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Research Article

Is a rapid expansion of the invasive amphipod *Gammarus tigrinus* Sexton, 1939 associated with its niche selection: a case study in the Gulf of Finland, the Baltic Sea

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Abstract

Among the recent non-indigenous species the gammarid amphipod *Gammarus tigrinus* is one of the more aggressive invaders in the Baltic Sea. Quantitative sampling of the shallow water habitats of the Gulf of Finland showed that *G. tigrinus* has become established in the whole coastal zone of the Gulf. Boosted Regression Trees modelling indicated that the abundance and biomass of *G. tigrinus* varied as a function of wave exposure, water salinity and transparency, with the invasive amphipod having higher abundance and biomass at less exposed, more dilute, and more turbid sites. *Gammarus tigrinus* appears to be competitively superior to the native gammarids, possibly leading to further decline of the native gammarid populations in the Gulf of Finland.

Key words: invasive species; Boosted Regression Tree modelling; environmental variability; spatial distribution; Baltic Sea

Introduction

Recently, the Baltic Sea, especially in its northern portion, has witnessed an unprecedented increase in the number of biological invasions. Although the exact cause of such a situation is unknown, the evidence suggests an intensified or modified invasion vector associated with ballast water and hull fouling. The recent invaders include many mobile phytophilous benthic macroinvertebrates such as the gammarid amphipod *Gammarus tigrinus* Sexton, 1939, the palaemonid shrimp *Palaemon elegans* Rathke, 1837, and the mudcrab *Rhithropanopeus harrisii* (Gould, 1841). All the species have rapidly increased their population densities, expanded their distribution area, and thus formed permanent populations (Berezina 2007; Packalén et al. 2008; Herkül et al. 2009; Kotta and

Kuprijanov 2012; Kotta and Ojaveer 2012; Katajisto et al. 2013). Besides, the Chinese mitten crab *Eriocheir sinensis* (H. Milne-Edwards, 1853) and some other non-indigenous species appear to have increased in abundance in recent years in the northeastern part of the Baltic Sea (e.g. Ojaveer et al. 2007, 2011). Such invasions have been shown to trigger major shifts in benthic and pelagic communities (e.g. Kotta et al. 2004; Kotta et al. 2006; Põllumäe et al. 2007; Ojaveer et al. 2011).

Among the recent non-indigenous species, the gammarid amphipod *G. tigrinus* is seemingly one of the most aggressive invaders. Recent experimental evidence indicates the species has a strong potential to modify benthic community structure and functioning in the whole coastal zone of the northern Baltic Sea (Orav-Kotta et al. 2009; Kotta et al. 2010, 2011, 2013; Sareyka et al.

2011). These recent studies show that *G. tigrinus* is competitively superior over all native amphipods except *Gammarus duebeni* Liljeborg, 1852 (see also e.g. MacNeil et al. 2003). The mechanisms through which competitive advantage is gained are as follows: *G. tigrinus* has a strong tolerance to adverse environmental conditions; it has a large brood size (Sareyka et al. 2011); and the species is behaviourly aggressive towards the native gammarids (Orav-Kotta et al. 2009). In fact, a co-occurrence of *G. tigrinus* with native gammarids increases exposure of native species to fish predation, especially in pebble habitat, and *G. tigrinus* can eventually outcompete the native gammarids in this habitat (Kotta et al. 2010).

It is surprising that despite of good knowledge on the ecological role of *G. tigrinus* in the Baltic Sea ecosystem, we know little of how variability in the environment shapes the distribution pattern of this invasive amphipod. Most studies report local distribution patterns of *G. tigrinus* (e.g. Jazdzewski et al. 2002; Jazdzewski et al. 2004; Szaniawska et al. 2003; Daunys and Zettler, 2006; Grabowski et al. 2006; Herkül and Kotta 2007; Packalén et al. 2008; Surowiec and Dobrzycka-Krahel 2008; Dobrzycka-Krahel et al. 2012; Strode et al. 2013) and increased observation frequency of the species in time (Ojaveer et al. 2011). Studies from outside of the Baltic Sea area report *G. tigrinus* has a wide tolerance of adverse environmental conditions (Pinkster et al. 1977; Wijnhoven et al. 2003; Devin and Beisel 2007) and low habitat selectivity (Bousfield 1973). Indeed, earlier experiments demonstrate that *G. tigrinus* tolerates very wide salinity ranges in estuaries (Normant et al. 2007) and in salt-polluted rivers (Koop and Grieshaber 2000). *G. tigrinus* was also experimentally shown to tolerate better oxygen depletion and heat stress compared to native gammarids (Sareyka et al. 2011). And ultimately, *G. tigrinus* has a large brood size and the species mature at a smaller size and earlier than the native gammarids (Sareyka et al. 2011). This allows us to conclude that *G. tigrinus* has a broad niche space and thus very strong invasion potential.

Ecological niche modelling, alternatively known as species distribution or predictive habitat distribution modelling, has been widely used to investigate the potential habitat range of species. Environmental niche modeling applies complex computer algorithms to predict the distribution of species in geographic space on the basis of a mathematical representation of their known distribution in environmental space (Morin and Thuiller 2009). Recently it has been shown that machine learning has high potential to become a leader in the field of ecological niche modelling (e.g. Lorena et al. 2008). To date, among machine learning algorithms, the novel predictive modelling technique called Boosted Regression Trees (BRT) performs best in terms of predictive validity and adequate descriptions of "reality" (Elith et al. 2006). Although correlative, the BRT modelling represents a sophisticated tool to improve our understanding on the relationships between environment and biota. Recently, Ba et al. (2010) used ecological niche modelling (not machine learning, though) to analyze the invasive potential of *G. tigrinus*. The algorithm they used sought nonrandom associations between environmental layers and presence of *G. tigrinus,* and predicted the global occurrence of the invasive amphipod. Due to the global approach, however, the study could not possibly involve the key environmental variables defining the patterns of fine and landscape-scale distribution of *G. tigrinus* (e.g. salinity, sediment characteristics, primary productivity); rather, they only showed its invasive potential based associations with air temperature, precipitation, and broad scale topography.

