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interactions of native and invasive  
predatory macroinvertebrates  
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*“With regard to the Malacostraca or crustaceans, .... another species is that of the carid, and another is that of the crab, and there are many kinds both of carid and of crab. Of carids there are the so-called cyphae, or “hunch-backs”, the crangons, or squillae, and the little kind, or shrimps, and the little kind do not develop into a larger kind.”*

*Perhaps the first scientific classification of crustaceans, made by Aristotle, 350 B.C.E., from his “History of Animals”*



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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications referred to in the text by their Roman numerals:

- I. Kuprijanov, I., Herkül, K., Kotta, J., 2017. Ecological niche differentiation between native and non-native shrimps in the northern Baltic Sea. *Aquatic Ecology*, 51 (2), 389–404.
- II. Kuprijanov, I., Kotta, J., Lauringson, V., Herkül, K., 2015. Trophic interactions between native and alien palaemonid prawns and an alien gammarid in a brackish water ecosystem. *Proceedings of the Estonian Academy of Sciences*, 64(4), 518–524.
- III. Nurkse, K.; Kotta, J.; Orav-Kotta, H.; Pärnoja, M.; Kuprijanov, I., 2015. Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisi* (Gould) in an invaded ecosystem: The north-eastern Baltic Sea. *Estuarine Coastal and Shelf Science*, 154, 152–157.
- IV. Kotta, J.; Kuprijanov, I., 2012. The first finding of the palaemonid shrimp *Palaemon elegans* Rathke in the Estonian coastal sea. *Estonian Journal of Ecology*, 61(2), 148–153.

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## AUTHOR'S CONTRIBUTIONS

Paper I – Led the concept and design of the study, carried out the field work and laboratory experiments, performed statistical analyses of the data, responsible for writing the manuscript

Paper II – Led the concept and design of the study, managed the field work, carried out the experiments, supervised the analyses of the samples in the laboratory, performed statistical analyses of the data, responsible for writing the manuscript

Paper III – Contributed to the concept and design of the study, assisted in the field work, assisted with sample analysis in the laboratory, supported the manuscript writing

Paper IV – Contributed to the concept and design of the study, participated in the field work, conducted analyses of the samples in the laboratory, involved in the manuscript writing.



# 1. INTRODUCTION

Marine ecosystems are vast and cover three-fourths of the earth's surface. Coastal habitats are particularly important as they alone account for approximately 30% of all marine biological productivity (Levinton, 1995). These highly diverse and productive environments are very important for humans as they provide a rich source of food and income and they also maintain other important services such as protecting the coastlines from wave action and erosion, and act as natural filtering systems through binding organic pollution and nutrients. Despite the importance of marine ecosystems, increased human activities have caused significant damage to marine biodiversity. Among these threats, eutrophication and introduction of exotic species notably jeopardize the future sustainability of marine species and ecosystems (e.g. Grosholz et al., 2000; Cloern, 2001; Edelist et al., 2013). Thus, understanding the role of marine ecosystems and the impact we have on them is critical to both conservation and sustainable use of marine resources.

Human activities are often concentrated in coastal regions and adverse human impacts are most apparent there. Due to restricted water exchange with the ocean, the coastal habitats of enclosed seas are particularly vulnerable to such threats. On the other hand, our knowledge of coastal ecosystems mostly originates from the true oceanic waters. As the coasts of oceans and enclosed seas are expected to function differently, considering the huge contrast in the physical environmental conditions, the knowledge and theories derived from open ocean often cannot be directly applied to the enclosed seas and this situation calls for regional-specific studies (Snoeijs-Leijonmalm and Andr en, 2017).

The Baltic Sea is an isolated area with only narrow connections to the Atlantic species pool. In a geological time scale, the Baltic Sea has had a very short lifetime as a brackish water environment following its origin as a freshwater lake, and is characterized by common features both of freshwater and marine systems (Snoeijs-Leijonmalm and Andr en, 2017). The number of species in the Baltic Sea decreases northwards and this has been explained primarily by concurrent reduction in salinity (Zettler et al., 2014). As a consequence, the Baltic Sea has also low functional diversity with only small number of species performing each ecological function (e.g. suspension feeding, benthic primary production) (Ojaveer et al., 2010).

The Baltic Sea area is under the pressure of various types of anthropogenic impacts, with eutrophication and introduction of non-indigenous species considered as the key factors for the dynamics of its ecosystem (Snoeijs-Leijonmalm and Andr en, 2017). A notable increase of successful introductions of non-native species to the Baltic Sea has been observed in the recent decades (Lepp koski and Olenin, 2000). This is very likely to exert a major ecological impact on the structure and function of the Baltic Sea ecosystem (Lepp koski et al., 2002a). Many of these non-native species have life-history traits that no other native species in the Baltic Sea possess, and thereby they add functional

complexity in the system (Ojaveer and Kotta, 2015). Others may share similar traits to the native species and under some environmental conditions exclude native species through different types of competitive interactions like competition for food or habitat or direct predation (e.g. Kotta et al., 2010).

Because of the low levels of biological diversity in the Baltic Sea, and the tendency for this system to be naturally regulated by bottom-up processes, top-down regulation by introduced predators can have particularly strong structuring effects (Flecker and Townsend, 1994; Worm and Myers, 2003), and the appearance of an additional effective predator may lead to reorganization of the entire food web through many direct and indirect effects (Carpenter et al., 1985). For instance, when occurring at high numbers, even small-bodied predators may greatly reduce populations of herbivores and thus indirectly intensify blooms of filamentous macroalgae in coastal ecosystems (Eriksson et al., 2009; Sieben et al., 2011).

Demersal predatory macroinvertebrates form an important link in coastal food webs worldwide. They prey on small benthic invertebrates and at the same time they are an important food item for upper trophic levels. In the coastal range of the Baltic Sea area macroinvertebrate predatory crustaceans form a trophic link to fish, being valuable prey for such commercially important predators as Atlantic cod (*Gadus morhua* Linnaeus, 1758) and perch (*Perca fluviatilis* Linnaeus, 1758) (Gruszka and Więcaszek, 2011; Järv et al., 2011). The predatory macroinvertebrates also have an important role in regulating the dynamics of species on lower trophic levels. Until recently, this group of macroinvertebrates consisted of only a few species in the northern Baltic Sea, including only two species of native caridean shrimps – *Crangon crangon* and *Palaemon adspersus*. However, very recently two non-native macroinvertebrate predators arrived – the caridean shrimp *Palaemon elegans* and the crab *Rhithropanopeus harrisii*. Furthermore, another potential invader – *Palaemon macrodactylus* – has recently established in the southern Baltic Sea (González-Ortegón et al., 2010; Janas and Tutak, 2014). Thus, the non-native macroinvertebrate predators are filling up this nearly unoccupied niche. This is particularly true in the context of recent establishment of the invasive *Palaemon elegans* that has spread to many parts of the Baltic Sea and formed dense populations only within a few years (e.g. Katajisto et al., 2013) and potentially intensified competition for food and space with the native *P. adspersus* (Grabowski, 2006). Moreover, in the last decade the invasive crab *R. harrisii* has colonized the northern parts of the Baltic Sea and is rapidly expanding its distribution range (Kotta and Ojaveer, 2012; Fowler et al., 2013). The growing number of invasions by predatory invertebrates has a potential to strongly modify coastal food webs, particularly if such a function (large predator) is absent or underrepresented in the recipient communities (Weis, 2011).

Previous studies have shown that the non-native shrimp can exploit a wide array of food by effectively preying on epibenthic amphipods and free swimming mysids but also grazing on macroalgae (Möller et al., 1985; Persson et al., 2008; Lesutienė et al., 2014). This feeding strategy is in accordance with

widely accepted knowledge in invasion ecology that, in case of crustaceans, generalist feeding strategy increases the chances of establishment of the non-indigenous species in new environments (Hänfling et al., 2011).

*R. harrisii* has formed self-sustaining populations and thereby added a completely new function of large-bodied predator and bioturbator to the local coastal ecosystems (Bonsdorff, 2006; Kotta and Ojaveer, 2012) because the northern Baltic Sea lacks native crabs. Experimental studies have demonstrated that this invasive crab species strongly affects food web dynamics and energy pathways, i.e. by removing a large proportion of native invertebrate biomass and modifying sediment characteristics and sediment dwelling micro-invertebrates (Lokko et al., 2015; Jormalainen et al., 2016). In order to assess the effects of *R. harrisii* across all different coastal habitats, the habitat occupancy of the invasive crab species needs to be quantified. As food availability and crab density are expected to modulate the habitat occupancy of mud crab, such linkages need to be evaluated.

These introductions have raised a question of whether the native predatory crustaceans are absent from a part of the environmental niche space of the Baltic Sea, which now is being filled up by non-native species. Alternatively, these non-native species may have the capability to outcompete native predatory crustaceans and they thereby may only marginally affect the overall functioning of the Baltic coastal ecosystems. Despite the accumulation of invasion history data on *R. harrisii* and *P. elegans* and other recent immigrants, we still lack sufficient knowledge on how these non-native species affect the structure and dynamics of the Baltic Sea ecosystems. To gain such knowledge, laboratory and field experiments are needed together with high-quality data on species distribution (Ojaveer and Kotta, 2015).

It is important to understand the ecological niches of native and invasive species, including their habitat preferences, feeding habits, and reproductive strategies (Castro and Huber, 2003). The ecological niche is conventionally defined by spatial constraints or functional position of the organism in the environment (e.g., Elton, 1927; Grinnell 1928). The most influential ecological concept associated with niche is its width along the array of ecological gradients (Pianka, 1981). The niche breadth is defined by a large number of environmental factors which ultimately results in trade-off between specialization and generalization. An understanding of factors governing the realization of ecological niches may fill gaps in our present knowledge on how the geographic range of particular species is formed and at the same time may help to reveal mechanisms involved in adaptive responses of the species to environmental variation (Polechová and Storch, 2008). If species have similar environmental requirements then such a similarity constitutes an overlap of their niches (Leibold, 1995) with associated competitive relationships involved. On the other hand, the same species may find separation of ecological space over several environmental gradients (e.g., Priddis et al., 2009). If native and non-native species are taxonomically close then their adaptive characteristics are likely similar and the latter may manifest through the similarity in environmental

niche space between novel and native species and may translate to better survival of non-native species in the recipient environment (e.g. Duncan and Williams, 2002). However, taxonomic affiliation may not play an important role in invasion success of some animal groups (e.g. fishes) as taxonomic similarity may be uncoupled with ecological similarity among native and non-native congeneric species (Ricciardi and Mottiar, 2006).

The spread of non-native species (*sensu* Olenin et al., 2010) provides valuable empirical support to fundamental ecological theories including relationships between niche space and community assembly rules. Following the recent mass invasions, classic views of community saturation have been reconsidered (Sax et al., 2007). Although introductions of non-indigenous species may locally increase total species richness (Stachowicz and Tilman, 2005), the ecological impacts of invaders may be very severe (e.g., Weis, 2011; Dick et al., 2013), especially if the established alien species possess novel function to the system. Non-native species are expected to alter the established interspecific interactions, with strongest potential effects on highly specialized species (Hobbs et al., 2006; Clavel et al., 2011).

The earlier studies indicate that non-native species often have broad environmental tolerance or a wide environmental niche space (Marvier et al., 2004). The most successful invaders are generalized in their feeding and have a strong capability to persist in a wide range of environmental conditions (Snyder and Evans, 2006; Evangelista et al., 2008). Often, non-native species further expand their niche breadth after invasion, conceivably due to lack of enemies (predators, parasites, competitors) in the recipient environment (Elton, 1958; Mack et al., 2000; Callaway and Ridenour, 2004). Opposing to this earlier theory, recent work from the shallow Baltic region contrastingly showed that non-native species may not necessarily expand their niche, but rather remain more specialized compared to native congeners (Herkül et al., 2016). This diverse evidence base suggests that niche width has not received a sufficient amount of attention in studies comparatively exploring environmental requirements of taxonomically or functionally close non-native and native species.

## Objectives

The general aims of this thesis were to describe distribution (I–IV), environmental niche space, habitat selection (I–III), and trophic interactions (II–III) of predatory macroinvertebrates in the coastal areas of the northern Baltic Sea. The specific objectives were to:

- Describe the establishment, range expansion and geographical distribution of the non-native shrimp *Palaemon elegans* in comparison with the native shrimp species (IV, I). It was hypothesized that the patterns of geographical distribution differ between the non-native and native shrimps.
- Measure habitat preferences and potential environmental niche separation between the non-native and native shrimp species (I). It was hypothesized

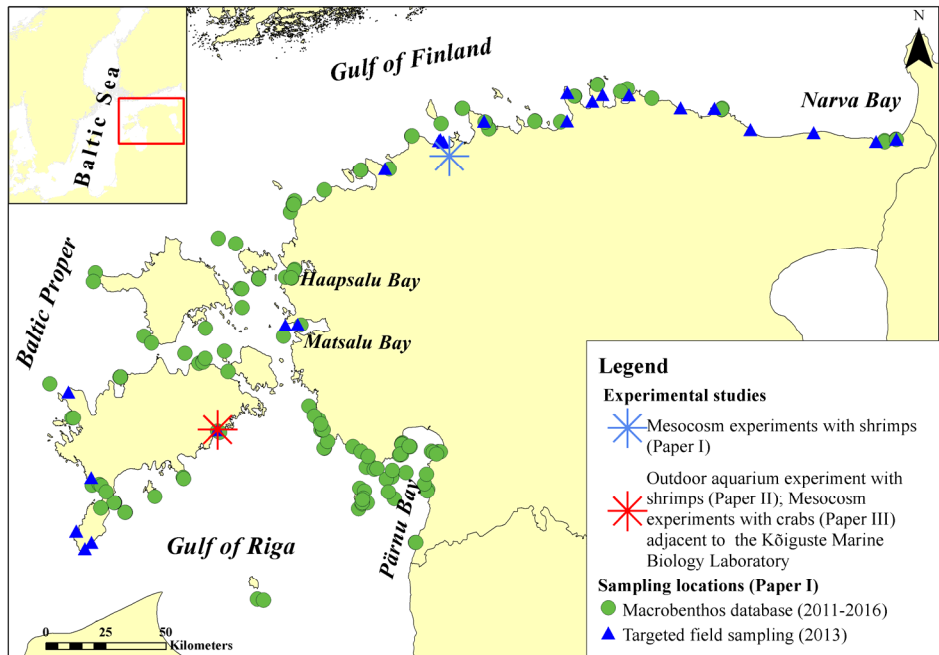
that the patterns of environmental niche space differ between the non-native and native shrimps.

