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Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea

Abstract Population dynamics and ecological impacts of the cirriped *Balanus improvisus*, the polychaete *Marenzelleria neglecta* and the cladoceran *Cercopagis pengoi* were investigated in the north-eastern Baltic Sea. After an increase during the first decade of invasion, the density of *M. neglecta* and *C. pengoi* declined afterwards. The studied abiotic environmental variables did not explain the interannual variability in the seasonal cycles of *M. neglecta* and *C. pengoi* indicating that the species are at their initial phase of invasion. The population dynamics of *B. improvisus* was best described by water temperature. *B. improvisus* promoted the growth of the green alga *Enteromorpha intestinalis*. *M. neglecta* enhanced the content of sediment chlorophyll *a* and reduced growth and survival of the polychaete *Hediste diversicolor* and growth of the amphipod *Monoporeia affinis*. Concurrent with the invasion of *C. pengoi* the abundance of small-sized cladocerans declined, especially above the thermocline. *C. pengoi* had become an important food for nine-spined stickleback, bleak, herring and smelt.

Keywords Baltic Sea · Benthic and pelagic systems · Ecological impact · Nonindigenous species · Interspecific interaction

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Introduction

The ecology and impact of marine invaders are little known. We rely on field data and there are a few papers linking experimental and field observations (Parker et al. 1999). In the Baltic Sea there exists some information on the impacts of benthic invasions (Kotta et al. 2001; Kotta and Møhlenberg 2002; Kotta and Ólafsson 2003) whereas data on pelagic species are rarer (Leppäkoski and Olenin 2001; Leppäkoski et al. 2002).

In this paper the population dynamics and ecological impacts of three established alien species the cirriped *Balanus improvisus* Darwin, the polychaete *Marenzelleria neglecta* (Sikorski and Bick sp. nov.) and the cladoceran *Cercopagis pengoi* (Ostroumov) are described in the north-eastern Baltic Sea. The first two species are benthic as adults and have pelagic larvae. The third species spends the whole life cycle in the pelagic system except for benthic resting eggs. *M. neglecta* and *C. pengoi* are among recent newcomers in the Baltic Sea (Bick and Zettler 1997; Ojaveer and Lumberg 1995) whereas the invasion of *B. improvisus* dates back to the late nineteenth century (Välikangas 1926; Lindquist 1959). *B. improvisus* and *M. neglecta* originate from North America and *C. pengoi* from Ponto-Caspian area. The transfer of ballast water between international ports is suggested as a potential vector of these invasions (Leppäkoski and Olenin 2001).

The first aim of the study was to observe the changes in mesozooplankton communities in relation to the establishment of *C. pengoi* and estimate the share of *C. pengoi* in the fish diet. Secondly, we tested the effect of *B. improvisus* on the growth of green algae. *B. improvisus* is a prevailing benthic suspension feeder in the north-eastern Baltic Sea (Segerstråle 1957; Kotta et al. 2003). Owing to considerable biodeposition the species is capable of promoting the growth of benthic macrophytes (Reusch et al. 1994; Kautsky 1995). Thirdly, we tested whether the presence of *M. neglecta* had an effect on the dominating macrofaunal species and whether

M. neglecta itself was affected by interspecific interactions. The addition of an efficient deposit feeder into the low nutrient benthic system is likely to stress the native fauna through competitive interactions for food and/or for space.

Materials and methods

Field sampling

Macrozoobenthos was annually sampled around the entire Estonian coastal sea in May during 1991–2004 (Fig. 1). The samples were collected by a van Veen grab (sampling area 0.10 m², one sample per station, total 336 samples, sediments ranging from coarse sand to silty bottoms, depth range 5–100 m). Material was sieved through a 0.25 mm net and then deep frozen at −20°C. Animals were identified to the lowest taxonomic classification possible, dry weights were obtained (±0.1 mg) after drying the material at 60°C for 48 h.

