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Role of invasive species in brackish benthic community structure and biomass changes

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Press

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LIST OF ORIGINAL PUBLICATIONS

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

I. **Nurkse, K.,** Kotta, J., Orav-Kotta, H. and 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(1), pp. 271–281.

II. **Nurkse, K**., Kotta, J., Rätsep, M., Kotta, I. and Kreitsberg, R., 2018. Experimental evaluation of the effects of the novel predators, round goby and mud crab on benthic invertebrates in the Gulf of Riga, Baltic Sea. Journal of the Marine Biological Association of the United Kingdom, 98(1), pp. 25–31.

III. Kotta, J., Wernberg, T., Jänes, H., Kotta, I., **Nurkse, K**., Pärnoja, M. and Orav-Kotta, H., 2018. Novel crab predator causes marine ecosystem regime shift. Scientific reports, 8, 4956.

IV. Kotta, J., **Nurkse, K**., Puntila, R. and Ojaveer, H., 2016. Shipping and natural environmental conditions determine the distribution of the invasive non-indigenous round goby *Neogobius melanostomus* in a regional sea. Estuarine, Coastal and Shelf Science, 169, pp.15–24.

V. Liversage, K., **Nurkse, K.**, Kotta, J. and Järv, L., 2017. Environmental heterogeneity associated with European perch *(Perca fluviatilis)* predation on invasive round goby *(Neogobius melanostomus)*. Marine Environmental Research, 132, pp.132–139

VI. **Nõomaa, K**., Kotta, J., Szava-Kovats, R., Herkül, K., Eschbaum, R. and Vetemaa, M., 2022. Novel fish predator causes sustained changes in its prey populations. Frontiers in Marine Science, 9:849878. https://doi.org.10.3389/fmars.2022.849878

AUTHOR'S CONTRIBUTION
('*' denotes a moderate contribution, '**' denotes a high contribution, '***' denotes a leading role).

	I	II	III	IV	V	VI
Original idea	***	***	*		***	***
Study design	***	***	*	**	**	***
Performing the experiments	***	***	**			
Data collection			**	***	**	***
Data analyses	***	***	**	***	***	***
Manuscript writing	***	***	*	**	*	***

LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
BRT	Boosted Regression Tree
CCA	Canonical Correspondence Analysis
EMI	Estonian Marine Institute
GAM	General Additive Model
GOF	Gulf of Finland
GOR	Gulf of Riga
HELCOM	Baltic Marine Environment Protection Commission (Helsinki Commission)
ICES	International Council for the Exploration of the Sea
MAD	Median Absolute Deviation
MAXENT	Maximum Entropy Modelling
NIS	Non-indigenous Species
nMDS	Non-metric Multidimensional Scaling
PERMANOVA	Permutational Multivariate Analysis of Variance
PERMANCOVA	Permutational Multivariate Analysis of Covariance
SCAM	Shape Constrained Additive Model
SIMPER	Similarity Percentage Analysis
WGITMO	Working Group on Introductions and Transfers of Marine Organisms

1. INTRODUCTION

Biological invasions in marine ecosystems

The spread of invasive marine species is escalating globally (Primack, 1993; Seebens et al., 2021). High levels of invasive species are recorded in the temperate regions of Europe, North America and Australia with shipping and aquaculture confirmed as primary pathways (Molnar et al., 2008; Seebens et al., 2016). Globally invasions are associated with biodiversity hotspots (Li et al., 2016) and non-indigenous species (NIS) have been shown to have profound impacts on native ecosystem biodiversity and functioning (Strayer, 2012; Pyšek et al., 2020). While it is known that only a small fraction of the new arrivals can establish in and impact their new habitats (Mack et al., 2000), over half of the arrivals are considered potentially harmful in many marine ecoregions, *e.g.* in northern California, North Sea, western Mediterranean, temperate Northern Atlantic, and others (Molnar et al., 2008).

Most of the documented impacts of NIS in the marine environment are described with expert judgment or noncausal correlations and cause-effect evidence, like manipulative experiments, are lacking (Katsanevakis et al., 2014b; Kumschick et al., 2015). In one of the highest recorded NIS area, the Mediterranean Sea (831 species), no general conclusions on their ecosystem level impact and magnitude have been drawn (AquaNIS. Editorial Board, 2015; Bonanno and Orlando-Bonaca, 2019). However, in some areas biodiversity patterns have been substantially modified, and locally NIS induce changes in species composition, abundance and richness (Katsanevakis et al., 2014a). It has been speculated that high native species richness in the Mediterranean may mitigate the effects of invasive species in some of its habitats (Buba et al., 2017), but recent evidence suggests that in some areas NIS dominate over native species and the new assembly cannot functionally compensate for native species disappearance (Albano et al., 2021; Steger et al., 2022). Thus, transitions to NIS-dominated assemblages could profoundly alter marine ecosystem functioning with unpredictable consequences.