In the current study we sampled the shallow water benthic communities all around the Gulf of Finland to cover wide gradients in salinity, exposure to waves, and eutrophication. Using the novel machine learning algorithm (BRT), we quantified how the abundance and biomass of *G. tigrinus* related to the key environmental variables and how the distribution pattern of *G. tigrinus* was related to other invasive and native species of the Gulf of Finland. In particular, we expected the following:

(1) The populations of *G. tigrinus* have high densities in sheltered areas characterised by mixed bottoms and lush vegetation;

(2) *G. tigrinus* benefits from elevated nutrient levels because eutrophied ecosystems are characterised by high food levels;

(3) The link between eutrophication and *G. tigrinus* population development is weaker in exposed areas than in sheltered areas;

(4) Owing to its wide salinity tolerance, *G. tigrinus* is relatively unresponsive to changes in salinity;

(5) Due to strong antagonistic interactions between the invasive and native gammarids, the populations of native gammarids are depressed in areas invaded by *G. tigrinus*.

Figure 1. Sampling stations in the Gulf of Finland (see details in Appendix 1).
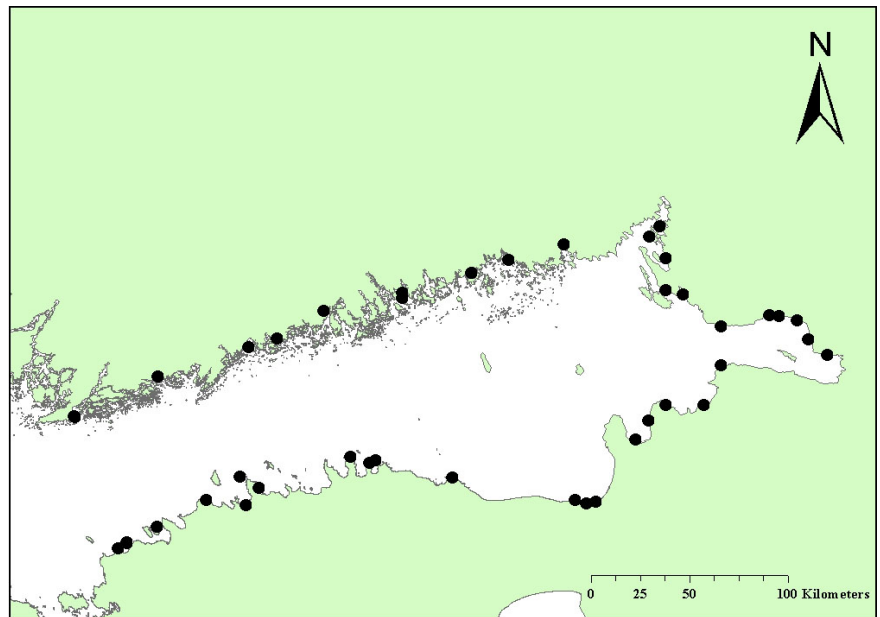
Material and methods

Study area

The shallow water benthic habitats of the Gulf of Finland are diverse spanning from granite bedrock and sandy shores in its western parts to silty reed bottoms in its eastern parts. Compared to other basins in the Baltic Sea, the Gulf of Finland has a relatively large catchment area and the greatest freshwater inflow. Therefore the Gulf has a strong horizontal salinity gradient. The surface salinity varies from 0 in its eastern end to 7 in the western parts (Leppäranta and Myrberg 2009). Near the bottom, the salinity increases from 5 in the eastern parts to approximately 10 in the western parts. Consequently, the western Gulf of Finland is characterised by algal communities of marine origin whereas the eastern Gulf is dominated by either freshwater algae or higher plants. The monthly average seawater temperature varies from 0 to 15 °C. The Gulf is among the most nutrient enriched basins in the Baltic Sea area with its more eutrophied areas located in the easternmost part of the Gulf (Pitkänen et al. 2007). Gammarid amphipods can be found all over the region, though, with different species and relative proportions in different communities.

Sample collection

The benthic community sampling and sample analysis followed the guidelines developed for the HELCOM COMBINE programme (HELCOM 1999). Along the Estonian shores of the Gulf of Finland an Ekman-type bottom grab sampler (0.02 m^2) was used on soft sediment, and a diver-operated metal frame (0.04 m^2) was used to collect samples on hard substrate. In general, three replicate samples were taken in each station. In Finnish and Russian waters quantitative sampling was carried out with a cylindrical corer (0.03 m^2) in two to five replicates. A total of 47 stations were sampled in summers 2010 and 2011 (Figure 1). During sampling the geographic coordinates, depth, and sediment types were recorded (Appendix 1).

Benthic samples were sieved through a 0.25 mm mesh and the residue was placed in plastic bags. Samples were preserved in a deep freezer at -20 °C in Estonia and in a 4% formalin solution in Finland and Russia. In the laboratory, all macroinvertebrate and macrophyte species were identified in the samples (See amphipod species in Appendix 2). Wet weights were recorded for the Finnish and Russian samples and then the wet weights were converted into dry weights based on the known relationship between species-specific

wet and dry weights. For the Estonian samples dry weights of all taxa were obtained after keeping the material 2 weeks at 60 °C.

Supporting environmental variables

The annual average of water temperature, salinity and current velocity were obtained from the results of hydrodynamic model calculations from the early April 2010 to the early August 2011 (Figure 2). The calculations were based on the COHERENS model (Luyten et al. 1999), which is a three-dimensional ocean circulation model. The model has a modular structure allowing users to select different processes, specific schemes and different types of forcing for a particular application. It was formulated with spherical coordinates on a horizontal grid of 1 × 1 nautical miles and 30 vertical sigma layers. The model was forced with hourly meteorological fields of air temperature at a height of 2 m, wind speed, wind stress vector, cloud cover and relative humidity. The meteorological fields were obtained from an operational atmospheric model (Brandt et al. 2001). The model was validated against water level, temperature, salinity and water velocity measurements from the study area (Bendtsen et al. 2009).

The Simplified Wave Model method was used to calculate the wave exposure for mean wind conditions represented by hourly wind data for period 2002−2007 (Isæus 2004). A nested-grids technique was used to take into account long-distance effects on the local wave exposure regime. The resulting grids had a resolution of 25 m. In the modelling the shoreline was divided into suitable calculation areas, fetch and wave exposure grids were calculated and subsequently the separate grids were integrated into a seamless description of wave exposure along the study area (Figure 3). This method results in a pattern where the fetch values are smoothed out to the sides and around island and skerries, in a similar way that refraction and diffraction make waves deflect around islands.