Long-term dynamics of mesozooplankton were studied at a 10 m station in Pärnu Bay. Zooplankton was weekly sampled from May to July during 1957–1969 and from May to October during 1970–2004. Additional zooplankton samples were collected at six stations near Tallinn Bay during 1997–2002 and in Narva Bay during 2001–2002. The sampling was done fortnightly from June to August and monthly in May, September and October. Mesozooplankton samples were collected by vertical hauls through the whole water column with a Juday net (mouth surface area 0.1 m², mesh size 90 μm, total 1,492 samples). Samples were preserved in a 4% formaldehyde solution and analysed by routine method (HELCOM 1988).

During sampling, water temperature and salinity were measured. Since 1993 water nutrients were also analysed at each site during winter. Because of the strong seasonality, the concentration of nutrients in the water column during winter may be used as a proxy for eutrophication in the Baltic Sea area (HELCOM 2002). Prior to 1993 river inflows were used as a proxy for eutrophication. Data on ice conditions were obtained from Estonian Hydrometeorological Institute.

Monthly daytime experimental bottom trawl surveys were performed at 6–54 m in the central and northeastern Gulf of Riga during June–September 1994–1998 (for details see Ojaveer 1997). In each sample, stomachs of 20 individuals were analysed according to Melnichuk (1980). Altogether 2,074 herring *Clupea harengus membras* L., 1,117 smelt *Osmerus eperlanus* (L.), 769 three-spined stickleback *Gasterosteus aculeatus* L., 80 nine-spined stickleback *Pungitius pungitius* (L.) and 71 bleak *Alburnus alburnus* (L.) individuals were analysed.

Experiments

The effect of the suspension feeder *B. improvisus* on the growth of the green alga *Enteromorpha intestinalis* (L.) was studied in the Gulf of Finland (59°30′N, 25°11′E) during June–September 2002. We used 3 l buckets that had 2 mm barnacles covered fully on the outside. By cleaning the bucket, the density of the barnacles was set at 0, 10, 20, 40, 70, 80 and 100%. Each density was replicated three times. Zero coverage represented control values. The buckets were filled with clean pebbles and covered with tightened mesh cloth to enable algal settlement without any space competition with barnacles, i.e. barnacles occurred only the outside and top edge of the bucket. The buckets were randomly placed on the exposed seafloor at a depth of 0.5 m. The average distance between the buckets was 0.5 m. At the end of the experiment the coverage and total dry weight of *B. improvisus* and *E. intestinalis* were determined and regressions between their densities were computed.

Fig. 1 Study area. *Dark circles* indicate the sampling sites of mesozooplankton and *stars* the sites of macrozoobenthos, respectively
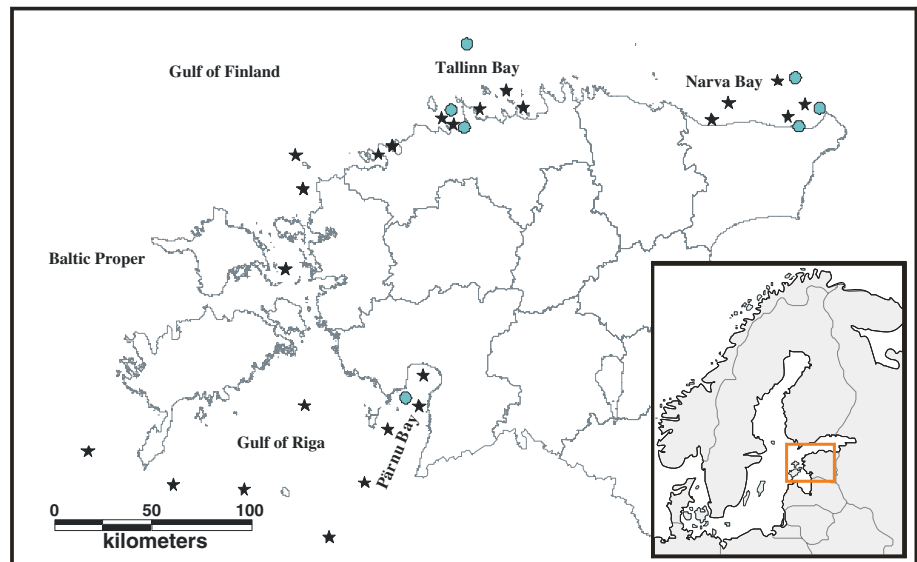
Competitive interactions between the shallow water species *Macoma balthica* L., *Cerastoderma glaucum* Bruguière, *Hediste diversicolor* (O. F. Müller), the deep water amphipod *Monoporeia affinis* Lindström and the introduced polychaete *M. neglecta*, were experimentally quantified (for details see Kotta et al. 2001; Kotta and Olafsson 2003). In short, test organisms were added in densities consistent with their values in the field (replicated thrice). At the end of the experiment the sediment in the mesocosms were sampled for chlorophyll *a* and phaeopigments (Strickland and Parsons 1972). Living animals were counted and changes in survival and the growth of test organisms were estimated.

