ORIGINAL ARTICLE

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Effects of nonindigenous species on diversity and community functioning in the eastern Gulf of Finland (Baltic Sea)

Abstract An increase of xenodiversity in plankton and benthos in the eastern Gulf of Finland was observed from 1998 to 2004. Nonindigenous species account for 4.8% of all species found and up to 96% of total biomass. Invasive benthic omnivores, the alien amphipods *Gmelinoides fasciatus* and *Pontogammarus robustoides* and the predaceous fish *Perccottus glenii* with their versatile diets strongly affect the community structure. Invasive sessile seston-feeders that directly (through grazing and water clearance) and indirectly (through recycling of nutrients) interact with other ecosystem components, are mainly represented by the zebra mussel *Dreissena polymorpha*, which affect the structure of benthic and planktonic communities as well as benthic-pelagic coupling. The invasive predatory cladocerans *Cercopagis pengoi* and *Evadne anonyx* and larvae of *D. polymorpha* are only temporary components in the zooplankton, which is limiting their overall effect. Alien benthic bioturbators, the polychaetes *Marenzelleria neglecta* and the oligochaete *Tubificoides pseudogaster* account for a high proportion of total abundance and biomass but their effects on native species need further research.

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Introduction

The eastern Gulf of Finland (EGOF) is an important part of the Volga-Baltic invasion corridor for freshwater and brackish water organisms. Dominant nonindigenous species (NIS) have originated from the Ponto-Caspian region, from the coastal waters of North America, and from inland waters of eastern Asia (Orlova et al. 1999; Gollasch and Leppäkoski 1999). These species have altered species diversity, community structure and function, and water quality parameters. Key species from the Ponto-Caspian region include the bivalve *Dreissena polymorpha* (Pallas, 1771) occupying shallow freshwater to oligohaline zones and are found in highest abundance along the northern shore (Antsulevich et al. 2003; Orlova et al. 2004), the predatory cladoceran *Cercopagis pengoi* (Ostroumov, 1891) widespread in EGOF except for freshwater areas, and the amphipod *Pontogammarus robustoides* (Sars, 1894). Two key NIS are from North America, the polychaete *Marenzelleria neglecta* (formerly *M. viridis*, see in Sikorski and Bick 2004) and the North Sea estuarine oligochaete *Tubificoides pseudogaster* (Dahl, 1960) inhabiting relatively deep regions of EGOF. Species from eastern Asia include the Baikalian amphipod *Gmelinoides fasciatus* Stebbing, 1899 and the fish *Perccottus glenii* Dybowsky, 1877 (amur sleeper or rotan) which originates from Amur River. *P. glenii* occurs in macrophyte vegetation in shallow freshwater. Both, *G. fasciatus* and *P. glenii* arrived in EGOF by secondary invasions from continental water bodies, while the others were introduced by shipping. The objective of this paper is to document the present state of xenodiversity in EGOF with results of sampling from 1998 to 2005, and to reveal possible impacts of NIS on the structure and function of selected communities.

Methods

Study area

The study area (EGOF) covers the Russian part of the Gulf of Finland ($59°40'$–$60°25'$N latitude and $27°12'$–$30°09'$ longitude). For a general description see Davidan and Savchuk (1997). The area may be subdivided into three regions (Fig. 1). The freshwater portion of Neva Bay (I) is separated from the gulf by a storm-surge barrier. The eastern shallow area (II) has a water depth above 30 m and salinity of 1–2 at the surface and up to 5–6 PSU at the bottom. The deep-water area (III) generally exceeds 30 m depth and near-bottom salinity is up to 6–7 PSU. The area is nontidal, but water level fluctuations (about 1 m) induced by wind, seiches and changes of the Neva River runoff are common. The near-shore zone from 0 to 7–8 m does not stratify in summer, but at depths more than 8–10 m a thermocline is often present. Ice usually covers the sea from December to April. As a result of eutrophication, intensive development of filamentous algae in the littoral zone is a characteristic feature.

