coast of northern Saaremaa Island in 1999 (Fig. 1). *O. cavimana* inhabited damp wrack cast up on shore. The species was restricted within 200 m shore area. The average abundance and biomass were 22,400 ind m⁻² and 14 g dw m⁻², respectively. In 2000 the species expanded its range to a few kilometres but the average abundance and biomass decreased down to 2,433 ind m⁻² and 2 g dw m⁻², respectively.

In 2002 *O. cavimana* was found in nine areas (Fig. 1.). In 2004 the distribution of *O. cavimana* had remained the same as in 2002. However, the abundance of the species had decreased considerably in the majority of stations. Only three locations had sufficiently high abundances for capturing animals into the sampling frame.

O. cavimana inhabited very exposed shores except for a partly sheltered site on the western coast of Saaremaa Island. However, there was no statistically significant difference in exposure between the sites with and without *O. cavimana*. Similarly, there were no statistical differences in the sediment characteristics regardless of the presence of *O. cavimana*. In the presence of *O. cavimana* the wrack coverage varied between 40–100 % with an average at 73 % and the wrack biomass varied between 1224–4924 g dw m⁻² with an average at 2712 g dw m⁻². In the absence of *O. cavimana* the average coverage and biomass were lower, 54 % and 1820 g dw m⁻², respectively. Altogether 14 algal species and 4 higher plants were found in the habitats of *O. cavimana*. The number of plant species in wrack varied between 3 and 13 with an average at 9. *F. vesiculosus* prevailed in the wrack in seven areas and *Polysiphonia fucoides* (Huds.) Grev. in the other two areas. *Pilayella littoralis* (L.), *Zostera marina* and *Ruppia maritima* L. were the second dominant plant species within the wrack.

The biomasses and abundances of *O. cavimana* ranged between 0.6–29.0 g dw m⁻² and 50–6275 ind m⁻², respectively. The average biomass was 9.1 g dw m⁻² and the average abundance was 1975 ind m⁻². The amphipod length varied between 3–20 mm with an average at 9.9 mm. The 9–10 mm size class formed nearly 40 % of the population density and biomass. The amphipod dry weight varied between 0.0001–0.0201 g with an average at 0.005 g. Males had significantly greater

average length than females (11.4 vs 10.4 mm, one-way ANOVA, $p < 0.001$). The differences in the weights were not statistically significant (one-way ANOVA, $p = 0.22$). The average sex ratio was female-biased (1:0.83, chi-square test, $p < 0.05$).

BIOENV analysis suggested that wrack biomass, humidity and interaction between wrack biomass and exposure were the best predictor of the abundances of *O. cavimana* whereas wrack biomass and interaction between wrack biomass and exposure explained the variability in biomasses. The size structure of the population of *O. cavimana* was mostly related to humidity and wrack biomass (Table 1).

The biomass of *O. cavimana* increased with the wrack biomass (Fig. 2). However, there was no significant relationship between the biomass of wrack and the abundance of *O. cavimana*. The abundance of *O. cavimana* correlated positively with the biomass of higher plants in the wrack (linear regression analysis, $r^2 = 0.52$, $p < 0.05$). The variability in juvenile dry weight correlated with average size of sediment particles (linear regression analysis, $r^2 = 0.83$, $p < 0.05$). The humidity of wrack was significantly related to the abundance of *O. cavimana*. The amphipod abundances were highest in moist, intermediate in wet and lowest in dry wrack, respectively. However, only dry and moist wrack were significantly different in terms of amphipod abundances (233 vs 4000 ind m^{-2} , ANOSIM, $p = 0.042$).

In the station of the first record of *O. cavimana* (northern coast of Saaremaa Island) the highest abundance and biomass of the talitrids were found in 1999. In the following years the abundance and biomass have stabilized on remarkably lower levels with a slight increase in 2004 (Fig. 3).

Discussion

In the northeastern Baltic Sea *O. cavimana* inhabits damp wracks cast up on shore and the upper layer of sediment. The habitat corresponds to the previous records in the Baltic and other seas (Den Hartog 1965; Lincoln 1979; Żmudziński 1974; Curry et al. 1972). The amphipod reaches its maximum length (Lincoln 1979) in the Estonian coastal sea suggesting that environmental conditions during summer are favourable in the area.

The studied environmental factors did not predict the presence of *O. cavimana* in a site. As the amphipod is a recent immigrant, it is likely that the species has not yet colonized all suitable habitats in the northeastern Baltic Sea due to the stochastic nature of invasion process.

Population characteristics varied considerably between and within sites. Most of the variability was explained by quantity and quality of wrack. Quantity, composition and other properties of wrack are important for aspects of foraging and habitat suitability (Backlund 1945; Persson 1999). In our study area the biomass of *O. cavimana* was higher in areas of more intensive accumulation of wrack whereas the abundances increased only with the biomass of higher plants.

The type and granulometry of sediment are also important habitat qualities of *O. cavimana*. The variability in juvenile weight increased with the average size of sediment particles indicating that juvenile amphipods are more associated with sediment than adults. Juveniles may require better protection in the exposed environments. Alternatively they may actively search for more decayed plant debris that can be found in the upper layer of sediment.

O. cavimana was found for the first time on the coasts of northern Saaremaa Island, the northeastern Baltic Sea in 1999 corresponding to the extension of its Baltic distribution of some 400 km. The species was observed only in a single site and the amphipod densities were very high. The exact time of the first inoculation of *O. cavimana* remains uncertain. Considering the high densities of the amphipod in 1999, it is likely that the species arrived on the Estonian shore either late 1998 or early 1999. Alternatively, the species may have arrived even earlier providing that the amphipods had densities below detection limits. However, this seems very unlikely as the site has

been regularly surveyed since 1994 (database of the Estonian Coastal Sea Monitoring Program, available at Estonian Marine Institute).

In the following years the amphipod abundances stabilized on remarkably lower levels. This is in agreement with earlier observations that in many cases invading species attain a peak of population density and then decline due to interactions between the invader and its resources or enemies (Carlton 1996; Williamson and Fitter 1996). In 2002 eight additional locations of *O. cavimana* were found in Saaremaa Island and northwestern Estonia corresponding to the additional extension of its Baltic distribution of some 150 km. The distribution of *O. cavimana* remained the same in 2004, indicating that the amphipod can survive extremely severe winters (e.g. 2002/2003) and therefore the species has a potential for invading coastal areas further north. However, the densities were extremely low in 2004 at most stations. In Britain a severe winter did not affect the populations of *O. cavimana* and the colonies of amphipod remained active beneath snow (Curry et al. 1972). The winter temperature, however, might become a regulating factor of the range expansion of *O. cavimana* in colder climate. In the Baltic Sea area the high temperature in the wrack banks through autumn to spring is an ecological factor which positively influences the populations of the talitrid amphipod *Orchestia gammarellus* (Backlund 1945).

The timing of the range expansion of *O. cavimana* may be connected with climate warming. Shorter period of ice cover and strong storms in autumn and winter may favour the transport of wrack over large distances. As the climate warming in northern Europe has been primarily expressed as warmer winters (Ottersen et al. 2001), it is likely that the hibernating conditions for the species have become more favourable.

The southern coast of the Baltic Sea may be regarded as the initial donor region for the Estonian populations of *O. cavimana*. It remains unknown whether *O. cavimana* first colonized northern coasts of Saaremaa Island and then dispersed to the other sites in the northeastern Baltic Sea or there have been several secondary introductions from the southern Baltic Sea to the northern Baltic Sea.