Statistics

For univariate analysis the statistical programme "Statistica" was used (StatSoft Inc. 2004). We employed correlation, linear and polynomial linear regression analyses to describe the relationships between abiotic and biotic environmental variables. Polynomial regression results are only reported if significantly better fits were achieved using this method compared with the linear model. The statistical differences between experimental treatments were obtained by ANOVA and *t*-tests (Sokal and Rohlf 1981).

Multivariate data analyses were performed by the statistical program "PRIMER" (Clarke and Warwick 2001). A Spearman rank correlation (ρ) was computed between the similarity matrices of mesozooplankton abundance and environmental data to examine the ecological significance of environmental variables in mesozooplankton dynamics (BIO-ENV procedure, Clarke and Ainsworth 1993) and the significance of the correlation was determined by the PRIMER programme RELATE (Clarke and Warwick 2001).

Results

Balanus improvisus was observed for the first time in the study area in the late nineteenth century (Välikangas 1926; Lindquist 1959). In the present study the species occurred in plankton at high densities along the whole Estonian coastal sea. *M. neglecta* and *C. pengoi* appeared in plankton samples in 1991 and *M. neglecta* appeared in benthos in 1995 (except for a single finding in the western Gulf of Riga in 1993). Since invasion the density of *C. pengoi* gradually increased until 2002 and then dropped to the level of the early 1990s. The abundance of pelagic larvae of *M. neglecta* peaked in 1998, 1999 and 2003, and adults in 1997 and 2004. Following the very harsh winter of 2002 the adult *M. neglecta* was not found in the shallow areas of Pärnu Bay and was rare in the deeper sea in 2003 (Figs. 2, 3).

Temperature at the bottom had the best match with the abundance of *B. improvisus* larvae (BIOENV,

$\rho = 0.624$). Other variables predicted less than 5% of the variability. The studied abiotic environmental variables (temperature, salinity, nutrient load, ice conditions) did not explain the interannual variability in the seasonal cycles of *M. neglecta* and *C. pengoi*.

Field experiments indicated that *B. improvisus* promoted the settlement success and growth of the green alga *E. intestinalis*. In the treatment without *B. improvisus* (control treatment), the algal coverage was below 5%. The coverage of *E. intestinalis* increased curvilinearly with the coverage and biomass of *B. improvisus*. The development of *E. intestinalis* was better explained by the coverage of the barnacles than their biomass (Fig. 4). No other macroalgal and attached invertebrate species were found on the buckets.