Invasion in the Baltic Sea

NIS establish better in areas with high propagule pressure, vacant or less inhabited functional niches, and communities under stress, *e.g.* from heat waves, eutrophication, habitat destruction (Wolff, 1973; Occhipinti-Ambrogi and Savini, 2003; Paavola et al., 2005; Simberloff, 2009). The impacts of NIS in these areas on local communities are expected to be strong. Increasing shipping and other invasion vectors result in high propagule pressure of NIS in the Baltic Sea. (HELCOM, 2010). In the Baltic Sea, where native species-richness is low and many ecological niches are underoccupied (Ojaveer et al., 2010), invasive species have very high potential to effect native biodiversity and ecosystem functioning (Olenin et al., 2007; Zaiko et al., 2011). Moreover, many other anthropogenic pressures (eutrophication, pollution) (HELCOM, 2018) and contemporary climate change pose a serious threat to the ecosystems of the Baltic Sea (BACC, 2008; Meier et al., 2012).

All these conditions make the Baltic Sea favourable for both new arrivals as well as secondary spread of already existing NIS. In 2015 the recorded NIS in the Baltic Sea was 130 and 220 species recorded by 2022 (AquaNIS. Editorial Board, 2015; Olenin et al., 2017). This increase in NIS numbers concurs with the invasion meltdown theory (Simberloff and Holle, 1999), where invasive species change the environment, thus facilitating the arrival of more novel species. The latter calls for studies that assess the diversity and magnitude of impacts that alien species cause on recipient systems by quantifying separate and interactive effects of NIS on local species and communities.

In general, biological invasions to a previously almost unoccupied predatory niche provide researchers with a unique opportunity to study changes caused by an addition of a predator to a community and to understand generic roles of predators in these ecosystems (Kraufvelin et al., 2020). Marine ecosystems are simultaneously regulated by resources from bottom-up and by predators from top-down (Lynam et al., 2017). These forces interactively determine community productivity, structure, and biomass. If a new invasive predator substantially increases top-down forcing, benthic community functioning changes and this could affect the whole ecosystem functioning via trophic cascades. It is known that benthic crabs and fish play an important ecological role in coastal food webs (Andersson et al., 1978; Rilov and Schiel, 2011; Winkelmann et al., 2011; de Aguiar et al., 2020); their grazing, predation and scavenging exert strong control over benthic communities (Ruitton et al., 2000; Gerke et al., 2018). In most of the Baltic Sea areas, such abundant benthic predators are lacking, and the arrival of invasive benthic predators could have severe impacts on the whole ecosystem functioning.

Marine benthic communities

Marine coastal communities in the Baltic Sea are facing severe changes from biological invasions, with novel species becoming a dominant component in the communities (*e.g.*, *Marenzelleria* spp., *Gammarus tigrinus* Sexton, 1939, *Dreissena polymorpha* (Pallas, 1771)) (Olenin et al., 2017, and references therein). These ecosystems contribute to human well-being by maintaining important ecosystem functions and providing food and other resources (Martínez et al., 2007). Although species diversity and community structure differ largely among regions, macroalgae and mussels are among the most common inhabitants in these areas (Wolff, 1973; Suchanek, 1985; Little and Kitching, 1996). These benthic communities are considered to play a key role in the stability of coastal ecosystems (Herman and Scholten 1990), *i.e.* acting as a natural filter, removing excess nutrients and thus mitigating eutrophication effects (Ehrnsten et al., 2019). Dominant bivalves in Baltic Sea benthic communities are *Mytilus trossulus* A. Gould, 1850 in mixed and hard bottom habitats and *Macoma balthica* (Linnaeus, 1758) in soft bottom habitats. The distribution and abundance patterns of these species have been monitored in Baltic Sea for a long period and so far changes have been largely attributed to varying abiotic and feeding condition of their habitat (Kube et al., 1996; Bonsdorff et al., 1997; Skov et al., 2020). With the arrival of two novel benthic predators, the round goby *Neogobius melanostomus* (Pallas 1811) and the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841), these dominant bivalve populations face for the first time, strong top-down pressure, raising the need for substantial research on the role of these predators in community functioning.

