

Research Article

The invasive amphipod species *Gammarus tigrinus* (Sexton, 1939) can rapidly change littoral communities in the Gulf of Finland (Baltic Sea)

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Abstract

The invasive amphipod *Gammarus tigrinus* was found for the first time and in abundant populations in shallow-water habitats in coastal areas of the city of Helsinki (Gulf of Finland, Baltic Sea). In summer-autumn 2007 the species occurred at four out of seven study sites, dominating almost exclusively at one site and comprising a progressively increasing share of the local gammarid community at another site with a reducing portion of the native *Gammarus zaddachi* during the study period. The species did not occur at the least polluted archipelago stations, which are also most exposed to wave action. With only single previous observations of this species in Finland the current findings show that *G. tigrinus* has now firmly established itself into the northern Baltic littoral ecosystem. As this exceedingly omnivorous species is able to outcompete and replace native herbivorous *Gammarus* species its environmentally detrimental effects may include lesser consumption of e.g. filamentous macroalgae, which are already highly abundant in the study region due to eutrophication.

Key words: *Gammarus tigrinus*, Baltic Sea, invasive species, non-indigenous species, food web structure

Introduction

Keys to the success of invasive species in establishing populations outside their natural distribution range usually include opportunistic use of resources, high fecundity, lack of efficient predation, tolerance to deteriorated water quality, and/or superior competitive abilities (Grabowski et al. 2007; MacNeil et al. 2007; Pöckl 2007). In the marine realm, the known success stories of invasive invertebrate species are based on strong competitive interactions (e.g. gammarid amphipods; Jazdzewski et al. 2004), lack of predation (e.g. the comb jelly *Mnemiopsis leidyi* (Agassiz, 1865); Lehtiniemi et al. 2007) and fast population growth (e.g. *M. leidyi*, Lehtiniemi et al. 2007; the zebra mussel *Dreissena polymorpha* (Pallas, 1771), Nalepa and Schloesser 1992). Most findings of invasive species originate from routine monitoring activities, which often take place in pelagic areas. Shallow littoral zones may,

however, remain largely unexplored, except for sporadic samplings often related to other research activities, and may thus hide new species for relatively long time until discovered (cf. Daunys and Zettler 2006).

Invasive species may cause severe changes in littoral communities hosting multiple inter-specific interactions (Menge 1995). Although some non-indigenous aquatic species have established in the northern Baltic Sea food web the region has faced relatively harmless changes compared to the southern Baltic (Olenin and Leppäkoski 1999). In the northern part the rocky littoral invertebrate communities consist of ca. 10 species of peracarid crustaceans including five species belonging to the genus *Gammarus* (Amphipoda) (Kautsky and van der Maarel 1990).

Gammarus tigrinus (Sexton, 1939) is a non-indigenous amphipod species to the Baltic Sea. The species has successfully invaded coastal ecosystems in the southern parts of the sea area

(Bulnheim 1976; Szaniawska et al. 2003; Jazdzewski et al. 2004) and has in recent years extended its range also to the northern parts (Pienimäki et al. 2004; Daunys et al. 2006; Herkül and Kotta 2006; Berezina 2007). In this paper, we show how *G. tigrinus* has established itself to rocky shores on the coastline of the city of Helsinki (Gulf of Finland), has altered the species composition of the local *Gammarus* assemblages, and that the species has high reproductive potential in the area.

Materials and methods

Gammarus spp. (Crustacea: Amphipoda) were collected from seven selected sites in the city of Helsinki, situated in the central Gulf of Finland (Figure 1). Two of the sites, Marjaniemi and Munkkiniemi are relatively sheltered locations in the vicinity of urban areas. The bridge-connected inner islands of Lauttasaari and Korkeasaari are sites exposed to moderate waves and situated close to large harbours and extensive boat traffic. The islands of Suomenlinna and Vasikkasaari are wave-exposed sites on islands adjacent to intensive harbour-bound ship traffic. Finally, the island of Kuiva Hevonen is farthest away from the shoreline, very exposed to waves and hence regarded as the least polluted sampling site in this study.