An in situ experiment combining the natural densities of native species and the introduced polychaete, showed that sediment chlorophyll *a* content in the treatment with *M. neglecta* was significantly higher than in all other treatments (one-way ANOVA, $df = 7$, $F = 24.5$, $P < 0.001$). *M. neglecta* was found to significantly reduce the survival of *H. diversicolor* (one-way ANOVA, $df = 1$, $F = 7.7$, $P = 0.024$) and the growth of *M. affinis* (one-way ANOVA, $df = 1$, $F = 4.8$, $P = 0.033$). The survival of *M. neglecta* was significantly reduced by the presence of *M. balthica* (one-way ANOVA, $df = 2$, $F = 18.8$, $P < 0.001$). Field data agreed with the experimental finding that *M. affinis* was not found even at moderate densities of *M. neglecta*. On the other hand, the negative effect of *M. balthica* on *M. neglecta* was observed in pristine conditions and not in eutrophicated areas (pooled data in the whole Gulf of Riga, Figs. 5, 6).

At higher abundance of *C. pengoi* above the thermocline, the cladoceran *Bosmina coregoni maritima* P. E. Müller stayed below the thermocline ($r = -0.61$, $P < 0.01$). In addition to changed vertical distribution, annual density of *B. c. maritima* and other less abundant cladocerans like *Evadne nordmanni* Lovén and *Pleopsis polyphemoides* (Leuckart) significantly declined after the invasion compared to the pre-invasion period ($\log(x + 1)$-transformed data, *t*-test, $P < 0.001$).

The contribution of *C. pengoi* in the diet of fish was high when the cladoceran was present in the water column (June-September). The nine-spined stickleback started feeding on the cladoceran when it had attained the length of 3.4 cm, the three-spined stickleback and herring at a length of 4.1 cm, the bleak at a length of 6.2 cm and the smelt at a length of 7.3 cm. However, *C. pengoi* was exceptionally found in the stomach of a herring larvae of 2.2 cm (length of *C. pengoi* was 1.0 cm) (Table 1). The consumption of *C. pengoi* by herring was size-dependent. The share of *C. pengoi* in the diet of large herring (15–16 cm) reached over 10% by wet weight and exceed by a factor of 2–3 that of smaller individuals (Fig. 7). Significant size-specific differences were not observed for other fish.