As a proxy of eutrophication we used the MODIS satellite derived water attenuation coefficient (Kd) and water chlorophyll *a* values in 2010−2011 (Figure 3). The MODIS data was obtained from http://www.myocean.eu/ . The frequency of satellite observations was generally once a week over the whole ice-free period; however, several observations were discarded due to cloudiness. The spatial resolution of satellite data was 1 km. False zeroes were removed from the data prior to the statistical analysis.
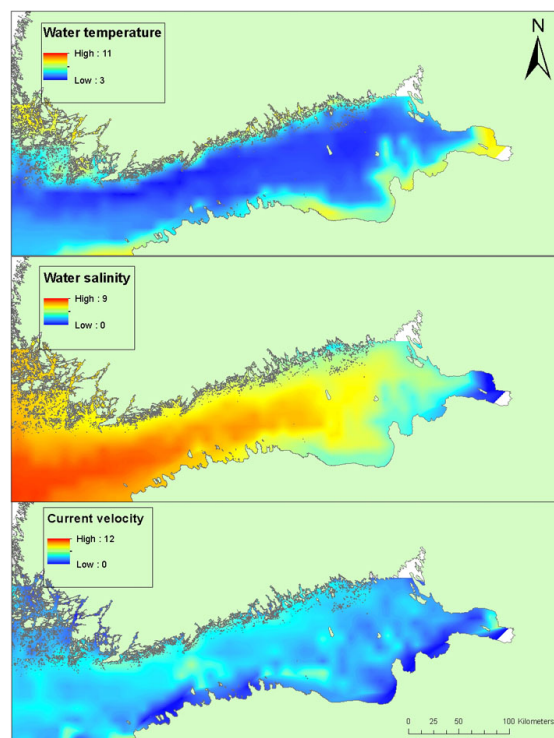

Figure 2. Modelled annual averages of water temperature (°C), salinity and current velocity (cm s^{-1}) in the Gulf of Finland.
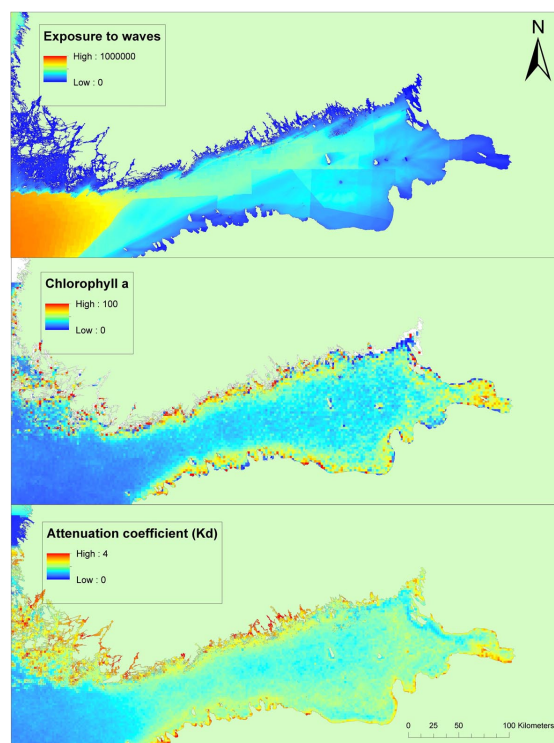

Figure 3. Wave exposure (m^2 s^{-1}), surface chlorophyll *a* (mg m^{-3}) and water attenuation coefficient (K$_d$).

Statistical analyses

Ecological understanding is a prerequisite when it comes to selecting model environmental variables. It is plausible that traditional statistical modelling may not be the most rewarding way to disentangle the environment−species relationships as it starts by assuming an appropriate data model and the model parameters are then estimated from the data. By contrast, machine learning avoids starting with a data model and rather uses an algorithm to learn the relationship between the response and its predictors (Hastie et al. 2009). The novel predictive modelling techniques called Boosted Regression Trees (BRT) combine the strength of machine learning and statistical modelling. The BRT iteratively develop a large ensemble of small regression trees constructed from random subsets of both the numerical and categorial data. Each successive tree predicts the residuals from the previous tree to gradually boost the predictive performance of the overall model. Although BRT models are complex, they can be summarized in ways that give powerful ecological insight. BRT has no need for prior data transformation or elimination of outliers and can fit complex nonlinear relationships. What is most important in the ecological perspective, it automatically handles the interaction effects between predictors (Elith et al. 2008). The BRT modelling was done in the statistical software R version 2.0.1 using the gbm package (RDC Team 2012). We used the BRT script provided by (Elith et al. 2008).

In this study we established relationships between environmental data, abundance, and biomass of *G. tigrinus* using the BRT modelling. For BRT modelling the independent variables were: sediment type, sampling depth, water temperature, salinity, velocity, exposure to waves, water chlorophyll *a* and water attenuation coefficient (K_d). They were regressed to predict the biotic patterns. Multiple models were run varying both the model learning rate (between 0.1 and 0.001) and the number of trees (between 1000 and 10,000). Then the best performing model was selected based on the model predictive power.

Multivariate data analyses were performed by the statistical program "PRIMER" version 6.1.5 (Clarke and Gorley 2006). Prior to analysis, a zero-adjusted Bray−Curtis similarity matrix was calculated using untransformed abundances. Then nonmetric multidimensional scaling (nMDS) was used to present visual images of the differences in variability among species in faunal assemblages.

Results

Macroinvertebrate species in the studied locations

During surveys of the shallow water habitats of the Gulf of Finland in 2010−2011, we recorded 10 non-native species of macroinvertebrates, including 4 species of alien molluscs [New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843), Conrad's false mussel *Mytilopsis leucophaeata* (Conrad, 1831), softshell clam *Mya arenaria* Linnaeus, 1758 and zebra mussel *Dreissena polymorpha* (Pallas, 1771)] and 6 species of crustacean invaders [acorn barnacle *Amphibalanus improvisus* (Darwin, 1854); Ponto-Caspian amphipods *Chelicorophium curvispinum* (Sars, 1895) and *Pontogammarus robustoides* (Sars, 1894); Baikalian amphipod *Gmelinoides fasciatus* (Stebbing, 1899); North-American amphipod *Gammarus tigrinus* Sexton, 1939, and grass prawn *Palaemon elegans* Rathke, 1837].

Native amphipods were represented by mud shrimp *Corophium volutator* (Pallas, 1766) and five species of gammarid amphipods: *Gammarus zaddachi* Sexton, 1912, *Gammarus duebeni* Liljeborg, 1852, *Gammarus salinus* Spooner, 1947, *Gammarus oceanicus* Segerstråle, 1947 and *Gammarus pulex* Linnaeus, 1758. Abundances of native and non-native amphipods are provided in Appendix 2.