The samples were collected from early July to mid-October in 2007 with qualitative methods (a hand net). The shallow littoral area, from <1 m depth to the surface, was sampled usually for ca. one hour, depending on the number of collectors. Each sample comprised of ca. 100–400 individuals of *Gammarus* spp. The gammarid fauna was collected from very variable habitats (under stones, bricks, pieces of wood and within the dense filamentous macroalgal zone). The sampling dates are listed in the Annex 1.

After sampling the individuals were transported in ambient water to the laboratory and stored at -80°C. Species and sex identification was performed from melted samples according to keys by Bousfield (1973), Lincoln (1979) and Barnes (1994) using Leica stereo microscope (up to 40× magnification). Individuals smaller than 4 mm were not identified to the species level and are therefore not included in the results.

Egg number and body length (from the tip of telson to the base of antennae) of gravid females

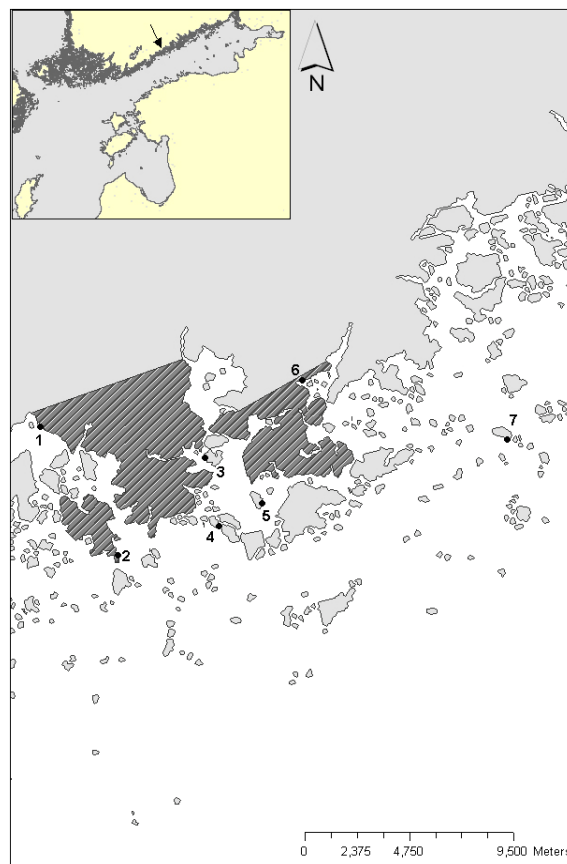


Figure 1. Map of the city of Helsinki coastal area in the central Gulf of Finland, northern Baltic Sea. Numbers refer to seven sampling sites: 1. Munkkiniemi, 2. Lauttasaari, 3. Korkeasaari, 4. Suomenlinna, 5. Vasikkasaari, 6. Marjaniemi and 7. Kuiva Hevonen.

were determined from 11 females in the summer (30 July) and from 31 females in the autumn (5 October) in Munkkiniemi in order to estimate the reproductive capacity of *G. tigrinus* in this sea area. The eggs were at the development stage I, i.e. relatively freshly produced.

Results

At the two inner sampling sites Munkkiniemi and Marjaniemi the invasive species *G. tigrinus* formed a marked share of the *Gammarus* spp. Community (Figures 2 and 3). In Munkkiniemi an average of 82% of the sampled individuals collected between July – October belonged to this species while *Gammarus zaddachi* (Sexton, 1912) (18%) and *Gammarus oceanicus* (Segerstråle, 1947) (< 1%) were also present. In Marjaniemi an average of 38% of the samples

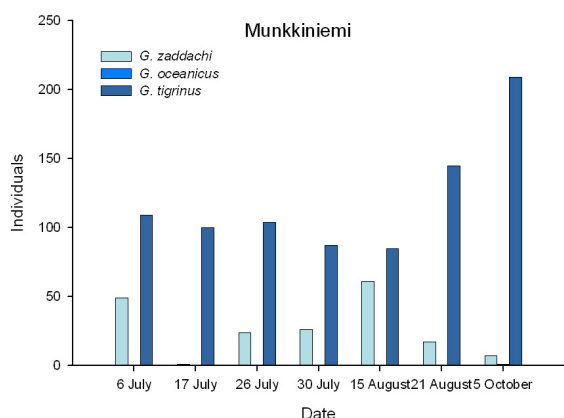


Figure 2. Proportion of different *Gammarus* species in samples collected from the Munkkiniemi sampling site at different times.

