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Crustacean invasions in the Estonian coastal sea

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Abstract. In this paper we describe the invasion history of benthic crustacean species that have recently invaded the Estonian coastal sea. Physical characteristics of their habitat and communities associated with the invasive species were explored. The crustaceans *Gammarus tigrinus*, *Chelicorophium curvispinum*, *Pontogammarus robustoides*, and *Paramysis intermedia* are the most recent newcomers in the Estonian coastal sea. All these species have formed permanent populations and more aggressive species have likely caused significant shifts in the community structure and functioning. Besides the true invasive species, some native amphipod species have significantly expanded their range in the Baltic Sea. This group consists of rare or previously not spotted benthic invertebrate species in the northern Baltic Sea range such as *Echinogammarus stoerensis*, *Calliopius laeviusculus*, and *Melita palmata*.

Key words: Baltic Sea, benthic invertebrates, nonindigenous, *Gammarus tigrinus*, *Chelicorophium curvispinum*, *Pontogammarus robustoides*, *Paramysis intermedia*.

INTRODUCTION

Together with habitat loss and climate change, invasions of nonindigenous species are one of the most serious threats to global biodiversity. This human-aided process has initiated significant, unpredictable, and irreversible changes to both the abiotic and the biotic environment and has caused severe economic damage in a variety of waterbodies worldwide (e.g. Carlton, 1996; Vitousek et al., 1997; Sala et al., 2000). Concurrently with this global trend several new crustacean species have also been found in the Estonian coastal sea in recent years.

The gammarid amphipod *Gammarus tigrinus* Sexton originates from the North American coast of the Atlantic Ocean. The species was introduced to Europe probably in ballast water and was first discovered in England in 1931 (Chambers, 1977). Although *G. tigrinus* was found in the Baltic Sea already in 1975, its significant range expansion started in the 1990s (Jazdzewski et al., 2002, 2005; Szaniawska et al., 2003). In the northern Baltic Sea *G. tigrinus* was first found in the northern Gulf of Riga (Herkül et al., 2006) and the northern Gulf of Finland in 2003 (Pienimäki et al., 2004). In 2005, *G. tigrinus* was found in the Neva Estuary, the easternmost part of the Gulf of Finland (Berezina, 2007). This species has caused a significant decrease in the diversity and density of native

amphipods in the southern Baltic Sea (Grabowski et al., 2006) and Estonian coastal sea (Kotta et al., 2006; Orav-Kotta et al., 2009).

The amphipod *Chelicorophium curvispinum* (Sars) originates from large rivers connected to the Black Sea and the Caspian Sea. It was found in the Baltic Sea already in the 1920s (Bij de Vaate et al., 2002). The species invaded to the Baltic and North seas through rivers and canals attached to the hulls of ships and in ballast water. Regardless of its long invasion history in the Baltic Sea, *C. curvispinum* was not found in the northern Baltic until 2005 when it was detected in the eastern part of the Estonian coast of the Gulf of Finland (Herkül & Kotta, 2007). In the next year, 2006, *C. curvispinum* was found in Luga Bay, Russia (Malyavin et al., 2008).

Similarly to *C. curvispinum*, the gammarid amphipod *Pontogammarus robustoides* (Sars) originates from the lower reaches of Ponto-Caspian rivers and from brackish and freshwater lakes around the Black Sea (Bij de Vaate et al., 2002). In 1960–1961, the species was intentionally introduced into the Kaunas Water Reservoir on the Nemunas River, Lithuania (Bij de Vaate et al., 2002; Gumuliauskaitė & Arbačiauskas, 2008). It successfully spread in the Nemunas drainage system including the Curonian Lagoon of the Baltic Sea. In 1999 *P. robustoides* was first found in Neva Bay, the easternmost part of the Gulf of Finland (Panov et al., 2003) and in 2006, in Lake Ladoga (Kurashov & Barbashova, 2008). In 2006 the species was recorded for the first time in the Estonian coastal sea. Similarly to *G. tigrinus*, *P. robustoides* has a potential to reduce the diversity and density of native gammarids (Panov et al., 2003; Gumuliauskaitė & Arbačiauskas, 2008).