Fig. 2 Long term changes of pelagic larvae of *B. improvisus* and *M. neglecta* and *C. pengoi* in Pärnu Bay, NE Gulf of Riga in 1957–2004
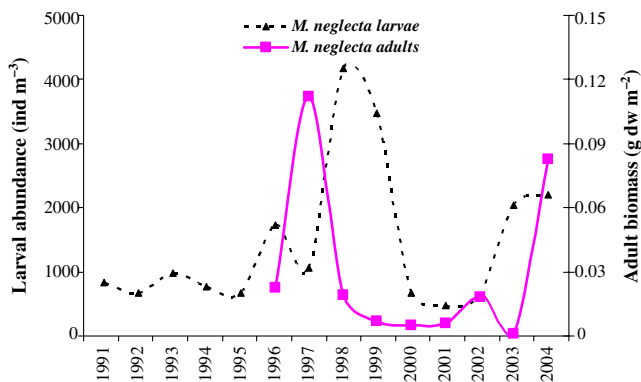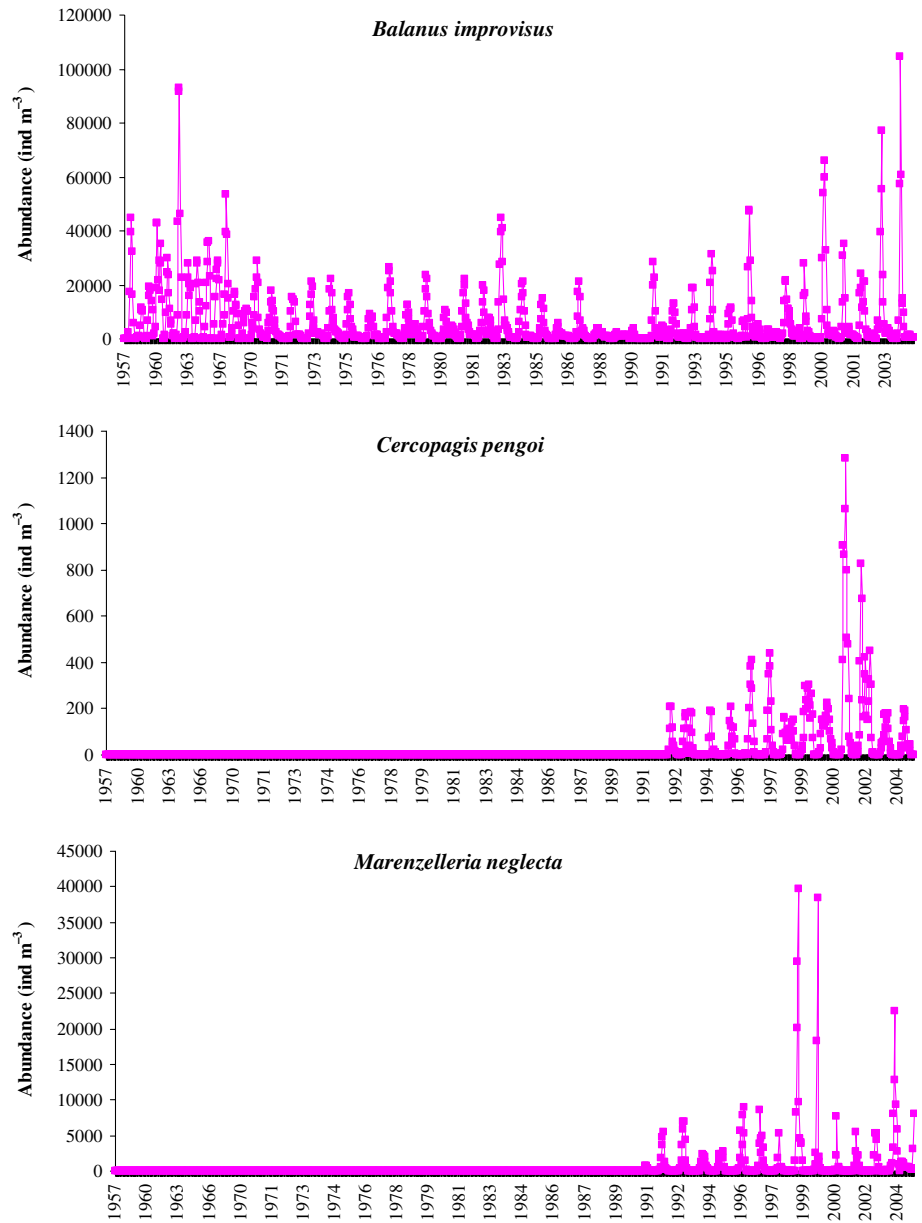

Fig. 3 Mean annual densities of *M. neglecta* in Pärnu Bay, NE Gulf of Riga in 1991–2004. The abundance of pelagic larvae is indicated by *dotted line* and the dry weight of adults by *solid line*