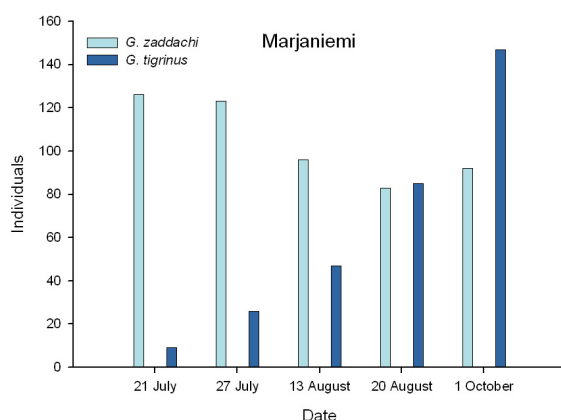


Figure 3. Proportion of different *Gammarus* species in samples collected from the Marjaniemi sampling site at different times.

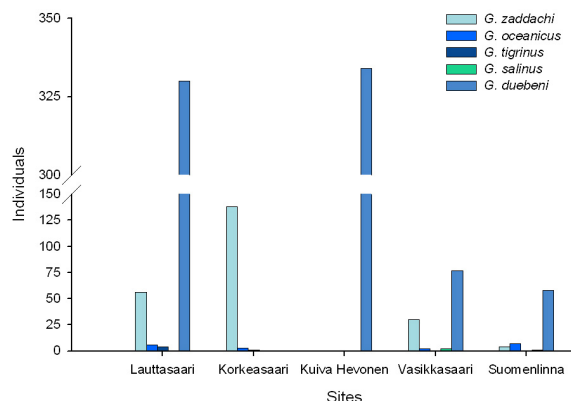


Figure 4. Proportion of different *Gammarus* species in samples collected at four sites further away from anthropogenic pressures.

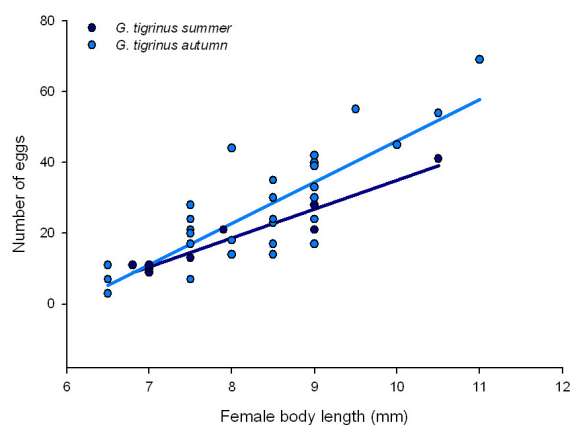


Figure 5. The number of eggs in *Gammarus tigrinus* compared to female body length in the summer and autumn. $R^2 = 0.93$ (summer, continuous line) and $R^2 = 0.68$ (autumn, broken line).

consisted of *G. tigrinus* with the rest (62%) being *G. zaddachi*. The proportion of *G. tigrinus* in the samples increased during the study period from 69 to 99% in Munkkiniemi and from 58 to 99% in Marjaniemi (Figure 3). Individuals of *G. tigrinus* were also found in the samples from Lauttasaari (four individuals, 1.0%) and Korkeasaari (one individual, 0.7%) (Figure 4), two sites moderately exposed to waves and human activities. The species was not recorded at the Suomenlinna, Vasikkasaari and Kuiva Hevonen sampling sites (Figure 4), the places most exposed to waves and least to anthropogenic pressures. At these sites the main

species was *Gammarus duebeni* (Liljeborg, 1851) (Figure 4).