The mysids *Paramysis intermedia* (Czerniavsky) and *P. lacustris* (Czerniavsky) are native to rivers connected to the Caspian Sea and Black Sea (Birshteina et al., 1968). In the 1970s *P. lacustris* and *P. intermedia* were introduced to Lake Peipsi but neither of the species has been sighted later (Timm et al., 2001). Both species were also introduced to Lake Võrtsjärv, southern Estonia, in the 1970s, but only *P. lacustris* formed a permanent population there (Kangur et al., 2004). However, there is only a single record of *P. lacustris* in the Estonian coastal sea dating back to 1963 (Yarvekyulg, 1979). We are not aware of any successful introductions of *P. intermedia* in the Baltic Sea drainage area while *P. lacustris* inhabits the Curonian Lagoon, the southern Baltic Sea, already since the 1960s. In 2008 *P. intermedia* was found for the first time in the Baltic Sea. There were two separate records in 2008, one from the Gulf of Riga and the other from the eastern Gulf of Finland.

Besides the true invasive species this paper reports recent findings of rare gammarid amphipods in the northern Baltic Sea range. *Echinogammarus stoerensis* (Reid), *Calliopius laeviusculus* (Kröyer), and *Melita palmata* (Montagu) are found on the north-eastern coast of the Atlantic (Barnes, 1994; Hansson, 1998; Bellan-Santini & Costello, 2001). There have been only a few documented records of *E. stoerensis* in the Baltic Sea region (Jazdzewski, 1976; Leineweber, 1985). The species was found for the first time in the Estonian coastal sea near Osmussaar Island, the western Gulf of Finland, in 2007. *Melita palmata* is known to inhabit the western and central Baltic (Yarvekyulg, 1979; Barnes, 1994; Hansson, 1998).

In 2006, *M. palmata* was found for the first time in Estonia. According to Yarvekyulg (1979), *C. laeviusculus* is found from the southern Baltic Sea to the western part of the Gulf of Finland. From the Estonian coastal sea, documented records of *C. laeviusculus* near Hiiumaa Island date from 1963. There were no further records of *C. laeviusculus* until 2006 when the species was found in the western part of the Gulf of Finland and off western Saaremaa Island.

The aims of this study are to report (1) new data on the distribution and habitats of recently arrived nonindigenous amphipods (*G. tigrinus*, *C. curvispinum*, *P. robustoides*) in the Estonian coastal sea, (2) the first record of *P. intermedia* in the Baltic Sea, and (3) new findings of rare amphipod species (*E. stoerensis*, *C. laeviusculus*, *M. palmata*) in the Estonian coastal sea.

MATERIAL AND METHODS

Data from more than 6900 quantitative benthos samples collected from the Estonian coastal sea (Fig. 1) in 2003–2008 (databases of the Estonian Marine Institute) were used in this study. The data were obtained from macrozoobenthos and macrophytobenthos mapping studies, the Estonian coastal sea monitoring programme, and field experiments. All benthos samples were collected and analysed according to the HELCOM standards (HELCOM, 2006). Additionally, some semiquantitative