- Examine habitat preferences of the non-native Harris mud crab (*Rhithropanopeus harrisii*) in response to population density, prey availability and habitat specification (III). It was hypothesized that *R. harrisii* actively choose habitat and the habitat selection is modulated by the crab density and food availability.
- Examine trophic interactions of the native and non-native shrimp species with the non-native amphipod *Gammarus tigrinus* (II). Given the taxonomical and morphological similarity between the native *P. adspersus* and non-native *P. elegans*, it was hypothesized that the feeding activity is similar in these species.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The experimental studies for this thesis were carried out at the Estonian Marine Institute (I), adjacent to the Kõiguste Marine Biology Laboratory (II–III) and the field studies were conducted all along the Estonian coastal sea (I–IV) located in the north-eastern Baltic Sea (Figure 1).



**Figure 1.** Study region, sampling sites and locations of the experimental studies.

Coastal waters of Estonia belong to northern part of the Baltic Sea encompassing the Gulfs of Finland and Riga, the Baltic Proper and the West Estonian Archipelago Sea. The area can be distinguished by various environmental gradients (e.g. salinity, wave exposure) and complex topography, including extensive shallows. Salinity can be above 7 PSU in the Baltic Proper, while river inflows result in a drop of salinity to nearly zero in the inner parts of some bays (e.g. Haapsalu Bay, Matsalu Bay). Areas highly exposed to waves are predominantly characterized by the presence of hard substrate, namely limestone or granite boulders. Moderately exposed areas have typically mixed sediments of sand, gravel, and pebbles. Along the coastline in most sheltered bays, bottom sediments are predominantly consisting of fine sand and silt (Martin et al., 2013).

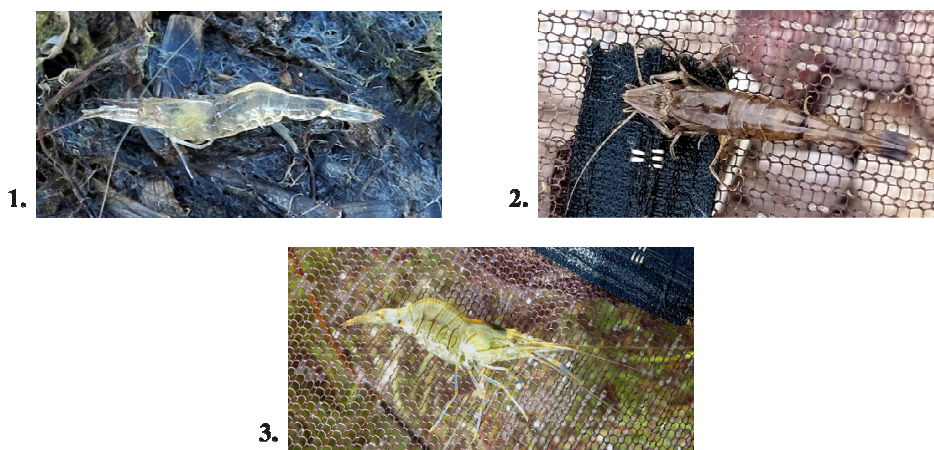
Benthic macrophytes in the study area are mainly represented by several algal and vascular plant species. Seabed habitats on the hard substrate are hosting important biotope forming species, such as brown alga *Fucus vesiculosus* Linnaeus, 1753 or the red alga *Furcellaria lumbricalis* (Hudson) J. V. Lamouroux,

1813. *F. vesiculosus* is usually found within the depth range of 1–4 m, while *F. lumbricalis* can be found within much wider depth zone (1–10 m) (Martin et al., 2013). Additionally, on the hard bottom habitats, several widespread filamentous green, brown, and red algae are present, such as *Ulva intestinalis* Linnaeus, 1753, *Cladophora glomerata* (Linnaeus) Kützing, 1843, *Battersia arctica* (Harvey) Draisma, Prud'homme & H.Kawai, 2010, *Pilayella littoralis* (Linnaeus) Kjellman, 1872, *Ectocarpus siliculosus* (Dillwyn) Lyngbye, 1819, *Ceramium tenuicorne* (Kützing) Waern, 1952, and *Polysiphonia* spp. (including *P. fucooides* (Hudson) Greville, 1824) (Martin et al., 2013). Vascular plants and charophytes are typical inhabitants of sandy and silty sediments of the shallow inner bays. Macrobenthic invertebrate communities of shallow areas are mainly associated to the plants and dominated mainly by different crustaceans (e.g. from orders *Amphipoda*, *Isopoda*), insect larvae (specifically in the diluted areas e.g. from orders *Diptera*, *Lepidoptera*) and brackish water snails (Kotta et al., 2008a; Kotta et al., 2008b).

As a consequence of eutrophication, extensive growth of annual filamentous algae and formation of drift algal mats are frequent events in coastal areas (Kotta et al., 2008c). Episodic hypoxia occurs all around the coastline (Conley et al., 2011).

## 2.2. Study species

Benthic communities in the northern Baltic Sea host four predatory macrofaunal species, which are studied in the present thesis: the Harris mud crab (*Rhithropanopeus harrisi* Gould, 1841), the brown shrimp (*Crangon crangon* Linnaeus, 1758), the Baltic prawn (*Palaemon adspersus* Rathke, 1837) and the rockpool prawn (*Palaemon elegans* Rathke, 1837). Caridean shrimps (Crustacea: Decapoda) are represented in the study area by two native species (*C. crangon* and *P. adspersus*) and one non-native species (*P. elegans*) (Figure 2).



**Figure 2.** Photographs of the studied shrimp species: (1) *P. adspersus* (2) *C. crangon*, (3) *P. elegans* (photograph by Ivan Kuprijanov).

*C. crangon* is a small epibenthic predator in the estuaries of northwest Europe, typical on unvegetated sandy or silty sediments. The Baltic Sea population of *C. crangon* is considered to belong to the north-eastern Atlantic phylogeographic group adapted e.g. to the low-salinity conditions (Luttikhuisen et al., 2008). In contrast to the *Palaemon* species, *C. crangon* is known to inhabit predominantly bottom habitats with soft sediment where it may demonstrate burrowing behaviour while having exclusively carnivore diet, preying on passing smaller invertebrates and even young benthic fish from the ambush (Oh et al., 2001).

*P. adspersus* in the oceanic waters typically inhabits seaweed habitats (Berglund, 1980; Manent and Abella-Gutierrez, 2006). Similarly, in the Baltic Sea, the main habitats of this shrimp are related to the lush benthic vegetation (Lapinska and Szaniawska, 2005). The species is sensitive to high fluctuations of salinity, temperature, and oxygen level (Berglund and Bengtsson, 1981). As many other species of the *Palaemon* genus, *P. adspersus* has specific migration pattern as it migrates into the coastal low salinity waters mainly during the summer months (Barnes, 1994).

In its native range, particularly in estuaries and coastal lagoons of Atlantic coasts of north-western Europe, *P. elegans* is characteristic to the areas with wave exposed macrophyte covered habitats (Barnes, 1994). In the Baltic Sea the shrimp was firstly found in the southern region in 2002 (Janas and Mańkucka, 2010) and in the northern region in 2011 (Paper IV). Currently, *P. elegans* is present almost in the entire Baltic Sea (Katajisto et al., 2013), but based on genetic evidence, the population originates from the Ponto-Caspian or Mediterranean region and was probably initially established in the southern Baltic Sea due to unintentional anthropogenic introduction (Reuschel et al., 2010). The further spread of the species inside the Baltic Sea has probably been natural but secondary introductions due to shipping are also possible. In the Baltic Sea, *P. elegans* is able to live under a wide range of environmental conditions; it can tolerate broad salinity variation (Janas et al., 2013) and even can survive during temporal hypoxia events (Taylor and Spicer, 1987). In the southern Baltic Sea, *P. elegans* seems to have a high overlap in environmental preferences with native shrimp species (Łapińska and Szaniawska, 2005, 2006). As a typical palaemonid prawn, *P. elegans* consumes smaller macrofauna species, such as amphipods and mysids as well as benthic macroalgae (Persson et al., 2008; Janas and Barańska, 2008; Moksnes et al., 2008; Lesutienė et al., 2014).

The native habitat range of *R. harrisii* is situated along the north-western part of the Atlantic Ocean and extends from Canada to Mexico (Williams, 1984; Projecto-Garcia et al., 2009). It is characterized by its small size (carapace diameter up to 26 mm), omnivorous feeding, euryhalinity, and high fecundity. While adult crabs can withstand fresh water, their larval development occurs at salinity values above 0.5 (Turoboyski, 1973; Boyle et al., 2010). *R. harrisii* was first observed in Western Europe already in the 19th century (Wolff, 2005). The species was introduced into the southern Baltic Sea by the 1950es (Schubert, 1936; Demel, 1953) but it was only in the 2000's when the species spread



northward. *R. harrisi* was first sighted in Lithuania in 2000 (Bacevičius and Gasiūnaitė, 2008) and in Estonia and Finland in 2011 (Karhilahti, 2010; Kotta and Ojaveer, 2012). In parallel with the range expansion in the Baltic Sea, the species also invaded inland water bodies such as the Caspian and Black Seas (Zaitsev and Ozturk, 2001). The pelagic larval stage has probably facilitated the spread of *R. harrisi* due to the intake of larvae into ships' ballast water and the intensification of ship traffic during recent decades has probably contributed to the new introductions of the invasive crab (Turoboyski, 1973; Gollasch and Leppäkoski, 1999; Forward, 2009). *R. harrisi* is suggested to compete strongly with other species e.g. native benthophagous fishes that share similar diets with the crab (Zaitsev and Ozturk, 2001). *R. harrisi* on rocky habitats could drastically deplete the previously abundant grazer taxa (Jormalainen et al., 2016) and likely shift the existing trophic interactions.

## 2.3. Data collection

### 2.3.1. Field sampling

The distribution data of shrimps were compiled from two different sources: a.) macrobenthos database of the Estonian Marine Institute, University of Tartu, which holds benthic invertebrate surveys mostly carried out by the same institution in the frame of the Estonian National monitoring; and b.) by use of targeted trap sampling funded by the Environmental Investment Centre of Estonia in the framework of the Project “Identifying an invasive potential of alien shrimp in the Estonian coastal waters” (I). Crayfish traps were used in the targeted field sampling. These traps were deployed in 23 locations in the Estonian coastal sea in 2013 (Figure 1). Subsequently in each location, traps were deployed at two visually distinguishable habitats according to the presence of distinct substrate type (e.g. soft and hard bottom) and macrophyte community (a depth range from 0.4 to 1 m, a period of deployment of 24 h). Three replicate traps were mounted on each habitat (Figure 3). Coverage of seabed substrate types and benthic macrophyte species in a radius of 3 m around traps was estimated visually to provide characteristics of the bottom habitats sampled.

All trapped predatory macrofauna individuals were identified and counted in the lab (I, II, III and IV). The body length of adult inter-molt shrimps used in the experiments was measured from the tip of the rostrum to the tip of the telson at the end of the experiment (I, II). Non-ovigerous adult *R. harrisi* individuals were categorized according to the measured carapace width before entry into the experimental mesocosms (III).



**Figure 3.** A cluster of crayfish traps, which were deployed at each sampling location. As generally visibility in the Baltic Sea is poor, shrimps rely often on chemoreception rather than visual sense organs (photograph by Ivan Kuprijanov).

Data on the occurrence of caridean shrimp species and phyto-benthic species from years 2011 to 2016 were extracted from the macrobenthos database of the Estonian Marine Institute and consisted of (a) quantitative samples (mainly frame samples, n=161) and (b) qualitative samples (n=35) derived e.g. from towed fishing gear or hand net. Quantitative sampling of benthic organisms used in the study was conducted according to HELCOM COMBINE guidelines (HELCOM, 2015). From the macrobenthos database, only shrimp species presence data were incorporated in this study (n=196, Figure 1).

### 2.3.2. Environmental variables

In paper I, shrimp distribution data was used together with abiotic and biotic environmental data on shrimp habitats collected either *in situ* or acquired from georeferenced GIS layers (Table 1). Seabed substrate, macrophyte cover, and water depth were recorded during field sampling. Another set of the environmental variables (slope of seabed, wave exposure, wave orbital velocity, near-bottom water velocity, sea surface temperature and salinity, water transparency, near-bottom oxygen concentrations, ice conditions, concentrations of chemical components and chlorophyll a) was obtained from different georeferenced raster datasets using geographical information system (GIS). Grid size in GIS-based data layers varied between 25 and 200 meters.

Cover of benthic macrophytes was assessed by visual estimation while snorkelling or scuba diving around the sampling location. Sediment types and macrophytes were identified simultaneously with field sampling. Among the 28

macrophyte species (aquatic macroalgae and vascular plants) that were recorded during *in situ* sampling, only the most frequently occurring species (see Paper I for details) were included in the following multivariate analysis. The information on coverage of the bottom by different hard sediment particles was consolidated into one parameter i.e. the proportion of coverage of hard substrate. In total, the environmental dataset included 24 variables (Table 1).