The number of eggs in female *G. tigrinus* depended strongly on body length (in the summer (regression analysis: $F_{1,9}=124.6$, $p<0.0001$, $R^2=0.93$) and also in the autumn ($F_{1,29}=63.3$, $p<0.0001$, $R^2=0.68$) (Figure 5). In the summer the female body length was 7.8 ± 1.2 mm (mean \pm SD) and in the autumn 8.4 ± 1.1 mm. The largest female was 11 mm in body length and had produced over 70 eggs while the smallest ones were only 6.5 mm with only ca. ten eggs (Figure 5).

Average sex ratios (% males in each sample, mean \pm SD) in *G. tigrinus* from Munkkiniemi

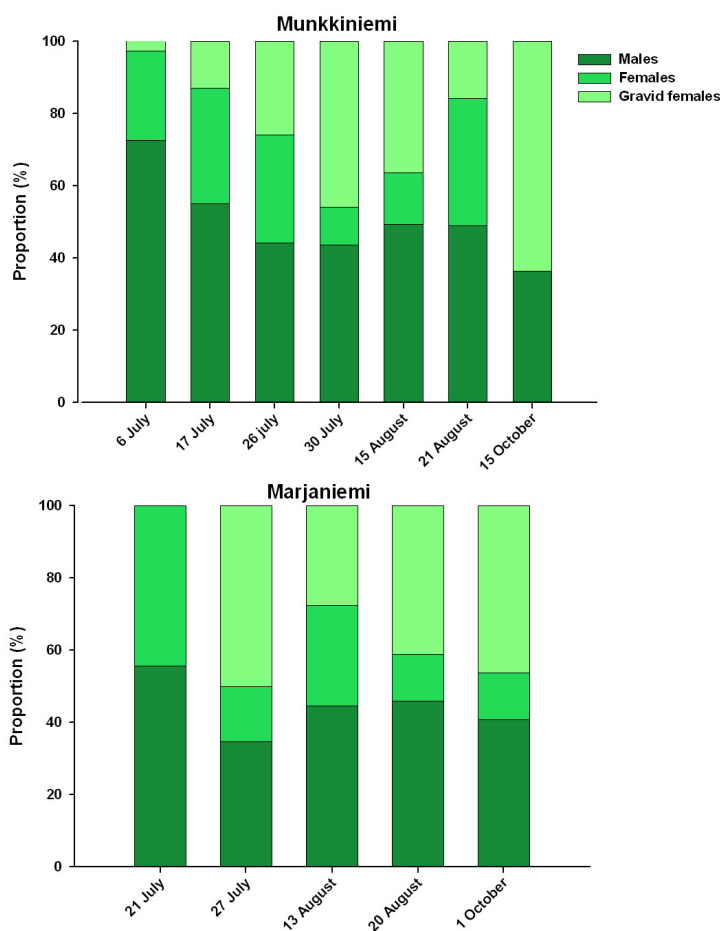


Figure 6. Population structure of *Gammarus tigrinus* in Munkkiniemi and Marjaniemi.

and Marjaniemi were 50 ± 11 and $44 \pm 8\%$, respectively. Fecund, egg-carrying females were found only from Munkkiniemi (in average $45 \pm 27\%$) and Marjaniemi ($56 \pm 33\%$). The proportion of egg-carrying females was higher at both sites later in the season (Figure 6).

Discussion

Since its first findings (Pienimäki et al. 2004), *G. tigrinus* is now, for the first time, shown to be firmly established in the littoral communities of the Gulf of Finland. In our samples collected from seven locations along the coastline of the City of Helsinki the species was observed at four locations and, being a prominent or dominant member of the *Gammarus* spp. assemblages at two of them. The sites occupied by *G. tigrinus*

are characterised as sheltered or semi-exposed shores close to the coastline and urban areas under various anthropogenic activities. In opposite, the sites lacking the species were the ones most exposed to waves and farthest away from the urban pollution sources. All established populations of *G. tigrinus* reported so far are from sheltered or near-shore locations in the Baltic Sea (Szaniawska et al. 2003; Jazdzewski et al. 2004; Daunys et al. 2006; Herkül and Kotta 2007) and in the species' native range in North America (Bousfield 1973). The present findings corroborate that wave-exposed shores, offshore reefs and similar habitats seem not favourable for the invasion of *G. tigrinus*.