The vector of this invasion is unknown but most likely it is related to the natural dispersal of the drifting algae. However, as the northern Saaremaa Island is an important recreational area unintentional introduction can not be excluded. Wildish (1970) showed that talitrid amphipods survived at least 14 days of submersion. In another experiment (Persson 2001) the mortality of submerged *O. gammarellus* and *Platorchestia platensis* was very low during first two weeks but some individuals of both species survived more than three months of submersion. The results suggest that long dispersal episodes are possible even entirely submerged. Animals may survive even longer episodes of dispersion when attached to material drifting on the surface of water. In the Baltic Sea dispersion probably takes place in late autumn when the water level is high and storms are frequent (Persson 2001).

Prior to 1999 the northernmost distribution limit of the amphipod was located at the southern coasts of the North and Baltic Seas (Żmudziński 1974; Lincoln 1979). To date *O. cavimana* is found as north as in Estonia. The incredible speed of the invasion of *O. cavimana* and its high biomasses indicate that the species has formed permanent populations and will very likely extend its distribution on the coasts of Estonia in the following years.

Acknowledgements

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Tables

Table 1. The combination of the best environmental variables that predicts abundance, biomass and biomass size structure of *O. cavimana* in the study area.

Similarity matrix	Significant environmental variables	Spearman ρ
Abundance	humidity of wrack wrack biomass wrack biomass \times exposure	0.676
Biomass	wrack biomass wrack biomass \times exposure	0.600
Abundance size structure	humidity of wrack wrack biomass	0.623
Biomass size structure	humidity of wrack wrack biomass	0.609

Figures

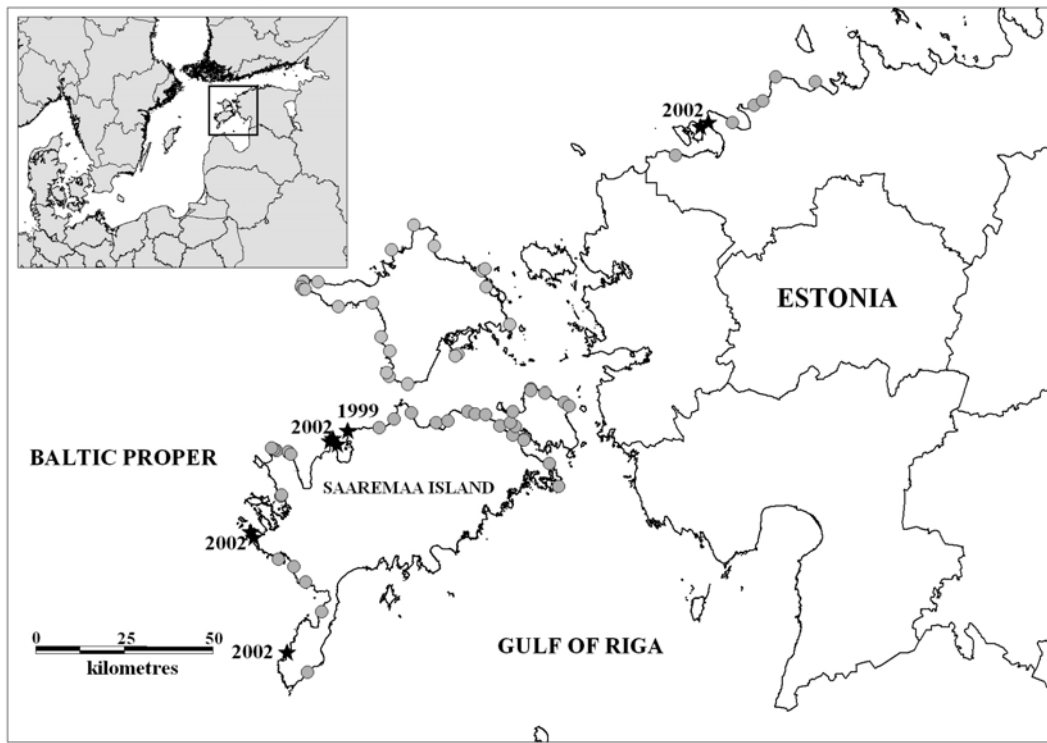


Fig. 1. Study area. Filled circles indicate the sampling sites of talitrid amphipods and stars the locations where *O. cavimana* were found. Years show the time of first record of *O. cavimana* in a site.

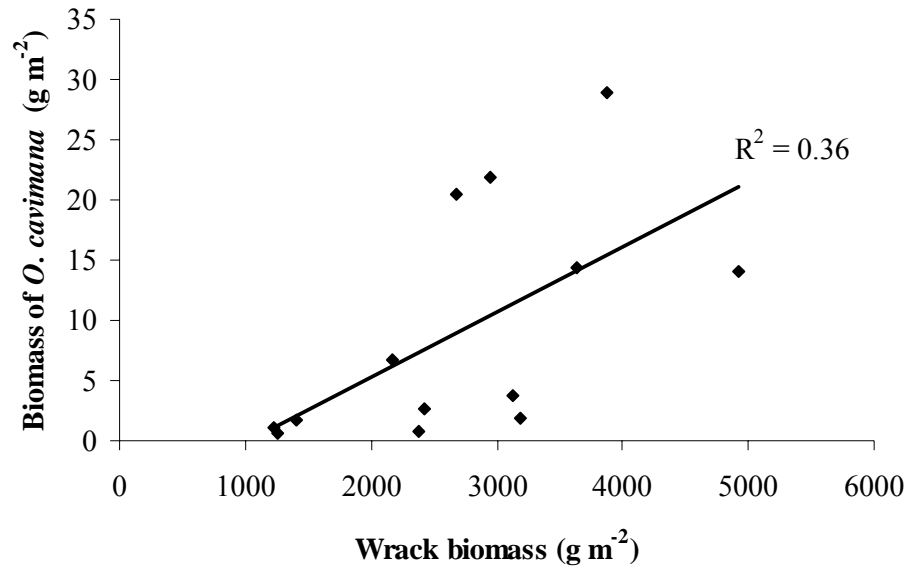


Fig. 2. Relationship between the biomass of wrack and the amphipod *O. cavimana* in the study area.

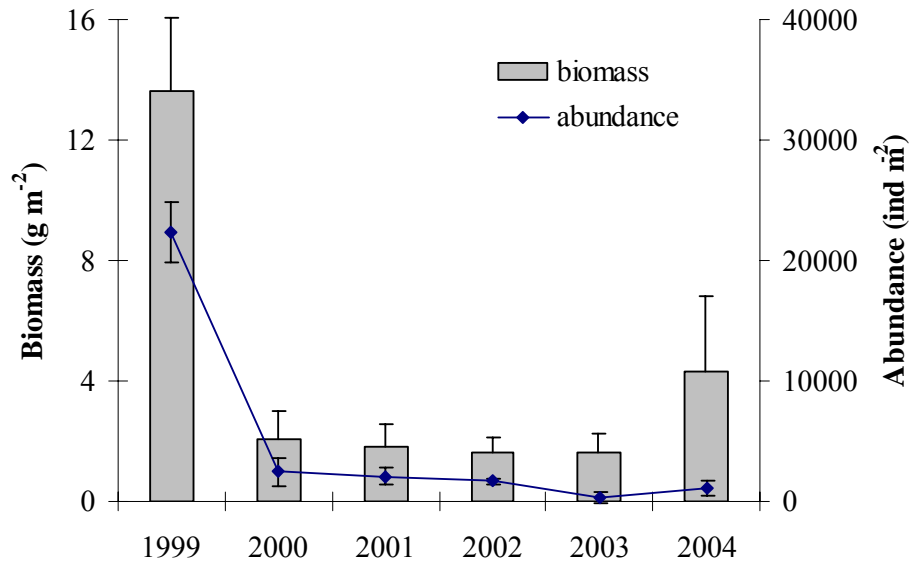


Fig. 3. Interannual variation in the abundance and biomass of *O. cavimana* (\pm S.E.) at the station of the first record of the species (northern coast of Saaremaa Island).