Discussion

Field experiments showed that *B. improvisus* promoted the settlement success and further development of the filamentous algae in the study area. The mechanism behind this relationship is likely the increased nutrient availability in benthic system through the biodeposition of suspension feeders (Reusch et al. 1994; Kautsky 1995). As macroalgal coverage was low in the treatment without *B. improvisus*, nutrients rather than the space was limiting algal growth in the experiment. Rising nutrient load has been shown to compensate the herbivore pressure on the early life stages of *E. intestinalis* (Lotze et al. 2000) as the spore germination and growth of the species may be reduced up to 99% by mesograzers (Lotze et al. 1999). Besides, the growth of an adult algal
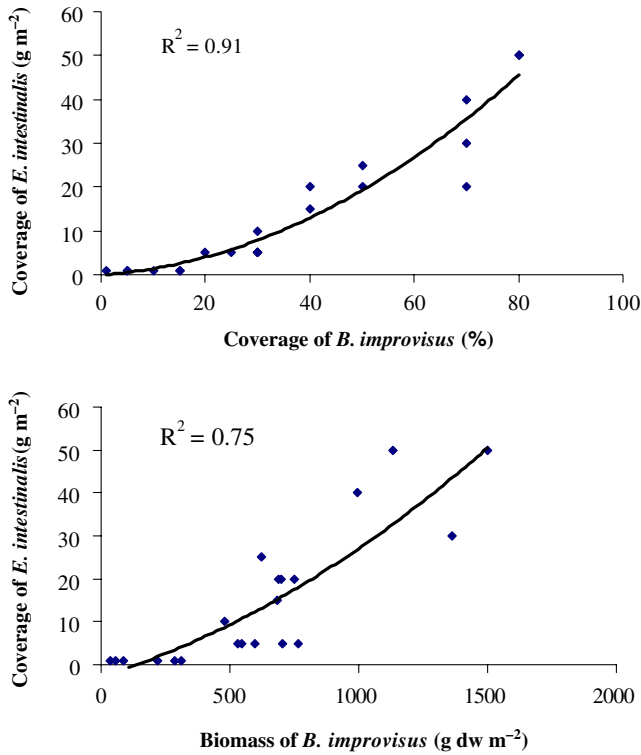
Fig. 4 Polynomial regressions between the densities of *B. improvisus* and *E. intestinalis* on the mesocosms in the Gulf of Finland in 2002

Fig. 6 Relationships between the biomass of *M. balthica* and *M. neglecta* at low and high eutrophication in the Gulf of Riga

canopy is also favoured by small-scale nutrient enrichment (Lotze et al. 2000).

Prior to the invasion of *B. improvisus* there was no benthic suspension feeding mode in the northern Baltic Sea where salinity is below 5 psu and the climate is too cold for another non-indigenous suspension feeder *Dreissena polymorpha* (Pallas) (Leppäkoski and Olenin 2001). Thus, the invasion of *B. improvisus* potentially increased the energy flows from pelagic system to benthos and caused a shift from pelagic production to benthic production.
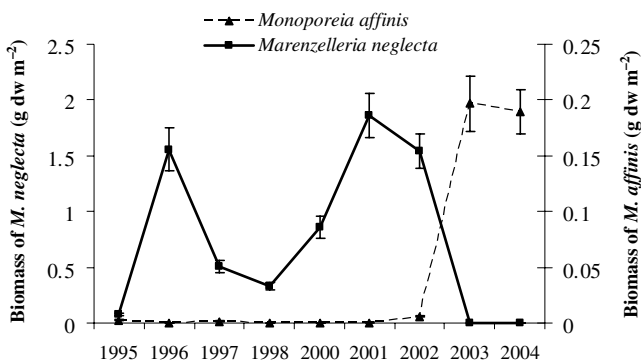