Sampling

Stations sampled in 2004 and 2005 were located in shallow waters along the northern and southern shores and also in offshore areas (Fig. 1). In near-shore waters samples were collected along short transects (2–4 sampling sites) from the "littoral" zone (depth 0.5–2 m) to 5–7 m. The principal sampling area was located in the shallow, near-shore region within the freshwater and oligohaline Northeastern waters of the Neva Estuary (region II, Fig. 1). This area covers about 17 km of the shoreline of the Resort District of St. Petersburg (N60°09.32′–60°11.37′; E29°38.34′–29°54.89′) within which transect 7 (Zelenogorsk) is an ideal location for a detailed study of the quantitative abundance and spatial and temporal variations in populations of key NIS, and for an evaluation of their role in community diversity and function.

Quantitative sampling of benthos in the littoral zone was carried out with a 0.03 m^2 cylindrical metal frame of a 0.7 m height (according to Berezina et al. 2005). At sites with mixed and stony bottoms in the near-shore zone, sampling was carried out using various modifications of SCUBA diving methods (Orlova and Panov 2004). Other sampling procedures for plankton and benthos were standard. Biomass is expressed as fresh weight. Fish were sampled by gillnets of various mesh sizes and by sweep-nets for quantitative investigations. Water samples were collected to determine particulate organic matter (POM) and dissolved inorganic phosphorus (DIP).

To determine feeding patterns (diet), individuals of *P. robustoides* and *G. fasciatus* were collected in the littoral zone in May–June, July–August, and September–October 2004. *Perccottus glenii* was collected in June 2004 and 2005.

Zebra mussels in benthic-pelagic coupling

To assess the potential role of *D. polymorpha* in benthic–pelagic coupling, we calculated the rate of DIP excretion, clearance capacity, and rates of consumption and assimilation by the population. Estimates of DIP excretion in zebra mussels are based on body mass (W) in a power function calculated from experiments: $DIP_{ind} = 2.77W^{0.565}$ (Orlova et al. 2004), extrapolated to population level by the following equation: $DIP_{pop} = \Sigma DIP_{cohort} = \Sigma(aW^b \cdot N \cdot 24)$, given in mgP m^{-2} per day, where DIP_{cohort} is the excretion in each size cohort and W is the average body mass for representatives of each cohort (g) and N is number of individuals in the cohort; $24 =$ time (hours).

Clearance capacity S_{pop} is the quantity of seston extracted by the population of zebra mussels from the water column and was calculated as the rate of individual filtration: $F = 85.5W^{0.605}$ (Alimov 1981), extrapolated to population level as above and multiplied by POM concentration in the water. Rates of consumption and transformation of POM were calculated with a balance approach (Winberg 1956). The balance equation describes the relationship between food consumption rate C_{pop} and the rate of food assimilation A_{pop}, and provides a coefficient u of efficiency of food assimilation: $C_{pop} = A_{pop}/u$. The assimilated matter A_{pop} is the sum of respiration R_{pop} and production P_{pop}. The rate of faeces and pseudofaeces production by molluscs was calculated as $f_{pop} = C_{pop}-(P_{pop} + R_{pop})$ and $pf_{pop} = S_{pop}-C_{pop}$ both in g m^{-2}. Respiraton rate was calculated from the power function $R_{ind} = 0.140W^{0.63}$ (Alimov 1981) and then extrapolated to the population.

Results

Updates to xenodiversity

In 2004–2005 six new NIS were recorded in EGOF: the carnivorous cladoceran *Evadne anonyx* Sars, 1897, the benthic isopod *Jaera sarsi* (Valkanov, 1936), the benthic cumacean *Stenocuma graciloides* (Sars, 1894) (Antsulevich 2005), the bivalve *D. rostriformis bugensis* (Andrusov, 1897), the Ponto-Caspian amphipod *Chaetogammarus warpachowskyi* (Sars, 1894), and the South Baltic estuarine nemertean *Prostoma puteale* (Beauchamp, 1932). We recorded 7 NIS in the littoral zone, 10 in near shore waters in mixed and 11 in sandy bottoms, and only 3 in deeper regions with silt/clay bottoms. For the three portions of the estuary (Fig. 1), the lowest number of NIS was reported from Neva Bay (4 species), and the highest number in the freshwater to oligohaline shallow region II (15 species). We found no