Appendix II

Effects of physical disturbance, isolation and macrofaunal feeding guild diversity on community development, recolonization and sedimentation process

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Abstract

In an in situ factorial field mesocosm experiment the relative effect of physical disturbance, isolation and macrofaunal feeding guild diversity on community development and sedimentation processes were studied in the northern Baltic Sea. Differences in abundance and biomass structure of recolonised macrobenthos were due to exposure and isolation. The initial feeding guild diversity had a negligible effect on macrofauna. However, higher feeding guild diversity increased the content of organic matter in sediment at high isolation level. The main conclusion of the study was that physically driven fluxes override the effects of biological interactions in shallow water systems of the northern Baltic Sea.

Keywords: Baltic Sea, ecosystem functioning, field experiment, functional diversity, physical disturbance

Introduction

Biodiversity is being lost globally at an unprecedented rate. The causes of this loss is of great importance in order to describe the potential effect of biodiversity loss on ecosystem processes (Vitousek et al. 1997, Loreau 2000, Loreau et al. 2001, Biles et al. 2003, Giller et al. 2004, Solan et al. 2004, Mermillod-Blondin et al. 2005). These recent studies have mainly aimed at resolving the question whether ecosystems with decreasing diversity would be able to maintain functioning comparable with 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) and only recently the topic has 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).

Impact of functions on ecosystem processes seems to be controversial. It is not clear how much ecosystems are controlled by the type and number of functions in the ecosystem (Tilman et al. 1997 and the references therein, Loreau et al. 2001). The presence of some functional groups seems 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. In the smaller spatial scales, however, ecosystem processes may be still 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 the colonization ability of individual species rather than biotic interactions might drive ecosystem processes (Loreau et al. 2001).

The knowledge on the relationships between functional diversity and ecosystem processes are currently more qualitative than quantitative (Hector et al. 2001). Experimental studies manipulating functional diversity and abiotic environment are needed to quantify how environmental variability modifies the relationships between functional diversity and ecosystem processes (Loreau et al. 2001). In this study the relationships between macroinvertebrate feeding guild diversity, community

development and ecosystem processes were investigated at different disturbance levels in a shallow water ecosystem of the northern Baltic Sea. The number of benthic invertebrate species is low there 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 being characterized by high 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 1996ab, Kotta et al. 1999, Paalme et al. 2002). We tested (1) whether ecosystem functioning is positively correlated to feeding guild diversity, (2) whether the systems with relatively few functions are less stable and have higher recolonization rate than more diverse communities and (3) if 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 utilization and declining functional diversity can result in a reduction of positive mutualistic interactions or complementary diversity effect (Emmerson & Raffaelli 2000, Loreau et al. 2001). If this is true then functionally rich communities are expected to decline the probability of invasion and/or recolonization through increased competition for space and food (e.g. Stachowicz et al. 1999). Strong fluctuation in abiotic factors such as oxygen concentration or wave induced disturbance is 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). With our experiment we aim to clarify the role of functional diversity on the stability of the simple benthic communities in the northern Baltic Sea, with the aim to help understanding the role of these processes in more complex ecosystems.

Material and methods

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. Experimental design included 96 plastic cages (11 cm diameter, 10 cm deep) attached to two floating rafts. The following factors were included: exposure (rafts in sheltered and exposed site; distance between rafts was 200 m), isolation (cages with and without 0.25 mm mesh screen) and initial feeding guild diversity.

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 abovementioned functions in the study area. All possible combinations of *C. glaucum*, *M. balthica* and *T. fluviatilis* and additional control treatment without animals served as the treatment of initial feeding guild diversity. The factor "isolation" involved both physical (i. e. high and low water exchange rate) and biological term (i.e. high and low recolonization level). The experiment was set up with 3 replicates of each exposure × isolation × diversity combination.

The cages were filled with sand from nearby seafloor to the amount of 2/3 of cage volume. Prior to experiment the sediment was sieved through a 1 mm mesh and dried in the sun for several days to assure that it was free of living benthic invertebrates. In order to obtain similar starting conditions sediment was homogenized before use. The test animals were collected from the neighbouring area in Kõiguste Bay. Prior to the experiment shell length was measured to the nearest 0.1 mm with dial calipers. 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 the densities of 228 ind m⁻² for *C. glaucum* and *M. balthica* and 570 ind m⁻² for *T. fluviatilis*. The selected densities of benthic invertebrates were similar to those earlier found in Kõiguste Bay (Kotta & Kotta 1997, Kotta et al. 2000, Lauringson & Kotta 2005). 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 were sampled for the content of organic matter and chlorophyll *a* with a 20 mm diameter metal tube. The care was taken that only samples with no

macrofauna were further analysed. Samples for organic matter content were deep-frozen and samples for chlorophyll *a* were extracted in 96% ethanol overnight. Organic matter content was measured as a percentage loss of ignition (3 h, 500°C). Chlorophyll *a* was quantified fluorometrically correcting for phaeopigments (Strickland and Parsons, 1972). Comparison of the content of organic matter and chlorophyll *a* was used to assess the changes in physical disturbance due to screening.

Remaining sediment was sieved through 0.25 mm mesh and the residuals were placed into plastic bags. The samples were kept deep-frozen until analyzing in laboratory. 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 animals were dried at 60 °C for 48 hours and plants for two weeks, respectively. The length of assembled individuals was measured to the nearest 0.1 mm.

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

Results

T. fluviatilis had significantly higher growth rates with the highest feeding guild diversity but only in sheltered site and at low isolation level (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 feeding guilds were due to the initial functional diversity (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 colonized 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.

Exposure (ANOSIM, $r = 0.504$, $p = 0.001$, Fig. 1A) and isolation level (ANOSIM, $r = 0.112$, $p = 0.001$) significantly affected the abundance structure of recolonizing macrofauna. The total abundance of recolonized invertebrates was significantly higher at low isolation level than at high isolation level (three-way ANOVA, $F_{1,62} = 5.6706$, $p = 0.020$). The total number of recolonized animal species was significantly higher in the sheltered site at low isolation level, whereas there were no differences due to exposure at high isolation level (three-way ANOVA, $F_{1,62} = 11.62$, $p = 0.001$). No significant differences in the recolonized community structure were due to the initial feeding guild diversity (ANOSIM, $p > 0.05$) Differences in abundance structure due to exposure were related to higher abundance of *Cerastoderma galucum* and Chironomidae larvae in exposed site and higher abundance of *Gammarus* juv. in sheltered site (SIMPER). The abundance of *Cerastoderma glaucum*, Chironomidae larvae and *Gammarus* juv. was higher at low isolation level (SIMPER).

Exposure (ANOSIM, $r = 0.333$, $p = 0.001$, Fig. 1B) and isolation level (ANOSIM, $r = 0.119$, $p = 0.001$) significantly affected the biomass structure of recolonizing benthic animals. At low isolation level the total invertebrate biomass was higher in sheltered site than in exposed site whereas at high isolation level the biomass was higher in exposed site than in sheltered site (three-way ANOVA, $F_{1,62} = 15.810$, $p < 0.001$). No significant differences in biomass structure were due to the initial feeding guild diversity (three-way ANOVA, $p > 0.05$). Differences in biomass structure due to exposure were related to higher biomass of three-spined stickleback (*Gasterosteus aculeatus* L.) larvae and *Saduria entomon* (L.) in exposed site and higher biomass of *Cerastoderma glaucum* and *Hydrobia ulvae* (Pennant) in sheltered site (SIMPER). With decreasing isolation level the biomass of *Cerastoderma glaucum* increased (SIMPER).