Fig. 5 Interannual changes in the biomass of *M. neglecta* and *M. affinis* in the Gulf of Riga in 1995–2004 (pooled data of 8 stations, mean ± SE, note differences in scales)
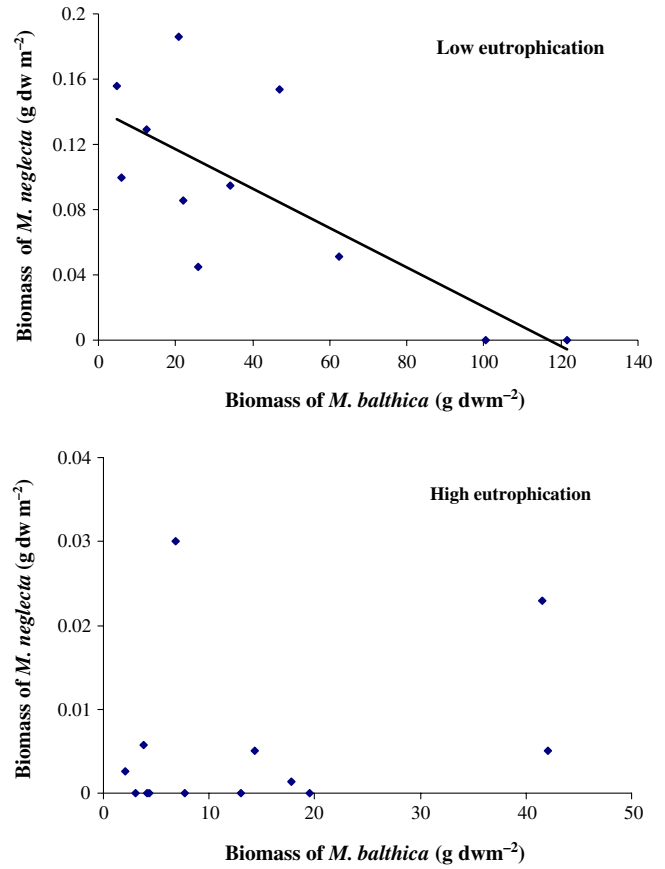
Competitive interactions between *M. neglecta* and native fauna may explain why the polychaete densities are low when the densities of *M. balthica* are high and why *M. affinis* did not recover in the area with high density of *M. neglecta*. Competitive superiority of *M. balthica* over *M. neglecta* is likely to be due to this species' efficient feeding modes and better tolerance of food shortages (e.g. Brafield and Newell 1961; Ólafsson 1986; Kotta et al. 2004a). Because *M. balthica* is one of the most common species in the soft bottom sediments (Segerstråle 1957; Hällfors et al. 1981), competitive interactions between *M. neglecta* and *M. balthica* appear to be a key factor limiting the further expansion of *M. neglecta* in the study area.

Higher sediment chlorophyll *a* content in the treatments with *M. neglecta* indicates higher biodeposition and/or bioturbating activity of the polychaete as compared to the native fauna. According to Pelegri and Blackburn (1995) polychaetes significantly accelerate nitrogen remineralisation and transformation processes within the sediment. As *M. neglecta* burrows much deeper and more actively than the native polychaetes the amount of reworked sediments, i.e. the availability of nutrients to microalgal growth, is higher in the presence of *M. neglecta*.

Table 1 Statistics of fish samples where at least one fish contained *Cercopagis pengoi* in the stomach

	L_{min} with *Cerc.*	L_{mean} with *Cerc.*	L_{mean} without *Cerc.*	Difference[b]	Percentage of fish with *Cerc.* in stomach	Percentage of *Cerc.* in stomach (wet wt.)	N
Herring (1+)		14.0	13.3	$P < 0.05$	53.6	45.7	256
0-Group	4.1	5.2	5.1	NS	7.7	1.4	40
Larvae[a]	2.2						
Smelt (1+)		13.1	10.5	$P < 0.001$	25.0	40.8	78
0-Group	7.3	8.1	7.9	NS	33.3	33.7	60
3-Spined stickleback	4.1	5.0	5.3	$P < 0.05$	25.0	26.9	94
9-Spined stickleback	3.4	4.3	5.0	$P < 0.001$	51.1	44.7	60
Bleak	6.2	9.8	10.2	NS	93.4	85.7	70

Samples collected in the main feeding areas of the Gulf of Riga during the main feeding period (June–September) in 1994–1998. Fish length (total length, L) is given in centimetre
[a]Single finding of *Cercopagis pengoi* in the larval fish intestine in Pärnu Bay (NE Gulf of Riga) in 2004
[b]Difference between the mean length of fish with and without *Cercopagis pengoi* in stomach (*P* significance level, *NS* not significant)

Our study indicates that *C. pengoi* preys on the small cladocerans that are important food items for mysids and fish (Kotta et al. 2004b). On the other hand the introduced species is preyed by fish. Thus, the effects of *C. pengoi* on the pelagic ecosystem are two sided as competing for food with other pelagic predators and reducing the efficiency of energy transfer to upper trophic levels.