Fig. 1 Study area. **a** Position of EGOF and Zooplankton survey in Augusts 1999 and 2004; **b** EGOF and its counterparts, fairway channel is indicated as *dashed line*; **c** principal area; **d** sampling sites for study of *Marenzelleria neglecta*. Legend: empty *arrows* position of transects; *circles* regular stations
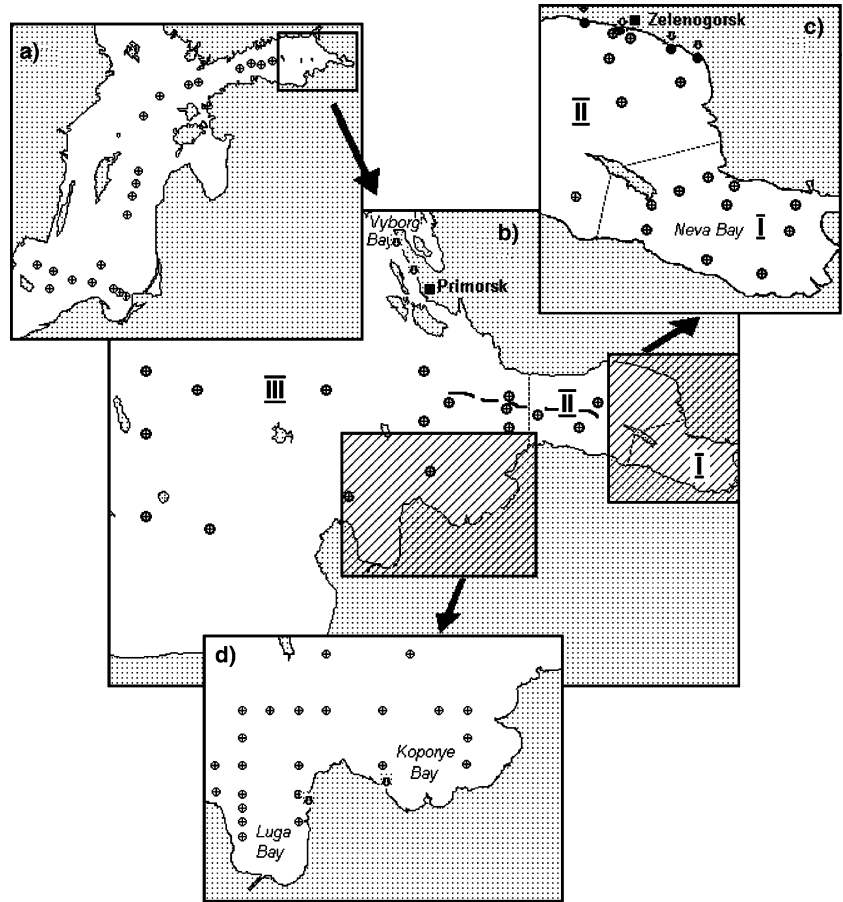
NIS among 147 species of phytoplankton identified in samples collected in 2004. There were 2 NIS among 68 macrophytes (3%), 7 NIS among 90 zooplankton species (8%, which includes larvae of benthic NIS), and 18 NIS in 196 benthic invertebrate species (9%). Over all in communities, NIS accounted for 4.8% of total species richness.

Abundance of key NIS and their relation to other species

Amphipods. In summer 2004 maximum biomass of *Gmelinoides fasciatus* and *P. robustoides* reached 13.2 g m^{-2} and 24.8 g m^{-2}, respectively. Together these two invasive gammarids contributed up to 45% of total biomass in littoral zones of regions I and II. Both amphipods are omnivorous and may affect numbers of small benthic invertebrate prey (Fig. 2). At densities > 5,000 ind.m^{-2}, there was a negative relationship between amphipods and oligochaetes ($r = -0.33$, $P < 0.25$) and chironomids ($r = -0.38$, $P < 0.17$). There was also a significant negative correlation between the biomass of *G. fasciatus* and *P. robustoides* ($r = -0.53$, $P < 0.05$).