Invasive species under investigation

Round goby

The round goby is a widespread Pontocaspian origin invasive fish, who successfully invaded freshwater and brackish water habitats in North America and Europe (Kornis et al., 2012 and references therein). In the Great Lakes of North America, the species spread potentially via ballast water transport to all of the lakes in 5 years and continues migrating upstream (Bronnenhuber et al., 2011; George et al., 2021). This fast dispersal in North America has resulted in environmental and economic impacts in the area. The round goby has impacted native communities as both a predator and prey object, in the short and long term, and both positively and negatively (Kuhns and Berg, 1999; Barton et al., 2005; Johnson et al., 2005; Krakowiak and Pennuto, 2008; Bergstrom and Mensinger, 2009; Burkett and Jude, 2015; Crane and Einhouse, 2016; Jacobs et al., 2017). Impacts to the ecosystem also include acting as a vector for hazardous substances and parasites (Hogan et al., 2007; Hannett et al., 2011). Initial dispersal of the round goby in the Baltic Sea has been much slower; after initial introduction in the southern Baltic Sea in 1990 (Skora and Stolarski, 1993), the fish was first observed in the north-eastern Baltic Sea in 2002 (Ojaveer, 2006). The substantial difference in invasion speed allows speculation that in the Baltic Sea the spread is possibly determined by anthropogenic and/or environmental factors, raising the need for further research.

In its native range the round goby preys upon bivalves, polychaetes, amphipods, fish and detritus (Skazhkina and Kostyuchenko, 1968). In invaded areas the species is shown to prey on different species, likely dependant on their availability in the environment. In North American rivers the round goby preys mostly on dreissenid mussels, instead of native bivalves, or on insect larvae in the absence of bivalves (Raby et al., 2010). However, so far prey consumption rates of the round goby in the Great Lakes have been shown not to control large bivalve populations (Johnson et al., 2005). In the Baltic Sea the round goby is known to prey upon different invertebrates (bivalves, decapods, amphipods) in different sub areas (Skora and Rzeznik, 2001; Azour, 2011; Järv et al., 2011; Hempel et al., 2019), thus raising the need to assess the benthic predators prey consumption rates and preference towards some prey species, as it could influence the ability of the species to spread and potentially impact native communities.

The round goby also plays an important role in the ecosystem as a novel prey species, increasing the need to evaluate its contribution to different predatory fish diet. In North America, in the Lake Erie burbot *Lota lota* likely controls the abundance of the round goby (Madenjian et al., 2011). In the Baltic Sea, so far the northern pike *Esox lucius* Linnaeus, 1758, the Atlantic cod *Gadus morhua* Linnaeus, 1758, burbot, European perch *Perca fluviatilis* Linnaeus, 1758, the zander *Sander lucioperca* Linnaeus, 1758, and turbot *Scophthalmus maximus* (Linnaeus, 1758) have been reported to prey on the round goby (Almqvist et al., 2010; Oesterwind et al., 2017). Less is known about prey consumption rates, and the ability of predators to control the round goby population in the Baltic Sea, as the predators themselves have declining populations due to contemporary climate, shifts in habitat quality, and overexploitation (Olsson, 2019).

Harris mud crab

The Harris mud crab is native to the east coast of the Atlantic Ocean (Williams, 1984) and has rapidly increased its distribution range globally (Figure 1), presumably with ballast water transport and ship's hull fouling (Projecto-Garcia et al., 2010; Fowler et al., 2013). The species is tolerant to a wide salinity range (Turoboyski, 1973) and contrary to earlier observations (Turoboyski, 1973; Boyle, Jr. et al., 2010), the species is able to successfully inhabit and reproduce in freshwater (Huebner et al., 2021). Although the mud crab has been increasing its abundance in the southern Baltic Sea since the 1950s (Demel, 1953; Czerniejewski, 2009), the crab invaded northern Baltic Sea in 2009, possibly due to a new invasion event in the Baltic Sea (Kotta and Ojaveer, 2012; Fowler et al., 2013; Forsström et al., 2017). In the Northern part of the Baltic Sea, the species is the first crab species able to reproduce in the area and has established a viable population (Kotta and Ojaveer, 2012). So far, only a few short-term impacts in the structure of invaded communities have been documented, but with the ongoing range expansion and increase in population abundance further impacts are expected (Forsström et al., 2015; Gagnon and Boström, 2016; Lokko et al., 2018).