**Table 1.** Variables used in the environmental niche analysis (see Paper I for a more complete version of the table).

Variable	Description of variable	Source
<i>Variables recorded in situ during sampling</i>		
Depth	Water depth (m)	B
hard_subst	Proportion of coverage of hard substrate (%)	B
Furcellaria	Cover of <i>Furcellaria lumbricalis</i> (%)	B
Fucus	Cover of <i>Fucus vesiculosus</i> (%)	B
Polysiphonia	Cover of <i>Polysiphonia fucoides</i> (%)	B
Battersia	Cover of <i>Battersia arctica</i> (%)	B
Ceramium	Cover of <i>Ceramium tenuicorne</i> (%)	B
Cladophora	Cover of <i>Cladophora glomerata</i> (%)	B
Pilayella/ Ectocarpus	Cover of <i>Pilayella littoralis</i> , <i>Ectocarpus siliculosus</i> (%)	B
<i>Variables obtained from GIS layers</i>		
slope	Slope of seabed (°)	A
chlorophyll	Chlorophyll <i>a</i> content of sea surface ( $\text{ml m}^{-3}$ ): based on long-term (2009–2012) mean of daily satellite remote sensing	B
transparency	Water transparency estimated as attenuation coefficient ( $\text{m}^{-1}$ ): based on long-term (2009–2012) mean of daily satellite remote sensing	B
Oxygen	Near-bottom oxygen concentrations ( $\text{mg l}^{-1}$ ): average over 2002–2008	F
PO <sub>4</sub>	Concentration of phosphates ( $\mu\text{g l}^{-1}$ ): long-term (1995–2005) mean values	F
NO <sub>3</sub>	Concentration of nitrates ( $\mu\text{g l}^{-1}$ ): long-term (1995–2005) mean values	F
ammonium	Concentration of ammonium ( $\mu\text{g l}^{-1}$ ): long-term (1995–2005) mean values	F
velocity	Near-bottom water velocity ( $\text{m s}^{-1}$ ): long-term mean values at seabed	F

Variable	Description of variable	Source
temp_cold	Bottom layer water temperature in cold season (November – April) (°C): long-term (1995–2005) mean values at seabed	F
temp_warm	Bottom layer water temperature in warm season (May – October) (°C): long-term (1995–2005) mean values at seabed	F
temp_sat	Sea surface temperature based on satellite imagery (°C): average over 2009–2010	B
salinity	Salinity (PSU): long-term (2002–2008) mean value at seabed based on hydrodynamic model corrected with local <i>in situ</i> measurements	B, G
Wave	Wave exposure based on simplified wave model (m <sup>2</sup> s <sup>-1</sup> ): based on long-term (1997–2006) mean wind speeds and directions	C
ice	Average ice thickness in winter (m): average over 2009–2011	D
Orbspeed	Wave orbital velocity (m s <sup>-1</sup> )	E

**Sources:**

A – Bathymetric raster (Estonian Maritime Administration)

B – Databases of the Estonian Marine Institute

C – Wave exposure calculations for the Estonian coast (Nikolopoulos and Isæus, 2008)

D – Finnish Meteorological Institute

E – SWAN hydrodynamic model (Suursaar et al., 2014)

F – Hydrographic model developed by the Marine Systems Institute, Tallinn University of Technology (Maljutenko and Raudsepp, 2014)

G – COHERENS ocean circulation model (Bendtsen et al., 2009)

### 2.3.3. Manipulative experiments

**Habitat occupancy of *P. adspersus* and *P. elegans* (I)** was studied by mesocosm experiments conducted at the laboratory of the Estonian Marine Institute, University of Tartu in June 2013. Different soft and hard bottom habitats were recreated in an aerated aquarium (1.20 × 1.0 × 0.50 m, Figure 4). The mesocosm setup consisted of four habitat patches (60×50 cm each); all the animals were collected from Kopli Bay (Gulf of Finland, northern Baltic Sea) and acclimatized prior to the start of the trials for at least 24 h. Experimental habitats reflected natural coastal conditions of the northern Baltic Sea (Figure 4).

The following treatments and treatment levels were used:

- Habitat treatment (levels: soft bottom without vegetation, soft bottom with vegetation, hard bottom without vegetation, and hard bottom with vegetation)
- *Palaemon* shrimp treatment (levels: *P. elegans*, *P. adspersus* and *P. elegans* + *P. adspersus*)



**Figure 4.** Setup of the experimental mesocosm in Paper I (photograph by Ivan Kuprijanov).

The soft bottom habitats consisted of medium sand with or without the vascular plants *Zannichellia palustris* and *Stuckenia pectinata*. The hard bottom habitats consisted of boulders either with or without the filamentous green algae characterized by the mixed community of *U. intestinalis* and *C. glomerata*. The cover of macrophytes in mesocosms corresponded to that observed in natural habitats of shallow coastal areas. Within each experimental habitat, different assemblages of *Palaemon* shrimps were deployed for 12-h period.

Radio frequency identification technology was used for locating shrimp individuals which were equipped with individually coded passive integrated transponder (PIT) tags. Habitat occupancy of each tagged individual was recorded with a portable FDX/HDX Reader at intervals of 1 h (I).

**Trophic interactions of *P. adspersus* and *P. elegans* with *G. tigrinus* and macroalgae (II)** were studied in an outdoor aquarium experiment conducted adjacent to the Kõiguste Marine Biology Laboratory in August 2012. The volume of filtered (mesh size 0.25 mm) sea surface water in experimental aquaria was 5 L. Experimental organisms were collected from the northern and southern coasts of Saaremaa Island, north-eastern Baltic Sea. The palaemonid prawns and gammarid amphipods were collected with a hand net from the depth of 0–1 m. Altogether 92 aquaria were used to deploy 23 treatments replicated four times (Figure 5).



**Figure 5.** Detail of the outdoor aquarium experiment in Paper II (photograph by Ivan Kuprijanov).

The following treatments and treatment levels were used:

- Shrimp assemblage treatment (levels: *P. elegans*, *P. adspersus*, mixed, none)
- *Palaemon* density treatment (levels: 1 or 2 individuals per aquarium, corresponding to 14 and 28 ind m<sup>-2</sup>)
- Macroalgae treatment (levels: vegetated boulders, unvegetated boulders)
- Gammarid amphipod treatment (levels: present at 10 ind per aquarium corresponding to 140 ind m<sup>-2</sup>, absent)

During the experiment, filamentous algae on the boulders served simultaneously as an object of grazing for crustaceans and as a refuge for gammarid amphipods. Visual estimation of amphipod density was performed every 12 h. The experiment was terminated after 48 h when about 50% of gammarids had been consumed in at least one experimental unit.

At the end of the experiment, algae were removed from their substrate and weighed (II). The gammarid amphipods were counted and species were identified using light microscopy. Their survival was calculated as the percentage of individuals of *G. tigrinus* and palaemonid shrimps that were alive at the end of the experiment. The individual lengths of amphipods and shrimps used in the study were assessed applying digital image-processing methods and using ImageJ software (Schneider et al., 2012) (I, II).

**Habitat preferences of *R. harrisii*** were studied in an outdoor mesocosm experiment conducted adjacent to the Kõiguste Marine Biology Laboratory, the north-eastern Baltic Sea, in June 2013. The experiment setup consisted of 12 aerated aquaria filled with 9 litres of filtered seawater.

The following treatments and treatment levels were used:

- Habitat treatment (levels: boulder with *F. vesiculosus*, boulder with *C. glomerata*, unvegetated boulder and sand).
- *R. harrisii* density treatment (levels: 1, 2 and 4 individuals per aquarium corresponded to low, medium and high densities).
- Food treatment (levels: no food, presence of slow-moving snails and presence of mobile gammarids).

The specimens of *R. harrisii* were brought from Pärnu Bay. *R. harrisii* were placed randomly into the aquaria and acclimatized prior to the start of the trials for 24 h. Other experimental material was collected from the coastal habitats adjacent to the Kõiguste Marine Biology Laboratory.

Two runs of the experiment were conducted under similar conditions. Only treatments with no food and treatments with non-mobile food were offered in the first run. For the second run, mobile food was added to 6 aquaria and all *R. harrisii* specimens were randomly reassigned among the aquaria.

Radio frequency identification technology was used for locating *R. harrisii*. All individuals were equipped with individually coded passive integrated transponder (PIT) tags (Figure 6). Occupancy of each tagged individual was recorded with Portable FDX/HDX Reader at an interval of 2 h during the period of 72 h. For further details see (III).



**Figure 6.** RFID-tagged *R. harrisii* (photograph by Ivan Kuprijanov).

## 2.4. Statistical methods

The habitat preferences of test animals were expressed as a frequency of occurrence of individuals on the studied experimental habitats (**I**). Two-way ANOVA was used to check if the habitat occupancy of a given palaemonid species was dependent on the presence or absence of the other caridean species. As it was not possible to demonstrate such dependence, data from single and two species treatments were pooled for further analyses. Thereafter, another two-way ANOVA with Tukey's HSD post-hoc procedure was used to analyze differences in habitat occupancy between habitat treatments and between the *P. elegans* and *P. adspersus* treatments.

Nested ANOVA with the density of shrimps nested within the *Palaemon* community factor followed by Post-hoc Bonferroni tests was used to analyse the separate and interactive effects of palaemonid shrimps on the macroalgal consumption and the survival of amphipod gammarids (**II**). In an experimental study on *R. harrisii*, three-way ANOVAs followed by Post-hoc Bonferroni tests were used to test if the habitat occupancy of the studied *R. harrisii* depended on habitat type, food type and *R. harrisii* density (**III**).

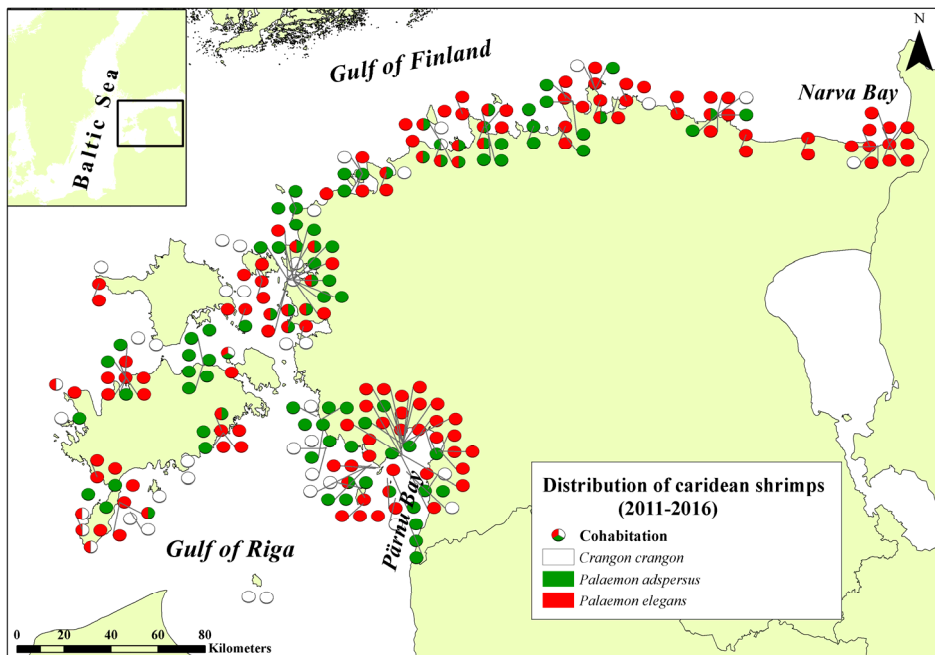
In paper **I**, canonical correspondence analysis (CCA) was used to visualize the occurrence of different shrimp species in relation to multiple environmental variables using the statistical software R version 3.2.0 (R Development Core Team, 2015) with the package "vegan" (Oksanen et al., 2013). To eliminate statistically non-significant environmental variables from CCA ordination, we previously tested multivariate relationships between environmental variables and shrimp species occurrence using a permutation test. The analysis of outlying mean index (OMI) was used to assess habitat specialization and separation of habitat niches between the shrimp species (**I**). OMI quantifies the distance between the mean habitat conditions used by the species (niche centre) and the mean habitat conditions of the sampling area (Dolédec et al., 2000). A permutation test was used to calculate the statistical significance of the values of OMI of each shrimp species. Hence the highest habitat specialization is indicated through the highest value of the OMI index of a species. The package "ade4" (Dray and Dufour, 2007) was used to perform OMI analysis in the statistical software R 3.2.0 (R Development Core Team, 2015). The environmental niche space of shrimp species was visualized by drawing a convex hull over the points where a given species was present.



### 3. RESULTS AND DISCUSSION

#### 3.1. Spatial distribution of caridean shrimps

The frequent occurrences of the studied shrimps in a broad range of coastal habitats indicate a wide distribution of these decapod crustaceans along the Estonian coastal sea (I, IV). We found that the non-native *P. elegans* inhabits almost the whole geographical extent of the study area (out of 239 sampling sites, 108 were occupied exclusively by *P. elegans*), whereas native species occurred within a smaller range (*P. adspersus* were found in 67 and *C. crangon* in 36 sites) (Figure 7). In addition, despite their recent arrival (Katajisto et al., 2013), the *P. elegans* were found at the lowest salinities (from 1.6 PSU, according to *in situ* measurements during targeted field sampling), contrary to native species that did not occur in places where water salinity was lower than 2.9 PSU.



**Figure 7.** Distribution of caridean shrimps in the studied area. Coexistence in the same sampling point is indicated by sectors of different colours. The leader next to the circle shows position of the sampling site. (Redrawn from Paper I).

Arrival, initial colonization and secondary spread of alien crustaceans are generally facilitated by high dispersal capacity (Hänfling et al., 2011). Larval drift has probably facilitated the rapid spread of *P. elegans* because an increased occurrence of *Palaemon* larvae (not feasible to identify to species level) was observed in planktonic samples after the introduction of the *P. elegans* (A. Põllumäe personal communication). The adults' ability to move actively may have

further facilitated the range expansion of *P. elegans*. According to our extensive field sampling, the *P. elegans* has established in areas along the Gulf of Finland, that were previously devoid of any native caridean shrimps, suggesting environmental niche separation between the studied shrimp species (Figure 7). This was further evidenced by the relatively low proportion of cohabitation of *P. elegans* and *P. adspersus* compared to single-species occurrences.

Our results indicate that primary factors leading to niche differentiation between the native and non-native shrimps include physical properties of the areas. In the eastern Gulf of Finland, specifically Narva Bay and in the north-eastern Gulf of Riga (i.e. inner part of Pärnu Bay), only the *P. elegans* were present at quantities more than 5 individuals per m<sup>2</sup>. These sub-basins have distinctly low salinity, elevated levels of nutrients, and naturally low water transparency (Kotta et al., 2008b; Pitkänen et al., 2008). This is in agreement with previous studies, that suggest salinity to be behind the observed spatial distribution of caridean shrimps (González-Ortegón et al., 2006) as higher occurrences of *P. elegans* in more diluted habitats are supported by the weaker osmoregulatory capacity of the native *P. adspersus* compared to that of the non-native *P. elegans* (Janas et al., 2013).

While the congeners *P. adspersus* and *P. elegans* mostly occurred sympatrically in a regional scale, they relatively seldom (only at 22 sites) co-occurred at local scales (I). The shrimp species were found on seabed habitats with mixed bottoms of soft and hard substrates where coverages of hard sediment types varied between 25 and 100% (I, IV). *C. crangon* primarily occurred in habitats that had a higher proportion of soft sediments (more than 50%) compared to habitats where *Palaemon* species were found (I).