Isolation level (ANOSIM, $r=0.077$, $p=0.003$) had a significant effect on the biomass structure of benthic macrophytes. No significant differences in the community structure were due to the initial feeding guild diversity. The main differences in the total biomass of plants were due to exposure and isolation level (three-way ANOVA, $F_{1,62} = 38.267$, $p < 0.001$). At high isolation level the number of macrophyte species was significantly higher in exposed site than in sheltered site whereas at low isolation level 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 isolation level than at high isolation level (SIMPER).

In control treatments (no added animals) the content of organic matter in sediment was significantly higher without mesh than with mesh. However, in other treatments (involving the studied feeding guilds) the screening did not reduce the sedimentation of organic matter (three-way ANOVA, $F_{7,62} = 2.970$, $p = 0.009$). The content of organic matter significantly increased with the number of feeding guilds in cages covered by mesh (i.e. high isolation level) whereas such relationship was not found for cages without mesh (i.e. low isolation level) (three-way ANOVA, $F_{3,78} = 4.910$, $p = 0.004$, Fig. 2).

The content of sediment chlorophyll *a* was significantly higher in exposed site than in sheltered site (three-way ANOVA, $F_{1,62} = 14.821$, $p < 0.001$) and at high isolation level (with mesh) than at low isolation level (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 feeding guild diversity. However, the content of chlorophyll *a* correlated positively with the number of recolonized animal species at low isolation level (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 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 recolonized macrofauna were found between treatments with and without *G. tigrinus*. The cages with *G. tigrinus* were characterized by lower abundance of *Cerastoderma glaucum* and Chironomidae larvae, and higher abundance of juvenile gammarid amphipod (SIMPER). Differences in the biomass structure were related to the higher biomass of *Cerastoderma glaucum* and *Hydrobia ulvae*, and lower biomass of *Gasterosteus aculeatus* in the cages with *G. tigrinus* than in the cages without the nonindigenous species. Both the number of recolonized macrozoobenthic species (one-way ANOVA, $F_{1,92} = 16.856$, $p < 0.001$) and the number of invertebrate feeding guilds (one-way ANOVA, $F_{1,92} = 4.697$, $p = 0.033$) were significantly higher in the presence of *G. tigrinus*.

Discussion

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

Relationships between functional richness 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 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) and this may partly explain the paucity of biotic interactions in this study.

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

The increased content of organic matter/chlorophyll *a* due to raised functional diversity may result from the complementary effect of functional diversity or positive mutualistic interactions between guilds as ecologically different species lead to greater resource utilization (Emmerson & Raffaelli 2000). Alternatively, increasing functional richness was 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 content of organic matter of 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 sedimentation of macroalgal debris at the end of the experiment may partly explain why we did not detect strong biotic control of ecosystem processes in the study area. Eutrophication induced proliferation of annual filamentous algae and the formation of drifting algal mats have increased organic matter content of sediment and occurrence of short term hypoxia practically in the whole coastal range of the Baltic Sea (Kiirikki & Blomster 1996, Norkko & Bonsdorff 1996ab, Bäck et al. 2000, Vahteri et al. 2000, Lehvo & Bäck 2001, Paalme et al. 2004). We found no clear indication of hypoxia in our treatments as the mortality of benthic invertebrates was low and not significantly higher in 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 functional diversity of assembled communities did not affect the subsequent recolonization of mesocosms, indicating that the colonisation is mainly driven by physical factors.

During this experiment *G. tigrinus* was found for the first time in the northern Baltic Sea. The number of recolonized macrozoobenthic species and feeding guilds was significantly higher in the cages with *G. tigrinus* than those without the invasive amphipod. Higher functional trait richness of benthic community seems to provide more resources for newcomers that likely have different food and habitat choice than the native species. Following physical disturbance dominant/opportunistic species recolonize quickly the sediment whereas rare species do not (Kenny & Rees 1996). Similarly, in our experiment the cages were mainly colonized by species dominating in the adjacent sea area. In that respect the opportunistic species like *G. tigrinus* has an advantage over other many native species being highly mobile, tolerating wide ranges of environmental conditions and having high reproduction rates (Dorgelo 1977, MacNeil & Prenter 2000, Wijnhoven et al. 2003).

It is suggested that the resistance of the community to biological invasions is related to its diversity (Stachovicz et al. 1999, Levine and D'Antonio 1999). The complexity of ecosystems may both

stabilize communities at a local scale (by dampening oscillations), and increase landscape-scale diversity (by promoting variability in time and space). Lowered diversity may destabilize ecosystem functioning making these communities more vulnerable to invasions (Stachovicz et al. 1999). Hence, low species diversity, together with the extensive anthropogenic impact in the Baltic Sea (Rosenberg 1985, Bonsdorff et al. 1997), may make the region prone to invasion (Stachovicz et al. 1999). However, the opposite relationship between community diversity and the occurrence of invasive species has been shown (Kaufman 1992, Lodge 1993, Cohen & Carlton 1998, Levine & D'Antonio 1999). Similarly, we found a significant positive correlation 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 recolonization. To date about one hundred non-native species have been reported in the Baltic Sea. Increasing invasion rates in the past 50 years (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 ecosystem and alter the fluxes of energy and matter (e.g. Loreau et al. 2001, Solan et al. 2004). This study indicated that physical factors controlled the ecosystem processes and biotic interactions were weak in the shallow water habitat of the northern Baltic Sea. With fluctuating environment the physically driven fluxes is 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 certain feeding guild may have a little impact on a particular ecosystem process the presence of any feeding guild may have a great impact on others, not involved in this study (Tilman et al. 1997). Our experiment lasted only for 38 days and it is possible that the role of biotic interactions may become more important in the longer time scales.

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Figures

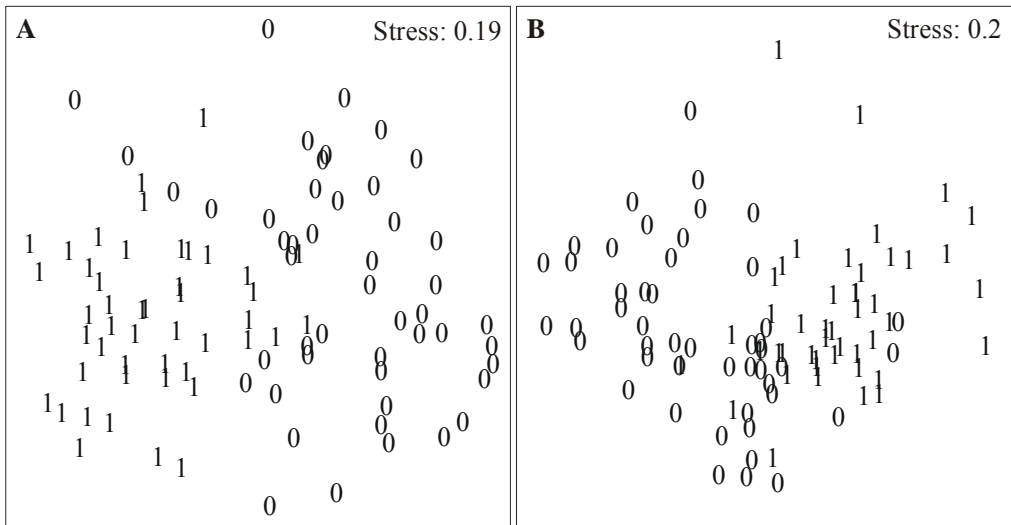


Fig. 1. nMDS ordination of recolonized macrobenthos abundance (A) and biomass (B) structure in mesocosms. 0 – sheltered site, 1 – exposed site.