The native *Gammarus* species in the study region were *G. zaddachi*, *G. salinus* (Spooner 1942), *G. oceanicus* and *G. duebeni*. When occurring together the native species have been

found to prefer distinct, although overlapping, depth zones, with *G. zaddachi* occupying the shallower and *G. salinus* the deeper waters and *G. duebeni* being restricted predominantly to rock pools and crevices over the water surface (Segerstråle 1950; Hartog 1964; Jazdzewski 1973; Kolding 1981; S. Korpinen, unpublished data). In experimental conditions, van Riel et al. (2007) showed how invasive amphipods competed with native amphipod species, resulting in microhabitat shifts by the native species. In this study, *G. tigrinus* was sampled only from the < 1 m depth zone where it has thus mostly competed with *G. zaddachi*, and possibly with *G. duebeni*, for space and resources. In the inner bays of the Helsinki region, such as Munkkiniemi and Marjaniemi, the native community in shallow water (and in above-surface crevices) has previously consisted mostly of these two species (Segerstråle 1950). At present, the amphipod assemblages have shifted to dominance by *G. tigrinus*.

Wherever the invader *G. tigrinus* has established itself it has replaced or outnumbered native amphipod species including *G. zaddachi*, *G. salinus*, and *G. duebeni*, e.g. in the inland waters of Holland and in the Baltic Sea (Nijssen and Stock 1966; Chambers 1987; Platvoet et al. 1989; Pinkster et al. 1992; Szaniawska et al. 2003; Jazdzewski et al. 2004; Daunys and Zettler 2006), causing a dramatic decline of native gammarid fauna and consequently altering species composition and interspecific interactions within these communities. In the Gulf of Finland it seems relatively improbable that *G. tigrinus* could replace *G. oceanicus*, which is a species up to 3–5 times larger in size. However, predation by *G. tigrinus* has been observed on the opossum shrimp *Mysis relicta* (Lovén, 1862) at both its adult and juvenile stages (Bailey et al. 2006), other *Gammarus* species (MacNeil et al. 2007) and also equally sized or even larger amphipod species when the latter are moulting and the carapace is soft (Dick 1996; Dick and Platvoet 1996). Thus, *G. tigrinus* may easily replace or outnumber the native *G. zaddachi*, similar to the events recorded in Polish coastal waters (Grabowski et al. 2006), thereby causing likely changes in the littoral food web. A decreased degree of herbivory in a coastal ecosystem could possibly increase e.g. the amount of filamentous macroalgae, which is in large areas of the Gulf of Finland and Archipelago Sea a major concern brought up by increased eutrophication during the past decades.

However, the predicted food web changes would probably occur only at lower trophic levels since the predators of gammarids are generalistic in their amphipod diet (MacNeil et al. 1999); e.g. Kelleher et al. (1998) found that *G. tigrinus* was as preferred food item for fish predators as any other amphipod species studied.

We found a markedly high reproductive potential of *G. tigrinus*, strongly related to female body length. Because in this study the sample size of *G. tigrinus* females was small, no reliable comparison of *G. tigrinus* to native species could be done. Therefore, more comprehensive studies on the reproductive potential of the species in comparison to native species are needed. Nonetheless, variability in the number of eggs was small, suggesting good reliability of the result, and similar observations have been made also outside the Baltic Sea (Chambers 1977; Pinkster et al. 1977, 1992). Although it was not possible to estimate further the species' reproduction period in this study, *G. tigrinus* in the southern Baltic Sea has been observed to reproduce from April to November, forming at least two generations within a year and producing several broods per generation (Wawrzyniak-Wydrowska and Gruszka 2005). According to Kolding (1986) the five native *Gammarus* species of the Baltic Sea have adapted to distinct breeding periods in order to avoid interspecific competition for mates. Whether the invasion by *G. tigrinus* mixes up this relatively young adaptation (the Baltic Sea is only ca. 7000 years old) remains to be seen.