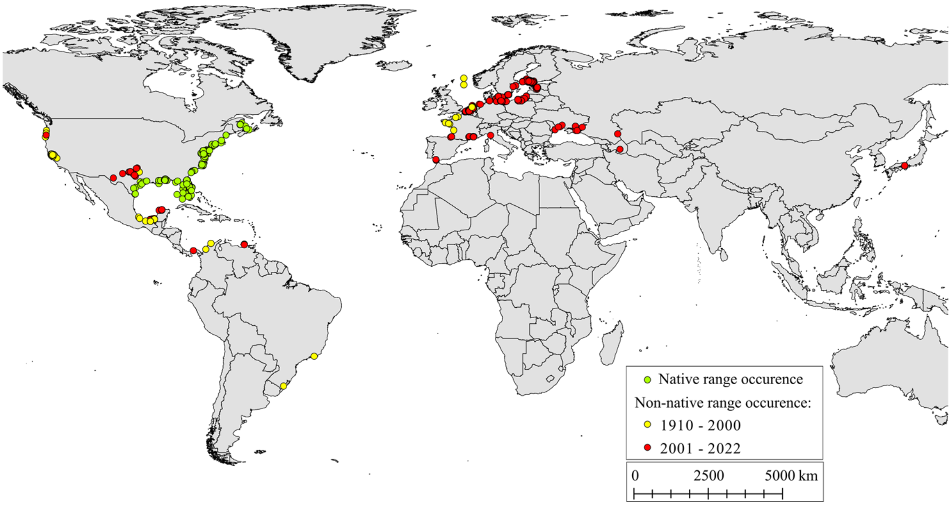

Figure 1. Global distribution of the Harris mud crab *(Rhithropanopeus harrisii)*. Data source: GBIF, 2022; Perry, 2022.

The feeding behaviour of mud crabs varies in different areas. In its native range barnacles, juvenile bivalves and detritus are the main components of their diet (Newell et al., 2007). In some invaded areas detritus dominates their diet (Hegele-Drywa and Normant, 2009) and in some areas they consume most of the native invertebrates (Forsström et al., 2015). There is a lack of knowledge on prey consumption rates and the crab's ability to affect native communities in the long-term, requiring further investigation, as the secondary production of benthic communities could compensate for the predation loss.

Population dynamics and abundance patterns for the Harris mud crab are not well-known. In its native range, population abundance is controlled mainly by a castrating parasite *Loxothylacus panopaei* (Gissler) (Turoboyski, 1973). In the Baltic Sea, no such parasite has been recorded, suggesting that populations are controlled by abiotic environment and biotic interactions (Hegele-Drywa and Normant, 2009; Fowler et al., 2013). Some predatory fish have been observed to occasionally consume some individuals (Puntila-Dodd et al., 2019), but their ability to control the population abundance of mud crabs remains to be investigated. With low predation pressure and lack of other natural enemies, stronger impact of the invasive crab on native communities is expected (Blumenthal, 2006).

Objectives

The overall aim of this thesis was to evaluate the role and impact of invasive species on native Baltic Sea communities, based on two novel benthic predators – the round goby and the Harris mud crab.

First, to assess the environmental impact of invasive species in the recipient ecosystems, it is necessary to determine the ability of the novel predators to consume native prey and whether they have a feeding preference. Preference toward some species would significantly reduce the ability of novel species to increase its abundance and could reduce the species ability for range expansion (Corkum et al., 2004; Kornis et al., 2012). For the round goby several studies referred to a preference for bivalves or higher consumption of some native prey (Skora and Rzeznik, 2001; Barton et al., 2005; Raby et al., 2010; Azour, 2011). Thus, it was hypothesized that the round goby has a preference towards native bivalves (**H1**) and the novel species consumption rates of the native species affect benthic communities in the north-eastern Baltic Sea area (**H2**). Manipulative experiments were conducted to determine the feeding strategy, prey consumption rates, and separate and interactive effects of invasive species on local benthic communities under changing environmental conditions (**I**, **II**, **III**).