Links between abiotic environment and G. tigrinus

The abiotic variables studied explained slightly over 50% of the variability of *G. tigrinus* abundance and biomass. Exposure to waves was by far the most important variable in the BRT model followed by average water salinity, water transparency (K_d), maximum chlorophyll *a* and average water velocity (Figure 4, 5). Sediment type described only a minor proportion in the variability of *G. tigrinus*. The amphipod abundance and biomass decreased in a logistic form with increasing exposure. Similarly, the reduced salinities favoured the invasive amphipod. In contrast, increasing water velocity at a site increased both abundance and biomass of *G. tigrinus*. Relationship between chlorophyll *a* and *G. tigrinus* abundance was unimodal with maximum *G. tigrinus* abundance estimated around 10–55 mg Chl *a* m^{-3} and biomass around 10–35 mg Chl *a* m^{-3}. Above and below this range, *G. tigrinus* abundance sharply decreased.
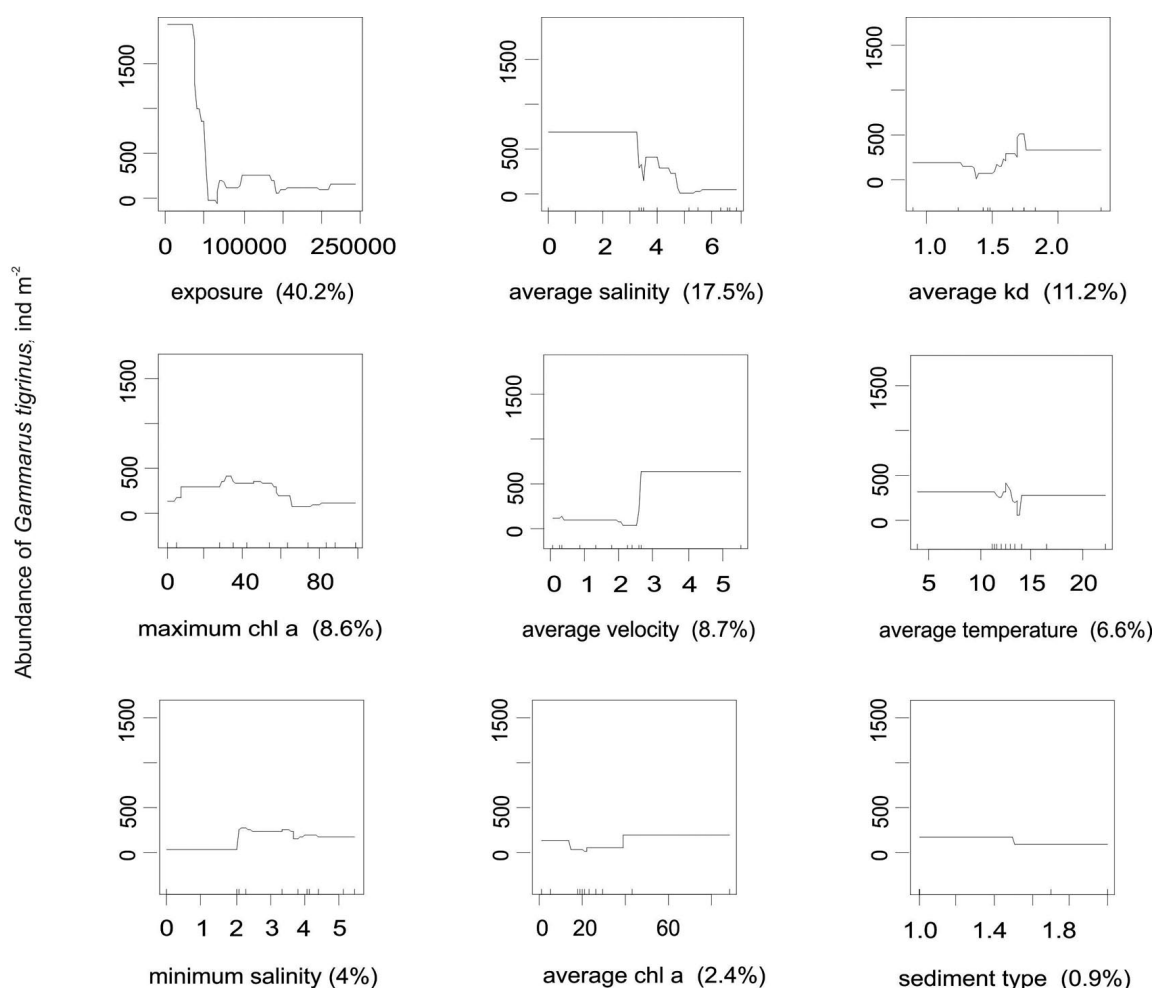
Figure 4. "Partial dependence" plots showing the effect of environmental variables on the abundance of *G. tigrinus* in the Gulf of Finland, whilst all other variables are held at their means. The upward tickmarks on x-axis show the frequency of distribution of data along this axis. The contribution of particular variable to the model is shown in brackets. The code of sediment types: 1 – sand, 2 – cobble.

The effect of exposure on the abundance and biomass of *G. tigrinus* depended heavily on the values of eutrophication-related variables (both maximum chlorophyll *a* and Kd) and the salinity level. *G. tigrinus* population had high abundance and biomass at low chlorophyll *a* when either salinity or exposure values were low. Similarly, the effects of exposure on *G. tigrinus* depended on water velocity values and highest abundance and biomass of *G. tigrinus* were recorded in the areas characterized by low exposure and high water velocity (Figure 6).