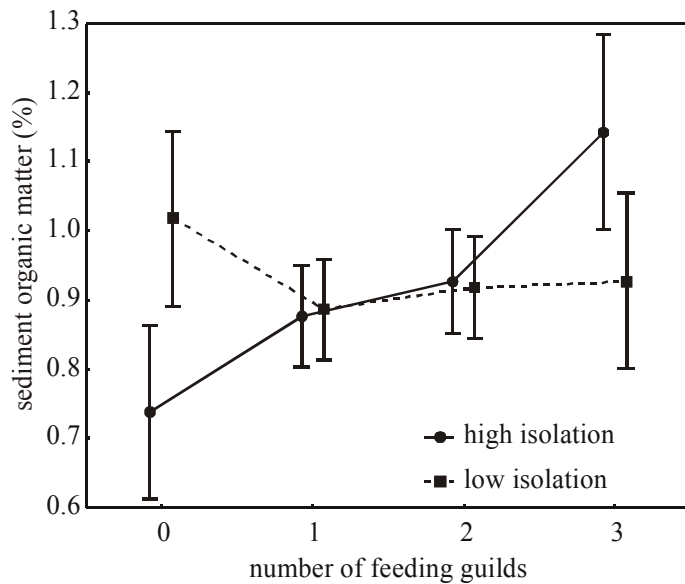


Fig. 2. Effects of isolation level and number of initial feeding guilds on the sediment organic matter content in cages. Vertical lines indicate 95 % confidence intervals.

Appendix III

Habitat and feeding choice of the invasive gammarid *Gammarus tigrinus* explain the decline of native gammarid diversity in the northern Baltic Sea

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Abstract

The North-American amphipod *Gammarus tigrinus* was observed for the first time in the northern Baltic Sea in 2003. Within two years the species has become one of the most abundant gammarid in the area. *G. tigrinus* occupied the same areas as compared to the native gammarid species, though, being more abundant in less exposed areas. Concurrent with this invasion the density of native gammarids declined manifold whereas the overall density of gammarids did not change. The addition of *G. tigrinus* reduced both overall and native gammarid diversity. Based on the microhabitat choice experiments the studied gammarids may be ranked as habitat generalists. The majority of gammarids hid under the stones. Amongst nine the most abundant macrophyte species and/or forms the gammarids had no clear preference. The presence of *G. tigrinus* reduced the affinity of native gammarids towards the brown alga *Pylaiella littoralis*. Feeding choice experiments indicated that *P. littoralis* was the most preferred macrophyte species followed by the green alga *Enteromorpha intestinalis*. Macrophyte species had no effect on the survival of gammarids. The presence of native gammarids had no impact on the survival of *G. tigrinus*. The presence of *G. tigrinus* reduced the survival of the native gammarids within *P. littoralis*. To conclude, *G. tigrinus* competes with the native gammarids for food and space. The competitive interactions between native gammarids and *G. tigrinus* may explain the reduction of amphipod diversity in the study area.

Keywords: Baltic Sea, *Gammarus tigrinus*, grazing rate, habitat choice, nonindigenous

Introduction

Human activities seriously modify the biogeographical distribution of species either by intentional acclimatisations or accidental introductions (Di Castri 1989). The introductions are known to cause large-scale ecological changes and economic damage world wide. The examples of invasions in the 1980s and 1990s have shown that successful exotics may render previously stable systems unbalanced and unpredictable (Carlton 1996; Ruiz et al. 1999) and may severely affect biological diversity in the area (Baker and Stebbins 1965; Levine and D'Antonio 1999).

The Baltic Sea is enclosed by land and communicates with the Atlantic by narrow outlets at its southwestern end. Owing to its isolation, short developing time, unstable salinity and temperature only a limited number of species have been able to adapt to the local conditions. The communities are characterised by a peculiar mixture of generalists mainly of marine and lacustrine origin. Specific brackish-water or endemic forms are nearly absent (Hällfors et al. 1981). In the northern Baltic Sea each ecosystem function is often represented by a single species. Thus, the loss or addition of a species may correspond to the loss or addition of ecosystem function.

Due to environmental instability, low number of species and increasing intensity of freight transportation the ecosystem of the Baltic Sea is very exposed to invasions. A number of benthic animals presently living in the Baltic have only recently invaded the area, some only in the last decades or years (Kotta 2000; Leppäkoski and Olenin 2001). A few of these non-native animals add unique ecological functions for the species-poor Baltic Sea ecosystem (Leppäkoski et al. 2002) whereas others share the same food resources with the local species and, thus, may reduce the native

biological diversity (Kotta et al. 2001; Kotta and Ólafsson, 2003). In either way the biological invasions potentially destabilise the functionality of whole ecosystem.

The gammarid amphipods are ranked among the most important necto-benthic herbivores in many coastal seas. The species are found on vegetated hard bottoms; however, the knowledge on their distribution, microhabitat and food selection is scarce. Earlier observations have indicated that gammarids choose their microhabitat according to the dimension of hiding place e.g. stone crevices, algae and mussel beds (Fenchel and Kolding 1979) and the quality and quantity of food (Kinne 1959). The gammarids are usually not microhabitat specialists (MacNeil et al. 1997a) and they have been recognized as both predators and herbivores (MacNeil et al. 1997b). However, fresh plants are necessary for their normal development (Kinne 1959). It is likely that gammarids graze algae more intensively than aquatic vascular plants (Cyr and Pace 1993).

Four gammarid species prevail in the northern Baltic Sea: *Gammarus oceanicus*, *G. salinus*, *G. zaddachi* and *G. duebeni* Lilljeborg (Hällfors et al. 1981; Kotta 2000). These species have different habitat requirements, though with significant overlap. *G. oceanicus* and *G. salinus* prefer deeper sites as compared to *G. duebeni* and *G. zaddachi*. *G. oceanicus* inhabits more exposed areas than *G. salinus*. Where *G. duebeni* and *G. zaddachi* coexist, there is in general a clearcut vertical zonation with *G. duebeni* along the shore and *G. zaddachi* mainly 30–40 cm lower (Vader 1977; Kotta et al. 2000; Herkül and Kotta 2007). Besides native gammarids the nonindigenous *Gammarus tigrinus* (Sexton) inhabits the region since 2003 (Kotta et al. 2006). The species was introduced into Europe from North America and was first recorded in England already in 1931 (Sexton 1939). *G. tigrinus* expanded into the Baltic Sea area in 1975 (Bulnheim 1976) but the further dispersal took place mainly in the 1990s and 2000s (Jazdzewski et al. 2002; Szaniawska et al. 2003; Pienimäki 2004; Kotta et al. 2006). *G. tigrinus* is euryhaline (Bousfield 1973), pollution tolerant (Savage 1996), with high reproductive rate (Chambers 1977) and, thus, has high potential to become a “pest species”.

It is likely that interspecific competition occurs between the native gammarids and *G. tigrinus* in the European fresh and brackish waterbodies. The examples from the Baltic Sea regions and elsewhere have shown that concurrent with the invasion of *G. tigrinus* the native gammarids have either disappeared or their densities have decreased manifold (e.g. Pinkster et al. 1992; Jazdzewski et al. 2002; Grabowski et al. 2006). Lacking the manipulative experiments we are not able to conclude whether this was due to the competitive interactions between gammarids or other factors (e.g. changing climate). Therefore, the aim of this paper was to investigate (1) whether *G. tigrinus* occupy same habitat and consume similar diet as the native gammarid species, (2) whether there is a competition for food and/or space between *G. tigrinus* and the native gammarids within different macrophyte species, and (3) whether we can see the reduction of abundance and diversity of native gammarids concurrent with the invasion of *G. tigrinus* in the northern Baltic Sea.