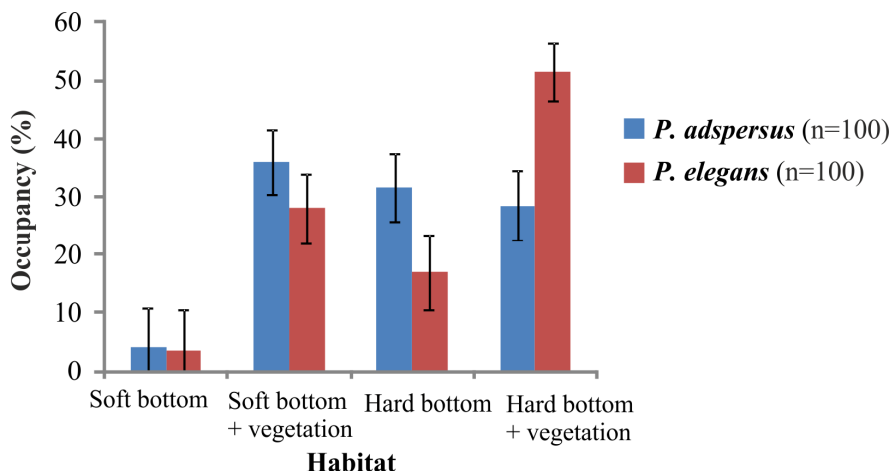
These results also suggest that the spatial distribution of species is determined by dispersal limitation, suitable habitat availability and habitat complexity. On sympatric habitats, the studied shrimp species may stay separated on the scale of microhabitats (I). Here, the habitat complexity at very small spatial scales enables co-existence of native and alien species within a guild, as this separation relieves competition induced by using same habitat resources (Hänfling et al., 2011). Data on distribution of shrimps along Estonian coastal waters covering a temporal extent from the first records of the non-native *P. elegans* to the colonization of the full coastal range of the region indicate the essential point of establishment, while wide geographic distribution refers to subsequent expansion of the population (I, IV). This information might help to prioritize sites as hot-spots for new introductions of invasive species (due to higher occurrences of *P. elegans* e.g. at ports of Tallinn and Pärnu) and distinguish geographic areas where impact on native ecosystem might be strongest (according to lower occurrences of native counterparts e.g. Narva bay).

Dedicated seasonal field studies are needed in future to clarify the seasonal component influencing the pattern of distribution as seasonal migration of palaemonid shrimps between shallow and deep water have been reported from the southern Baltic and the Black Sea areas (Łapińska and Szaniawska, 2005; Bilgin et al., 2009).

## 3.2. Habitat occupancy and preferences of predatory macrofauna

### 3.2.1. Habitat occupancy of *Palaemon* shrimps

According to our field sampling in the northern Baltic Sea region, the palaemonid shrimps co-occurred on stony habitats rather than on soft bottom habitats (I). The experimental study, in turn, showed that palaemonid species preferred distinct habitats (Figure 8). In the laboratory experiment, the non-native *P. elegans* was found mostly on hard bottom habitats with vegetation (average occupancy 51%), while the native *P. adspersus* was almost uniformly observed on vegetated soft (36%) and hard (29%) substrates, and hard substrates without vegetation (32%) (Figure 4) (I). Both species were rarely observed on unvegetated soft bottom habitat (average occupancy 4%) and they showed similar rates of occupancy within vegetated soft bottom habitat. *P. elegans* stayed within unvegetated hard bottom habitat less frequently than *P. adspersus* (17 and 32%, respectively).



**Figure 8.** Average ( $\pm$ SE) habitat occupancy of palaemonid shrimps within the studied habitats.

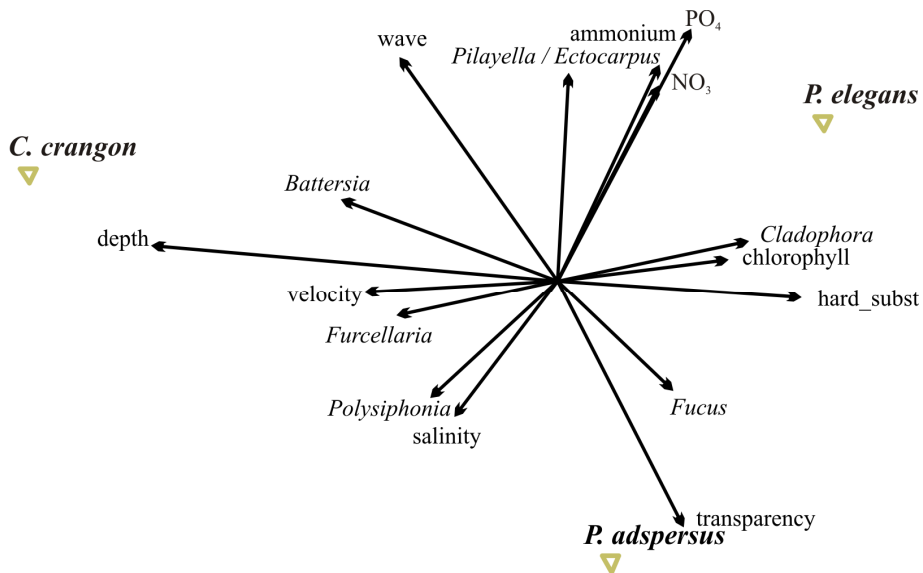
Our laboratory experiment with the non-native *P. elegans* and native *P. adspersus* demonstrated substantial differences in microhabitat selection (I). This result corresponds to previous field studies in the North Atlantic coast and the fjords of southern Sweden suggesting that the coexistence of palaemonid shrimps relies on differences in microhabitat selection (Berglund, 1980; Barnes, 1994) along with dissimilarity in body size (Berglund, 1980). In accordance with our earlier field observations (IV), the *P. elegans* had a high affinity towards hard bottom habitats covered with annual filamentous algae. The prevalence of such habitats in the shallow waters of the northern Baltic Sea has potentially supported the rapid spread of *P. elegans* in the study area. Compared to the

native *P. adspersus*, the non-native *P. elegans* was more frequently observed among filamentous algae. This may be related to the larger body size and lower mobility of the native species (Berglund, 1980) that might hamper foraging in the dense mats of filamentous algae.

The results derived from the habitat occupancy experiment support the idea that a coexistence of the two congeneric shrimp species in shallow heterogeneous habitats probably does not affect the species-specific habitat occupancy patterns (Berglund, 1982), as even over short time periods the niche partitioning may be expected at small spatial scales. The analysis of field sampling data covering a broad range of environmental niche space provided further evidence on the environmental niche separation between the studied shrimp species (I).

### 3.2.2. Realized niches and habitat specialisation of the caridean shrimps

Our field data showed that compared to the native shrimps, the invasive *P. elegans* more often occurred in low saline eutrophicated shallow water areas characterized by hard substrates covered with filamentous algae (I). Contrastingly, the native *P. adspersus* was mostly restricted to areas with higher water transparency dominated by the perennial brown alga *F. vesiculosus*. In contrast to the *Palaemon* species, *C. crangon* were found at greater depths and higher wave exposure (Figure 9) (I).

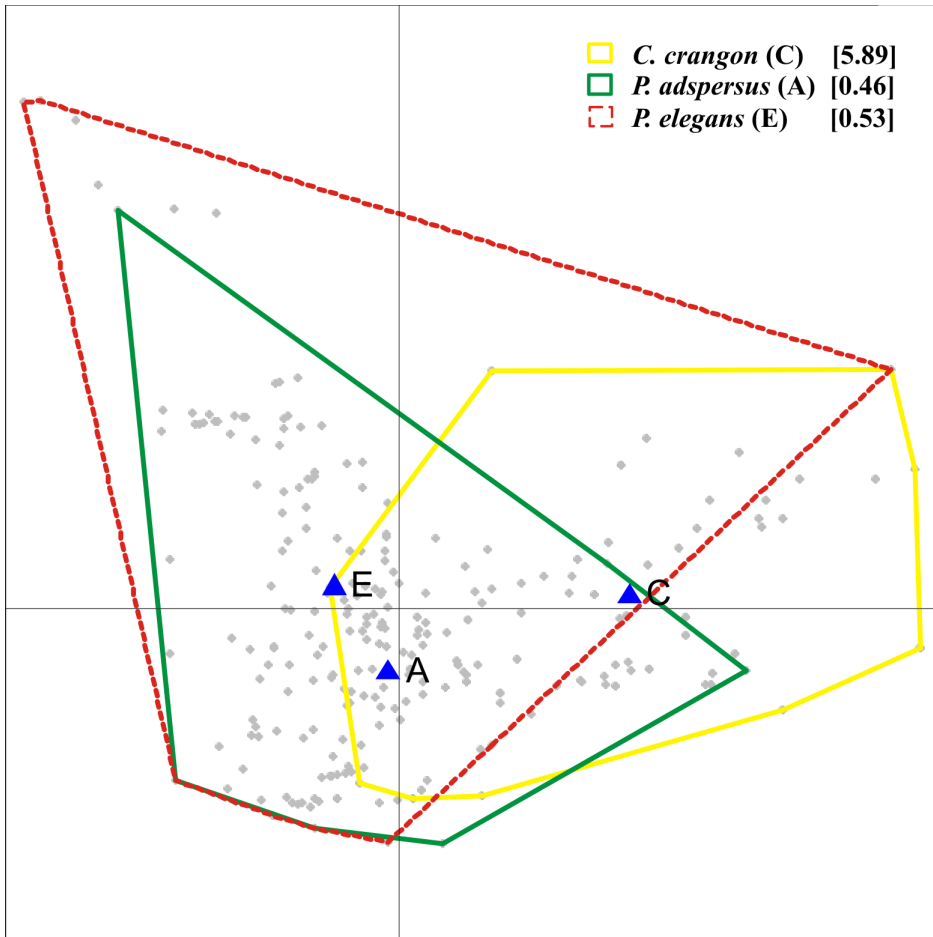


**Figure 9.** CCA ordination visualizing the occurrence of studied shrimp species in relation to environmental variables derived from *in situ* measurements (i.e. seabed substrate, macrophyte cover, water depth) or acquired from georeferenced GIS layers. (Redrawn from Paper I).

Results from both the field sampling and the habitat occupancy experiment indicated that hard substrates overgrown with filamentous algae are favourable habitats for *P. elegans* and this is probably because such habitats simultaneously provide the shrimps food and shelter from predators. The observed divergence in the habitat preferences among the studied caridean shrimps also indicates that the *P. elegans* will not likely become the dominant shrimp species all over the coastal habitats of the northern Baltic region already because it was absent in deeper wave exposed areas.

According to the analysis of habitat specialization (OMI values) (**I**), *C. crangon* was more specialized than the palaemonid shrimp species, among which the non-native *P. elegans* was slightly more specialized than its native counterpart (Figure 10). The latter result is different to the findings from the coastal fjords of western Baltic Sea where *P. elegans* had a broader ecological niche than *P. adspersus* (Berglund, 1980). The centre of the realized niche of the *P. elegans* was substantially closer to *P. adspersus* than to *C. crangon*, but did not coincide with that of *P. adspersus* (Figure 10). A partial overlap of the environmental niche space of the studied species indicates their potential interspecific competition. However, a broader environmental niche space of the native palaemonid shrimp enables the species to partly escape from this interference competition. Field observations are often limited in spatial and temporal coverage, i.e. they represent only episodic measurements of variables or species distribution patterns, and may not reflect the full range of variability. In the southern Baltic Sea the habitat occupancy of the studied shrimps varies along seasons (Łapińska and Szaniawska, 2005) and such migrations are likely taking place in the Northern Baltic Sea. Thus, a degree of the habitat overlap and the strength of competitive interactions among the studied shrimps may have a seasonal component. Targeted seasonal field studies are needed to clarify the seasonal patterns of habitat use.

The width of the realized niche of an introduced species in its new geographic range is defined by the available niche space and biotic interactions with other species (Polechová and Storch, 2008). Our study demonstrated that the invasive *P. elegans* currently occupied marginally narrower niche (indicated by higher OMI value) than its native congener, *P. adspersus*, which was not determined by an inferiority of the invasive species but rather by its true preference to more eutrophicated and diluted environments. Since the introduction of *P. elegans* is a very recent event, its further range expansion and niche widening together with intensified interspecific competition among the palaemonid shrimps is expected in the future. The continuation of targeted sampling of shrimps in future is needed in order to answer the question of potential widening of the niche of the *P. elegans*.



**Figure 10.** Environmental niche characteristics of the studied shrimp species based on PCA ordination of environmental variables in sampling sites. Dots represent sampling sites ( $n=239$ ), polygons represent the realized niches, and letters on the plot mark the centres of niche spaces of the shrimps. The OMI identified axes that are positioned in the multidimensional space according to optimal separation between studied species as a function of environmental parameters. The values of OMI are shown in square brackets. OMI evaluate the distance between the mean habitat conditions used by the species (niche centre) and the mean habitat conditions of the sampling area. The highest value of the OMI index of a species indicates highest habitat specialization. (Redrawn from Paper I).

As compared to *P. adspersus*, *P. elegans* is thought to be more euryoecious in its native distribution range and can better withstand extreme conditions such as low salinity, hypoxia, and thermal stress (e.g. Taylor and Spicer, 1987; Janas et al., 2013). Nevertheless, a presence of vacant habitats in its introduced range (*in sensu* Ricciardi et al., 2013) together with a low genetic diversity of introduced population(s) (genetic bottleneck; Lee, 2002), may promote specialization of the

*P. elegans* in a recipient environment compared to its native environment. The findings of this study and the recent invasion events by the amphipod *G. tigrinus* (Herkül et al., 2016) suggest that wider environmental tolerance does not necessarily result in a broader realized environmental niche space of a non-native species in a recipient environment.

Furthermore, recent introductions of round goby (*Neogobius melanostomus*) and mud crab (*Rhithropanopeus harrisi*) into the northern Baltic Sea have a potential to drastically change benthic communities (Lokko et al., 2015; Nurkse et al., 2016; Jormalainen et al., 2016) with expected effects on native and invasive shrimp species. Due to dietary overlap between the palaemonid shrimps and the invasive crab, stronger predation pressure through the cascading effects of the predation of shrimps on the gammarid amphipods are expected in the presence of the *R. harrisi*. Moreover, *N. melanostomus* and *R. harrisi* are large generalist predators that likely compete with shrimps but likewise exert predation pressure on them.