The population of the cladoceran *B. c. maritima* has collapsed in the whole north-eastern Baltic Sea including those sub-areas where the density of *C. pengoi* was low. Our results point out that the invasion of *C. pengoi* is at least partly behind this decline. In the Gulf of Finland the deeper water layers may be considered as a refuge for *B. c. maritima* as no diurnal vertical migration of *C. pengoi* has been recorded in invaded systems and the majority of the population is located in the upper water layer (e.g. Gorohhova et al. 2000).

Fish predation on *C. pengoi* was species-specific and size-dependent. When *C. pengoi* occurred in the plankton then its share in the diet of fish was noticeable. *C. pengoi* primarily contributed to the diet of small-sized fish inhabiting coastal areas, e.g. bleak and nine-spined stickleback due to strong overlap of spatial distribution. The pelagic species herring, smelt, three-spined stickleback, that are abundant in open and deeper areas, consumed less *C. pengoi*. Consumption of *C. pengoi* by smelt enhances energy transfer from the surface waters to the cold deeper water layers. This is especially important during the periods of food shortage in deep water layers due to oxygen deficiency and mild winters that do not favour the formation of abundant cold arctic invertebrate community in this deep environment.

To conclude all studied alien species are potentially able to affect biodiversity and modify organic matter and energy transfer pathways compared to the pre-invasion time. Further studies should quantify the changes in energy flow through the food-web as a result of alien species and assess the realised potential of competition between alien invertebrates and native species for the same food and habitat resource.
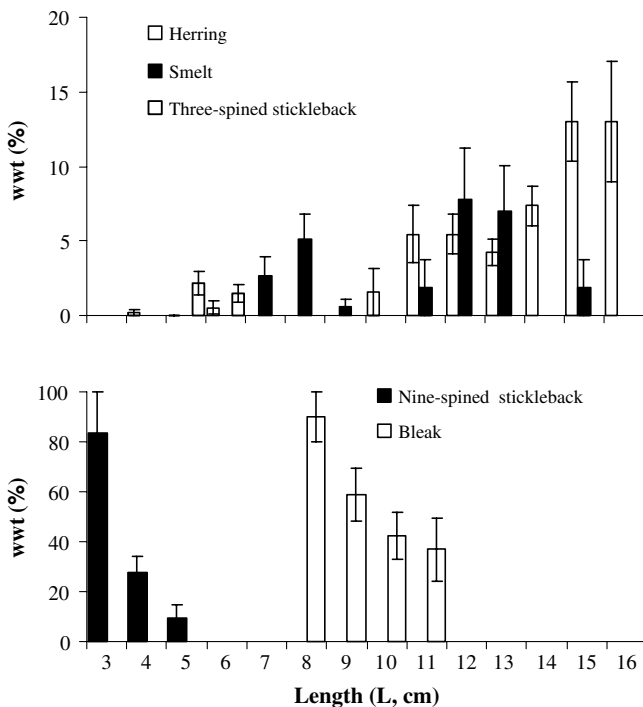

Fig. 7 Contribution (wet weight %, mean ± SE) of *Cercopagis pengoi* in the diet of herring *Clupea harengus membras*, smelt *Osmerus eperlanus*, three-spined stickleback *Gasterosteus aculeatus*, nine-spined stickleback *Pungitius pungitius* and bleak *Alburnus alburnus* in the Gulf of Riga during the main feeding period in the main feeding grounds in 1994–1998

MPS-06005 of MarBEF. The experiments comply with the current laws of the country in which they were performed.

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