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In the Wrong Place – Alien Marine Crustaceans: Distribution, Biology and Impacts

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Alien Malacostracan Crustaceans in the Eastern Baltic Sea: Pathways and Consequences

Nadezhda A. Berezina, Victor V. Petryashev, Arturas Razinkovas, and Jūratė Lesutienė

Abstract The recent invasion history of malacostracan crustaceans into the eastern Baltic Sea is reviewed with 16 alien species being recorded from the easternmost area. These invasives constitute 3% of the total species richness (50% of the alien biota), and comprise up to 80% of the total benthic biomass in several localities. The Ponto-Azov-Caspian species are the most diverse and abundant component. Their taxonomical and ecological dominance could be explained by a combination of factors including similarities between the Baltic, the donor regions and the waterway network that allows their dispersal. The high vulnerability of the Baltic Sea to invasion may be a consequence of low native biodiversity coupled with anthropogenic and natural factors. The potential impact of alien Malacostraca on the native community was assessed following predatory studies of alien amphipods on native benthic biota. These studies indicated that the alien amphipods may alter the structure of their prey communities. Alien crustaceans have outnumbered or even completely replaced native species and/or earlier established invaders locally in the eastern Baltic Sea.

Keywords Alien Malacostraca • Benthic Community • Invasion History • Predatory Impact • Baltic Sea • Curonian Lagoon • Vistula Lagoon • Neva Estuary

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1 Introduction

The Baltic Sea is a brackish ecosystem characterized by low species diversity, and as other mesohaline seas, is easily colonized by alien species (Stachowicz et al. 1999). The increasing number of newly recorded aliens in the last decades has been attributed to the escalating anthropogenic stress on the Baltic Sea ecosystem (Gomoiu et al. 2002).

A large catchment area combined with dense human population and intensive exploitation of natural resources of the Baltic Sea have caused the destabilization of a marine ecosystem already disturbed by natural or anthropogenic factors (e.g., extreme storms, bottom dredging), alteration due to previous introductions (habitat engineering), and eutrophication (Schernewski and Schiever 2002; Schiewer 2008). As a result a number of species are no longer recorded from the region and the food web has become weakly articulated giving rise to “vacant niches”. These according Zaiko et al. (2007) are then occupied by alien species. Such species as a rule are eurybiotic organisms, *r*-strategists and able to establish themselves in new habitats, including environments that have been disturbed. About 100 alien species have been recorded in the Baltic Sea during the last two centuries, and most of them have been unintentionally introduced by ballast water, hull fouling or by spreading from their primary sites of introduction into adjacent water bodies (Leppäkoski et al. 2002).

The main introductory pathways of crustaceans into the Baltic Sea basin have been analyzed in details (see Jażdżewski 1980; Bij de Vaate et al. 2002; Leppäkoski et al. 2002; Berezina 2007b; Ojaveer et al. 2007). The most important factors facilitating the arrival and successful establishment of alien species are the elimination of natural barriers due to construction of canals, reservoirs, drainage systems, the network of waterways cross Europe, shipping, climatic change and destruction of habitats. The Baltic Sea is susceptible to invasions as it forms a nexus of waterways connecting the North, White, Black, Azov and Caspian Seas, and it is the recipient of ca. 250 rivers. Assessment of impact in newly invaded habitats and preventive control of alien species are important ecological problems for the Baltic Sea ecosystem, especially in coastal and estuarine areas (Schernewski and Schiever 2002).

This chapter reviews the history of invasive malacostracans in the coastal habitats in the eastern Baltic Sea (primarily Gulf of Finland, Curonian and Vistula (Russian part) lagoons), describes the biological traits that make these crustaceans successful invaders and attempts to characterize their effects on native invertebrate communities (mainly through trophic interactions) in recipient ecosystems.

2 The Study Area

The tidal less Baltic is a shallow brackish inland sea with a mean depth of 55 m of which 17% is <10 m deep (Voipio 1981). The area of study is focused on the coastal areas in the eastern region to include the Gulf of Finland in the northeast and the Curonian and Vistula lagoons in the southeast (Fig. 1). The salinity in

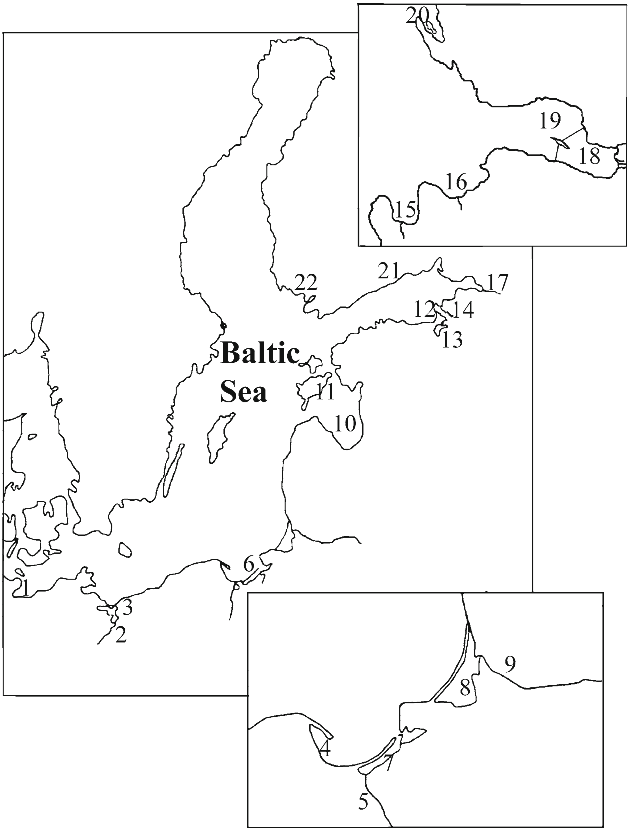

Fig. 1 Study regions of the Baltic Sea: 1. Mecklenburg Bay, 2. Oder River, 3. Oder Estuary, 4. Puck Bay, 5. Vistula River, 6. Gulf of Gdansk, 7. Vistula Lagoon, 8. Curonian Lagoon, 9. Neman River, 10. Gulf of Riga, 11. Saaremaa Island, 12. Narva Bay, 13. Lake Peipsi, 14. Luga River, 15. Luga Bay, 16. Koporskaya Bay, 17. Neva River, 18. Neva Bay, 19. Neva Estuary, 20. Vyborg Bay, 21. Kotka, 22. Turku

these areas varies from 0 to 3 psu in inner and estuarine waters, through 7 psu in the open areas.