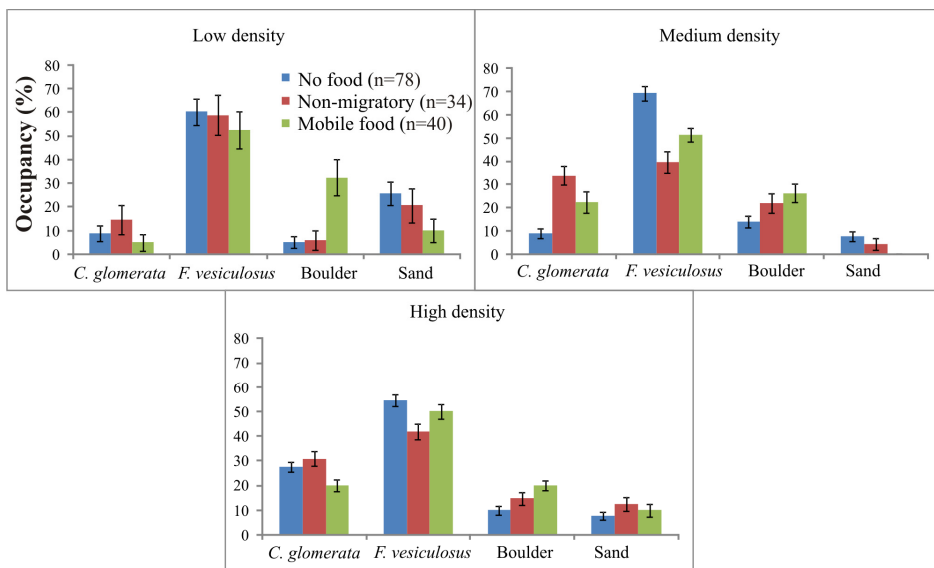
The differential environmental preferences of native and non-indigenous species (**I**) are in accordance with the theory that states a separation of native species and successful invaders in environmental niche space in a recipient ecosystem (Stachowicz and Tilman, 2005). *P. adspersus* had an affinity towards temporally stable habitats inhabited by perennial brown algae whereas the non-native *P. elegans* preferred habitats dominated by annual opportunistic filamentous algae. Differences in the habitat preference of the studied shrimps have a potential link to differences in their life strategies. *P. adspersus* is known to have typical features of K-strategist (e.g. larger body size and lower mobility) while *P. elegans* exhibits life-history traits linked to r-selection strategy (e.g. rapid growth, early maturity) (Berglund, 1980). In addition to the differences in habitat preferences and life strategies, the invasive *P. elegans* can better withstand different stresses such as low salinity and low-oxygen environments compared to the native species (Taylor and Spicer, 1987; Janas et al., 2013). Generally, the invasiveness of an alien species within a recipient ecosystem is directly linked to its life-history traits, and often related to elevated tolerance to stresses as well as possessing some traits of adaptability (e.g. elevated fecundity) (McMahon, 2002; Jänes et al., 2015). Consequently, the *P. elegans* is able to colonize habitats formerly lacking native shrimps and therefore adding a novel function i.e. epibenthic predation to some coastal habitats of the Baltic Sea (e.g. in the Gulf of Finland).

The changes enforced by the invasive species are not taking place in isolation of other elements of global change. Since the 1980's several significant shifts in Baltic Sea ecosystems have been detected including changes in summer plankton community structure (Suikkanen et al., 2013) and phytoplankton dynamics (Kahru et al., 2016), and increasing hypoxia in coastal areas (Conley et al., 2011). The future environment of the Baltic Sea is expected to be more diluted resulting in a significant areal shrinkage of species of marine origin such as the perennial brown alga *Fucus vesiculosus* (Jonne Kotta, unpublished data). The loss of areal cover of such important habitat forming species may have implications on

environmental niches and the species realized niche space. It is not unlikely that the local species being less adapted to the new conditions will disappear and be replaced by invasive species that will form novel communities. Although the potential cascading effects of climate change on native and invasive species are yet to be fully understood (Clavel et al., 2011), the *P. elegans* is expected to be a “winner” as it prefers lower salinity, elevated eutrophication, and ephemeral algal communities (I). Shifts in community composition in the Baltic Sea may also result from trophic cascades caused by the introduction of other species from warmer regions (Leppäkoski et al., 2002b). Therefore the ongoing increase in sea water temperature in the Baltic region (Belkin, 2009) might further intensify stresses caused by the introduced species (Occhipinti-Ambrogi, 2007) ultimately resulting in a complete reorganization of community composition and associated ecological functions.

### 3.2.3. Habitat occupancy of *R. harrisii*

There were statistically significant effects of habitat type and interactive effects of prey and crab density on the habitat occupancy of *R. harrisii* (III) (Figure 11). The *R. harrisii* preferred hard substrate over soft substrates. The *R. harrisii* were found mostly burrowed under the boulders covered by *F. vesiculosus* (average occupancy 52%), while significantly lower occupancy was observed in sand (20%), boulders covered with *C. glomerata* (15%), and boulders without vegetation (13%) (Figure 11).



**Figure 11.** Average ( $\pm$ SE) habitat occupancy by *R. harrisii* in experimentally studied habitats at three levels of crab densities were used: low (1 individual per aquaria), medium (2 individuals per aquaria) and high (4 individuals per aquaria) and three types of food conditions (no food, presence of slow-moving snails and presence of mobile gammarid amphipods).

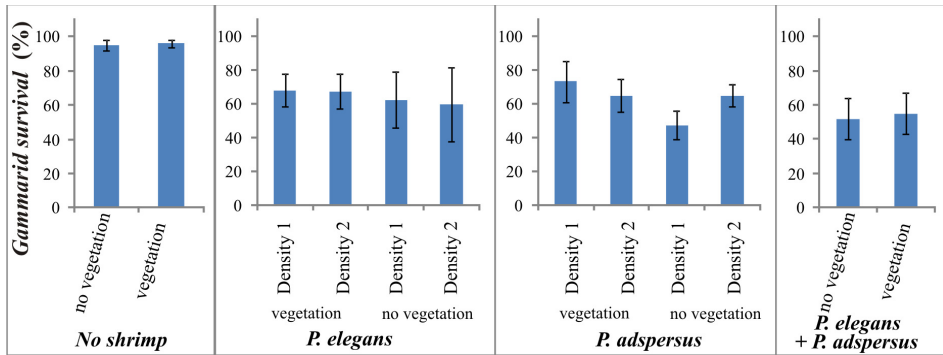


Crab density and presence of food interactively influenced the habitat choice of *R. harrisii* (Figure 11) (III). Habitat occupancy at low and medium crab densities was significantly affected by the availability of food. Namely, non-migratory food in the case of medium crab density significantly decreased the crab presence within boulders covered with the perennial *F. vesiculosus*, while presence of the same food type significantly increased the habitat occupancy within another habitat, boulders with filamentous *C. glomerata*. The availability of food had no effect on the habitat occupancy of crabs in the high crab density treatment. The only difference was a more uniform distribution of crabs among different habitats at high compared to low density treatments (Figure 11). In addition, the experiment showed that increased aggression between *R. harrisii* individuals increased their occupancy of otherwise less favourable habitats: in the presence of competition (in case of medium and high crab densities) less favored habitats (others than boulders covered with *F. vesiculosus*) were mostly inhabited by smaller individuals (III).

A possible explanation of the observed pattern of habitat occupancy of *R. harrisii* is that thin and flat blades of perennial brown algae thallus provides a substrate and shelter not only for associated epiphytes and herbivores (e.g. Wallentinus, 1991) but likewise for the predatory crab. Moreover, the furoid alga may provide the *R. harrisii* a lush feeding ground as previously described for nectobenthic fish (Aneer, 1985). Large thalli of *F. vesiculosus* likely offer the *R. harrisii* with year-round and stable habitat in the coastal ecosystem of the Baltic Sea. As compared to other perennial macroalgal species, the *F. vesiculosus* habitat hosts a high number of macroalgal and invertebrates species, and in addition, benthic biomass is highest there (Kautsky et al., 1992; Wikström and Kautsky, 2007). Similarly, in the Finnish Archipelago Sea, the habitat choice of *R. harrisii* seems to be determined by physical habitat properties (i.e. shelter) rather than food availability (Riipinen et al., 2017). In addition to the currently invaded two contrasting habitats, silty bottoms and hard bottom habitats overgrown with the brown alga *F. vesiculosus*, it is likely that critically important meadows of eelgrass (*Zostera marina*) are invaded next in concurrent with the further range expansion of *R. harrisii* (Gagnon and Boström, 2016).

### 3.3. Effects of *P. elegans* on trophic interactions

The feeding experiment (II) showed that the grazing of palaemonid shrimps on the filamentous *C. glomerata* was negligible. Similarly, *P. adspersus* and *P. elegans* did not impact macroalgal biomass through the removal of the meso-herbivore *G. tigrinus*. Both the invasive and native shrimps did significantly reduce the survival of gammarids in all treatments (Figure 12) (II). The invasive *P. elegans* and the native *P. adspersus* had no significant difference in their feeding activity and the presence of macrophytes did not influence how much amphipods were preyed. Furthermore, neither did shrimp density affect the predation of shrimps on gammarid amphipods. Thus, the experiment indicated that the ecological roles of *P. elegans* and *P. adspersus* are similar.



**Figure 12.** Effect of vegetation (factor levels: absent, present), *Palaemon* community (factor levels: no shrimp, *P. elegans*, *P. adspersus*, mixed community of *P. elegans* and *P. adspersus*) and *Palaemon* density (factor levels: 0, 1 (Density 1), 2 (Density 2) individuals per aquarium) on survival of gammarids. Vertical bars denote SE of the mean (n=4).

Although the palaemonid prawns can potentially feed on both macroalgae and benthic invertebrates (e.g. Janas and Barańska, 2008; Moksnes et al., 2008; Persson et al., 2008), the experiments showed that the effect of the *P. elegans* does not likely cascade down to algal biomass. As both studied palaemonid shrimps exerted a strong predatory pressure on their gammarid prey, it is likely that the invasion of the *P. elegans* does not necessarily lead to the rearrangement of established trophic interactions in the coastal sea, unless *P. elegans* becomes established in areas where *P. adspersus* is not presented or has low densities.

Caridean shrimps, similarly to other decapod crustaceans, are able to effectively use their chemical senses in detection and localization of food-related compounds (Solari et al., 2017). However, *P. elegans* has been shown to be more effective than *P. adspersus* at finding immobile food items (Berglund, 1980). According to our experiment, both studied species consumed mobile prey with equal efficiency (II). Nonetheless, in treatments where two different shrimps co-occurred, the consumption of amphipods by any palaemonid species might have been impacted by the presence of its congeneric neighbour, but this effect was not controlled in the context of the current experiment.

According to Janas and Barańska (2008), various filamentous algae (e.g. *Cladophora* spp.) are important components in the diet of the naturalized *P. elegans* in the southern Baltic Sea. Animal components were also present together with algal food, but the proportions of animal and algal food differed strongly between areas and seasons. Our work suggested that plants have minor importance in the diet of the shrimps, but this evidence might be related to the temporal limitation of our experimental study as well as lack of invertebrate food in habitats studied by Janas and Barańska (2008). Long-term and seasonally repeated experiments and measurements of isotopic signatures of food may elucidate the dietary composition and its seasonal variability in various coastal habitats of the Baltic Sea.

A lack of the effect of shrimp density on gammarid mortality suggests that shrimps were food limited in the experimental conditions. Under natural conditions the densities of gammarids are expected to be occasionally much higher (up to three times) than used in the current study (e.g. *sensu* Reialu et al., 2016). Moreover, this study also suggested that if a shoal of prawns with the density within the studied (i.e. natural) range remained at a place for about two days, then local gammarid population would be reduced by approximately 50% and the palaemonids might have to change their feeding grounds to meet their nutritional demands.

Although the non-native amphipod *G. tigrinus* was heavily consumed by shrimps, it has high potential to overcome the high mortality owing to its higher reproduction rate, shorter development time, and longer reproduction period compared to native gammarids (Kotta et al., 2010; Sareyka et al., 2011; Jänes et al., 2015). Thus, it is likely that *P. elegans* populations may have ultimately stronger impacts on native gammarids than *G. tigrinus*. Moreover, the invasive gammarid may potentially assist the establishment of other non-native predators (the invasional “meltdown” hypothesis by Simberloff and Von Holle, 1999) by improving the food base and contributing as a more accessible food source compared to the native prey species. This indirect effect may also shape the trophic pathways in the invaded assemblages as a coexistence with the opportunistic non-native predatory shrimp eventually helps the invasive *G. tigrinus* to outcompete more vulnerable native gammarid amphipods.

To summarize, the trophic experiment suggests that both palaemonid prawns act as important predators in the coastal ecosystem of the Baltic Sea. Although the predatory function of the non-native *P. elegans* largely overlaps with that of the native *P. adspersus*, it could introduce a new ecological function of epibenthic invertebrate predator when colonizing areas that were previously devoid of shrimps (I).

## CONCLUSIONS

1. The current thesis updates the distribution data of the caridean shrimp species and shows that, despite of a short invasion history, the non-native *P. elegans* inhabits almost the full extent of Estonian coastal sea and has the largest geographic range among all caridean shrimps in the study area (**I, IV**). Only very rarely, the native *P. adspersus* and the invasive *P. elegans* co-occurred (**I**). The *P. elegans* spread into the most diluted and eutrophicated coastal sea areas, where no native shrimps occur, and thereby intensifies predation pressure on mesoherbivores in such habitats.
2. Under field conditions, the native and invasive shrimp species had different habitat associations along the studied biotic and abiotic environmental gradients (**I**). *P. elegans* was associated with habitats characterized by lower salinity and higher concentrations of nutrients compared to the habitats used by *P. adspersus*. Key phytobenthic species were among the most significant variables behind the habitat segregation of the studied shrimps. Among the studied caridean shrimps, *C. crangon* was the most specialized species. Under experimental conditions, the non-native species was mostly associated with vegetated hard bottom habitats whereas the native shrimp was almost uniformly observed on all studied habitat types (**I**).
3. The experimental study on trophic interactions (**II**) showed that palaemonid shrimps can efficiently prey on the invasive amphipod *Gammarus tigrinus*. The two *Palaemon* species had no difference in their feeding rates and the presence of macrophytes did not affect shrimp predation on amphipods. Thus, *P. adspersus* and *P. elegans* seem to perform similar roles in the coastal food webs of the Baltic Sea. However, *P. elegans* may rearrange trophic interactions in areas previously lacking any native shrimp species e.g. in the eastern Gulf of Finland.
4. The invasive crab *R. harrisi* selected hard bottom habitats covered by *F. vesiculosus* over other habitat types (**III**). There was an interactive effect between the presence of prey and crab population density with prey availability increasing the crab's affinity towards less favoured habitats when the population density of crabs was low or medium.

## SUMMARY

Decapod crustaceans are an important component of coastal food webs as they prey on small benthic invertebrates and at the same time they are an important food item for upper trophic levels. This group of invertebrates includes many important alien invasive species. The Baltic Sea with its low taxonomic and functional diversity is particularly vulnerable to be impacted by such invasions. Recent years have witnessed the establishment of several invasive decapod crustaceans into the Baltic Sea area. These broad-scale “natural experiments” provide valuable empirical evidence on the roles of different species and functions in the Baltic Sea ecosystem. The relative simplicity of the Baltic Sea ecosystem allows the testing of many ecological theories e.g. fundamental “Darwin’s naturalization” or “pre-adaptation hypothesis”. The former theory emphasizes the importance of biotic resistance to establishment of non-native species (through negative interspecific interactions), whereas the latter emphasizes the significance of the invader’s tolerance to local abiotic factors for invasion success. Furthermore, by quantifying species-specific separation along environmental gradients of niche space and determining the degree of specialization for habitats between native and invasive species we may further advance the niche partitioning theory considering spatial concept of the niche while the “invasional meltdown hypotheses” and top-down regulation mechanisms may be addressed by studying interspecific interactions and trophic relationships. If we know the roles and impacts of invasive decapod species, management actions can be planned to oppose the threats that may accompany the introductions.