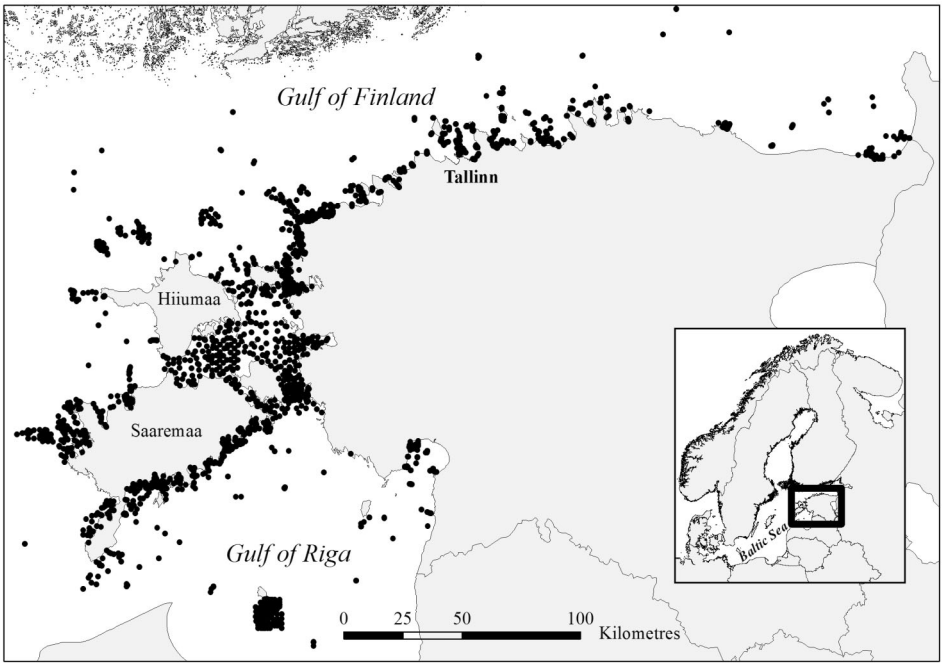

Fig. 1. Sampling stations in the Estonian coastal sea in 2003–2008.

samples were collected with a hand net and Rass dredge in Narva Bay, the eastern Gulf of Finland, in 2008. All biomasses in this paper are represented in dry weight.

RESULTS AND DISCUSSION

Table 1 presents information on the first records of the crustaceans studied in the Estonian coastal waters and physical characteristics of their populations (biomass, abundance) and habitat (depth, sediment type).

In the Estonian coastal sea ***Gammarus tigrinus*** was first found in Kõiguste Bay, northern Gulf of Riga, in 2003 (Fig. 2) when the benthic colonization and community development were studied in a mesocosm experiment in the shallow water area of this bay. The alien amphipod had colonized several experimental mesocosms (Herkül et al., 2006), but despite intensive sampling throughout the ice-free season, the species was not observed in regular monitoring stations (Kotta et al., 2006). In the mesocosm experiment the abundance and biomass of *G. tigrinus* ranged between 100 and 800 ind. m^{-2} and 0.2 and 2.3 g m^{-2}, respectively. In 2003 *G. tigrinus* was also found for the first time in the Gulf of Finland near Hamina and Turku (Pienimäki et al., 2004). In 2004 *G. tigrinus* had already spread all over Kõiguste Bay with densities up to 4700 ind. m^{-2} and biomass reaching 12.22 g m^{-2}. In 2005 the alien amphipod was found all over the northern Gulf of Riga, throughout the southern coast of Saaremaa Island, and in Rame Bay, western mainland. By 2006 *G. tigrinus* had reached Pärnu Bay and the eastern bays of the West Estonian Archipelago Sea. The amphipod was first found in the western part of the Gulf of Finland in 2007 and in its central and eastern parts in 2008 (Fig. 2). By the end of 2008 *G. tigrinus* had been found from a total of 350 benthos samples from the Estonian coastal sea. Based on all the samples containing *G. tigrinus*, the amphipod's abundance varied between 0.118 and 5150 ind. m^{-2} and its biomass was from <0.001 to 12.22 g m^{-2}. The average values of abundance and biomass were 418 ind. m^{-2} and 0.654 g m^{-2}, respectively. The alien amphipod reached its maximum biomasses already in the second year of invasion in Kõiguste Bay in 2004. It inhabited a broad depth range from 0.2 to 20.5 m, but the mean depth of the finds was only 1.7 m (Table 1). The species preferred sandy and silty sediments associated with charophytes, phanerogams (*Myriophyllum spicatum* L., *Potamogeton pectinatus* L.), and the green alga *Cladophora glomerata* (L.) Kützing. Invertebrate species most frequently co-occurring with *G. tigrinus* were chironomid larvae, the cockle *Cerastoderma glaucum* (Poiret), and the gastropod *Theodoxus fluviatilis* (L.). There is some circumstantial evidence that *G. tigrinus* is competitively superior over most other native gammarid species in European fresh and brackish waterbodies (e.g. Pinkster et al., 1992; Grabowski et al., 2006). Similarly, we observed a significant decline of native gammarids associated with the invasion of *G. tigrinus* in the Estonian coastal range (Kotta et al., 2006). A recent experimental study on the feeding preferences and the aggressiveness of gammarid amphipods also corroborated these