Secondly, the knowledge gained from laboratory experiments must also be tested in the field. The species represent a novel function in the Baltic Sea and their *in situ* impacts need to be properly investigated. Field studies of invasive species face the problem of the availability of targeted pre-invasion data. Therefore, the effects of invasive species in the Baltic Sea have been shown only in experimental studies (Pagnucco et al., 2016; Henseler et al., 2021) or short-term field observations (Kornis et al., 2013; Skabeikis et al., 2019; Armoškaitė et al., 2021; van Deurs et al., 2021). It is difficult to include all components of an ecosystem in short-term experimental studies and therefore such experiments may look at only a specific time frame during an invasion. Consequently, these studies may over- or underestimate the impact of an invasion, as communities may recover after the introduction of a novel species, or there may be a delayed effect in some neighbouring communities which allows buffering of the impact. (Thorlacius and Brodin, 2018; Catford et al., 2019). Moreover, it is essential to consider changing environmental conditions as climate change is shown to directly and indirectly modify the effects of invasive species (Denley et al., 2019; Dickey et al., 2021). Based on the high consumption rates observed in laboratory conditions, it was hypothesized that the studied novel species reduce in long-term benthic community biomass (**H3**). Long-term field data along with changing environmental conditions were used to investigate the role of these invasive species in benthic communities (**III**, **VI**). In addition, it was hypothesized that the density of round goby defines the feeding rates of larger predatory fish (**H4**). Long-term field data was used to quantify the integration of the novel species in fish diet under field conditions (**V**).

Third, the distribution and abundance patterns of these novel species were described (**III**, **IV**) and environmental variables that best describe the observed distribution patterns in the Baltic Sea were assessed (**IV**). It was hypothesized that local abiotic conditions along with anthropogenic effects are shaping the distribution patterns of the round goby (**H5**). To date, there was very little knowledge of the distribution of these species in the Baltic Sea, thus there was need to investigate distribution and factors influencing the species spread.

2. MATERIALS AND METHODS

2.1 Study area

According to the study, I examined the entire Baltic Sea (**IV**) (Figure 2), the whole Estonian coastal sea (**V**, **VI**) (Figure 3) or the Gulf of Riga (**III**). Some activities were performed at the Kõiguste field station (**I**, **II**, **III**).

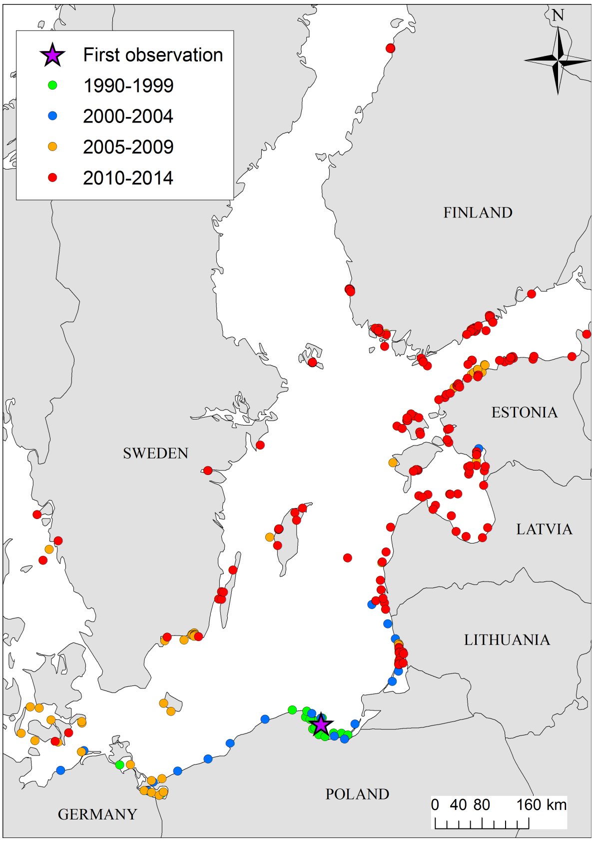

Figure 2. The Baltic Sea. Observations of the round goby in the Baltic Sea (**IV**).

The Baltic Sea is a brackish semi-enclosed tideless sea with a significant eastward salinity gradient. It has extensive coastal areas characterized by basin-scale gradients of temperature, salinity, and oxygen content (Segerstråle, 1957). The Estonian marine area (36,481 km^2) includes three major sub-basins of the Baltic Sea: the Baltic Proper, Gulf of Finland, and Gulf of Riga. All sub-basins exhibit strong gradients of wave exposure, depth, and salinity (HELCOM, 2013). Salinity exceeds 7 in the westernmost study area while it falls to almost 0 in the inner parts of bays with riverine inflow (Kotta et al., 2008; Martin et al., 2013; Snoeijs-

Leijonmalm et al., 2017). The coastal sea is generally rocky till shores at the tips of the peninsulas, mixed shores with cobbles, gravel-pebble and sand particles are common on the sides of the peninsulas, while finer grained sandy and silty shores are characteristic of the bay ends. The biological communities of seabeds are affected mostly by depth, salinity, wave exposure, and seabed substrates in the area.