Because the native gammarids occupy basically the same ecological niches as the invaders, the invasion of new species cannot be explained by empty niches in those ecosystems (Jazdzewski et al. 2004). Therefore, the success of *G. tigrinus* is more likely based on its predatory nature, high fecundity, wide salinity tolerance range, and tolerance to poor water quality (e.g. chemical contamination, occurrence of pathogens, or eutrophication) (Wijnhoven et al. 2003; Grabowski et al. 2007; Normant et al. 2007). Concerning the latter alternative, similar to many invasive species *G. tigrinus* tolerates poor water quality rather well and is therefore able to migrate and establish into areas characterised by deteriorated environmental conditions (Savage 1996; MacNeil et al. 2001, 2007). For example, in the southern Baltic Sea the species has successfully inhabited severely eutrophicated estuaries (Szaniawska et al. 2003; Jazdzewski et al. 2004; Wawrzyniak-Wydrowska

and Gruszka 2005). In the Rhein estuary, deteriorated conditions resulted in a severe decline of all native amphipod species and an increase in *G. tigrinus* populations (Platvoet and Pinkster 1995). In Northern Ireland native gammarid species are able to co-exist with *G. tigrinus* only in good quality habitats (MacNeil et al. 2001). The co-existence is maintained by complex competitive/predatory patterns between gammarid species (Dick et al. 1993; Dick 1996; Bailey et al. 2006). Thus, native species may successfully resist invaders if their living conditions are optimal (Grabowski et al. 2007). In this way, the deteriorating environmental conditions of the Baltic Sea are probably paving the way for the success of more tolerant non-native species. Actions to improve the state of the Baltic Sea are therefore important to safeguard the region from these invasions and prevent unwanted effects on the local food web structures.

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Annex 1. Records of amphipods in the Helsinki area in 2007: GZ - *Gammarus zaddachi*, GS - *Gammarus salinus*, GO - *Gammarus oceanicus*, GD - *Gammarus duebeni*, GT – *Gammarus tigrinus* (figures indicate number of collected specimens). Collector - Anna Packalén.

Map ref.	Location	Geographic coordinates		Sampling date	GZ	GS	GO	GB	GT
		Latitude, °N	Longitude, °E						
1	Munkkiniemi	60.200930	24.856164	6.7.2007	49	0	0	0	109
	Munkkiniemi	60.200930	24.856164	17.7.2007	1	0	0	0	100
	Munkkiniemi	60.200930	24.856164	26.7.2007	24	0	0	0	104
	Munkkiniemi	60.200930	24.856164	30.7.2007	26	0	0	0	87
	Munkkiniemi	60.200930	24.856164	15.8.2007	61	0	0	0	85
	Munkkiniemi	60.200930	24.856164	21.8.2007	17	0	0	0	145
	Munkkiniemi	60.200930	24.856164	5.10.2007	9	0	1	0	209
2	Lauttasaari	60.143792	24.877719	23.8.2007	56	0	6	330	4
3	Korkeasaari	60.174413	24.978351	27.8.2007	138	0	3	0	1
4	Suomenlinna	60.145868	24.978583	10.8.2007	4	1	7	58	0
5	Vasikkasaari	60.152056	25.015138	10.8.2007	30	0	2	77	0
6	Marjaniemi	60.199013	25.070680	21.07.2007	126	0	0	0	9
	Marjaniemi	60.199013	25.070680	21.07.2007	123	0	0	0	26
	Marjaniemi	60.199013	25.070680	21.07.2007	96	0	0	0	47
	Marjaniemi	60.199013	25.070680	21.07.2007	83	0	0	0	85
	Marjaniemi	60.199013	25.070680	21.07.2007	92	0	0	0	147
7	Kuiva Hevonen	60.092223	25.132816	17.8.2007	0	0	0	334	0