Table 1. Population characteristics of the studied crustacean species and physical characteristics of their habitat

Species	First record (year)	No. of samples	Biomass, g dw m^{-2}			Abundance, ind. m^{-2}			Depth, m			Sediment
			Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
Gammarus tigrinus	2003	350	<0.001	12.220	0.654	0.118	5 150	418.39	0.2	20.5	1.7	Sand, silt
Chelicorophium curvispinum	2005	21	<0.001	1.975	0.246	0.017	10 950	1 078.85	0.2	4.9	1.2	Sand, pebbles
Pontogammarus robustoides	2006	33	<0.001	3.460	0.641	0.033	1 200	214.87	0.1	2	0.6	Sand, pebbles
Paramysis intermedia	2008	3	<0.001	0.020	0.007	0.042	25	8.64	1	2.1	1.4	Sand
Echinogammarus stoerensis	2007	10	0.001	0.131	0.049	25	250	77.50	3.2	10.7	7.5	Rock
Calliopius laeviusculus	2006*	41	0.003	0.180	0.037	25	450	109.15	0.5	18	8.1	Rock, pebbles
Melita palmata	2006	14	0.002	0.085	0.034	25	150	57.86	0.5	13	2.8	Rock, sand

* There are historical records of *C. laeviusculus* also from 1963.

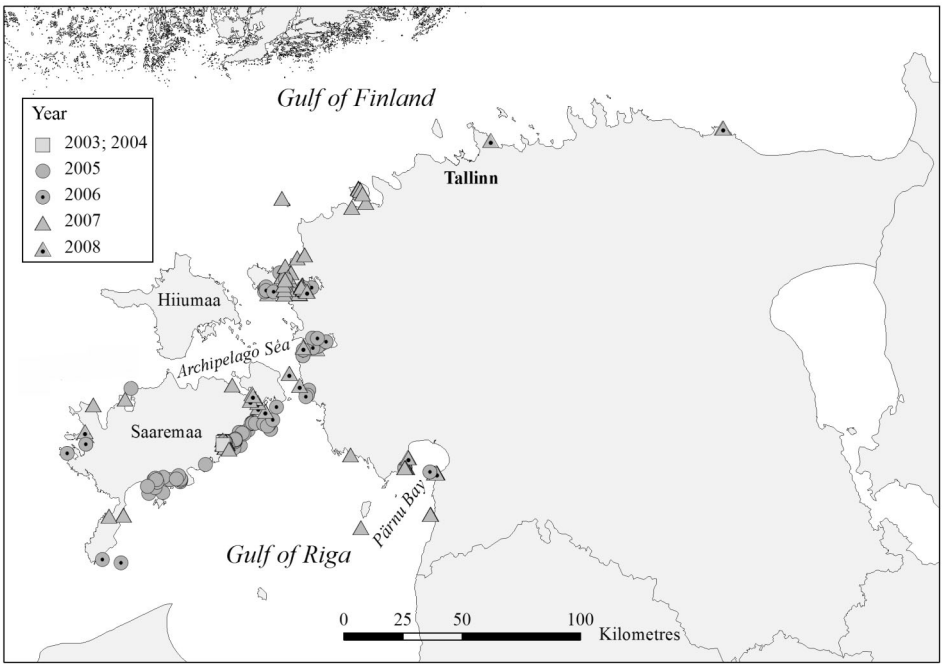

Fig. 2. Invasion and range expansion of *Gammarus tigrinus* in the Estonian coastal sea.

findings and we concluded that the competitive interaction between *G. tigrinus* and the native amphipods within the prevailing macrophyte communities is the likely explanation of the decline of the native gammarid amphipods after the establishment of *G. tigrinus* in the northern Baltic Sea (Orav-Kotta et al., 2009).