In this thesis, four species of predatory macrofauna were chosen as research objects: the native shrimps *Crangon crangon* and *Palaemon adspersus*, the non-native shrimp *Palaemon elegans* and the crab *Rhithropanopeus harrisi*. Although the invasion histories of these non-native shrimp and crab species are well documented, prior to this thesis their environmental preferences and complex trophic interactions with native species within northern Baltic were under-examined. Moreover, there was no comprehensive information on the distribution of caridean shrimps along different environmental gradients in the studied region.

We provided information on the first observations of the non-native *P. elegans* in the Estonian coastal sea. The samples of shrimp species were mostly collected in the frame of regular macrobenthos monitoring. In addition, the monitoring data were supplemented by a semi-quantitative sampling with a benthic hand-net, dredge and by diver’s visual observations. The frequent occurrences of the studied shrimps showed that all studied shrimp species were widely distributed in the Estonian coastal sea. The spatial distribution of the non-native *P. elegans* was wider than that of native species. The presence of the *P. elegans* in the most diluted and eutrophicated coastal sea areas suggests the introduction of a new ecological function in such areas.

The updated distribution data of the shrimp species was used together with relevant environmental variables to describe environmental niches and to quantify habitat segregation of the non-native and native shrimps. Radio frequency positioning technology was used in a laboratory experiment to investigate patterns of habitat occupancy between sympatric *P. adspersus* and *P. elegans*. The results revealed significant differences in habitat preferences between native and non-native shrimp species. *P. elegans* was associated with habitats characterized by lower salinity and higher concentrations of nutrients, relative to *P. adspersus*. The cover of key phytobenthic species were among the most influential habitat variables behind the habitat segregation of the studied shrimps.

Among the studied shrimps, *C. crangon* was the most specialized. The non-native *P. elegans* showed slightly higher habitat specialization compared to the native *P. adspersus*. The habitat differentiation suggests that *P. adspersus* can at least partly escape from potential interference competition with *P. elegans* in areas that are not optimal for *P. elegans*. The study also suggested that higher tolerance to environmental stress promotes invasiveness of the shrimp species.

Then we analysed the feeding behaviour and activity of palaemonid prawns with the filamentous macroalga *C. glomerata* and the alien gammarid amphipod *G. tigrinus*. The two *Palaemon* species had no difference in their feeding rates, and the presence of macrophytes did not modulate shrimp predation on amphipods. Thus, *P. adspersus* and *P. elegans* seem to perform a similar role in the coastal food webs of the Baltic Sea. However, *P. elegans* may rearrange trophic interactions in areas previously lacking any native shrimp species.

Habitat occupancy of *R. harrisii* in response to its population density, prey availability and habitat specification was studied using a mesocosm experiment. Radio frequency positioning technology enabled us to evaluate habitat occupancy patterns between different crab specimens as they were equipped with individually coded tags. The experiment indicated a significant difference of habitat occupancy among investigated habitats. The experiment also indicated that the habitat occupancy was influenced by food levels and *R. harrisii* density. The study suggests that furoid algal habitat offers the *R. harrisii* a favourable year-round and stable habitat, where the diverse native community may become heavily impacted by this novel generalist feeder.

To sum up, the Baltic Sea is undergoing dramatic changes involving introduction of multiple invasive species, often decapod crustacean. Recent decapod invaders are situated at various trophic levels, some of which levels are completely novel to the system, e.g. the infaunal predator *R. harrisii*. The establishment of just one of such decapod species has a potential to reorganize coastal food webs and cause regime shifts in the Baltic Sea environments. However, due to the generic lack of knowledge on the roles of most invasive species and many confounding stressors (e.g. climate change, pollution) such shifts are increasingly difficult to demonstrate. This thesis showed that the successful establishment and rapid expansion of non-native predatory invertebrates within the Northern Baltic can introduce new ecological functions or

considerably strengthen already existed ones. Impacts of novel species on coastal ecosystems are difficult to predict as such impacts are very context specific and tipping points are controlled by local and large scale variability of environmental background conditions and anthropogenic stressors. This has important implications to sustainable water management in the Baltic Sea basin as the outcome of a given invasion may range from no shift, to dramatic reorganization of communities and impacts to ecosystem services and socio-economic benefits. The results suggested that ecological state and heterogeneity of habitats affected the potential for spread of native or invasive species variably. If the invasive species were often associated with eutrophicated habitats characterized by the excessive growth of filamentous algae then the native species were often found within habitats characterised by better water quality and the prevalence of perennial species. Thus, future studies should reveal such habitat features (e.g. filamentous algal blooms) that can facilitate the establishment and spread of invasive species. This knowledge should be then used to suggest opposing or compensatory measures (e.g. the reduction of nutrient loads) to control the further spread of invasive species. Commercial harvesting should also be considered as an additional measure to decrease the negative impacts of non-native species as some of these recent invasive species may have potential commercial interest and be used in fisheries.

## SUMMARY IN ESTONIAN

### Kohalike ja invasiivsete röövtoiduliste suurselgrootute elupaigakasutus ja toitumissuhted Läänemere põhjaosas

Rannikumere ökosüsteemid on kõrge produktiivsusega ning pakuvad inimühiskonnale olulist toiduressurssi. Rannikualade kõrge asustustiheduse ja rannikumere intensiivse kasutuse tõttu on rannikumere ökosüsteemid väga tugeva inimtegevuse surve all. Läänemere puhul on kõige olulisemateks inimsurveteks eutrofeerumine ja võõrliikide sissetoomine. Kuna Läänemeri on geoloogiliselt arengult noor, ookeanist isoleeritud ja madala soolsusega, siis on liigiline mitmekesisus meres väga madal. Madala liigilise mitmekesisuse foonil on võõrliikide levik Läänemeres eriti olulise mõjuga, kuna võõrliigid võivad lisada ökoloogilisi funktsioone, mida kohalikud liigid ei täida. Näiteks puudus Läänemere põhjaosas alles hiljuti suuremõtmeline selgrootu kiskja-bioturbaator, kes suudab purustada limuste kodasid.

Röövtoidulised suurselgrootud, peamiselt vähilaadsed, on rannikumere toitumisvõrgustikes oluliseks lüliks põhjaelustiku ja kalade vahel ning ühtlasi nad reguleerivad väiksemate selgrootute arvukust. Läänemere põhjaosas elas selle rühma esindajaid seni ainult kaks liiki – läänemere krevett (*Palaemon adspersus*) ja põhjamere garneel (*Crangon crangon*). Hiljuti lisandusid neile kohalikele liikidele kaks võõrliiki – elegantne krevett (*Palaemon elegans*) ja rändkrabi (*Rhithropanopeus harrisi*). Rändkrabiga lisandus Läänemere põhjaosa ökosüsteemi täiesti uus suuremõtmelise kiskja-bioturbaatori funktsioon. Uute kiskjate lisandumine tõstatas küsimuse nende sobitumisest keskkonnaruumi ja toiduvõrgustikesse. Võõrliikide lisandumine Läänemere põhjaosa madala liigilise mitmekesisuse tingimustes annab suurepärase võimaluse uurida liikide rolli kooslustes ja testida ökoloogilisi teooriaid kohalike ja võõrliikide nišširuumi eristumise kohta. Võõrliikide „looduslikud eksperimendid“ Läänemeres võimaldavad testida teooriaid nagu näiteks Darwin'i naturaliseerumise hüpotees, mille kohaselt võõrliikide naturaliseerumine on raskendatud, kui piirkonnas esinevad võõrliigi sugulasliigid. Kvantifitseerides kohalike ja võõrliikide levikut keskkonnagradienditel ja nende spetsialiseerumise taset on võimalik edasi viia niššide jaotamise teooriat ning invasiivsete liikide vastastikuse soodustamise hüpoteesi (*invasional meltdown*) ja ülalt-alla kontrolli mehhanisme on võimalik kontrollida uurides liikidevahelisi troofilisi suhteid. Lisaks olulistele baasteaduslikele teadmistele võimaldavad sellised uuringud saada teavet võõrliikidega seotud mõjudest ja ohtudest seoses mereressursside haldamisega, keskkonnaseisundiga ja looduskaitsete tegevustega. Selgrootute kiskjate roll Läänemere põhjaosa rannikumere ökosüsteemis oli seni vähe uuritud ning uute liikide ja ökoloogiliste funktsioonide lisandumise mõju täiesti teadmata. Nende teadmiste hankimiseks uuriti röövtoiduliste selgrootute levikut (I–IV), elupaiganišše (I–III) ja toitumissuhteid (II, III). Doktoritöö konkreetsed eesmärgid olid:

- invasiivse kreveti *P. elegans* leviku kirjeldamine ja võrdlus kohalike krevetiliikidega (IV, I);



- krevetiliikide elupaigaeelistuste ja võimalike keskkonnaniššide eristumise väljaselgitamine (I);
- rändkrabi elupaigavaliku uurimine sõltuvalt krabide asustustihedusest ja toitumistingimusest (III);
- kohalike ja võõrliigist krevettide ja võõrliigist kirpvähi *Gammarus tigrinus* toitumissuhete uurimine (II).

Uuringutes kasutati olemasolevaid põhjaelustiku seire andmeid, spetsiaalselt uuritavatele liikidele suunatud proovide kogumist loodusest ja laborikatseid. Krevettide levikuinfo pärines peamiselt põhjataimestiku seire proovidest, aga lisaks ka semi-kvantitatiivsetest või kvalitatiivsetest kahvapüükidest, põhjatraalist ja sukeldujate visuaalsetest vaatlustest. Lisaks sellele teostati eraldi väliuuring, kus proove koguti vähimõrdadega. Levikuandmestikule toetudes uuriti krevetiliikide levikut erinevate keskkonnagradiendite suhtes ja selleks kasutati suurt hulka georeferentseid topograafilisi, füüsikalisi, keemilisi ja bioloogilisi keskkonnaandmeid. Täiendavalt teostati elupaigavaliku laborikatsed, kus kasutati loomade raadiomärgistamist ja -jälgimist. Andmetöötluseks kasutati peamiselt dispersioonanalüüsi, mitmemõõtmelisi ordineerimisi ja võimendatud regressioonipuude meetodit.

Kõik kolm krevetiliiki olid Eesti merealal laialt levinud. Võõrliigi levik oli ulatuslikum kui kohalike liikide levik ulatudes ka väga madala soolusega ja kõrge toitelisusega merelahtedesse, kus kohalikud krevetiliigid puudusid. *P. elegans*'i tungimine varem krevettide poolt asustamata piirkondadesse tähendab ka uue ökoloogilise funktsiooni sissetoomist ja kiskluse mõju intensiivistumist nendel aladel.

Kohalike ja võõrliigist krevettide vahel esines elupaikade eristumine uuritud keskkonnagradiendidel. Võõrliik oli kohalike krevettidega võrreldes enam seotud elupaikadega, millele on iseloomulik madal soolus, madal vee läbipaistvus ja kõrgemad toitainete kontsentratsioonid. Lisaks eristusid uuritud krevetid elupaiku moodustavate põhjataimestiku liikide alusel. Kõige kitsama elupaigakasutusega oli põhjamere garneel. *Palaemon* liikidest oli võõrliigi *P. elegans* spetsialiseerumise tase mõnevõrra kõrgem kui kohalikul liigil. Elupaikade eristumine *Palaemon* liikide vahel võib olla seotud sellega, et võõrliik on asustanud elupaigad, mis ei ole kohalikule liigile parima sobivusega või ka et võõrliik on kohaliku liigi teatud elupaikadest välja tõrjunud.

Krevettide toitumisuuringud näitasid, et uuritud *Palaemon* liikide toitumiskiirgus ja toidu koosseis ei erinenud ja taimestiku olemasolu ei mõjutanud krevettide kisklussurvet kirpvähkidele. Seega on kohaliku ja võõrkreveti roll rannikumere toiduvõrkudes ilmselt sarnane, ent võõrliik võib troofilisi suhteid ümber kujundada piirkondades, kus kohalikud krevetid puuduvad.

Rändkrabi elupaigavalikut ja selle seoseid krabide asustustihedusega, saakloomade olemasoluga ja elupaiga omadustega uuriti mesokosmidega laborikatsetes. Krabi eelistas põisadruga (*Fucus vesiculosus*) elupaika. Elupaigavalikut mõjutasid saakloomade olemasolu ja krabide asustustihedus. Tulemused viitavad sellele, et põisadruga elupaik pakub krabile aastaringset stabiilset elupaika ja

põisadruga seotud mitmekesine põhjakooslus võib saada seetõttu krabidest oluliselt mõjutatud.

Läänemere ökosüsteemid on muutumas seoses võõrliikide levikuga. Mitmed uued võõrliigid kuuluvad kümnejalaliste vähkide hulka, nagu ka hiljuti Läänemere põhjaossa jõudnud rändkrabi, kes esindab kooslustes seni puudunud suuremõõtmelise kiskja-bioturbaatori funktsiooni. Ka juba ühe uut funktsiooni omava liigi sissetung võib oluliselt ümberkujundada rannikumere toiduvõrkusid ja põhjustada režiimihkeid. Paraku on uute liikide mõjude kohta teadmisi vähe ja mitmete teiste samaaegsete survete (nt kliimamuutused, reostus) koosmõjus on ka muutuste empiiriline demonstreerimine üha keerulisem. Doktoritöö tulemused näitasid, et võõrliikidest selgrootute kiskjate saabumine ja kiire levila laienemine Läänemere põhjaosas toovad kaasa täiesti uute ökoloogiliste funktsioonide lisandumise või juba varem regionaalselt esinenud funktsioonide leviku piirkondadesse, kus see varem puudus. Uute liikide mõju ennustamine on keeruline, sest mõjud on kontekstispetsiifilised ja muutuste murdepunktid on seotud nii lokaalsete kui suureskaalaliste keskkonnatingimustega ja inimtekkeliste survetega. Doktoritöö tulemused näitasid, et elupaikade iseloom ja seisund mõjutab kohalike ja võõrliikide levikumustreid ning sellel on olulised järelmid Läänemere piirkonna veemajanduse kujundamisele – võõrliigid olid kohalikest enam seotud eutrofeerunud elupaikade tunnustega (nt lühiealiste niitjate vetikate vohamine). Tulevikus tehtavad tööd peavad seega üheaegselt arvestama nii loodusliku elupaikade muutlikkusega, liikide bioloogiliste omadustega kui ka suureskaalaliste inimtekkeliste survetega. Saadud teadmisi tuleb seejärel kasutada võõrliikidega seotud negatiivsete mõjude vähendamise meetmete väljatöötamisel, sealhulgas toitainete koormuste vähendamine ja võõrliikide tõenduslik püük.