The Baltic Sea is connected to the Atlantic Ocean through the Danish Straits, and to the Ponto-Caspian region via a system of waterways, for which construction began in the 1770s (Bij de Vaate et al. 2002). The estuaries, the Neva Estuary, Curonian and Vistula lagoons, serve as halfway houses for alien species and centres of xenodiversity. These transitional waters are affected by wind-mixing, stochastic water exchange with the Baltic Sea proper, horizontal gradients of salinity, high nutrient load leading to occasional phytoplankton blooms, high productivity, accumulation of humic material, and domination by eurybiotic species (Telesh et al. 2008; Schiewer 2008).

The Neva Estuary (3,600 km^2) is one of the largest in the Baltic. The Neva River (74 km long) flows out of Lake Ladoga, the largest lake in Europe, and discharges 76 km^3 water annually into the inner and outer parts of the Neva Estuary. The total particulate organic matter (POM) of the river ranges between 4.6 and 12.0 mg l^{-1} (Telesh et al. 2008). The surrounding Neva Bay is shallow with a mean depth of 4 m, (maximum depth 12 m), and oligohaline (ca. 0.1 g l^{-1}). A storm-surge barrier has separated the bay from the estuary since the early 1980s. The mean and maximal depths of the inner and outer estuary are 12 and 60 m respectively, and the salinity ranges from 0.21 to 2.5 gl^{-1}. The total phosphorus in the estuary ranges between 30 and 340 mgm^{-3}.

Curonian Lagoon (1,584 km^2) is separated from the sea by a sand spit, with a narrow (0.4–1.1 km) opening (Klaipeda port area). The average depth of the lagoon is 3.8 m, with a dredged waterway to 14 m depth (Gasiūnaitė et al. 2008). This freshwater lagoon is greatly influenced by the Neman River inflow. The eastern side of the lagoon (mainland shore) slopes gently westward to a depth of 1–2 m, whereas the western side is up to 4 m depth (Gasiūnaitė et al. 2008).

The Vistula Lagoon (838 km^2) has an average and maximal depth of 2.7 and 5.2 m respectively, excluding the dredged navigable channel, and is separated from the sea by a sandy barrier. The lagoon was formed in 1916 when the Vistula River was diverted to the Baltic Sea and changed from a freshwater estuary to an estuarine lagoon (Chubarenko and Margoński 2008).

3 Invasion History of Crustaceans in the Gulf of Finland, Curonian and Vistula Lagoons

The majority of alien crustaceans arrived in the Baltic Sea from the Volga River, Caspian Sea, Black Sea and the Sea of Azov, following the construction of waterway systems that formed inland invasion corridors (Bij de Vaate et al. 2002; Leppäkoski et al. 2002). Large-scale intentional introductions with the aim of improving fisheries by augmenting the food items of fish species of commercial interest are to blame for the amphipod, mysid and isopod invasions of the inland waters of European Russia (Nikolaev 1963; Arbačiauskas 2002; Orlova et al. 2006; Berezina 2007b). Between the 1950s and 1980s scores of amphipod and mysid species from Ponto-Caspian region were transported through the former USSR (Jażdżewski 1980; Arbačiauskas 2002; Berezina 2007b).

Climate change such as warming could trigger the expansion of alien species of Malacostraca from the Ponto-Caspian and the Black Sea to the Baltic Sea (Berezina 2007b). Some Ponto-Caspian gammarids and the mysid *Hemimysis anomala* have reached the northeastern Baltic (including Neva Bay), and other Ponto-Caspian mysids, *Paramysis lacustris* and *Limnomysis benedeni*, are currently restricted to the southern Baltic (Razinkovas and Zemlys 2008). Effects of climate change in the Baltic Sea forecast a significant rise in sea level, decreased salinity and an increase of temperature especially during winter (Razinkovas and Zemlys 2008). These changes would be reasonable to expect that alien species limited by cold winter and tolerant to oligohaline waters (such as crustaceans from Ponto-Caspian and Mediterranean regions) will continue to expand their ranges into the northeastern part of the Baltic Sea

4 Amphipods

Nine alien amphipod species have been recorded in the eastern Baltic Sea (Table 1). The species of Ponto-Caspian origin, *Chaetogammarus ischnus* (Stebbing, 1899), *C. warpachowskyi* (Sars, 1894), *Chelicorophium curvispinum* (Sars, 1895), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Obesogammarus crassus* (Sars, 1894) and *Pontogammarus robustoides* (Sars, 1894), form the leading group among amphipod invaders (Berezina and Panov 2003; Ezhova et al. 2005; Orlova et al. 2006; Malyavin et al. 2008). Two amphipod species, *Gmelinoides fasciatus* (Stebbing, 1899) and *Gammarus tigrinus* Sexton, 1939, originate in Lake Baikal, Siberia (Panov and Berezina 2002), and the Atlantic coast of North America respectively (Ezhova et al. 2005; Berezina 2007b; Bacela et al. 2008). Another Ponto-Caspian species, *Dikerogammarus villosus* (Sowinsky, 1894), is widespread in Europe (Grabowski et al. 2007; Bacela et al. 2008) and may further disperse into the eastern Baltic Sea in the near future.