Chelicorophium curvispinum was found for the first time in the Estonian coastal sea near Sillamäe in Narva Bay, the eastern Gulf of Finland, in 2005. The salinity in the area is about 4.5. The species was observed in the depth range of 1 to 4.9 m in places where the bottom substrate was dominated by sand and boulders. The bottom vegetation was characterized by a belt of the green algae *Cladophora rupestris* (L.) Kützing and *C. glomerata*. The average abundance of *C. curvispinum* varied between 125 and 1425 ind. m^{-2} and its average biomass was 0.05–0.27 g m^{-2}. The minimum and maximum densities were found at 4.9 and 3 m depths, respectively. After juveniles of gammarid amphipods, *C. curvispinum* was the second most abundant taxon at 3 m depth. By 2008 *C. curvispinum* was found some 3 km westwards and 15 km eastwards (mouth of the Narva River). Then its abundance and biomass reached 10 950 ind. m^{-2} and 1.975 g m^{-2}, respectively. The depth range at which *C. curvispinum* has been found is 0.2 to 4.9 m (Table 1). The nonindigenous amphipod co-occurred mainly with *Gammarus* spp., chironomid larvae, and another Ponto-Caspian invader in the region, *P. robustoides*. *Cladophora glomerata* and *Ulva intestinalis* (L.) Nees were the dominant macrophytobenthic species in the locations of *C. curvispinum*. At high densities *C. curvispinum* is known

to reduce the species richness of macroinvertebrates and decreases, through high filtration capacity, total suspended matter. Additionally, by constructing tubes on solid substrate *C. curvispinum* may alter the physical properties of the benthic environment (Bij de Vaate et al., 2002). Because of the short invasion history and limited distribution of *C. curvispinum* in the Estonian coastal waters, we lack evidence for the negative effects of the species on local communities so far.

Pontogammarus robustoides was recorded for the first time in the Estonian coastal sea in Narva Bay, eastern Gulf of Finland, in 2006 (Fig. 3). The amphipod inhabited the sandy–pebbly seabed at 2 m depth, co-occurring with the amphipods *Gammarus* spp., *Chelicorophium curvispinum*, the barnacle *Balanus improvisus* Darwin, and chironomid larvae. *Ulva intestinalis* and *Cladophora glomerata* prevailed in phytobenthos. When first found in 2006, *P. robustoides* was present only in one sample. The abundance and biomass were 300 ind. m^{-2} and 0.698 g m^{-2}, respectively. In 2007 and 2008 the invader was found ca. 7 km eastwards of the location of the first record. The abundance and biomass were up to 1200 ind. m^{-2} and 2.044 g m^{-2}, respectively (Table 1). The amphipod co-occurred with the same benthic species as in 2006. In the northern Baltic Sea *P. robustoides* has a localized distribution. However, the species is very abundant in the southern Baltic Sea and is together with *Obesogammarus crassus* (Sars) the most invasive