Material and Methods

The study was conducted in the shallow semi-enclosed Kõiguste Bay, Gulf of Riga, NE Baltic Sea. The prevailing sediment types of the bay are sandy clay mixed with pebbles, gravel or boulders. The prevailing depths are between 1 and 4 m. The area is influenced by a diffuse nutrient load from the moderately eutrophicated Gulf of Riga (Astok et al. 1999). The benthic vegetation is well developed and extensive proliferation of ephemeral macroalgae and the appearance of drift algal mats have been reported from the area in the recent years (Paalme et al. 2004; Lauringson and Kotta 2006).

Benthos samples were collected from 23 stations all over Kõiguste Bay in spring, summer and autumn 2003–2005 (Fig. 1). A modified Ekman type bottom grab (0.02 m²) was used for the sampling of benthic invertebrates. Sediment samples were sieved in the field on 0.25 mm mesh screens. The residuals were stored in a deep freezer at –20 °C and subsequent sorting, counting and determination of biomass of invertebrate species (dry weight g m⁻², 48h at 60°C) were performed in the laboratory using a stereomicroscope.

Habitat choice and grazing experiments were performed in Kõiguste Bay in May, July and September 2005. Depending on the natural occurrence of the macrophytes in the field different species were deployed in the experiment (Table 1). Macrophytes were collected from a shallow (1–3 m) area adjacent to Kõiguste Marine Biological Laboratory. Nine different macrophyte species and/or forms were used in the habitat choice and grazing experiments: the brown algae *Fucus vesiculosus* L. and *Pylaiella littoralis* (L.) Kjellm., the red alga *Ceramium tenuicorne* (Kütz.) Waern and *Furcellaria lumbricalis* (Huds.), the green algae *Cladophora glomerata* (L.) Kütz. and *Enteromorpha intestinalis* (L.) Nees. and the higher plant *Myriophyllum spicatum* L. Besides the typical *F. vesiculosus*, the dwarf form, nowadays described as *F. radicans* sp. nov. (Bergström et al. 2005), and both attached and free-floating forms of *F. lumbricalis* were deployed. *Gammarus* spp. were collected at the same site either under the stones by means of handnet or within the stands of *F. vesiculosus* by shaking the algae. Only adult specimens were used in the experiment.

Grazing was studied in 5×5×20 cm nylon netbags of 1 mm mesh size. Each macroalgal treatment was added either six specimens of *G. tigrinus*, six specimens of native *Gammarus* spp. or three specimens of *G. tigrinus* and native *Gammarus* spp. Three replicates of each treatment were used. Additionally, three control netbags contained algae relevant to each algal treatment and no amphipods. The wet weight of algae was determined prior to the experiment to the nearest of 0.01 g. Before weighing the algae were gently dried on plotting paper until the paper did not become wet any more. Additional three replicates of each macroalgal treatment served as control to obtain the ratio of wet to dry weight. The algae were dried at 60 °C during 48 h. On average 0.2 g dw of algae was deployed in each netbag. The netbags were placed at 2 m depth about 0.5 m above the bottom. Each series of the experiment lasted 15–20 days. At the end of the experiment the test animals were counted and the dry weights of macroalgae were determined. The changes in the dry weight of algae per individual of invertebrates in the nylon mesocosms served as the estimates of invertebrate grazing in the field. These values were corrected to the weight increment due to the photosynthetic activity of the algae i.e. control values.

The habitat choice of *Gammarus* spp. was studied in 3 replicate 100 l aquaria with a light regime similar to the field conditions. The aquaria received running seawater at a flow rate of 3 l h⁻¹. The water was taken from 2 m depth nearby Kõiguste Marine Biological Laboratory. Each aquarium were added available macrophyte in field and either ten native gammarids, ten *G. tigrinus* or the mixture of five specimens of native gammarids and five specimens of *G. tigrinus*. The algae were attached to the aquarium floor by pebbles. Additionally a few pebbles without macroalgae were added. The coverage of algae, pebbles and the area without vegetation in the aquaria was 20%, 10% and 70%, respectively. The number of *Gammarus* spp. on different macroalgae, under pebbles and those swimming freely were recorded every hour for 30 h. During dark periods artificial red light was used during the observations. All water was exchanged and new test organisms were collected prior to each experiment. The survival of *Gammarus* spp. in the habitat choice experiment was 100%.

For univariate analyses the statistical programme "Statistica" was used (StatSoft Inc. 2004). The analysis of variance (ANOVA) was employed to describe the effect of years and experimental treatments on gammarid diversity, abundances, habitat and grazing selectivity and survival. The percentage data sets were arcsine transformed before statistical analysis. The package "PRIMER" was used for the calculation of Shannon diversity index (Clarke and Warwick 2001). The distribution maps of gammarid abundance were made with MapInfo Vertical Mapper v3.0 (MapInfo 2003). For the gridding Kriging method was used.

Results

In 2003 only native gammarid species *G. oceanicus*, *G. salinus* and *G. zaddachi* were found from benthos samples in Kõiguste Bay. The invasive gammarid *G. tigrinus* was not found in the area although the bay was intensively monitored throughout the ice-free season. Since 2004, however, *G. tigrinus* was common all over the Kõiguste Bay area. The species occupied the same areas as compared to the native gammarid species, though, being more abundant in less exposed areas. The abundance of *G. tigrinus* were usually around 25 ind. m⁻² but in the inner bay area the values exceeded

250 ind. m⁻². The share of *G. tigrinus* usually reached to 25% in total gammarid abundances, with maximum values above 75% in the inner part of Kõiguste Bay. The invasive species had higher abundances in autumn than in spring and summer (Fig. 2, 3).

Concurrent with the invasion of *G. tigrinus* the abundance of native species have significantly declined (one-way ANOVA, $p < 0.001$) whereas the overall abundance of gammarids did not change in 2003–2005 ($p = 0.87$) (Fig. 4). On the other hand the addition of *G. tigrinus* reduced both overall and native gammarid diversity in the study area (one-way ANOVA, $p < 0.001$) (Fig. 5). Prior to the invasion of *G. tigrinus* the native gammarids had high densities both in the inner and outer parts of Kõiguste Bay. After the invasion *G. tigrinus* prevailed in the inner parts of Kõiguste Bay and the native gammarids had higher densities in more exposed parts of the bay.

Habitat selection experiments showed that the majority of studied gammarids hid under the stones regardless of macrophyte community. Amongst nine most abundant macrophyte species and/or forms the gammarids had no clear preference. The presence of *G. tigrinus* reduced the affinity of native gammarids towards the brown alga *Pylaiella littoralis* (two-way ANOVA, $p < 0.001$) whereas other differences were not statistically significant ($p > 0.05$). Based on the visual observations *G. tigrinus* had substantially higher swimming speed as compared to the native gammarids.

Feeding choice experiments indicated that *P. littoralis* was the most preferred macrophyte species followed by the green alga *E. intestinalis*. Grazing was lower in spring than in other seasons (one-way ANOVA, $p < 0.001$). Macrophyte species had no effect on the survival of gammarids ($p > 0.05$). The presence of native gammarids had no impact on the survival of *G. tigrinus*. The presence of *G. tigrinus* reduced the survival of the native gammarids within *P. littoralis* (two-way ANOVA, $p = 0.03$).