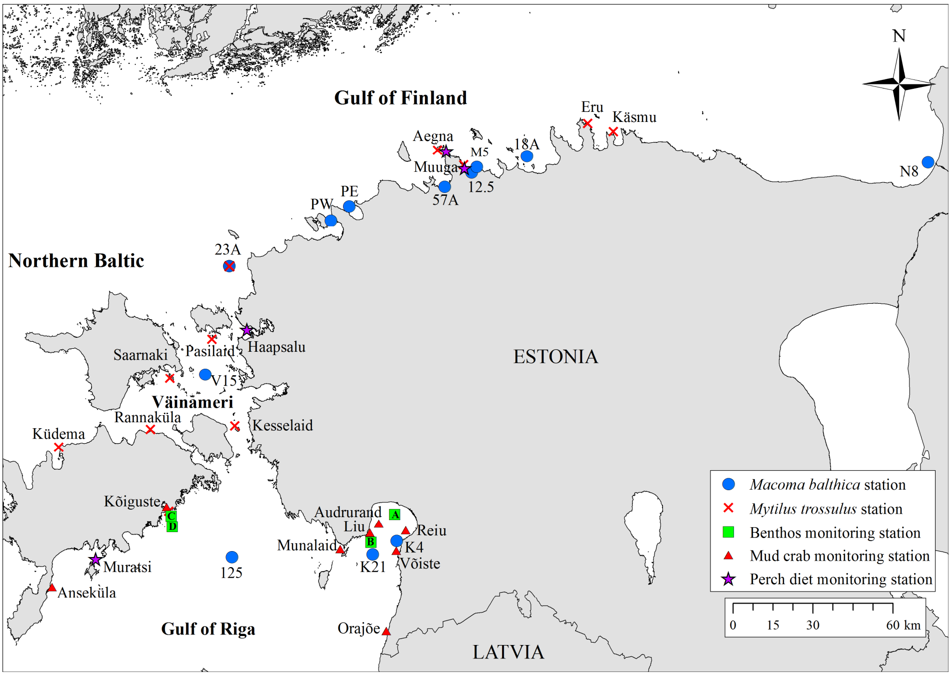

Figure 3. Study area. The Estonian coastal sea.

Species richness is relatively low and spatially variable (Ojaveer et al., 2010). Soft bottom infauna in the Baltic Sea is poor in overall species composition with low functional complexity (Andersin et al., 1978; Bonsdorff and Pearson, 1999; Laine, 2003). One of the main reasons is that very few species are endemic to brackish conditions, and both marine and limnic species have difficulty surviving in brackish conditions (HELCOM, 2009). In addition to the extensive natural environmental gradients (*e.g.*, salinity) of the Baltic Sea, 85 million people living within its drainage area result in multiple pressures, *e.g.* eutrophication (Snoeijs-Leijonmalm and Andrén, 2017), and thereby significant efforts must be made to take these factors into account when assessing the impact of invasive species in the region.

2.2 Data

Benthic community data

To assess the effects of round goby (**VI**) and Harris mud crabs (**III**) on benthic communities, the data of the Estonian national coastal monitoring programme (accessible at the Estonian Marine Institute) was used. In paper **VI** data from altogether 23 benthic sampling stations (Figure 3; *Macoma balthica* stations and *Mytilus trossulus* stations) from 1995 to 2020 was used. Data for the impact assessment of mud crab (**III**) were obtained from 4 stations (Figure 3; benthos monitoring stations A, B, C, D) in summer from 2000–2015.

The Estonian national coastal monitoring programme follows guidelines developed for the HELCOM combine programme (HELCOM, 2015). In general, Ekman and Van Veen type bottom grab samplers were used in soft sediment habitat sampling and scuba divers collected samples with a 0.04 m^2 metal frame on hard substrates. When possible, each sampling event included 3 replicates. Physical variables, such as depth and areal coverage of substrates, were recorded during sample collection.