Perccottus glenii was more abundant in 2005 than in 2004 and this was likely related to temperature differences between the 2 years. In the relatively warm summer of 2005, the abundance of this species reached a maximum of 1,550 ind ha^{-1} and it contributed up to 85% of total fish abundance in the littoral zone. In the relatively cool summer of 2004, abundance was 450 ind ha^{-1} and it accounted for 4.5% of total fish abundance. The average number of fish species collected per catch was 7 in 2004 and but only 4 in 2005.

Cercopagis pengoi abundance averaged at 60.4 ind m^{-3} and biomass at 57.34 mg m^{-3}. It contributed up to 33% of the zooplankton total community biomass in the second half of summers 2004 and 2005. Total zooplankton abundance (excluding protozoans) in the two years ranged from 5,400 to 182,200 ind m^{-3}. The dominant zooplankton groups, which could serve as prey for C. *pengoi*, were nauplii and copepodites of calanoids (*Acartia bifilosa* Giesbrecht, 1881, *Centropages hamatus* Lilljeborg, 1853 and *Eurytemora* spp.), and small Cladocera. *Cercopagis pengoi* coexists with the native carnivorous cladocerans *Bythotrephes brevimanus* Lilljeborg, 1901 and *B. cederstroemii* Schoedler, 1863 in EGOF. In an area where both cladoceran genera co-occurred in August 2004, *Bythotrephes* spp. was absent from stations where C. *pengoi* was abundant (Fig. 3).

D. polymorpha biomass varied significantly between years ($F_{(6,45)} = 1.000$, $P < 0.001$; samples collected at Zelenogorsk transect from depth 3 and 5 m) over the period of 1998–2005. High biomass (maximum 3,000 g
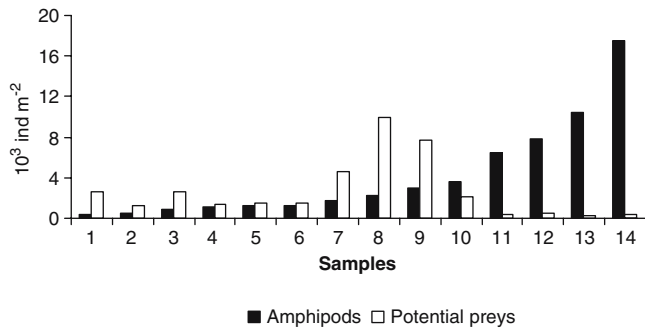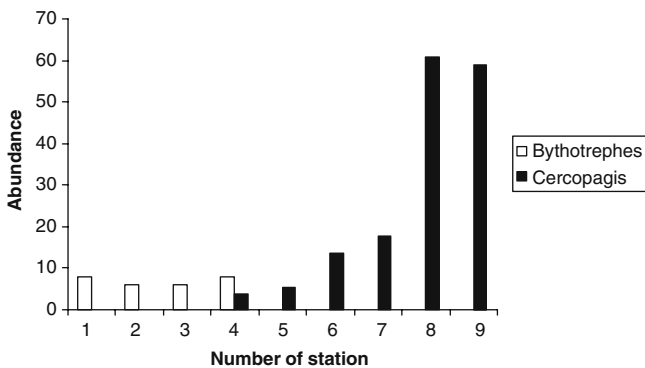
Fig. 2 Abundances of nonindigenous amphipods and their potential prey (benthic oligochaetes and aquatic insects) at 14 locations in the Neva estuary

m^{-2}) was observed in 2000–2001 and in 2004–2005. Zebra mussels dominated the benthic communities at stony and mixed bottoms, contributing up to 96% of total biomass over this period. We found that biomass of associated detritivores was positively ($P < 0.05$) related to *Dreissena* biomass (Chironomidae: $r = +0.779$ and Oligochaeta: $r = +0.876$), while Gastropoda (phytophagous grazers and predators) were unrelated ($r = +0.120$). Total number of other NIS in these communities was also positively ($P < 0.05$) correlated to *Dreissena* biomass ($r = +0.716$) and abundance ($r = +0.705$), while there was no significant relationship between the number of Ponto-Caspian invaders and *Dreissena* biomass ($r = +0.430$, $P < 0.13$) and abundance ($r = +0.438$, $P < 0.10$).