Discussion

The North-American amphipod *G. tigrinus* was observed for the first time in the northern Baltic Sea in summer 2003 in connection to another experiment carried out in Kõiguste Bay. At the end of experiment the invasive species *G. tigrinus* was observed in many mesocosms. The species was mainly associated to the bare sand communities that contained the cockle *Cerastoderma glaucum* Bruguière. Densities ranged between 100 and 800 ind. m⁻² (Kotta et al. 2006). Despite of intensive monitoring we failed to find the invasive gammarid from traditional benthos samples in 2003 and earlier (Kotta 2000; Orav-Kotta 2004; Lauringson and Kotta 2006; this study) and there were no other records of *G. tigrinus* in the northern Baltic Sea except for a single finding of the species in the Finnish coast of the Gulf of Finland in summer 2003 (Pienimäki 2004). Thus, it is likely that *G. tigrinus* established in the study area in late 2003 and become a dominant member of amphipod community all over Kõiguste Bay in 2004.

In its native range the distribution area of *G. tigrinus* overlap with some gammarids that are also common in the Baltic Sea area. But due to the differences in habitat selectivity these species rarely co-exist (Steele and Steele 1972). In the Baltic Sea, however, many euryhaline species widen their ecological range due to low and stable salinities (Dahl 1973; Fenchel and Kolding 1979) and therefore *G. tigrinus* may be found in same habitats as *G. oceanicus*, *G. salinus*, *G. zaddachi* and *G. duebeni*.

Following the establishment of *G. tigrinus* the abundance of native species significantly declined whereas the overall abundance of gammarids did not change in the study period. This indicates that food and/or space is limiting the population growth of gammarids and there is a food and/or space competition between *G. tigrinus* and the native species in the study area. The experiments supported the field observation as there were no differences in the microhabitat and grazing preferences of native gammarids and *G. tigrinus*. When *G. tigrinus* was present then the native gammarids avoided *P. littoralis* i.e. the prime diet of the invasive species. Besides, the presence of *G. tigrinus* induced higher mortality of native gammarids within *P. littoralis*.

We are aware that besides macrophytes small amphipods may graze periphytic algae (Duffy 1990; Olsen and Lubchenco 1989) and this may explain why we were not able to demonstrate strong grazing selectivity of the studied gammarids. Whether periphyton or macrophytes are grazed may depend on periphyton density and this needs to be clarified in future studies. However, in light of high grazing pressure and strong competitive interactions within *P. littoralis*, it is likely that macrophytes at least partly contribute to the diet of gammarids in the northern Baltic Sea.

Despite of broad ecological niche *G. tigrinus* was more abundant in less exposed parts of the bay. This is in agreement with earlier studies from the Baltic Sea area (Jazdzewski et al. 2002; Szaniawska et al. 2003) and might be associated to the better tolerance of *G. tigrinus* to fluctuating life condition e.g. salinity and hypoxia (Bousfield 1973; Platvoet and Pinkster 1995; Gerhardt and Quindt 2000). Despite of adverse oxygen conditions these sites are characterised by high food availability and may support dense population of gammarids. Alternatively, the density of *G. duebeni* is very high in the upper reaches of the shore of exposed Kõiguste Bay (Herkül and Kotta 2007) i.e. in the most preferred depth range of *G. tigrinus*. *G. duebeni* is known to outcompete *G. tigrinus* in freshwater biotope (MacNeil and Prenter 2000) and the same mechanism is possible in the brackish Baltic Sea.

Thus, based on the field observations and experimental evidence, *G. tigrinus* competes with the native gammarids for food and space. The competitive interactions between native gammarids and *G. tigrinus* may explain the reduction of amphipod biodiversity in the study area. The effect of *G. tigrinus* is likely more severe in less exposed parts of bays where *G. tigrinus* may outcompete native gammarids in near future.

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Table 1. Different macrophyte species and forms used in the habitat choice and grazing experiments. The choice of macrophyte species depended on their natural occurrence in the field.

<i>Macrophyte species</i>	<i>May</i>	<i>July</i>	<i>September</i>
<i>Fucus vesiculosus</i>		+	+
<i>Fucus radicans</i>		+	
<i>Pylaiella littoralis</i>		+	
<i>Ceramium tenuicorne</i>			+
<i>Furcellaria lumbricalis</i> attached		+	+
<i>Furcellaria lumbricalis</i> floating		+	
<i>Cladophora glomerata</i>		+	
<i>Enteromorpha intestinalis</i>	+	+	+
<i>Myriophyllum spicatum</i>	+	+	+

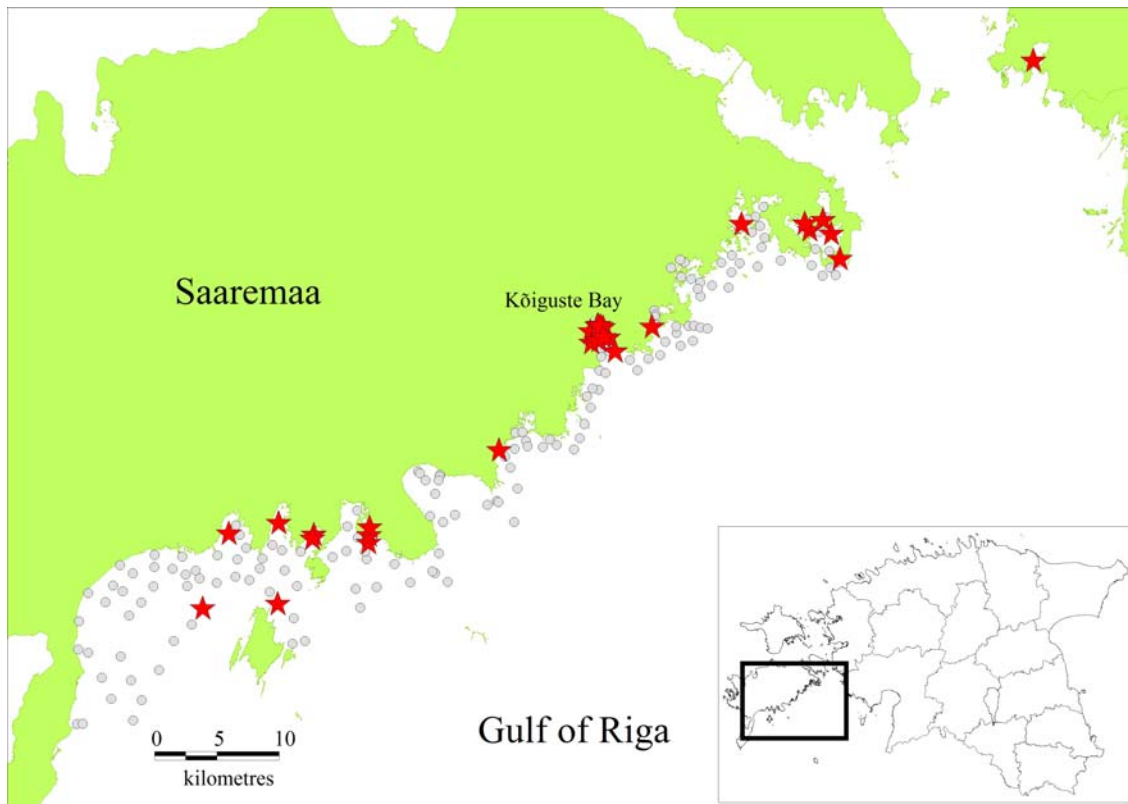


Fig. 1. Study area. Circles indicate sampling stations and stars the locations where.