Invasive species data

For the impact assessment of round goby under field conditions (**VI**), annual landings of the round goby by coastal fishermen were used as a proxy of the areal biomass of the invasive fish in each station. The landing statistics were obtained from the Veterinary and Food Board based on obligatory catch data submitted by coastal fishermen for each small statistical quadrat. For each quadrat total annual biomass (kg) was divided by surface area (km^2) obtained with ArcMap 10.8.1. Annual round goby biomass (kg km^{-2}) was assigned to each station based on its location within a specific quadrat. For stations located near the border of two or more small catch quadrats, the biomass was calculated as the mean of the quadrats. For stations located offshore, the nearest shoreline quadrat was used. The trend of fishermen landings was compared with the census of national coastal fish monitoring in areas with data overlap. Strong correlations in all three stations between annual catches (2007–2020) reported by fishermen and coastal monitoring were observed (Spearman rank correlation: Station 125 rs=0.87, p<0.05; station Kõiguste rs=0.86, p<0.05; station Eru rs=0.83, p<0.05).

To assess the spatial patterns of the mud crab (**III**), the crab's abundance and distribution data were collected with artificial collectors in 8 sites (Figure 3; mud crab monitoring stations) along the coastline of the Gulf of Riga in 2012, 2014 and 2015. The artificial samplers were made of two hollow bricks (with a dimension of 28 × 8 × 5 cm and each brick having 20 different size holes) attached to each other with cable ties. The collectors were deployed at 2, 3 and 4 m at all 8 sites from June to August and provided habitat for natural recruitment of both juvenile and adult macroalgae and invertebrates. Collectors were retrieved gently by diver to avoid any losses of mobile invertebrates. Crabs collected from the collectors were counted and measured.

When investigating patterns in round goby distribution (**IV**), occurrence data from various sources was collected: literature (Corkum et al., 2004; Sapota, 2004; Ojaveer, 2006; Rakauskas et al., 2008, 2013; ICES, 2012; Kornis et al., 2012); public web pages presenting round goby observations (ArtDatabanken, 2014; Finnish Alien Species Database, 2014); authors own data, originating both from coastal fish monitoring programs as well as contacts with local professional and recreational fishermen (mainly from Estonia, Lithuania and Latvia). All round goby observations (n=333) where used in the distribution map (Figure 2) and in the MaxEnt model (see below).

For perch diet analysis (**V**), round goby density within the sampled areas was estimated monthly from diver surveys. In each area (Figure 3; perch diet monitoring stations), six locations were visited monthly in which the abundance of round goby was counted in 10 random 1 m^2 quadrats. Simultaneously, the coverage of soft sediment and macrophytes was estimated. A monthly average from the six locations were further used in the analyses.

Perch stomach content analysis

Perch diet (**V**) was measured from fish caught at four coastal locations in the North-eastern Baltic Sea (Figure 3; Perch diet monitoring station) between April 2015 and October 2016. Perch was collected from fyke nets (14–16 mm mesh size) during catches over single nights by commercial fishermen. Based on availability, an average of 40 fish was collected for each month and location. Fish samples were kept in a freezer (−20 °C) until dissection in the laboratory. Total and standard length (1 mm precision), sex, and maturity stage were measured according to the 2007 Manual for the Baltic International Trawl Surveys. Age and stomach content of each fish was also determined. Stomach contents were sorted under a binocular microscope and all diet items were identified to species level whenever possible. The wet weight of all fish species ingested by perch was determined (0.1 g precision) or if the prey was semi-decomposed, the allometric length-weight relationships were used based on databases of benthic monitoring in the Estonian coastal sea (EMI database). Invertebrate prey items were classified into size classes, and size-class specific wet weights were also obtained from the allometric length-weight relationships. Diet components were classified into broader diet types (separate fish species, fish eggs, invertebrates). Diet items that were accidentally caught by piscivorous fish were excluded (*e.g.,* plants, non-organic material).

Environmental variables

The round goby distribution dataset (**IV**) was supplemented by environmental data potentially impacting the establishment and spread of this invasive fish species. Investigated variables included the following proxies of propagule pressure: shipping intensity (density of ships equipped with Automatic Identification System, monthly average per pixel of 2200 × 2200 m size; HELCOM, 2014), amount of annual cargo traffic at a nearest port (tons; HELCOM, 2014) and distance to nearest port (km). Variables characterizing the tolerance of round goby to abiotic environment included vertically aggregated mean seawater temperature (°C), maximum salinity (psu), stratification (mean difference in water density between surface and bottom layers *i.e.*, mixing intensity, kg m^{-3}), exposure to waves (m^2 s^{-1}) and depth (m). As a proxy for eutrophication, the surface water chlorophyll a (chl a, mg m^3) and water attenuation coefficient (K_d) were used.