Table 1 List of alien species and their first records in the eastern Baltic Sea according to Berezina and Panov 2003; Ezhova et al. 2005; Pienimäki et al. 2004; Daunys and Zettler 2006; Orlova et al. 2006; Berezina 2007a, b, c and unpublished data; Herkül and Kotta 2007; Ojaveer et al. 2007; Malyavin et al. 2008; Herkül et al. 2009; Kalinkina and Berezina 2010

Species	Gulf of Finland	Gulf of Riga	Curonian Lagoon	Vistula Lagoon (Russian part)
Amphipoda				
Chaetogammarus warpachowskyi	2004	–	1960s	–
Chaetogammarus ischnus	–	–	1920s	1920s
Chelicorophium curvispinum	2005	–	1920s	1920s
Dikerogammarus haemobaphes	–	–	–	1999
Obesogammarus crassus	–	–	2000	2000s
Pontogammarus robustoides	1999	2009	1999	1999
Gmelinoides fasciatus	1996	–	–	–
Gammarus tigrinus	2003	2003	2003	1999
Orchestia cavimana	2002	2002	–	1980s
Mysidacea				
Hemimysis anomala	2003	–	1960s	–
Limnomysis benedeni		–	1960s	–
Paramysis lacustris	–	–	1960s	–
Paramysis intermedia	2008	2008	–	–
Isopoda				
Jaera sarsi	2004	–	–	–
Decapoda				
Eriocheir sinensis	1933	1990s	1980s	1980s
Palaemon elegans	2003	–	2004	2000

In the 1960s three Ponto-Caspian amphipods, *P. robustoides*, *O. crassus* and *C. warpachowskyi*, had been introduced from the Black Sea basin to Kaunas Reservoir (Neman River), from which they spread to Lithuania, Latvia and Russia (Leningrad province). Their native regions include brackish and freshwater bays in the Marmara, Black, Azov and Caspian seas, coastal lakes and lagoons and the lower courses and estuaries of the rivers Volga, Don, Bug, Dnepr, Dniester, Danube, Prut, Terek, Kura, Kuban, etc. (Kalinkina and Berezina 2010). By the end of the twentieth century, *P. robustoides* had spread along the Vistula, Oder, Neman, and Elbe Rivers, also entering some lakes and reservoirs (Rudolph 1997; Zettler 1998; Arbačiauskas 2002; Jażdżewski and Konopacka 2002; Jankauskienė 2002; Ezhova et al. 2005). It is common in the Vistula and Curonian lagoons where it coexists with another common Ponto-Caspian amphipod alien, *O. crassus* (Berezina, unpublished data). In the past decade it was recorded in the Neva Estuary (Berezina and Panov 2003), Narva Bay, Estonia (Herkül et al. 2009), the lower reaches and mouths of Latvian rivers (Grudule et al. 2007), and along the Gulf of Riga (Kalinkina and Berezina 2010). *Chaetogammarus warpachowskyi* was reported from the Curonian Lagoon and inland lakes of Lithuania in the 1990s (Olenin and Leppäkoski 1999; Jankauskienė 2002). In addition, during 2004 it was recorded near St. Petersburg, where likely it had arrived with ballast water from other parts of the Baltic Sea. However, subsequent surveys of this area in 2005–2008 failed to record *C. warpachowskyi*. Consequently it may have been an ephemeral population, or it is only present in small number (Berezina et al. 2008).

Chelicorophium curvispinum is native to the Caspian and Azov-Black Seas. The species has been recorded from the Volga, Don, Ural, Dnepr, Dniestr and Danube rivers (Malyavin et al. 2008). This amphipod species arrived in the Baltic Sea probably through the waterway network in 1920–1930s, and established populations in the Curonian and Vistula lagoons (Nikolaev 1963; Jażdżewski 1980; Malyavin et al. 2008). In 2005 it was found along the Estonian coast (Herkül and Kotta 2007), and in 2006 it reached abundances of 29–171 ind. m^{-2} at the mouth of the Luga River and at Luga Bay (Malyavin et al. 2008).

Chaetogammarus ischnus has spread like the previous species and has been established in the Baltic basin since the early twentieth century. It has been recorded in the Vistula and in the Curonian Lagoon, but has not been found to date along the Russian coast (Jażdżewski and Konopacka 2002; Jankauskienė 2002; Berezina and Razinkovas, unpubl. data).

Gammarus tigrinus is native to estuaries of the Atlantic coast of North America and has an extensive invasion history (Pinkster et al. 1977). The first Baltic record dates to 1975, when it was found in Schlei fjord, Germany (Bulnheim 1976). By 1994 it reached the Mecklenburg (Rudolph 1994), the Odra Estuary (Gruszka 1999; Jażdżewski and Konopacka 2000) and spread along the entire Baltic coast of Germany (Zettler 2001), Puck Bay on the western Gulf of Gdańsk, Poland (Szaniawska et al. 2003), and the Vistula Lagoon (Jażdżewski et al. 2002; Ezhova et al. 2005). In 2003 it was recorded in the northern Gulf of Riga (Herkül et al. 2006), off the Finnish coast (Pienimäki et al. 2004), the Curonian Lagoon (Daunys and Zettler 2006), and, in 2005, from the Neva Estuary (Berezina 2007a). It is likely that these have been secondary introductions due to ballast water. In 2008 and 2009, *G. tigrinus* was frequently recorded from the northern and western regions of the Neva Estuary. It may now spread through the extensive waterway networks to many Eastern European lakes.

Gmelinoides fasciatus is native to Lake Baikal and Siberian rivers (Angara, Barguzin, Irtysh, Lena, Pyasina, Tunguska, Selenga, Yenisey). In the 1970s it was intentionally introduced into lakes and reservoirs in the former USSR, including the Baltic Sea basin (lakes of the Karelian Isthmus) to supplement fish feed (Berezina 2007b). As a consequence this species spread through the aquatic systems of Eastern Europe. During the 1990s it reached Neva Bay and the oligohaline Neva Estuary. At present, it is common in habitats of the eastern Gulf of Finland with salinity range of 0.05–2.0 psu (Berezina and Panov 2003). It has established an abundant population in the mouth of the Luga River, where it was first recorded in 2004 (Berezina 2008) This species may have arrived here either from the Neva Estuary or the Narva River, where it has been abundant since the 1990s (Panov et al. 2000).