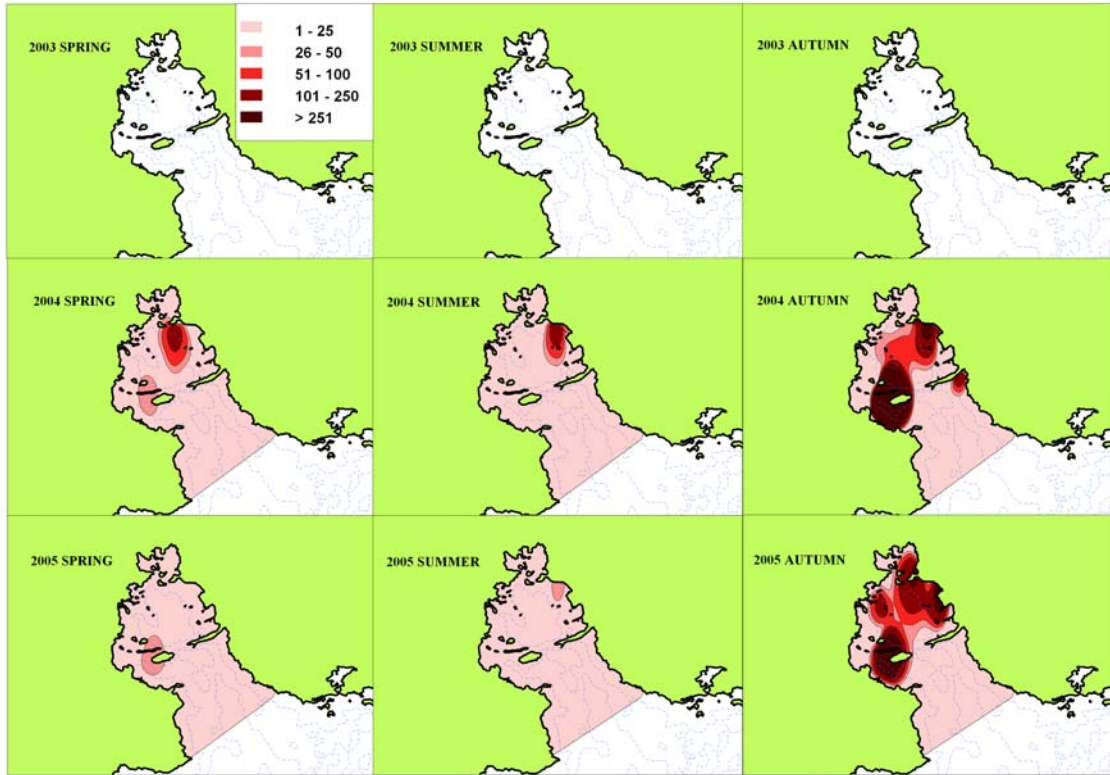


Fig. 2. Abundance distribution of *G. tigrinus* (ind. m⁻²) in Köiguste Bay in 2003–2005.

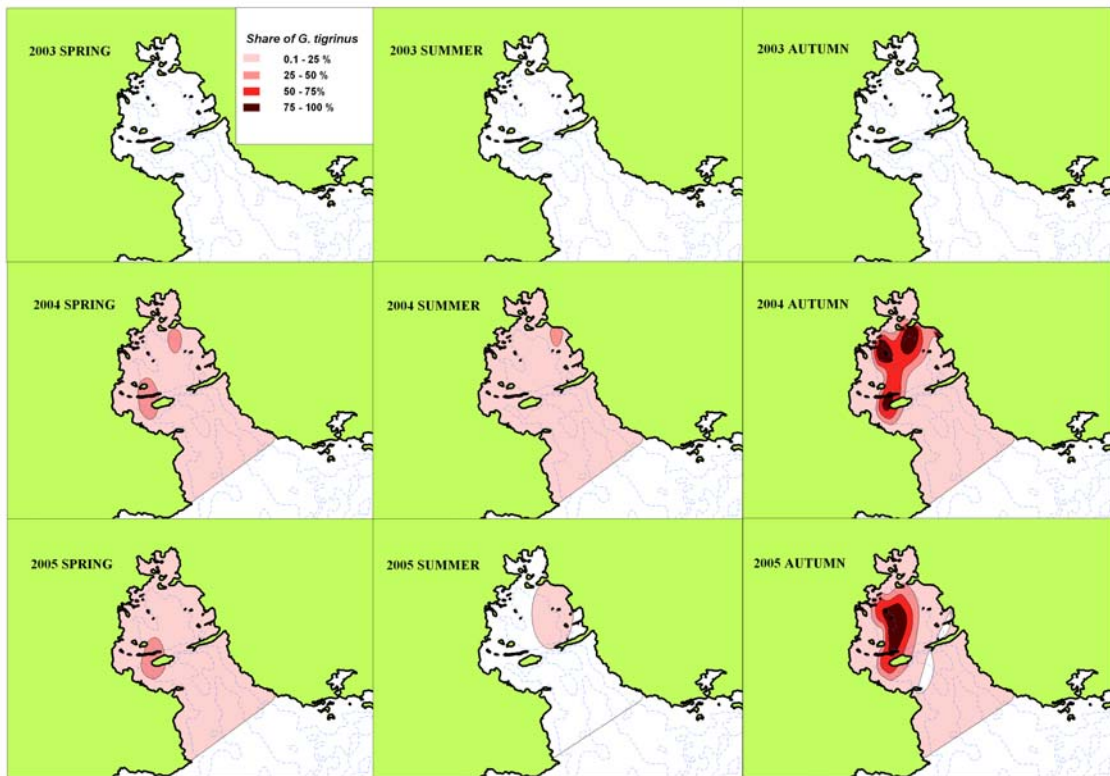


Fig. 3. Share of *G. tigrinus* to the total abundance of gammarids (%) in Köiguste Bay in 2003–2005.

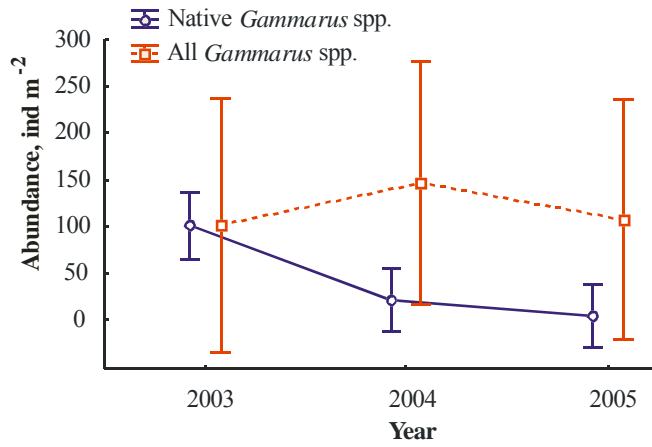


Fig. 4. Mean abundance (ind. m⁻²) (\pm 95% C.I.) of native and all gammarid species in Kõiguste Bay in 2003–2005.

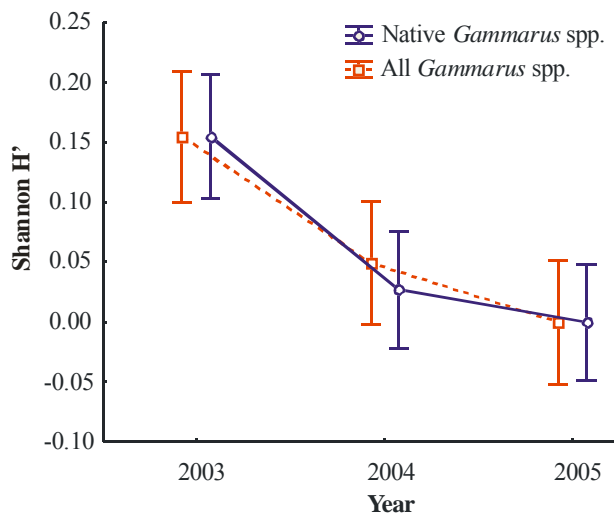


Fig. 5. Shannon diversity index (\log_e) (\pm 95% C.I.) of native and all gammarid fauna in Kõiguste Bay in 2003–2005.