No more than 70% of native unionid bivalves collected in EGOF (region II) had attached zebra mussels upon them. Numbers of fouling mussels per basibiont were 2–6 individuals and biomass 3–4.5 g.

Dreissena polymorpha: larvae first appeared in the plankton in late June and remained until late October, 2004. In July 2004 abundance varied from 1 to 108 ind l^{-1}, while in 2005 only single individuals were found in several samples through the season.

Annelids: In 2003–2004 *Marenzelleria neglecta* extended its range eastward to region II, where it was found on sandy and clay bottoms. At some sites, *M. neglecta* became the dominant species, forming 70–90% of total macrozoobenthic biomass. Maximum biomass (30 g m^{-2}) was observed in Koporye Bay. We did not find significant negative correlations between *M. neglecta* biomass and any other benthic organisms. Positive correlations ($P < 0.05$) were found with *Macoma baltica* (L., 1758) ($r = +0.80$), Oligochaeta ($r = +0.64$), *Monoporeia affinis* (Lindström, 1855) ($r = +0.51$) and Chironomidae ($r = +0.65$).

A local population of *Tubificoides pseudogaster* (about 6,000 ind. m^{-2} and 5.8 g m^{-2}) in 2004 was observed at a depth of 36 m adjacent to fairway channel (Fig. 1b). This oligochaete accounted for about 99% of total macrofauna abundance and biomass in this area in 2004. The native bottom community at this station was dominated by the amphipod *Monoporeia affinis* in 2003 before *T. pseudogaster* became established. During the subsequent two years after the invasion *M. affinis* was absent.
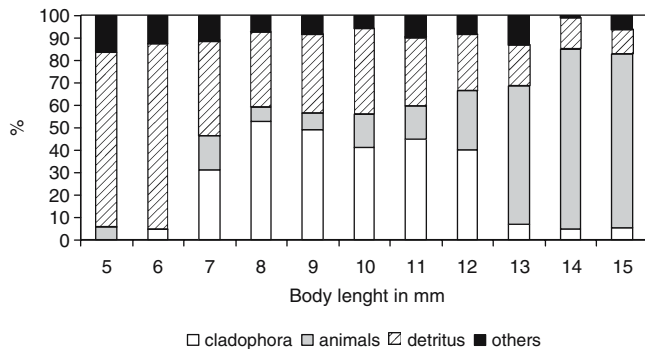
Key NIS and intra-population diversity in food spectra

Amphipods: Microscopic analysis of gut content showed that both amphipod species demonstrated high variability in food spectrum as a function of size. Juveniles of *P. robustoides* with body lengths up to 7 mm fed mainly on detritus, and the proportion of filamentous algae [mainly *Cladophora glomerata* (Kutz.)] in their diets was low. However, in adults (8–12.5 mm), the proportion of filamentous algae increased, exceeding 50% of total food mass. Specimens with body lengths of 13–16 mm consumed considerably less algae (5–7%) as a result of the increasing portion of animal food in their diets. The largest specimens were mainly predators and the proportion of animals in their diet reached 80% (Fig. 4).

Pecrcottus glenii was studied in 2004 and 2005 years and has also demonstrated variability between ages and sizes in content of stomachs (see Table 1 for more details). All dissected juvenile and adult amur sleepers contained food in their stomachs.

Assessment of potential benthic–pelagic coupling by *Dreissena polymorpha*

Local zebra mussel populations demonstrated high water clearance capacity (S_{pop}) and produce a significant amount of faeces (f_{pop}) and pseudofaeces (pf_{pop}). About 50% of consumed matter (C_{pop}) is incorporated by the population (A_{pop}) whereas the other 50% is biodeposited to the sediment as faeces and pseudofaeces (Table 2). Mussels also play a major role in nutrient recycling and clearing water of POM (Table 1). For example, at Zelenogorsk transect the population excreted 5–159 mg m^{-2} DIP per day through the 5-year period of observations (Table 2).