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## REFERENCES

- Aneer, G., 1985. Some speculations about the Baltic herring (*Clupea harengus membras*) in connection with the eutrophication of the Baltic Sea. *Can. J. Fish. Aquat. Sci.* 42, 83–90.
- Bacevičius, E., Gasiūnaitė, Z.R., 2008. Two crab species – Chinese mitten crab (*Eriocheir sinensis* Edw.) and mud crab (*Rhithropanopeus harrisi* (Gould) ssp. *tridentatus* (Maitland)) in the Lithuanian coastal waters, Baltic Sea. *Transitional Waters Bulletin* 2, 63–68.
- Barnes, R.S.K., 1994. The brackish-water fauna of northwestern Europe: an identification guide to brackish-water habitats, ecology and macrofauna for field-workers, naturalists and students. Cambridge University Press, Cambridge, pp. 406–411.
- Belkin, I.M., 2009. Rapid warming of large marine ecosystems. *Progr. Oceanogr.* 81, 207–213.
- Bendtsen, J., Gustafsson, K.E., Söderkvist, J., Hansen, J.L.S., 2009. Ventilation of bottom water in the North Sea-Baltic Sea transition zone. *J. Mar. Syst.* 75, 138–149.
- Berglund, A., 1980. Niche differentiation between two littoral prawns in Gullmar Fjord, Sweden: *Palaemon adspersus* and *P. squilla*. *Ecography* 3, 111–115.
- Berglund, A., Bengtsson, J., 1981. Biotic and abiotic factors determining the distribution of two prawn species: *Palaemon adspersus* and *P. squilla*. *Oecologia* 49, 300–304.
- Berglund, A., 1982. Coexistence, size overlap and population regulation in tidal vs. non-tidal *Palaemon* prawns. *Oecologia* 54, 1–7.
- Bilgin, S., Ozen, O., Samsun, O., 2009. Sexual seasonal growth variation and reproduction biology of the rock pool prawn, *Palaemon elegans* (Decapoda: Palaemonidae) in the southern Black Sea. *Scientia Marina* 73, 239–247.
- Bonsdorff, E., 2006. Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. *J. Exp. Mar. Biol. Ecol.* 330, 383–391.
- Boyle, J.T., Keith, D., Pfau, R., 2010. Occurrence, reproduction, and population genetics of the estuarine mud crab, *Rhithropanopeus harrisi* (Gould, 1841) (Decapoda, Panopidae) in Texas freshwater reservoirs. *Crustaceana* 83, 493–505.
- Callaway, R.M., Ridenour, W.M., 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Front. Ecol. Environ.* 2, 436–443.
- Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. *BioScience* 35, 634–639.
- Castro, P., Huber, M.E., 2003. *Marine biology*, 4th edn. McGraw-Hill, New York, pp. 219–221.
- Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* 9, 222–228.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210, 223–253.
- Conley, D.J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T. et al., 2011. Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environ. Sci. Technol.* 45, 6777–6783.
- Demel, K., 1953. Nowy gatunek w faunie Bałtyku. *Kosmos* 2, 105–106.
- Dick, J.T., Gallagher, K., Avlijas, S., Clarke, H.C., Lewis, S.E., Leung, S. et al., 2013. Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biol. Invasions* 5, 837–846.
- Dolédéc, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: a new method. *Ecology* 81, 2914–2927.

- Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* 22, 1–20.
- Duncan, R.P., Williams, P.A., 2002. Ecology: Darwin's naturalization hypothesis challenged. *Nature* 417, 608–609.
- Edelist, D., Rilov, G., Golani, D., Carlton, J.T., Spanier, E., 2013. Restructuring the Sea: profound shifts in the world's most invaded marine ecosystem. *Divers. Distrib.* 19, 69–77.
- Elton, C.S., 1927. The nature and origin of soil-polygons in Spitsbergen. *Quarterly Journal of the Geological Society* 83, 163.
- Elton, C.S., 1958. *The ecology of invasions by plants and animals*. Methuen, London.
- Eriksson, B.K., Ljungren, L., Sandström, A., Johansson, G., Mattila, J., Rubach, A., et al. 2009. Declines in predatory fish promote bloom-forming macroalgae. *Ecol. Appl.* 19, 1975–1988.
- Evangelista, P.H., Kumar, S., Stohlgren, T.J., Jarnevich, C.S., Crall, A.W., Norman III, J.B., Barnett, D.T., 2008. Modelling invasion for a habitat generalist and a specialist plant species. *Divers. Distrib.* 14, 808–817.
- Flecker, A.S., Townsend, C.R., 1994. Community-wide consequences of trout introduction in New Zealand streams. *Ecol. Appl.* 4, 798–807.
- Forward, R.B., 2009. Larval biology of the crab *Rhithropanopeus harrisi* (Gould): a synthesis. *Biol. Bull.* 216, 243–256.
- Fowler, A.E., Forsström, T., von Numers, M., Vesakoski, O., 2013. The North American mud crab *Rhithropanopeus harrisi* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. *Aquat. Invasions* 8, 89–96.
- Gagnon, K., Boström, C., 2016. Habitat expansion of the Harris mud crab *Rhithropanopeus harrisi* (Gould, 1841) in the northern Baltic Sea: potential consequences for the eelgrass food web. *BioInvasions Records* 5, 101–106.
- Gollasch, S., Leppäkoski, E., 1999. Initial risk assessment of alien species in Nordic coastal waters, Nord. Counc. Minist., Copenhagen, 244 pp.
- González-Ortegón, E., Pascual, E., Cuesta, J.A., Drake, P., 2006. Field distribution and osmoregulatory capacity of shrimps in a temperate European estuary (SW Spain). *Estuar. Coast. Shelf. Sci.* 67, 293–302.
- González-Ortegón, E., Cuesta, J.A., Pascual, E., Drake, P., 2010. Assessment of the interaction between the white shrimp, *Palaemon longirostris*, and the exotic oriental shrimp, *Palaemon macrodactylus*, in a European estuary (SW Spain). *Biol. Invasions* 12, 1731–1745.
- Grabowski, G., 2006. Rapid colonization of the Polish Baltic coast by an Atlantic palaemonid shrimp *Palaemon elegans* Rathke, 1837. *Aquat. Invasions* 1, 116–123.
- Grinnell, J., 1928. *A distributional summation of the ornithology of Lower California*. University of California Publications in Zoology 32, 1–300.
- Grosholz, E.D., Ruiz, G.M., Dean, C.A., Shirley, K.A., Maron, J.L., Connors, P.G., 2000. The impacts of a nonindigenous marine predator in a California bay. *Ecology* 81, 1206–1224.
- Gruszka, P., Więcaszek, B., 2011. *Palaemon elegans* Rathke, 1837 in the food of Baltic cod (*Gadus morhua callarias* L., 1758) from the Gulf of Gdańsk. *Mar. Biol. Res.* 7, 100–105.
- HELCOM, 2015. Manual for marine monitoring in the COMBINE programme of HELCOM. <http://www.helcom.fi/action-areas/monitoring-and-assessment/manuals-and-guidelines/combine-manual>. Accessed February 2016

- Herkül, K., Lauringson, V., Kotta, J., 2016. Specialization among amphipods: the invasive *Gammarus tigrinus* has narrower niche space compared to native gammarids. *Ecosphere* 7, e01306.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A. et al., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecol. Biogeogr.* 15, 1–7.
- Hänfling, B., Edwards, F., Gherardi, F., 2011. Invasive alien Crustacea: dispersal, establishment, impact and control. *BioControl* 56, 573–595.
- Janas, U., Barańska, A., 2008. What is the diet of *Palaemon elegans* Rathke, 1837 (Crustacea, Decapoda), a non-indigenous species in the Gulf of Gdańsk (southern Baltic Sea)? *Oceanologia* 50, 222–237.
- Janas, U., Mańkucka, A., 2010. Body size and reproductive traits of *Palaemon elegans* Rathke, 1837 (Crustacea, Decapoda), a recent colonizer of the Baltic Sea. *Oceanol. Hydrobiol. St.* 39, 3–24.
- Janas, U., Piłka, M., Lipińska, D., 2013. Temperature and salinity requirements of *Palaemon adspersus* Rathke, 1837 and *Palaemon elegans* Rathke, 1837. Do they explain the occurrence and expansion of prawns in the Baltic Sea? *Mar. Biol. Res.* 9, 293–300.
- Janas, U., Tutak, B., 2014. First record of the oriental shrimp *Palaemon macrodactylus* MJ Rathbun, 1902 in the Baltic Sea. *Oceanol. Hydrobiol. St.* 43, 431–435.
- Jormalainen, V., Gagnon, K., Sjöroos, J., Rothäusler, E., 2016. The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. *Biol. Invasions* 18, 1409–1419.
- Jänes, H., Kotta, J., Herkül, K., 2015. High fecundity and predation pressure of the invasive *Gammarus tigrinus* cause decline of indigenous gammarids. *Estuar. Coast. Shelf. Sci.* 165, 185–189.
- Järv, L., Kotta, J., Raid, T., 2011. Linking the structure of benthic invertebrate communities and the diet of native and invasive fish species in a brackish water ecosystem. *Ann. Zool. Fenn.* 48, 129–141.
- Karhilahti, A., 2010. Taskurapu tarttui pyydykseen. *Suomen Luonto* 4, 12–13.
- Katajisto, T., Kotta, J., Lehtiniemi, M., Malavin, S.A., Panov, V.E., 2013. *Palaemon elegans* Rathke, 1837 (Caridea: Palaemonoidea: Palaemonidae) established in the Gulf of Finland, the north-eastern Baltic Sea. *BioInvasions Records* 2, 125–132.
- Kautsky, H., Kautsky, L., Kautsky, N., Kautsky, U., Lindblad, C., 1992. Studies on the *Fucus vesiculosus* community in the Baltic Sea. *Acta Phytogeogr. Suec.* 78, 33–48.
- Kahru, M., Elmgren, R., Savchuk, O.P., 2016. Changing seasonality of the Baltic Sea. *Biogeosciences* 13, 1009–1018.
- Kotta, J., Jaanus, A., Kotta, I., 2008a. Haapsalu and Matsalu Bays. In: Schiewer, U. (Ed.), *Ecology of Baltic coastal waters. Ecological studies* 197. Springer, Berlin, pp. 245–258.
- Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K., Ojaveer, H., 2008b. Gulf of Riga and Pärnu Bay. In: Schiewer, U. (Ed.), *Ecology of baltic coastal waters. Ecological studies* 197. Springer, Berlin, pp. 217–243.
- Kotta, J., Paalme, T., Püss, T., Herkül, K., Kotta, I., 2008c. Contribution of scale-dependent environmental variability on the biomass patterns of drift algae and associated invertebrates in the Gulf of Riga, northern Baltic Sea. *J. Marine Syst.* 74, 116–123.

- Kotta, J., Orav-Kotta, H., Herkül, K., 2010. Separate and combined effects of habitat-specific fish predation on the survival of invasive and native gammarids. *J. Sea Res.* 64, 369–372.
- Kotta, J., Ojaveer, H., 2012. Rapid establishment of the alien crab *Rhithropanopeus harrisi* (Gould) in the Gulf of Riga. *Estonian J. Ecol.* 61, 293–298.
- Łapińska, E., Szaniawska, A., 2005. Seasonal variations in the occurrence of the prawns *Crangon crangon* (L., 1758), *Palaemon adspersus* (Rathke, 1837) and *Palaemon elegans* (Rathke, 1837) in the littoral zone of the Gulf of Gdańsk. *Oceanol. Hydrobiol. St.* 34, 95–110.
- Łapińska, E., Szaniawska, A., 2006. Environmental preferences of *Crangon crangon* (Linnaeus, 1758), *Palaemon adspersus* Rathke, 1837, and *Palaemon elegans* Rathke, 1837 in the littoral zone of the Gulf of Gdańsk. *Crustaceana* 79, 649–662.
- Lee, C.E., 2002. Evolutionary genetics of invasive species. *Trends Ecol. Evol.* 17, 386–391.
- Leibold, M.A., 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76, 1371–1382.
- Leppäkoski, E., Olenin, S., 2000. Non-native species and rates of spread: lessons from the brackish Baltic Sea. *Biol. Invasions* 2, 151–163.
- Leppäkoski, E., Gollasch, S., Gruszka, P., Ojaveer, H., Olenin, S., Panov, V., 2002a. The Baltic a sea of invaders. *Can. J. Fish. Aquat. Sci.* 59, 1175–1188.
- Leppäkoski, E., Olenin, S., Gollasch, S., 2002b. The Baltic Sea – A Field Laboratory for Invasion Biology. In: Leppäkoski, E., Gollasch, S., Olenin, S. (Eds.), *Invasive Aquatic Species of Europe. Distribution, Impacts and Management*. Springer Netherlands, Dordrecht, pp. 253–259.
- Lesutienė, J., Gasiūnaitė, Z., Strikaitytė, R., Žilienė, R., 2014. Trophic position and basal energy sources of the invasive prawn *Palaemon elegans* in the exposed littoral of the SE Baltic Sea. *Aquat. Invasions* 9, 37–45.
- Levinton, J.S., 1995. *Marine Biology: Function, Biodiversity, Ecology*. Oxford University Press, New York, 420 pp.
- Lokko, K., Kotta, J., Orav-Kotta, H., Nurkse, K., Pärnoja, M., 2015. Introduction of a functionally novel consumer to a low diversity system: effects of the mud crab *Rhithropanopeus harrisi* on meiobenthos. *Estuar. Coast. Shelf Sci.*, doi: 10.1016/j.ecss.2015.11.017.
- Luttikhuisen, P.C., Campos, J., van Bleijswijk, J., Peijnenburg, K.T., van der Veer, H.W., 2008. Phylogeography of the common shrimp, *Crangon crangon* (L.) across its distribution range. *Mol. Phylogenet. Evol.* 46, 1015–1030.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710.
- Maljutenko, I., Raudsepp, U., 2014. Validation of GETM model simulated long-term salinity fields in the pathway of saltwater transport in response to the Major Baltic Inflows in the Baltic Sea. In: Carroll, J. (Ed.), 2014 IEEE/OES Baltic International Symposium (BALTIC), IEEE/OES, Tallinn, pp. 23–31  
<http://ieeexplore.ieee.org/lpdocs/epic03/wrapper.htm?arnumber=6887830>. Accessed February 2016
- Manent, P., Abella-Gutiérrez, J., 2006. Population biology of *Palaemon adspersus* Rathke, 1837 (Decapoda, Caridea) in Fornells Bay, Balearic Islands, western Mediterranean. *Crustaceana* 79, 1297–1308.