The first record of the semi-terrestrial talitrid amphipod, *Orchestia cavimana* (Heller, 1865), was from the Northeastern Baltic Sea. It dates to 1999 when it was found in damp wracks cast up on Saaremaa Island, Estonia (Kotta 2000). In the early 2000s the species spread to Northwestern Estonia. *Orchestia cavimana* is widely distributed in the Mediterranean, Black Sea, Red Sea, and the eastern Atlantic, from North Africa to the Southern North Sea. In the Baltic Sea it reported from German and Polish estuaries and lagoons (Żmudziński 1990; Spicer and Janas 2006). The latter are the likely donor populations. In 2009 *O. cavimana* was found for the first time in the main Vistula channel at Świbno, colonizing this locality by a natural spread up the river obviously from the Baltic coast (Konopacka et al. 2009). These records of *O. cavimana* and its high biomass in newly invaded habitats indicate that the species continues to extend its range along the Baltic coastline. Algal biomass has increased in recent decades with the eutrophication of the Baltic Sea. Since wrack biomass appears to be a predictor of *O. cavimana* abundance, this amphipod may have dispersed with drifting algae, although unintentional anthropogenic transport cannot be excluded.

5 Mysids

Four Ponto-Caspian species, *Hemimysis anomala* Sars, 1907, *Limnomysis benedeni* (Czerniavsky, 1882), *Paramysis lacustris* (Czerniavsky, 1882), and *Paramysis intermedia* (Czerniavsky, 1882), have been established in the eastern Baltic Sea basin. *Hemimysis anomala* is native to the western and northwestern coast of the Black Sea, the Azov Sea, mouth of the Don River, the eastern Caspian Sea and the Volga River delta. *Limnomysis benedeni* and *P. lacustris* are native to the Black and Azov Seas, and the shallow waters of the Caspian Sea mostly in river mouths (Derjavin 1939; Pauli 1957; Bacescu 1969). The latter species has a native distribution that includes the Marmara Sea and adjacent river basins. Following the description of the southern Russian congener, *P. sowinskii* (Daneliya, 2002), the Baltic basin population of *Paramysis* is in need of clarification.

In the 1950s large-scale introductions from Ponto-Caspian basin into different lakes, rivers and reservoirs of Ukraine, Moldova and southern Russia took place. Between 1962 and 1985, the three mysid species had been repeatedly introduced from the Dnieper basin to lakes and reservoirs in Lithuania, including the Kaunas reservoir on the Nemunas River (Arbačiauskas 2002). Here they have established viable populations and have spread downstream to the Curonian Lagoon.

In the Curonian Lagoon, *L. benedeni* and *P. lacustris* are common species (Arbačiauskas 2002; Lesutienė 2009), whereas *H. anomala* is much less abundant (Razinkovas A. pers. comm. 2008). Only *H. anomala* was recorded in the Gulf of Finland. It was first found in the open marine area of the Baltic Sea near western edge of the Gulf of Finland in 1992 (Salemaa and Hietalahti 1993), and later dispersed eastwards to the inner parts of the gulf. At present *H. anomala* is a common species near the northern coast of the Gulf of Finland from Turku to Kotka, as well as along the eastern coast of Sweden and in the Gulf of Gdansk (Lundberg and Svensson 2004; Janas and Wysocki 2005). The species is known to be transported in ballast tanks (Gollasch et al. 2002). A single record, dating back to 1963, of *P. lacustris* is known from the Estonian coast (Yarvekyulg 1979), but no further occurrences in the Gulf of Finland have been confirmed.

Paramysis intermedia was first found in the Baltic Sea in 2008, near Ruhnu Island in the Gulf of Riga and close to the mouth of the Narva River. Like its congener, it was intentionally introduced to serve as food for commercially valuable fish. It was introduced to Lake Peipsi, bordering Estonia and Russia, in the 1970s. Although it had not established a population in the lake, the species may have survived in the Narva River, later dispersing to the Baltic Sea (Herkül et al. 2009).

6 Isopods

The isopod *Jaera sarsi* Valkanov, 1936, was first found in 2004, in the brackish waters (2 psu) of Koporskaya Bay, in the Gulf of Finland (Orlova et al. 2006). The Baltic specimens are similar to the subspecies *sarsi* from the Black Sea (Petryashev, unpublished data). The species may have been vessel-transported, or associated with the intentional introduction of mysids and amphipods mentioned above (Nikolaev 1963; Orlova et al. 2006). Its native distribution is limited to the brackish water lagoons of the Black and Azov Seas, the lower reaches of their rivers (Danube, Dnepr, Don, Volga, Ural), some adjacent lakes (Abrau Lake, Lake Varna-Beloslav Lake complex), and in the Caspian Sea (Kussakin 1988; Schotte et al. 1995; van der Land 2001).

7 Decapods

The Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards, 1853, is native to the Northwestern Pacific. Its global dispersal with ballast water and trade together with its environmental and economic impacts, make it one of the most cited examples of invasive alien species (see Bentley 2011). The crab is well established in many estuaries and adjacent rivers bordering the North Sea (Peters et al. 1936; Ojaveer et al. 2007). The species may have entered the Baltic Sea by current-swept larvae, active migration of adults or in ballast tanks (Ojaveer et al. 2007).

In the North Sea basin *E. sinensis* was first found in 1912 in the Aller River, Germany. In 1926–1928 it was recorded in the Baltic Sea near German and Polish coasts (Boettger 1933), and in 1933 in Vyborg Bay, Gulf of Finland (Haahtela 1963; Herborg et al. 2003). According to Haahtela (1963), specimens inhabiting the Baltic may have been transferred from the North Sea as larvae or juvenile specimens. In the 1980s this species was recorded in the River Vistula mouth and Gdansk Bay (Normant et al. 2000), and in the Russian part of the Vistula Lagoon (near Kaliningrad). In the eastern Gulf of Finland, near St. Petersburg, *E. sinensis* was first found in 1982 (Panov et al. 2003). Since 2000, it was amply recorded from the inner Neva Estuary (Zelenogorsk-Ushkovo, to the north-west of St. Petersburg), in the city port and in the Neva River itself (Petryashev V.V. 2000). In spite of numerous findings of adult specimens in different parts of the eastern Baltic Sea, there is still no evidence that the species is able to reproduce successfully in waters of eastern part of the Baltic Sea. Obviously it can establish stable self-reproducing populations only in marine waters of the Vistula Lagoon, near German and Danish coasts. Whereas megalops and young crabs drifting eastwards support the ephemeral population in the eastern Baltic Sea.