Spatial distribution and interaction with other species

The densest *G. tigrinus* populations were located in the eastern and northeastern parts of the Gulf of Finland whereas the species was relatively rare in the southwestern parts of the Gulf (Figure 7; Appendix 2). *G. tigrinus* could share its habitat with other invasive amphipods such as *Pontogammarus robustoides* but in general the abundance and biomass of *G. tigrinus* was lower in these habitats compared to areas where *P. robustoides* were not found (Figure 7; Appendix 2).
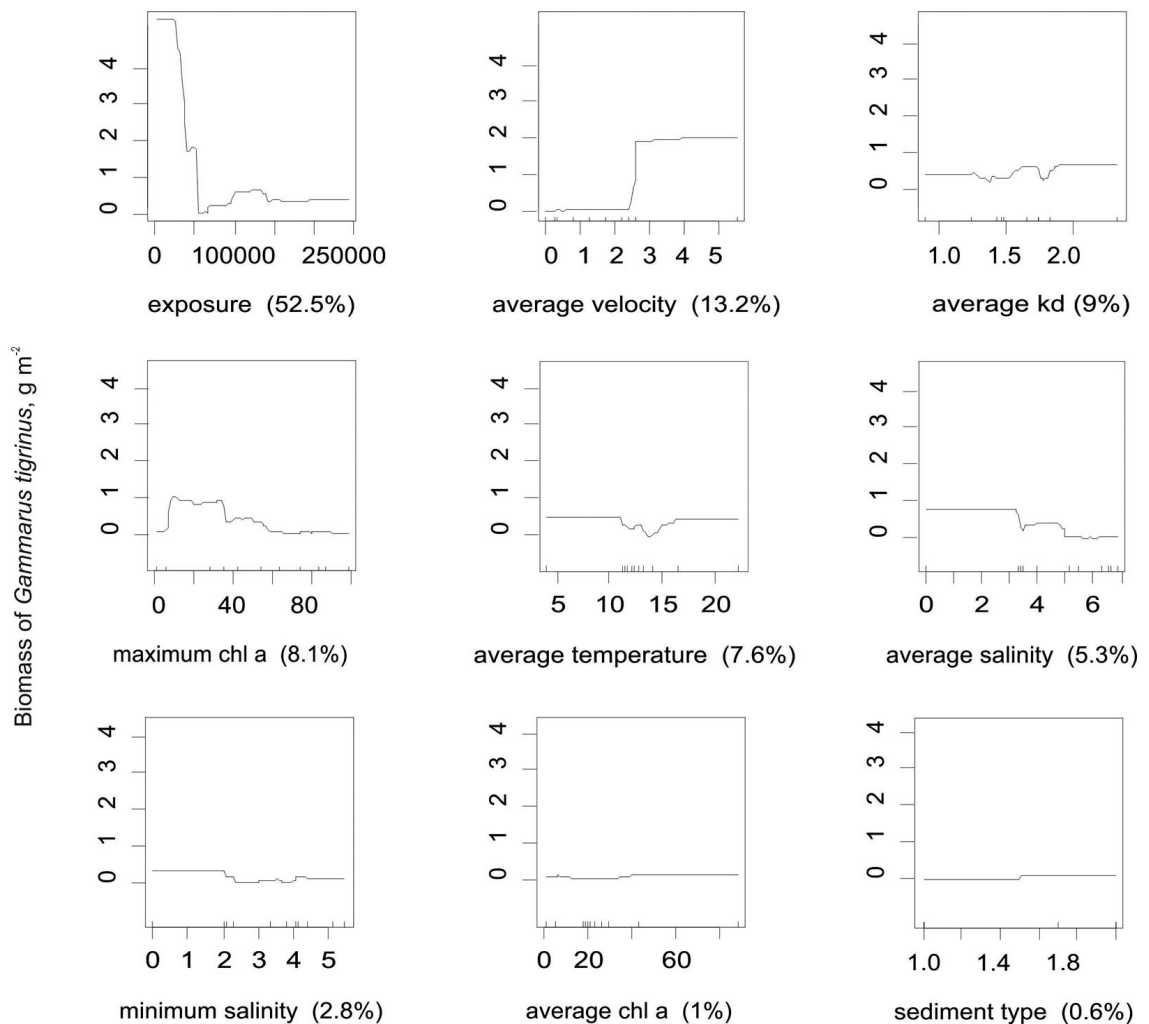
Figure 5. "Partial dependence" plots showing the effect of environmental variables on the biomass of *G. tigrinus* in the Gulf of Finland, whilst all other variables are held at their means. The upward tickmarks on x-axis show the frequency of distribution of data along this axis. The contribution of particular variable to the model is shown in brackets. The code of sediment types: 1 – sand, 2 – cobble.

The nMDS analysis (Figure 8) showed that the distribution range of *G. tigrinus* was relatively broad and similar to those of native gammarids. Only *G. duebeni* occurred primarily close to the waterline where other gammarid amphipods were rare (Figure 8). Thus, *G. tigrinus* is exceptional among the invasive species as all other invasive species in the Gulf of Finland formed two distinct groups in terms of their habitat requirement. One group consists of the amphipods *Gmelinoides fasciatus*, *Pontogammarus robustoides*, *Chelicorophium curvispinum*, the bivalve *Dreissena poly-*morpha. The second group consisted of the shrimp *Palaemon elegans*, the cirriped *Amphibalanus improvisus*, and the bivalves *Mytilopsis leucophaeata* and *Mya arenaria*. *G. tigrinus* may occasionally share habitat with those invasive species but currently such habitat overlap was negligible in the Gulf of Finland.

The native gammarid species were found at higher abundances and biomasses in the areas where *G. tigrinus* was rare or lacking (Figure 9). Without *G. tigrinus* the abundance of the native gammarids was 980 ± 154 ind m^{-2} (average $\pm$ SE)
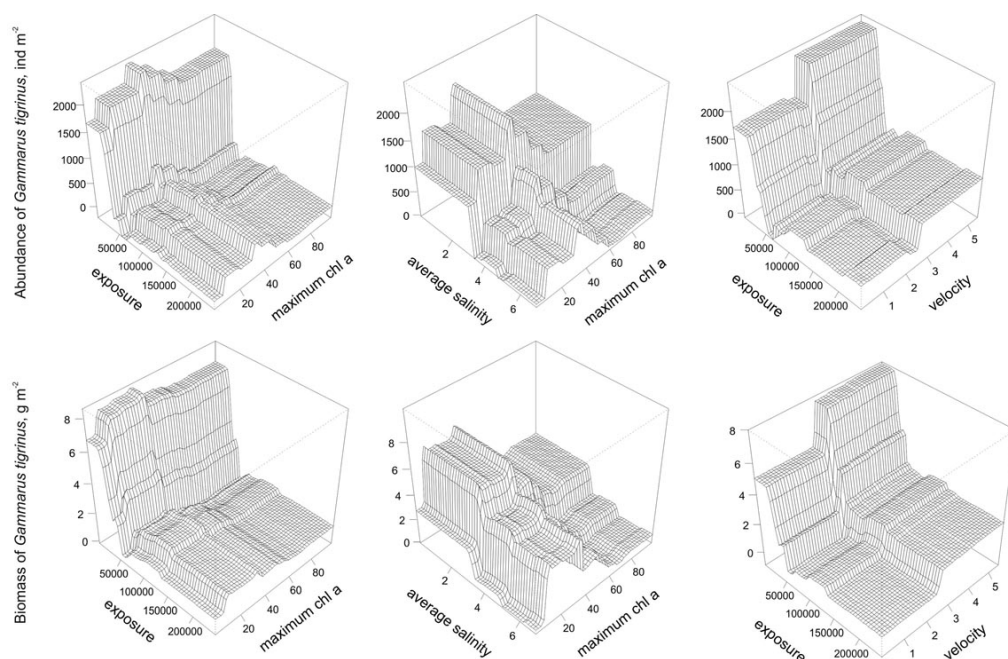
Figure 6. Three-dimensional partial dependence plots in the BRT model for the abundance (top) and the biomass (bottom) of *G. tigrinus* in the Gulf of Finland. Note how the effect of one variable is dependent on another.