- Martin, G., Kotta, J., Möller, T., Herkül, K., 2013. Spatial distribution of marine benthic habitats in the Estonian coastal sea, northeastern Baltic Sea. *Estonian J. Ecol.* 62, 165–191.
- Marvier, M., Kareiva, P., Neubert, M.G., 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Anal.* 24, 869–878.
- McMahon, R.F., 2002. Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. *Can. J. Fish. Aquat. Sci.* 59, 1235–1244.
- Moksnes, P.O., Gullström, M., Tryman, K., Baden, S., 2008. Trophic cascades in a temperate seagrass community. *Oikos* 117, 763–777.
- Möller, P., Pihl, L., Rosenberg, R., 1985. Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats. *Mar. Ecol. Prog. Ser.* 27, 109–121.
- Nikolopoulos, A., Isæus, M., 2008. Wave exposure calculations for the Estonian coast. AquaBiota Water Research, Stockholm, p 26.
- Nurkse, K., Kotta, J., Orav-Kotta, H., Ojaveer, H., 2016. A successful non-native predator, round goby, in the Baltic Sea: generalist feeding strategy, diverse diet and high prey consumption. *Hydrobiologia* 777, 271–281.
- Occhipinti-Ambrogi, A., 2007. Global change and marine communities: alien species and climate change. *Mar. Pollut. Bull.* 55, 342–352.
- Oh, C.W., Hartnoll, R.G., Nash, R.D., 2001. Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea. *Mar. Ecol. Prog. Ser.* 214, 211–223.
- Ojaveer, H., Jaanus, A., MacKenzie, B.R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M.L., Zaiko, A., 2010. Status of biodiversity in the Baltic Sea. *PLoS Biol* 5, e12467.
- Ojaveer, H., Kotta, J., 2015. Ecosystem impacts of the widespread non-indigenous species in the Baltic Sea: literature survey evidences major limitations in knowledge. *Hydrobiologia* 750, 171–185.
- Olenin, S., Alemany, F., Cardoso, A.C., Gollasch, S., Gouletquer, P., Lehtiniemi, M., McCollin, T., Minchin, D., Miossec, L., Occhipinti-Ambrogi, A., Ojaveer, H., Jensen, K.R., Stankiewicz, M., Wallentinus, I., Aleksandrov, B., 2010. Marine strategy framework directive—task group 2 report. Office for Official Publications of the European Communities, Non-indigenous species. Luxembourg.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. Vegan: community ecology package. R package version 2.0–10. <http://CRAN.R-project.org/package=vegan>. Accessed February 2016
- Persson, M., Andersson, S., Baden, S., Moksnes, P.O., 2008. Trophic role of the omnivorous grass shrimp *Palaemon elegans* in a Swedish eelgrass system. *Mar. Ecol. Prog. Ser.* 371, 203–212.
- Pianka, E.R., 1981. Competition and niche theory. In: May, R.M. (Ed.), *Theoretical Ecology*, 2-nd edn. Blackwell Scientific, Oxford, pp. 167–196.
- Pitkänen, H., Lehtoranta, J., Peltonen, H., 2008. The Gulf of Finland. In: Schiewer, U. (Ed.), *Ecology of baltic coastal waters*. Ecological studies 197. Springer, Berlin, pp. 285–308.
- Polechová, J., Storch, D., 2008. Ecological niche. In: Jørgensen, S.E., Fath, B.D. (Eds.), *Encyclopedia of ecology*. Elsevier, Oxford, pp. 1088–1097.



- Priddis, E., Rader, R., Belk, M., Schaalje, B., Merkley, S., 2009. Can separation along the temperature niche axis promote coexistence between native and invasive species? *Divers. Distrib.* 15, 682–691.
- Projecto-Garcia, J., Cabral, H., Schubart, C.D., 2009. High regional differentiation in a North American crab species throughout its native range and invaded European waters: a phylogeographic analysis. *Biol. Invasions* 12, 253–263.
- R Development Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed February 2016
- Reisalu, G., Kotta, J., Herkül, K., Kotta, I., 2016. The invasive amphipod *Gammarus tigrinus* Sexton, 1939 displaces native gammarid amphipods from sheltered macrophyte habitats of the Gulf of Riga. *Aquat. Invasions* 11, 45–54.
- Reuschel, S., Cuesta, J.A., Schubart, C.D., 2010. Marine biogeographic boundaries and human introduction along the European coast revealed by phylogeography of the prawn *Palaemon elegans*. *Mol. Phylogenet. Evol.* 55, 765–775.
- Ricciardi, A., Mottiar, M., 2006. Does Darwin's naturalization hypothesis explain fish invasions? *Biol. Invasions* 8, 1403–1407.
- Ricciardi, A., Hoopes, M.F., Marchetti, M.P., Lockwood, J.L., 2013. Progress toward understanding the ecological impacts of nonnative species. *Ecol. Monogr.* 83, 263–282.
- Riipinen, K., Mikkola, S., Ahola, M.K., Aalto, M.M., Olkinuora, A., Vesakoski, O., 2017. Habitat selection of the mud crab *Rhithropanopeus harrisi* in its newly invaded range. *Aquat. Invasions* 12, 191–200.
- Sareyka, J., Kraufvelin, P., Lenz, M., Lindström, M., Tollrian, R., Wahl, M., 2011. Differences in stress tolerance and brood size between a non-indigenous and an indigenous gammarid in the northern Baltic Sea. *Mar. Biol.* 158, 2001–2008.
- Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I., Rice, W.R., 2007. Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* 22, 465–471.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671–675.
- Schubert, K., 1936. *Pilumnopeus tridentatus* Maitland, eine neue Rundkrabbe in Deutschland. *Zoologischer Anzeiger* 116, 320–323.
- Sieben, K., Ljunggren, L., Bergström, U., Eriksson, B.K., 2011. A meso-predator release of stickleback promotes recruitment of macroalgae in the Baltic Sea. *J. Exp. Mar. Biol. Ecol.* 397, 79–84.
- Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1, 21–32.
- Snoeijs-Leijonmalm, P., Andrén, E., 2017. Why is the Baltic Sea so special to live in? In: Snoeijs-Leijonmalm, P., Schubert, H., Radziejewska, T. (Eds.), *Biological Oceanography of the Baltic Sea*. Springer, Netherlands, pp. 23–84.
- Snyder, W.E., Evans, E.W., 2006. Ecological effects of invasive arthropod generalist predators. *Annu. Rev. Ecol. Evol. Syst.* 37, 95–122.
- Solari, P., Sollai, G., Masala, C., Loy, F., Palmas, F., Sabatini, A., Crnjar, R., 2017. Antennular morphology and contribution of aesthetascs in the detection of food-related compounds in the shrimp *Palaemon adspersus* Rathke, 1837 (Decapoda: Palaemonidae). *Biol. Bull.* 232, 110–122.
- Stachowicz, J.J., Tilman, D., 2005. Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: Sax, D.F.,

- Stachowicz, J.J., Gaines, S.D. (Eds.), Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Massachusetts, pp. 41–64.
- Suikkanen, S., Pulina, S., Engström-Öst, J., Lehtiniemi, M., Lehtinen, S., Brutemark, A., 2013. Climate change and eutrophication induced shifts in northern summer plankton communities. PLoS ONE 8, e66475.
- Suursaar, Ü., Alari, V., Tõnisson, H., 2014. Multi-scale analysis of wave conditions and coastal changes in the north-eastern Baltic Sea. J. Coastal Res. 70, 223–228.
- Taylor, A.C., Spicer, J.I., 1987. Metabolic responses of the prawns *Palaemon elegans* and *P. serratus* (Crustacea: Decapoda) to acute hypoxia and anoxia. Mar. Biol. 95, 521–530.
- Turoboyski, K., 1973. Biology and ecology of the crab *Rhithropanopeus harrisi* ssp. *tridentatus*. Mar. Biol. 23, 303–313.
- Wallentinus, I., 1991. The Baltic Sea gradient. In: Mathieson, A.C., Nienhuis, P.H. (Eds.), Ecosystems of the World 24, Intertidal and Littoral Ecosystems. Elsevier, Amsterdam, pp. 83–108.
- Weis, J.S., 2011. Invasion and predation in aquatic ecosystems. Curr. Zool. 57, 613–624.
- Wikström, S.A., Kautsky, L., 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuar. Coast. Shelf Sci. 72, 168–176.
- Williams, A.B., 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington D.C, p. 550.
- Wolff, W.J., 2005. Non-indigenous marine and estuarine species in the Netherlands. Zoologische Mededelingen Leiden 79, 1–116.
- Worm, B., Myers, R.A., 2003. Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. Ecology 84, 162–173.
- Zaitsev, Y., Ozturk, B., 2001. Exotic Species in the Aegean, Marmara, Black, Azov and Caspian Seas. Turkish Marine Research Foundation, Istanbul Turkey, p. 267.
- Zettler, M.L., Karlsson, A., Kontula, T., Gruszka, P., Laine, A.O., Herkül, K., Schiele, K.S., Maximov, A., Haldin, J., 2014. Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data. Helgoland Mar. Res. 68, 49–57.

## **PUBLICATIONS**

## CURRICULUM VITAE

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2011–2013 Tallinn University, master's degree (Marine Biology and Environmental Sciences)  
2008–2011 University of Tartu, bachelor's degree (Ecology)  
1992–2005 Mustamäe Gymnasium of Humanities in Tallinn (Silver Medal)

### Professional career:

2008–... University of Tartu, Faculty of Science and Technology, Estonian Marine Institute, technician  
2014–... Tallinn University, School of Natural Sciences and Health; zoology lecturer

### Language skills:

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**Research interests:** Biological diversity in coastal waters of the Baltic Sea; monitoring of marine environment; ecology of predatory macrofauna in marine benthic communities.

### Publications:

- Kuprijanov, I., Herkül, K., & Kotta, J. 2017. Ecological niche differentiation between native and non-native shrimps in the northern Baltic Sea. *Aquatic Ecology* 51, 389–404.
- Jaanus, A., Kuprijanov, I., Kaljurand, K., Lehtinen, S., & Enke, A. 2017. Optimization of phytoplankton monitoring in the Baltic Sea. *Journal of Marine Systems* 171, 65–72.
- Kuprijanov, I. 2017. Shrimps in Estonian coastal sea. Pajuste, M. (Ed.). *Kalale!* 26, 10–14.
- Kuprijanov, I., Kotta, J., Lauringson, V. & Herkül, K. 2015. Trophic interactions between native and alien palaemonid prawns and an alien gammarid in a brackish water ecosystem. *Proceedings of the Estonian Academy of Sciences* 64, 518–52.
- Nurkse, K., Kotta, J., Orav-Kotta, H., Pärnoja, M. & Kuprijanov, I. 2015. Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisi*

- (Gould) in an invaded ecosystem: The north-eastern Baltic Sea. *Estuarine, Coastal and Shelf Science* 154, 152–157.
- Kuprijanov, I & Kotta, J. 2013. First evidence on the epiphytic macroalga *Pylaiella littoralis* on the prawn *Palaemon adspersus*. *Estonian Journal of Ecology* 60, 287–291.
- Kotta, J. & Kuprijanov, I. 2012. The first finding of the palaemonid shrimp *Palaemon elegans* Rathke in the Estonian coastal sea. *Estonian Journal of Ecology* 61, 148–153.
- Kuprijanov, I., Kotta, J., Pärnoja, M., Herkül, K. & Kersen, P. 2011. Scale-specific effects of environmental variables on benthic macrophyte and invertebrate communities in the Vaindloo area, the central Gulf of Finland. *Estonian Journal of Ecology* 60, 4–17.

#### **Conference presentations:**

- Kuprijanov, I., Kotta, J., Pärnoja, M., Herkül, K., Kersen, P. Scale-specific effects of environmental variables on benthic macrophyte and invertebrate communities in the Vaindloo area, the central Gulf of Finland (poster presentation). MAREANO – International workshop on seabed mapping methods and technology, Trondheim, Norway, 16–18 October 2012
- Kuprijanov, I., Kotta, J., Herkül, K. Distribution and habitat preferences of the invasive and native palaemonid prawns in the northeastern Baltic Sea (oral presentation). 49<sup>th</sup> European Marine Biology Symposium, St. Petersburg, Russia, 8–12 September, 2014
- Kuprijanov, I., Kotta, J., Herkül, K. Ecological niche differentiation between native and alien caridean shrimps in the northern Baltic Sea (oral presentation). 51<sup>st</sup> European Marine Biology Symposium, Rhodes, Greece, 26–30 September, 2016

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#### **Dissertations supervised:**

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- Kuprijanov, I., Herkül, K., & Kotta, J. 2017. Ecological niche differentiation between native and non-native shrimps in the northern Baltic Sea. *Aquatic Ecology* 51, 389–404.
- Jaanus, A., Kuprijanov, I., Kaljurand, K., Lehtinen, S., & Enke, A. 2017. Optimization of phytoplankton monitoring in the Baltic Sea. *Journal of Marine Systems* 171, 65–72.
- Kuprijanov, I. 2017. Krevetid Eesti rannikuvetes. Pajuste, M. (Toim.). *Kalale!* 26, 10–14.
- Kuprijanov, I., Kotta, J., Lauringson, V. & Herkül, K. 2015. Trophic interactions between native and alien palaemonid prawns and an alien gammarid in a brackish water ecosystem. *Proceedings of the Estonian Academy of Sciences* 64, 518–52.
- Nurkse, K., Kotta, J., Orav-Kotta, H., Pärnoja, M. & Kuprijanov, I. 2015. Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisi* (Gould) in an invaded ecosystem: The north-eastern Baltic Sea. *Estuarine, Coastal and Shelf Science* 154, 152–157.

- Kuprijanov, I. & Kotta, J. 2013. First evidence on the epiphytic macroalga *Pylaiella littoralis* on the prawn *Palaemon adspersus*. *Estonian Journal of Ecology* 60, 287–291.
- Kotta, J. & Kuprijanov, I. 2012. The first finding of the palaemonid shrimp *Palaemon elegans* Rathke in the Estonian coastal sea. *Estonian Journal of Ecology* 61, 148–153.
- Kuprijanov, I., Kotta, J., Pärnoja, M., Herkül, K. & Kersen, P. 2011. Scale-specific effects of environmental variables on benthic macrophyte and invertebrate communities in the Vaindloo area, the central Gulf of Finland. *Estonian Journal of Ecology* 60, 4–17.

#### **Konverentsiettekanded:**

- Kuprijanov, I., Kotta, J., Pärnoja, M., Herkül, K., Kersen, P. Scale-specific effects of environmental variables on benthic macrophyte and invertebrate communities in the Vaindloo area, the central Gulf of Finland (stendettekannet). MAREANO – International workshop on seabed mapping methods and technology, Trondheim, Norra, 16–18.10. 2012
- Kuprijanov, I., Kotta, J., Herkül, K. Distribution and habitat preferences of the invasive and native palaemonid prawns in the northeastern Baltic Sea (suuline ettekannet). 49<sup>th</sup> European Marine Biology Symposium, St. Petersburg, Venemaa, 8–12.09. 2014
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