The euryhaline rockpool prawn *Palaemon elegans* Rathke, 1837, is distributed in the Mediterranean, Black, Caspian seas and in the African and European coast of the Atlantic (from Namibia to Norway) (Udekem d'Acoz 1999). In the 1950s it was unintentionally introduced to the Aral and Caspian Seas (Zenkevich 1963). A massive increase occurred during 2001 in the Vistula Lagoon and along the Russian shoreline (Ezhova 2009). In 2002 it was first found in the Arkona Basin and the Gulf of Gdańsk, in the southern Baltic Sea (Janas et al. 2004; Grabowski et al. 2005) Later in 2003 it was reported from the Gulf of Finland (Kekkonen 2003), and in 2004 from the Curonian Lagoon (Daunys and Zettler 2006).

8 Species Richness and Abundance of Alien Species in the Eastern Baltic Sea

Alien crustaceans constitute over 40% of the total number of introduced invertebrate species in the Baltic Sea. In the easternmost Baltic Sea they contribute up to 3% of the total species richness (50% of the aliens), and dominate (up to 80%) the benthic biomass.

Alien amphipods alone (*P. robustoides, G. fasciatus, G. tigrinus*) contribute more than 50% of the total biomass in the littoral zones of the Neva Estuary. The abundance of *P. robustoides* and *G. fasciatus* in Neva Bay has changed significantly since the early post-establishment period in the late 1990s. An early period (2002–2005) of high abundance (up to 2,500–3,500 ind. m^{-2}) was followed (2006–2008) by decline and stabilization (1,000–2,000 ind. m^{-2}), dynamics that correspond to the classic scenario for the species entering new habitats (Odum 1975).

In the Vistula Lagoon (Russian) littoral zones, *P. robustoides*, *O. crassus* and *D. haemobaphes* constitute over 80% of the zoobenthic biomass. These species dominated in August 2002, near Kaliningrad, over all other amphipods with their combined abundance reaching 25–30% of the total (Berezina, unpublished data). In the (Lithuanian) Curonian Lagoon, *P. robustoides, O. crassus* and *G. tigrinus*, had the highest occurrence (79%) of all benthic malacostracan crustaceans (Daunys and Zettler 2006), during 2004, while the other alien crustaceans (*P. lacustris*, *L. benedeni*, *C. warpachowskyi* and *C. curvispinum*) were much less frequent (1–13%). In July 2005 the freshwater part of the Curonian Lagoon was dominated by *P. robustoides*, while in the oligohaline area *O. crassus* was the most numerous (Arbačiauskas 2008). In 2008 and 2009 *O. crassus* was the most abundant species (up to 4,500 ind. m^{-2}) in several coastal areas of the Curonian Lagoon while *P. robustoides* dominated the biomass with values reaching 30 gm^{-2} (Berezina and Razinkovas, unpublished data).

Chelicorophium curvispinum was common in macrophyte covered habitats, while *G. tigrinus* was rarely found. The alien mysid *L. benedeni* is abundant in the submersed vegetation zone of the Curonian Lagoon, especially in June-August (Razinkovas 1996; Lesutienė et al. 2005). In August 2008, it is abundance in *Potamogeton* beds reached (0.5–1 m) 500–800 ind. m^{-2}, 20 times that of *P. lacustris* (Petryashev and Berezina, unpublished data). The latter species is abundant in summer at 1.5–2.5 m depths, reaching 50–60 ind. m^{-2}. In late summer and autumn the population density increases significantly (Razinkov 1990; Lesutienė et al. 2008). There is little quantitative data on *E. sinensis* catches in the eastern Baltic Sea, though scores of specimens were collected near Kotka and Neva Bay (Ojaveer et al. 2007).

9 Role of the Alien Crustaceans in the Food Web and Assessment of Possible Predation Impact

Although the number of alien crustaceans in the Baltic Sea has increased considerably in recent years, only a few species can be considered as invasive or hazardous. The alien crustaceans may interact with native species by predation, resource competition or habitat modification, causing the decimation or even local extinction of species (or genetically unique populations), resulting in irreversible losses of genetic diversity. The impact of the alien species is mainly related to species characteristics (primarily with its abundance, food habits and behaviour) and hierarchical complexity and anthropogenic disturbance of the recipient ecosystem (Elton 1958; Lozon and MacIsaac 1997). Several attempts to evaluate or compare possible predation impacts of alien crustaceans have been made (e.g., Telesh et al. 2001; Berezina 2008; Bollache et al. 2008), revealing the ecological significance of the alien species.

The selective predation on planktonic and benthic invertebrates by some amphipods, mysids and decapods is considered the main mechanism explaining the replacement and shifts in density of native species. Examples of impact by predatory crustaceans on native populations/communities have been described in detail (Dick et al. 2002; Kelly et al. 2006; Berezina 2007b, c). As a rule, the predation pressure depends on the predatory nature of invasive crustacean species and the abundance and availability of prey in particular habitats.