Figure 7. The abundance of the invasive amphipods *Gammarus tigrinus* and *Pontogammarus robustoides* in the Gulf of Finland (exact numbers provided in Appendix 2).
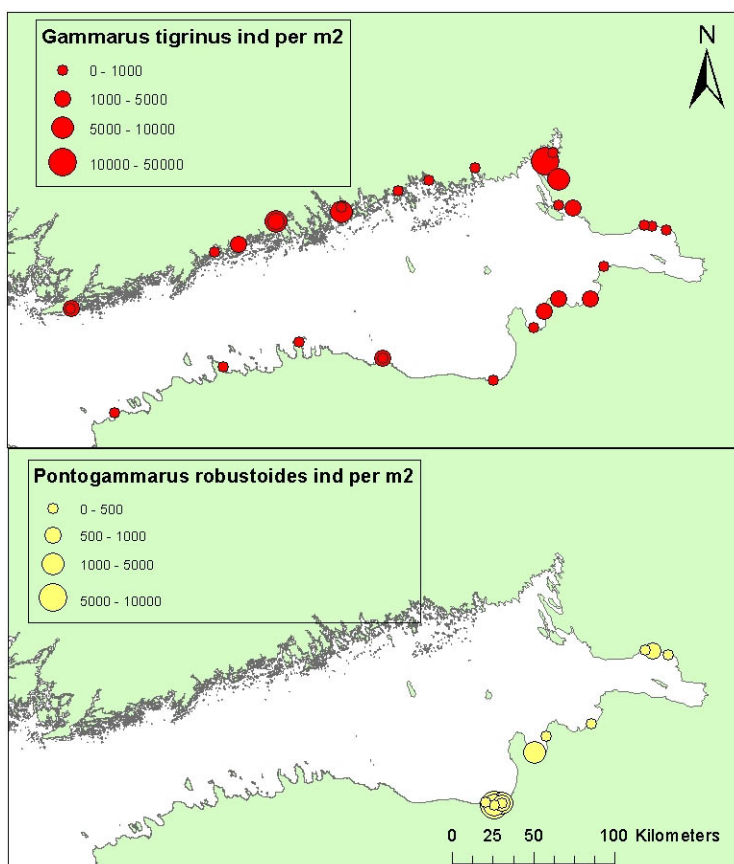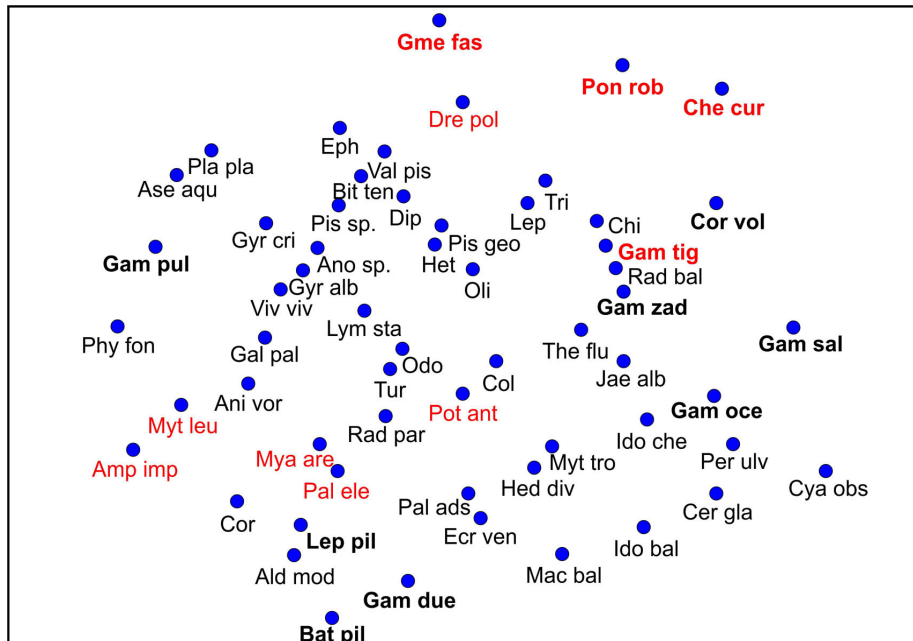
Figure 8. Non-metric multidimensional scaling (nMDS) plot showing similarities in the variability of abundances among benthic species in the Gulf of Finland. All amphipods are marked in bold. All non-indigenous species are marked in red. Blue dots mark the centre of species in the nMDS plot. Those species that are close on the figure have similar spatial patterns. The code of species: Ald mod - *Alderia modesta*, Amp imp – *Amphibalanus improvisus*, Ani vor – *Anisus vortex*, Ano sp. – *Anodonta* sp., Ase aqu – *Asellus aquaticus*, Bat pil – *Bathyporeia pilosa*, Bit ten – *Bithynia tentaculata*, Cer gla – *Cerastoderma glaucum*, Che cur – *Chelicorophium curvispinum*, Chi – Chironomidae, Col – Coleoptera, Cor – Corixidae, Cor vol – *Corophium volutator*, Cya obs – *Cyanophthalma obscura*, Dip – Diptera, Dre pol – *Dreissena polymorpha*, Ecr ven – *Ecrobia ventrosa*, Eph – Ephemeroptera, Gal pal – *Galba palustris*, Gam due – *Gammarus duebeni*, Gam oce – *Gammarus oceanicus*, Gam pul – *Gammarus pulex*, Gam sal – *Gammarus salinus*, Gam zad – *Gammarus zaddachi*, Gam tig – *Gammarus tigrinus*, Gme fas – *Gmelinoides fasciatus*, Gyr alb – *Gyraulus albus*, Gyr cri – *Gyraulus crista*, Hed div – *Hediste diversicolor*, Het – Heteroptera, Ido bal – *Idotea balthica*, Ido che – *Idotea chelipes*, Jae alb – *Jaera albifrons*, Lep – Lepidoptera, Lep pil – *Leptocheirus pilosus*, Lym sta – *Lymnaea stagnalis*, Mac bal – *Macoma balthica*, Mya are – *Mya arenaria*, Myt leu – *Mytilopsis leucophaeta*, Myt tro – *Mytilus trossulus*, Odo – Odonata, Oli – Oligochaeta, Pal ads – *Palaemon adspersus*, Pal ele – *Palaemon elegans*, Per ulv – *Peringia ulvae*, Phy fon – *Physa fontinalis*, Pis geo – *Piscicola geometra*, Pis sp. – *Pisidium* sp., Pla pla – *Planorbis planorbis*, Pon rob – *Pontogammarus robustoides*, Pot ant – *Potamopyrgus antipodarum*, Rad bal – *Radix balthica*, Rad par – *Radix parapsilia*, The flu – *Theodoxus fluviatilis*, Tri – Trichoptera, Tur – Turbellaria, Val pis – *Valvata piscinalis*, Viv viv – *Viviparus viviparus*.