Fig. 3 Abundance (ind./m³) of *Bythotrephes* spp. and *Cercopagis pengoi* in the Gulf of Finland in August 2004 at nine sampling stations

Fig. 4 Body length of the amphipod *Pontogammarus robustoides* ($N = 184$) and changing weight proportions of food categories

Discussion

Xenodiversity

Xenodiversity increased further with a high contribution from Ponto-Caspian species. *Evadne anonyx* was first recorded in 2004 but may have been overlooked because of its close similarity to the native *E. nordmanni* Loven, 1836 (Litvinchuk 2005). The single records of *Stenocuma graciloides* and *Dreissena rostriformis bugensis* are not yet sufficient to regard these as established populations.

The total number of NIS recorded in 2004 and 2005 was 24 invertebrates, 1 fish and 2 vascular plants. The overall share of 4,8 % NIS may be lower than in other inshore waters (Cohen et al. 2005). However, in EGOF 20% of NIS have mass occurrences attaining up to 96% of total biomass. The aquatic ecosystem now differs widely from its "pristine" state. Similar patterns have been observed in other Baltic coastal waters (Kotta et al. 2006) and in the Caspian Sea. The latter water body was dramatically changed after intentionally introduced fishes and invertebrates (Karpevich 1975) and more than 20 other newcomers invaded from the Black Sea since the Volgo-Don channel opened in 1952 (Mordukhai-Boltovskoi 1960).

Effects of key NIS

In the *pelagic compartment of the ecosystem*, the cladoceran NIS in EGOF is parthenogenetic polyphemids, which exist in the plankton for a rather short time. When abundances are high, these invaders may compete with other planktonic predators. Negative relation between the invader *C. pengoi* and native *Bythotrephes spp.* may suggest competition for food, while no significant correlations were found between the invading *E. anonyx* and the native *E. nordmanni* or the invader *C. pengoi*. However, it is expected that food competition between *E. anonyx* and *E. nordmanni* and predation of *C. pengoi* on *E. anonyx* will arise in the future (Litvinchuk 2005).

At maximum densities *C. pengoi* can eliminate a large portion of the assemblage of smaller zooplankters in the water column (Telesh et al. 2001). In EGOF, this results in a strong correlation ($R^2 = 0.82$) between the calculated consumption rates of *C. pengoi* and mean individual body mass of herbivorous cladocerans (Telesh and Ojaveer 2002). *C. pengoi* affects the size structure of the zooplankton community and modifies the trophic web in the Gulf of Finland by eliminating small planktonic filtrators (Telesh et al. 2000). According to Gorokhova (1998), in the northern Baltic proper nauplii of the copepods *Acartia*, *Eurytemora* and *Temora*, rotifers (*Synchaeta*), and cladocerans (*Evadne*) constitute 60, 20 and 20% of the diet of *C. pengoi*, respectively.

Cercopagis pengoi itself is the preferred prey of the Baltic herring (Antsulevich and Välipäkka 2000) and native mysids (Gorokhova 2005). However, taking into account both the seasonal and interannual dynamics of *C. pengoi*, this species may affect communities for only a period of some weeks when densities are at a peak.

Three benthic NIS, *D. polymorpha*, *Balanus improvisus* and *Marenzelleria neglecta*, as well as the "native" bivalve *Macoma baltica*, contribute to zooplankton by supplying larvae in summer and autumn. Based on a survey of *Dreissena* larvae (Telesh and Orlova 2004), we assume a minor role in changing the microzooplankton because of the short time present, which is similar to the cladoceran NIS.