10 Amphipoda

Microscopic analysis of gut contents of the alien gammaridean amphipods demonstrated that they are omnivorous, possessing mixed feeding strategies and acting as grazers, collector/gatherers and predators (Dick and Platvoet 2000; Devin et al. 2003; Kelly et al. 2006; Berezina 2007c; Bollache et al. 2008). The authors here suggest that their diverse diets allow them to partition resources when available and to successfully compete with native species that tend to be more stenophagous. Although being omnivorous, differences in the food spectra were identified between the alien amphipod species and mean proportions of animal food in the diet increased from smaller to larger species. The large-sized amphipod *P. robustoides* starts to predate at a young age (body length 6–7 mm) attacking the larvae of chironomids and oligochaetes, which are often larger than the species itself (Berezina and Panov 2003). In the littoral zone of Neva Bay, predation by *P. robustoides* on other benthic organisms was the main reason for the densities of prey species to decrease, and the main cause by which the native *G. lacustris* and an earlier established alien amphipod, *G. fasciatus*, were replaced or notably decreased in abundance (Berezina and Panov 2003; Orlova et al. 2006).

The distinct ontogenetic differences in diet and proportion of consumed animal and plant food were recorded for many amphipods (Limen et al. 2005; Berezina 2007c). For example, there were significant differences in the proportion of food categories in the gut contents of *P. robustoides* from the Neva Estuary with size-dependent food preferences (see Fig. 2; Berezina 2007c). The contribution of animal food increased significantly with body size. The juveniles (body length 5–7 mm) were mainly detritivorous (70–80% gut content). Macrophytes (mainly *Potamogeton* sp.) and small invertebrates associated with macrophytes (small oligochaetes, infusorians, rotifers and chironomid larvae) were main food items of middle-sized specimens (8–12 mm). Large *P. robustoides* specimens (larger than 13 mm) are preferentially predaceous, consuming ephemeropteran and chironomid larvae, oligochaetes, isopods, planktonic crustaceans and their own juveniles.

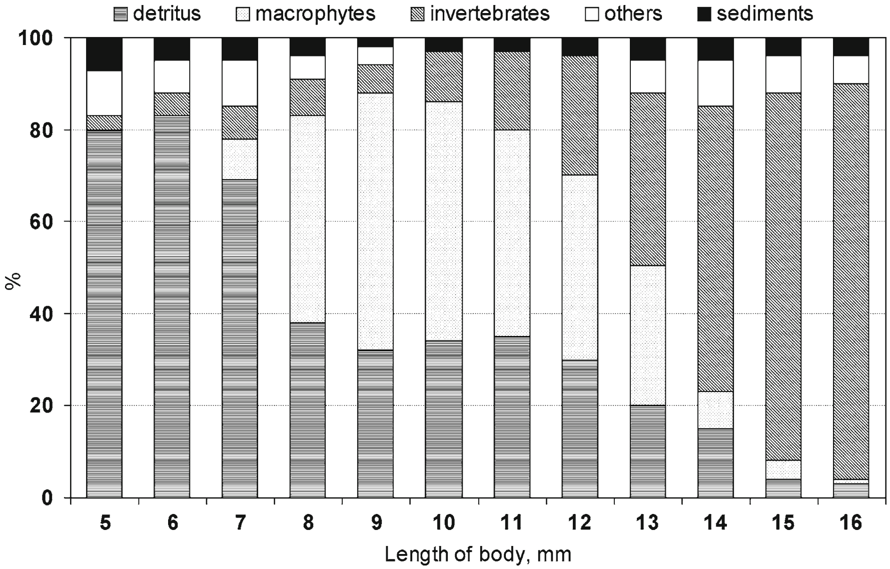

Fig. 2 Differences in proportion of food categories in gut content of *Pontogammarus robustoides* from Neva Estuary with size-dependent differentiation in food preferences (Developed from Berezina 2007c)

The predation impact index (IP) was proposed for assessment of alien amphipod predation pressure on benthic invertebrates (Berezina 2008). It is calculated as the ratio between consumption rate (C_{pop}) of the population and sum production of their preys (P_{prey}) for a given period ($IP = C_{pop}/P_{prey}$). The IP of *P robustoides* was ranked as high ($IP > 1$), middle ($0.5 < IP < 1$) and low ($0 < IP < 0.5$). Data on the dynamics of invertebrate communities in the coastal zone of the Neva Estuary in 2002–2008 were used for examination. Food spectra and the proportion of different food items in the diet of both amphipod species depending on their body length were analyzed microscopically and the consumption rates of the invaders measured experimentally (Berezina et al. 2005; Berezina 2008).

The proportion of animal food in the diet of i-sized group of *P. robustoides* (K_i, %) was calculated as: $K_i = 0.01 \times L_i^{3.22}$. Consumption rate ($C_i$, %) was calculated as: $C_i = 2.72 \times W_i^{-0.79}$; $W = 0.027 \times L_i^{2.75}$ or $C_i = 47.2 \times L_i^{-2.17}$, where L_i is body length (mm) and W_i is wet weight of i-sized specimens. The consumption rate of the predaceous part of the amphipod population was estimated as $C_{pop} = \sum K_i \times C_i \times B_i$, where B_i is biomass of all i-sized groups in habitats. Oligochaetes, isopods, juvenile amphipods (body length 1.5–6 mm) and chironomid larvae, ephemeropterans, trichopterans and other insects were considered as potential prey following earlier gut content studies (Berezina et al. 2005; Berezina 2008). The production rate of each taxon was calculated using rates of their somatic growth or specific production rate (p_s, Golubkov 2000) and biomass ($P_j = p_s \times B_j$).