while with *G. tigrinus* there were only 308 ± 127 ind m^{-2}. In the areas already invaded by *G. tigrinus* the abundance of native gammarids never reached over 1000 ind m^{-2}. Without *G. tigrinus*, however, values over 2000 ind m^{-2} and occasionally even over 5000 ind m^{-2} were recorded (Appendix 2).

Discussion

This study identified and tested the relative contribution of the key abiotic environmental predictors on the abundance and biomass of *G. tigrinus* at basin scale using a fine-scale modelling framework. Although correlative in nature, the resulting response curves matched well with the current understanding on the interdependence of abiotic environment and the distribution of this invasive amphipod species. The models also provided many novel ecologically-realistic separate effects and second-order interactions that can be tested in controlled experimental conditions. Potentially, the current models can be used to predict the abundance of the invasive gammarid under current environmental conditions but likely also for a range of human stress-gradients and climate change scenarios.

Often the environment of the large-scale ecological niche modelling studies is represented only by climate data (temperature and precipitation). Such global climate variables were also used by Ba et al. (2010) to predict the invasive potential of *G. tigrinus*. However, as seen from recent studies, the dynamics of marine benthic populations is often uncoupled from the global climate trends (e.g. Veber et al. 2009; Lauringson et al. 2012)

Figure 9. The abundance of native gammarids in the Gulf of Finland (exact numbers provided in Appendix 2).
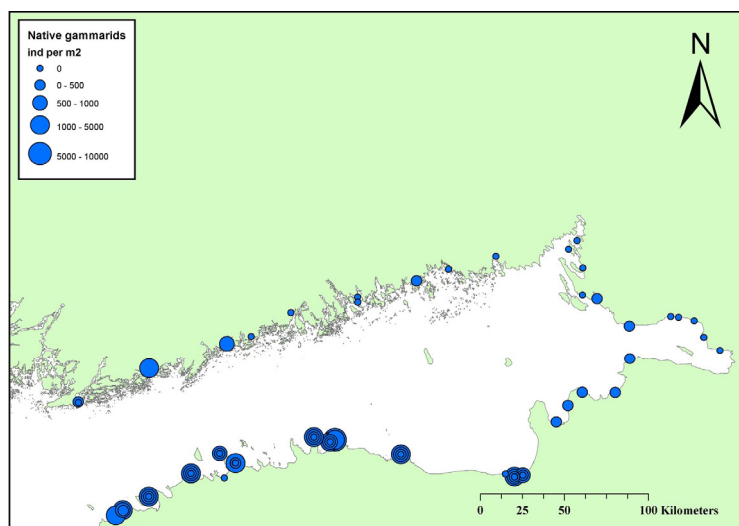
due to large variation in the interaction between large-scale and small-scale environmental factors (Hewitt and Thrush 2009). Thus, it is expected that models that rely on global climate variables only do not reproduce adequate descriptions of distributions at the finer scale.

Our models showed that the invasive *G. tigrinus* was selective in its environment occupied in the Gulf of Finland contrasting to very broad habitat range of the species in its native habitats (Steele and Steele 1972; Bousfield 1973; Kelly et al. 2006). In its native range, *G. tigrinus* is widespread in intertidal and subtidal benthic habitats including reeds, algae, hard or soft substratum, and sand both in fresh and brackish water (e.g. Steele and Steele 1972). In the Gulf of Finland ecosystem, however, *G. tigrinus* is currently abundant only in the eastern and northeastern parts of the Gulf. These habitats range from sheltered to moderately exposed coasts, salinity is low, and eutrophication level is moderate-high. Among the bottom substrates, mixed sediments prevailed; filamentous macroalgae, higher order plants and organic debris were plentiful; and visibility was moderate to poor.

In its native range, *G. tigrinus* is represented by two main cryptic species with 6 genetically distinct lineages (Kelly et al. 2006). The population introduced to Europe represents only two of these lineages (Bulnheim 1985; Kelly et al. 2006). This restricted genetic makeup may explain why the habitat occupancy of *G. tigrinus* is narrower in the invaded area than in its native range.

Our expectation that less exposed areas were characterised by higher number of *G. tigrinus* was confirmed. This effect was not due to seafloor characteristics because contribution of the type of sediment did not exceed 1% in the BRT models. Thus, *G. tigrinus* seemingly selected less exposed areas by some other attributes e.g. the ample presence of organic debris as a food or poor visibility (acting as a predatory refuge).

Our hypothesis that *G. tigrinus* benefits from elevated eutrophication was rejected. Instead, the moderate levels of nutrient enrichment most-favoured *G. tigrinus*. To a point, increasing nutrient levels leads to filamentous macroalgal blooms and greater sedimentation of organic material (Paalme et al. 2002). This enriched food supply usually promotes higher species richness, abundances and biomasses of macroinvertebrates including those of gammarid amphipods (Edgar et al. 1994; Kotta et al. 2000; Kotta and Ólafsson 2003; Lauringson and Kotta 2006). The macroalgal blooms can also result in the mass development of drifting algal mats (Berglund et al. 2003), which can accumulate in more sheltered areas (Kotta et al. 2008), where they provide a habitat and food for mobile macroinvertebrates all the year round (Thiel and Watling 1998; Kotta et al. 2008). Excessive nutrient loading, however, results in the intense sedimentation of organic matter and overgrowth of sediments by thick mats of higher plants and algae, which results in severe hypoxia and dramatic changes to the local animal communities (Karlson et al. 2002; Conley et al. 2011). *G. tigrinus* tolerates higher levels of eutrophication (Grabowski et al. 2007) and oxygen depletion than native gammarids and can, therefore,

better cope with such adverse conditions (Sareyka et al. 2011). This may give the species a competitive advantage over native gammarids. Nevertheless, an increasing extent and intensity of hypoxia may still explain an abrupt decline of the abundance and biomass of *G. tigrinus* in the most nutrient-enriched areas of the Gulf of Finland. Only in those highly eutrophied areas where water exchange is high can *G. tigrinus* maintain high densities.