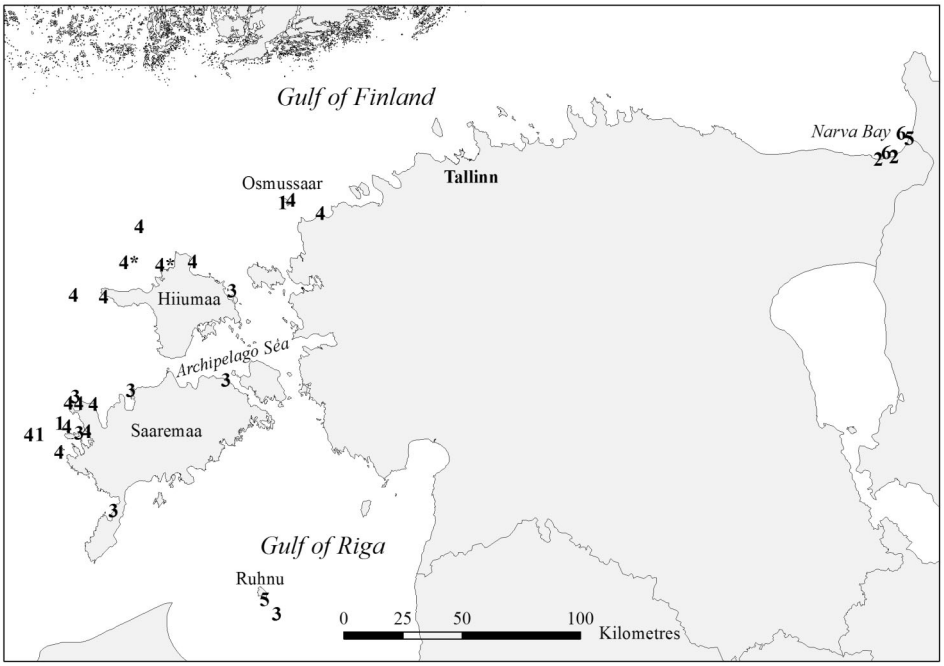

Fig. 3. Distribution of the studied crustacean species in the Estonian coastal range: 1 – *Echinogammarus stoerensis*, 2 – *Pontogammarus robustoides*, 3 – *Melita palmata*, 4 – *Calliopius laeviusculus* (* denotes historical records from 1963), 5 – *Paramysis intermedia*, 6 – *Chelicorophium curvispinum*.

among gammarid amphipods (Grabowski et al., 2007). Thus, in a near future other major shifts in macrophyte–herbivore assemblages can be expected together with the retreat of *G. tigrinus* and the establishment of *P. robustoides* and *O. crassus*. As the effects of these species on native amphipods and macrophytes are not known in the northern Baltic Sea, it is difficult to predict the effects of the invasions on the ecosystem.

There were two parallel finds of ***Paramysis intermedia*** in 2008: near Ruhnu Island, the Gulf of Riga, and in the coastal sea adjacent to the mouth of the Narva River, the eastern Gulf of Finland (Fig. 3). These are the first records of the species in the Baltic Sea range. In the Narva River site, *P. intermedia* was found on a shallow (1 m) sandy bottom co-occurring with the other two Ponto-Caspian invaders, *C. curvispinum* and *P. robustoides*. In the Ruhnu Island site, *P. intermedia* was found at 2.1 m depth on a sandy–rocky bottom together with the gastropod *T. fluviatilis*, amphipods *Gammarus* spp., isopods *Idotea* spp., the barnacle *B. improvisus*, and chironomid larvae. Henn Timm (2007, pers. comm.) found unknown mysids from the Narva River in 2007. Later these animals were identified as *P. intermedia*. Although *P. intermedia* did not form a permanent population in Lake Peipsi after its deliberate introduction in the 1970s, the species might have survived in the Narva River and is currently invading the coastal sea. The invasion corridor of the Gulf of Riga population remains unknown. There are no documented ecological impacts of *P. intermedia*.