Table 1 Parameters of dissected individuals ($N = 45$) of *Perccottus glenii* and content of their stomachs

Age	L (mm)	Body mass (g)	N (ind.)	Mass of food in stomach (g)	Content of food with percentage of dominant food item
0+	–	–	25	0.001–0.007[a]	Zooplankton (close to 100%): Cladocera (*Daphnia sp., Ceriodaphnia sp.*), Copepoda (*Mesocyclops leucartii, Eurytemora sp.*); swimming larvae of Chironomidae; small Hydracarina
2+	45–60	1.23–3.14	18	0.004–0.05	Zoobenthos (close to 100%): Gastropoda, Chironomidae, Isopoda, Amphipoda, Odonata, Diptera n/det, Hemiptera (single *Corixa sp*)
3+	65	7.24	1	0,065	Zoobenthos (99%): Chironomidae, Isopoda, Amphipoda, Odonata; Zooplankton: *Mesocyclops* sp., *Chydorus spahaericus*; remnant of fish (Cyprinidae n/det, juv.)
6+	166	92.2	1	2.710	Pisces (94%): *Rutilus rutilus*; Gastropoda (*Cincinna sp*)

[a]With mass of stomach

Table 2 Biotic balance of *Dreissena polymorpha* populations from Resort District, Zelenogorsk transect

Year	S_{pop} (g m^{-2})	P_{pop} (g m^{-2})	R_{pop} (g m^{-2})	$A_{pop} = P+R$ (g m^{-2})	$C_{pop} = A_{pop}/u$ (g m^{-2})	f_{pop} (g m^{-2})	pf$_{pop}$ (g m^{-2})
1998	106 ± 54	7.7	22.3 ± 21	30 ± 21	51 ± 34	20 ± 18	65 ± 52
2000	442 ± 314	53 ± 35	155	208 ± 134	347 ± 314	139 ± 90	95 ± 90
2001	343 ± 126	42 ± 9	121 ± 25	163 ± 34	271 ± 51	109 ± 22	72
2002	96 ± 61	15	44 ± 36	59 ± 52	106 ± 76	60 ± 48	0
2004	204 ± 107	47 ± 12	137 ± 98	184 ± 95	324 ± 151	120 ± 195	0

In the benthic compartment of the ecosystem, NIS is often a permanent component of communities, and we suggest that they are responsible for many variations in habitat properties and community structure where they have attained dominance .The benthic NIS may be classified into three functional categories based on traits expected to affect ecosystem processes (Hooper et al. 2002): (1) vagile omnivores, (2) sessile seston-feeders and (3) infaunal bioturbators.

Vagile omnivores include the alien amphipods and the amur sleeper. We suggest that their diverse diets allow these species to partition resources and to successfully compete with native species that tend to be more stenophagous. On littoral hard bottoms in Neva Bay (region I), predation by the invasive amphipod *P. robustoides* on other benthic organisms was the main mechanism by which invertebrate density decreased and by which native or earlier established alien species was replaced. At sites where the native *Gammarus lacustris* and the invasive *G. fasciatus* were found together, a considerable decline in density and even disappearance of *G. lacustris* occurred (Berezina 2004). *G. fasciatus* has a short life cycle and high fecundity that allows it to reach high densities over short periods of time, while *G. lacustris* has a longer life cycle with lower reproductive potential. Also, *G. lacustris* has low tolerance to wave action (Bekman and Basikalova 1951), which limits its habitat range in the exposed littoral zone of large lakes and estuaries.

G. fasciatus and *P. robustoides* also play a role in the functioning of littoral communities in EGOF through their grazing activities. According to consumption rates of *P. robustoides*, the dense population found in EGOF littoral zone is able to consume up to 1.9–2.4 gCm^{-2} day^{-1} of algae (Berezina et al. 2005). The average biomass of *Cladophora glomerata* was 68 ± 25 gCm^{-2} and primary production 7 gCm^{-2} day^{-1}. Amphipod consumption rates are thus only twofold to threefold lower than *C. glomerata* production and grazing effects will be significant. In locations with high densities of *P. robustoides* and *G. fasciatus*, these amphipods may actually cause a decline in *Cladophora* biomass, alleviating an eutrophication effect.