We also proposed that the relationship between nutrient levels and the abundance and biomass of *G. tigrinus* would be weaker in more exposed areas than in sheltered areas. This hypothesis was supported in that in areas with low exposure, the invasive amphipods occurred in high abundance at relatively moderate chlorophyll *a* values. Nevertheless, exposure did not change the functional form of the relationship between eutrophication and *G. tigrinus* occurrence but acted like a scaling factor by changing overall abundance levels.

We also expected that, owing to its wide tolerance, *G. tigrinus* would be unresponsive to changes in salinity. This expectation was rejected; the invasive amphipod was much more abundant in less saline areas compared to more saline areas. However, salinity levels were confounded with levels of many variables. For example, the strongest effects of exposure and eutrophication were observed in less saline areas. Seemingly, *G. tigrinus* prefers salinities between freshwater and 5 but the species can be likewise found in the most saline parts of the Gulf of Finland, albeit at much lower abundances. The model suggests, however, that there is a true salinity effect separate from those related to the other studied variables. This is especially true for the numerical abundance of *G. tigrinus* whereas the amphipod biomass is less coupled with separate salinity effects. Thus, *G. tigrinus* tends to have smaller-sized and denser populations at lower salinities. The results are quite surprising considering increasing maintenance energy cost for *G. tigrinus* with decreasing salinity from 20 down to freshwater conditions (Normant et al. 2007). The authors of this paper asked why *G. tigrinus* does not inhabit α-mesohaline zones (salinity 10−18) but thrive in freshwater and oligohaline areas of the Baltic Sea. In the light of our study, however, their hypotheses to explain the gammarid distribution paradox (e.g. strong preference to shallow water habitats, unknown interactions with key environmental variables, lowest biodiversity i.e. invasional resistance at 5−8) seem not very

likely. Alternatively, Kelly et al. (2006) suggested that differences in salinity tolerance among genetic lineages may be behind the recent patterns of habitat colonization. Specifically, in eastern Europe the populations of *G. tigrinus* consist of a mixtures of the two invading clades and were characterized by higher genetic diversity than source populations (Kelly et al. 2006). In its native area, different clades do not spatially coincide whereas in Europe those clades are found at the same sites. Thus, at the seascape scale, the genetic diversity of *G. tigrinus* is higher in Europe than in its native area. At the broader spatial scales, however, the opposite is true as only a few clades are found in Europe. It is expected that broader niche space or width and better tolerances to adverse environmental conditions (including low salinity) would result if multiple source populations, each with distinctive genetic composition, contributed to the genetic structure of founding populations.

With regards to predators, fish can cause heavy mortality on the *G. tigrinus* population (e.g. Kotta et al. 2010). In the turbid environments, however, *G. tigrinus* may escape heavy predation if benthivorous fish locate their prey visually. In fact, the three spine stickleback *Gasterosteus aculeatus* and the Eurasian perch *Perca fluviatilis* are major predators of gammarid amphipods in our study area and both fish species depend on vision as their main source of sensory information (Kotta et al. 2010; Järv et al. 2011). Thus, even relatively small increases in turbidity are expected to change predation efficiency of fish on such a large and mobile prey as gammarid amphipods (Utne-Palm 2002). This may explain why *G. tigrinus* has very high densities at less exposed areas where finer sediments are more common and thus water transparency is low. In freshwater environments, high water turbidity often associated with clay substrate is a key characteristic of the *G. tigrinus* habitat (e.g. Grigorovich et al. 2005). It would be useful to conduct experiments to identify potential threshold value in water transparency, below which fish feeding activity is limited and therefore the establishment of the invasive amphipod is favoured. If such a threshold exists, the abatement of eutrophication may actually reduce abundance of the invasive *G. tigrinus* in its current range and prevent its further spread.

Based on earlier experimental evidence and this study, *G. tigrinus* seems not to have important competitors in the Baltic Sea, except for *G. duebeni* and *P. robustoides* (Rolbiecki and Normant

2005; Grabowski et al. 2006). Our study showed that the other amphipods seem competitively inferior or neutral to *G. tigrinus*. We also have evidence that interspecific interactions between invasive amphipod species vary even within the Baltic Sea range. The Ponto-Caspian species *Pontogammarus robustoides* is very invasive in the southern Baltic Sea and is known to have caused a major decline of the *G. tigrinus* in this ecosystem (Grabowski et al. 2006). Nevertheless, in the Gulf of Finland ecosystem *P. robustoides* is limited to very narrow coastal range and in these habitats the two invasive species cohabit. Surprisingly, this is not due to a more recent arrival of *P. robustoides* into the southern shores of the Gulf of Finland. In fact *P. robustoides* was found for the first time in the easternmost Gulf of Finland in 1999 (Panov et al. 2003) and only in 2006 the species spread into the Estonian coastal waters (Herkül et al. 2009). At that time *G. tigrinus* occurred only at very low densities in the western Gulf of Finland. During the last 6−8 years the distribution range of *P. robustoides* has remained almost the same and the species is still confined to the limited coastal habitats of the eastern Gulf of Finland. On the other hand *G. tigrinus* has spread practically all over the Gulf including those sites where *P. robustoides* are found. Seemingly, the spatial limits of distribution of *P. robustoides* in the Gulf of Finland are controlled by some unknown abiotic or biotic variable giving *G. tigrinus* a clear competitive advantage. Such a dispersal pattern also suggests that *P. robustoides* may not be dominant over *G. tigrinus* in the coming years.

Our study supported earlier experimental evidence (Orav-Kotta et al. 2009; Kotta et al. 2010; Sareyka et al. 2011) that *G. tigrinus* is competitively superior to the majority of native gammarids in the Gulf of Finland. The study also suggests that the population of *G. tigrinus* is still in its growth phase in the Gulf of Finland. Although the invasive amphipod almost covers the whole coastal range of the gulf, some favourable habitats are still to be invaded e.g. in the southern and eastern parts of the Gulf of Finland. Thus, we expect that in a near future further decline of the native gammarids is possible.

To conclude, (1) *G. tigrinus* is still expanding its range in the Gulf of Finland ecosystem; (2) the gammarid is more selective in its environment compared to its native range; (3) the invasive species is competitively superior to the native gammarids leading to further decline of the native gammarids in the Gulf of Finland ecosystem.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Sampling stations in the Gulf of Finland.

Appendix 2. Abundances of amphipods in the Gulf of Finland.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2013/Supplements/AI_2013_Kotta_etal_Supplement.pdf