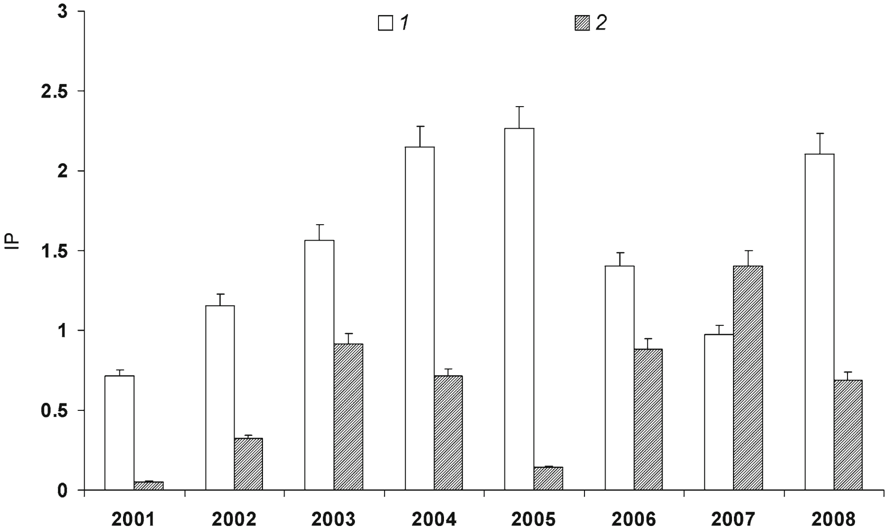

Fig. 3 Changes in IP indices (mean ± SE) for *Pontogammarus robustoides* in the southern (1) and in the northern (2) locations of the Neva Estuary between 2001 and 2008

The index varied between sampling dates, reaching a maximum in the beginning of summer and autumn, when large specimens were abundant. According to the 2005 data, predation pressure was strongest in June and low (<1) in August, when juveniles constituted a large component in the population. In autumn IP increased to 1.2–1.9 (with a maximum in late September, IP = 4.7), which demonstrates a strong predation impact on the invertebrate community including other crustaceans (native amphipods, isopods and the previously introduced amphipod *G. fasciatus*). Assessment of this impact in 2002–2008 demonstrated that the influence of alien amphipods on the littoral macrofauna reached a maximum in 2005–2006, and later decreased (Fig. 3).

11 Mysidacea

Alien mysids are abundant of in the Curonian Lagoon, and play an important part in its trophic structure (Razinkov 1990; Lesutienė 2009). Vertical nocturnal migrations emerged as an important feature of mysid feeding behaviour (Razinkovas 1996; Lesutienė et al. 2005). Stomach content analysis of *P. lacustris* revealed a significant proportion of planktonic crustaceans, suggesting that the mysids feed on mesozooplankton during their nocturnal migrations (Jankauskienė 2003). These results contradict previous works claiming *P. lacustris* fed preferentially on phytoplankton and phytodetritus (Komarova 1991). Stable isotopes were used to reconstruct its diet i.e., identify the primary carbon sources ($\delta^{13}C$) and estimate the

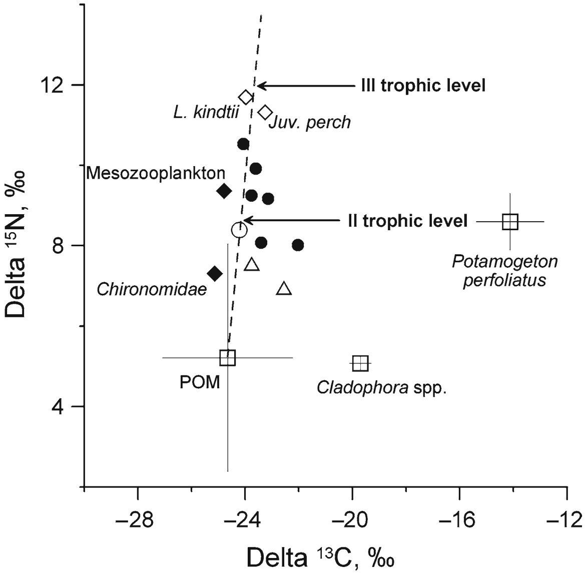

Fig. 4 Position of the Ponto-Caspian crustaceans in the food web of the Curonian Lagoon revealed by stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$, ‰; mean ± SD). Squares denote primary sources of organic matter (POM- particulate organic matter over past 3 weeks); filled diamonds – primary consumers, open diamonds – carnivores. Circles indicate mysids: filled – *Paramysis lacustris*, open – *Limnomysis benedeni*; triangles – amphipods of the family Pontogammaridae. Dashed line shows the hypothetical food chain for POM as primary source of organic matter, 3.4 and 0.5‰ enrichment per trophic level for $\delta^{15}N$ and $\delta^{13}C$, respectively

position of Ponto-Caspian mysids in the food chain ($\delta^{15}N$) in the Curonian Lagoon (Lesutienė et al. 2007; Lesutienė et al. 2008). All investigated consumers used POM as primary source of organic matter, whereas distinct $\delta^{13}C$ ratios from that in littoral macrophytes indicate minor importance of this source in the secondary production (Fig. 4). A similar $\delta^{13}C$ signal in mesozooplankton and chironomids implies that the isotopic ratios in suspended and sedimented POM are indistinguishable. This however hampers further evaluation of mysid relative use of water column or epibenthic surfaces as feeding environments (Fig. 4). The third trophic level in the POM based food chain is taken by the carnivorous cladoceran *Leptodora kindtii* and planktivorous juvenile perch (Fig. 4). All individuals of *P. lacustris* are less enriched in ^{15}N than the cladoceran and the perch, and take intermediate position between the herbivores and true carnivores. *Limnomysis benedeni*, feeding on detritus, phytoplankton and occasionally rotifers, represented the true herbivore on the $\delta^{15}N$ to $\delta^{13}C$ plot (Jankauskienė 2003).

The variability of $\delta^{15}N$ signatures in *P. lacustris* is largely determined by ontogenetical diet changes (Lesutienė et al. 2007). The significant enrichment of mysid $\delta^{15}N$ values with the increasing size about 3 PSU between the smallest (3 mm) and largest (12 mm) individuals, suggests that during the ontogenetic development, mysid diet changes nearly one trophic level (assuming 3.4 psu as one trophic level enrichment factor).

Juvenile mysid diet is composed largely by phytoplankton, whereas immature or subadult individuals have mixed diets. As indicated by the similarity between the $\delta^{15}N$ values in the stomachs and ambient zooplankton, mysid become largely carnivorous and start to feed actively on mesozooplankton at the threshold size of 8.7 ± 0.7 mm (Lesutienė et al. 2007). Individuals of >8.7 mm length prevail in the population only from late autumn to spring.