Perccottus glenii either directly (by predation) or indirectly (by food competition) may affect native fishes such as roach and various juveniles. The feeding range of *P. glenii* is exceptionally wide (Bogutskaya and Naseka 2002). Juveniles of *P. glenii* are zooplanktivorous, at 1–3 years *P. glenii* is mainly benthivorous, and when older it is preying on the juveniles of other fish. *P. glenii* is more resistant to hypoxia, high temperatures, and other abiotic stresses compared to many native fishes (Bogutskaya and Naseka 2002). A higher tolerance may explain the dominance of *P. glenii* in the fish community during the hot summer of 2005 even better than causing a decline in fish diversity by predation.

At sites where the sessile seston-feeder *D. polymorpha* is abundant, populations may change the trophic web as well as habitat conditions. A calculated energy budget indicates that 50% of consumed food is assimilated and the other half rejected as faeces and pseudofaeces. Thus, the invasion of zebra mussels in EGOF has formed a fouling assemblage similar to those found in the marine environment (see Dolmer and Frandsen 2002; Thiel and Ullrich 2002). Accumulation of organic material within zebra mussel beds provides food for detritivores species, and may explain the observed correlation between biomass of zebra mussels and detritivores. However, abundance and biomass of these detritivores account for only a small percentage of the total community, probably because faeces and pseudofaeces do not remain for long in the benthos due to high turbulence in the nearshore zone (Orlova et al. 2004). *Dreissena polymorpha* can facilitate colonization by other invaders. This is shown by positive relationships to the number of other NIS. However, we did not find an "invasion meltdown" effect sensu stricta (as described by Ricciardi 2001). Based on our study, the idea of an "invasion meltdown" not only applies to invaders that originate from the same but also from other regions.

Zebra mussels also play an important role in benthic–pelagic coupling through the recycling of nutrients, which may in turn facilitate benthic filamentous green algae (*Cladophora glomerata*), already promoted by eutrophication (Golubkov et al. 2003). Orlova et al. (2004) compared the contribution from external (input from small brooks and recalculated Neva River input) and internal sources (zebra mussel populations) to the DIP pool along a transect of 17 km with an area of 4.7 km^2 and 6,510 tons of *D. polymorpha*. It was found that the daily contribution from mussels was of 514 kg DIP compared to only 7 and 25 kg DIP from small brooks and the Neva River, respectively. However, the zebra mussels are distributed in patches and the overall effect at the scale of the Gulf of Finland may be small.

It is further suggested that *D. polymorpha* epizootic growth on unionids in EGOF is not as adverse as reported from North America (Burlakova et al. 2000). This may be explained by the wide availability of hard substrates in the Neva Estuary and by irregular

recruitment in the *D. polymorpha* populations (Orlova and Panov 2004).

Although the *Marenzelleria neglecta* has become common and abundant in EGOF, no adverse effects on the native fauna have been observed. However, the role of *M. neglecta* as a dominant species in some shallow areas, combined with its high burrowing activity may transform the benthic community in the future. The lack of the native amphipod *Monoporeia affinis* in an area with *Tubificoides pseudogaster* cannot be attributed to the invasion of this oligochaete. No habitat changes were noted in the study area that can sufficiently explain the extinction of the amphipod population (Maximov 2003). Thus, the interaction of *T. pseudogaster* with *M. affinis*, which is a key species in the Baltic benthos, is a field for future research.

Despite high numbers of NIS in EGOF, the effects of NIS on local species and on community structure along with potential impacts on energy exchange between benthic and pelagic compartments of the ecosystem of EGOF is apparently not as dramatic as in the Black and Caspian Seas (see Shiganova et al. 2004a, b). We cannot determine with certainty that current changes in the EGOF ecosystem are caused primarily by NIS. Also, it is difficult to determine whether effects of NIS are negative, positive or neutral. However, two functional groups of benthic invaders, the sessile seston-feeders and mobile omnivores are suggested to play a particularly important role in the utilization and transformation of energy via benthic-pelagic coupling (first group) and in grazing (the second group). They may also change species composition via the "invasion meltdown" effect, which includes trophic, habitat and historical components (first group) and predation and competition (second group).

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