Echinogammarus stoerensis was found for the first time in the Estonian waters in 2007 near Osmussaar Island, the western Gulf of Finland, at 5 m depth on a rocky bottom (Fig. 3). The species was found only in one sample with the abundance and biomass of 50 ind. m^{-2} and 0.001 g m^{-2}, respectively. The dominant species in the sample were the gastropods *Theodoxus fluviatilis* and *Hydrobia ulvae* (Pennant), the bivalve *Macoma balthica* (L.), and amphipods *Gammarus* spp. In 2008, *E. stoerensis* was found in several sampling sites near western Saaremaa Island in the depth range of 3.2–10.7 m. These sites were characterized by a rocky seabed with the brown algae *Pilayella littoralis* (L.) Kjellman and *Chorda filum* (L.) Stackhouse dominating in the phytobenthos and the bivalve *Mytilus trossulus* Gould, the barnacle *B. improvisus*, amphipods *Gammarus* spp., and the isopod *Jaera albifrons* Leach being dominant invertebrates. The abundance and biomass of *E. stoerensis* reached 250 ind. m^{-2} and 0.131 g m^{-2}, respectively (Table 1).

Calliopius laeviusculus was previously found in 1963 near Hiiumaa Island (Yarvekyulg, 1979). Since then there were no records of the species until 2006 when it was found in the western part of the Gulf of Finland (Fig. 3). Later on there were several finds near Osmussaar Island, Hiiumaa Island, and western Saaremaa Island in 2007–2008 (Fig. 3). The depth in the locations of *C. laeviusculus* varied between 0.5 and 18 m with the average being 8.1 m. Rocky and pebbly substrate dominated with the brown alga *P. littoralis* and the red alga *Ceramium* spp. The bivalve *M. trossulus*, amphipods *Gammarus* spp., and the isopod *J. albifrons* were the dominant invertebrates found in the samples with *C. laeviusculus*. The abundance and biomass of *C. laeviusculus* reached 450 ind. m^{-2} and 0.180 g m^{-2}, respectively (Table 1).

Melita palmata was first found on the northwestern coast of Saaremaa Island in 2006 (Fig. 3). There were several additional records around Saaremaa Island, eastern Hiiumaa Island, and near Ruhnu Island in 2007–2008. The invertebrate was mainly found on a rocky and sandy seabed in the depth range of 0.5 to 13 m (Table 1). The dominating plant species in the locations of *M. palmata* were *P. littoralis*, *Ceramium* spp., and *Cladophora* spp. and of invertebrates *Gammarus* spp., *Idotea* spp., *T. fluviatilis*, and *M. trossulus* prevailed. The abundance and biomass of *M. palmata* were up to 150 ind. m^{-2} and 0.085 g m^{-2}, respectively (Table 1).

To conclude, all crustacean amphipods that have recently invaded had formed permanent populations and most of them are commonly found all over the studied Estonian coastal sea. Due to their aggressiveness and high densities some of these species have probably caused significant shifts in the community structure and functioning. As we lack consistent time series and experimental studies it is difficult to say what factors are behind these recent invasions and range expansions. It is plausible, though, that recent changes in climate associated with milder winters have supported the blooms of filamentous algae throughout the Baltic Sea range. This together with prevailing westerlies and increased salinities has favoured the survival, reproduction, and eastward dispersal of phytophilous crustacean species.

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Uute ja haruldaste vähiliikide levik Eesti rannikumeres

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Kirpvähilised *Gammarus tigrinus* ja *Pontogammarus robustoides*, kaspia kootvähk *Chelicorophium curvispinum* ning müsiid *Paramysis intermedia* on Eesti rannikumere kõige uuemad võõrliigid, kes leiti esmakordselt vastavalt 2003., 2006., 2005. ja 2008. aastal. Lisaks võõrliikidele leiti aastail 2006–2008 Eesti rannikumerest kolm Läänemere põhjaosas harva esinevat kirpvähilist – *Echinogammarus stoerensis*, *Melita palmata* ja *Calliopius laeviusculus*. Kirpvähiliste *E. stoerensis* ja *M. palmata* puhul oli tegu esmaleidudega Eestis, kirpvähilist *C. laeviusculus* on varem leitud 1963. aastal. Artiklis on esitatud uusimad andmed võõrliikidest vähkide ja harva esinevate kirpvähiliste levikust ning elupaikadest aastatel 2003–2008.