Paramysis lacustris does not have a significant effect on the zooplankton community in the Curonian Lagoon in summer, as the population consists largely of small herbivorous and omnivorous individuals. The largest carnivorous specimens of *P. lacustris* accumulate at greater depths (>2 m) in the summer (Razinkovas 1996), which reduces their competition with the zooplanktivorous juvenile fish that are largely distributed at shallower depths. Indeed, the spring diet and habitat overlap between *P. lacustris* and fish larvae is highly possible and needs further investigations. In addition, after establishment of the Ponto-Caspian mysids, fish larvae were gradually replaced with mysids in the diet of juvenile predatory fish (Razinkov 1990). Nowadays mysid share in the diet of >1–2 years age perch and pikeperch is 62% and 98%, respectively (Ložys 2003). Tus, reduced mortality of fish larvae is likely to compensate for possible negative mysid effect of competition for zooplankton.

During the autumn *P. lacustris* becomes the key species in the littoral food web. The use of littoral particulate organic matter, detritus from the decaying macrophytes, and some meiobenthos as food sources by mysids improves their nutritional conditions when phytoplankton and zooplankton decline. The differences of $\delta^{15}N$ values between the size groups minimizes during this period (Lesutienė et al. 2007, 2008), which corresponds well to decreased zooplanktivory of large sized mysids. Mysids increase organic matter transfer efficiency in the macrophyte detritus food chain during autumn when other important littoral consumers, such as amphipods, are scarce (Lesutienė pers. obs.). Calculated *Paramysis lacustris* cumulative consumption is 9 g DW m^{-2} (estimated using data from the three autumn months). This is a substantial quantity of the organic material, mainly originating from the decaying submersed vegetation that is remineralized by the mysids in the littoral zone and becomes available to the higher trophic levels. In the meantime, inshore-offshore horizontal migrations of mysids can increase the horizontal transport of assimilated organic matter.

12 Decapoda

The Chinese mitten crab feeds on a wide variety of benthic invertebrates (Anger 1990). Too little is known of its impact in the eastern Baltic Sea; however, predation pressure on native plants and small macroinvertebrates was recorded from other regions (Ojaveer et al. 2007) and likely competes for food with fish and birds. Some fishermen from eastern Gulf of Finland testified also about the negative influence of the crabs on the local fisheries, i.e., destroying nets (Petryashov, unpublished data). The crab may transport sessile biota attached to its carapace, and smaller member of the Nematoda, Bivalvia, Crustacea, Oligochaeta and Gastropoda in the dense setal patches on its claws (Ojaveer et al. 2007).

Palaemon elegans plays a significant role in the trophic web of the coastal areas of the Baltic Sea in that it forages on certain food components and is itself consumed by predators (Berglund 1980; Janas and Barańska 2008). It could potentially affect the assemblages of aquatic plants and benthic animals. In the Puck Bay (Poland), detritus (>80%) and filamentous algae (36–88%) was the dominant food item with respect to frequency of occurrence in *P. elegans* diet (Janas and Barańska 2008). Also, crustaceans (Ostracoda, Amphipoda, Harpacticoida) and insect larvae (Chironomidae) made an important contribution to the stomach content. Occupying the same habitat as native prawn species *P. adspersus* Rathke, 1837 and *Palaemonetes varians* (Leach, 1814), *P. elegans* often dominates in the assemblages and even has replaced the natives (Grabowski 2006; Janas and Barańska 2008).

The recent increase in abundance of alien malacostracan crustaceans poses an additional risk of both structural and functional changes in the Baltic Sea ecosystems. The invasion of malacostracans may results in a high ecological impact, leading to changes in pre-existing biota, losses of species diversity and destabilization of recipient ecosystems through food web alterations. The results indicate that alien amphipods, mysids, decapods and other crustaceans have become important components of the food web of the Baltic littoral. Their role is dependent on their ontogenetic stage and food supply. The dietary plasticity and ability to alternate feeding strategies allows these crustaceans to turn from predatory to non-predatory (scavenging) mode on low-calorie food (detritus or plants) when prey is scarce. *Pontogammarus robustoides* and the Chinese mitten crab are invaders with potentially high ecological impacts. Other alien crustaceans have low impact on the Baltic food webs as they do not have the potential to dominate the ecosystems and coexist with populations of native species without affecting the dynamic structure and stability of the ecosystem.

13 Management

The contemporaneous development of regional commercial fishery in newly built reservoirs based on alien crustaceans and invasive species research effort during the last decade resulted in a body of scientific knowledge useful for management purposes.

The first Baltic Sea Alien Species Database provided a reference system on alien species in the Baltic Sea area. It has been available online since 1997 for environmental management, research and education (Baltic Sea Alien Species 2006). Lithuanian, Russian and Polish scientists have attempted to develop environmental and risk assessment indices (Olenin et al. 2007; Arbačiauskas et al. 2008; Panov et al. 2009), with particular reference to range expansion by inland waterways and the most important vectors of introduction for malacostracans (Jażdżewski 1980). These attempts are regarded as useful suggestions in establishing a framework for the incorporation of alien species into the European Water Framework Directive (Cardoso and Free 2008). In spite of the continued attention being paid by the scientific community, the local governments of the Eastern Baltic Sea still have little concern with regard to preventing new aliens from entering the Baltic Sea. Introduced higher crustaceans are included in the 'black' lists of species that are under control of environmental agencies. However, enforcement of the local regulations is partial.

The prevention of species crossing borders, including international commitments such as the regulations concerning trade in wildlife (European Community 1997) and use of alien and locally absent species in aquaculture (European Community 2007), could be more powerful than local laws. The HELCOM countries have agreed to ratify by 2010, or at the latest by 2013, the 2004 International Convention on the Control and Management of Ships' Ballast Water and Sediments initiated by International Maritime Organization. This will help to reduce the ballast-transported aliens and may prevent the further spread of mysids, decapods and amphipods (Ovčarenko et al. 2006).

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