The impact assessment of the round goby in the field (**VI**) required information on the physical and biogeochemical conditions (temperature, salinity, oxygen, chlorophyll a, nitrogen, and phosphorus) in the Baltic Sea for 1995–2020, which was downloaded from the EU Copernicus Marine Service data portal (https://marine.copernicus.eu/).

To complement the mud crab time-series with environmental data (**III**), data on the annual point and diffuse sources of total N and total P loads into the study area in 2000–2015 were obtained from the Estonian Ministry of the Environment and literature (HELCOM, 2011). Discharges from point sources include municipal effluents, industrial effluents, and pollution from fish farms. Diffuse sources of nutrients are defined as any anthropogenic sources of nutrients not accounted for as point sources, *e.g.*, agriculture, forestry, storm water from built-up areas and atmospheric deposition to inland waters. In addition, from June to August water samples for nutrients and phytoplankton were taken from the study areas fortnightly.

To model the role of the round goby in perch diet (**V**), I used wind-speed and air temperature. The maximum wind-speeds reached within the five days preceding sampling was used as a wind-speed proxy. Only ecologically relevant wind (*i.e.*, directions that produce waves) was included. As a long period of cold temperatures is known to reduce metabolism and feeding activity of poikilotherms (*e.g.*, Biro et al., 2010), the minimum air temperatures reached within the five days preceding perch sampling was use as a proxy for temperature. Weather data were gained for each sampling date and location from nearby Estonian Weather Service stations.

Experiments

The *in situ* experiment on the effect of the mud crab on benthic invertebrate community (**III**) was conducted in the Gulf of Riga, Kõiguste Bay (Figure 3) from June to August 2015 (62 days). This time period corresponds to the season when seawater temperature is above 5−10 °C and thereby benthic communities are the most developed. The experiment contained 4 treatment combinations with crab absence or presence and natural nutrients or elevated nutrient, each replicated 5 times. The mesocosms (10 L containers with a diameter of 24 cm) were filled with a 15 cm layer of sediment with associated benthic macrophytes and invertebrates, collected by the same sized corer from a shallow embayment adjacent to the experimental site, and allowed to settle for 6 hours. One crab was added to each mesocosm with crab presence treatment and mesocosm were closed with a mesh net (0.5 cm mesh size) to avoid emigration of the crabs and at the same time assuring water exchange and immigration of benthic invertebrates from adjacent benthic communities. Nutrient addition was administered to mesocosms with elevated nutrient treatment using commercial NPK fertilizer sticks at the beginning of experiment. The added nutrient treatment simulated high eutrophication conditions at the most polluted embayments of the Gulf of Riga. The experimental containers were distributed haphazardly on the seafloor at a depth of 1 m. Nutrient and chlorophyll a samples were collected at the beginning and after the experiment. At the end of experiment all mesocosms were retrieved from the seafloor and sediment and associated macrophytes and invertebrates were sieved through a 0.25 mm mesh sieve. The residues were stored at −20 °C and subsequent sorting, counting, and determination of macrophyte and invertebrate species were performed.

An indoor laboratory experiment assessing separate and interactive effects of round goby and mud crab on benthic invertebrate community (**II**) was conducted at the Kõiguste field station (Figure 3) at the start of November 2015 for 48h. The experiment was conducted in 50 l aquaria (bottom area 0.11 m2), with sand and medium macroalgal covered boulder for shelter and habitat. The invertebrate community in each aquarium consisted of local dominant invertebrates at natural densities: the mussel *Mytilus trossulus* Gould, 1850 (50 ind.); the clam *Macoma balthica* (Linnaeus, 1758) (46 ind.); the gastropod *Theodoxus fluviatilis* (Linnaeus, 1758) (45 ind.); and gammarid amphipods (45 ind.) (mainly *Gammarus tigrinus* Sexton, 1939, *Gammarus duebeni* Lilljeborg, 1852, *Gammarus salinus* Spooner, 1947, *Gammarus zaddachi* Sexton, 1912, *Gammarus oceanicus* Segerstråle, 1947). The experiment included altogether the following treatments and treatment levels: predator community (no predators, round goby, mud crab, both round goby and mud crab) and temperature (7 °C and 20 °C). Such experimental design resulted in 8 combinations of treatments each replicated 5 times.

To determine round goby feeding strategy (**I**), an experiment was conducted in 50 l aquaria (bottom surface area 0.11 m2) in a temperature-controlled room (21 °C). The aquaria were covered with a 3 cm layer of sand, filled by 40l of seawater and an empty medium sized flowerpot and a plastic plant were provided for shelter. One round goby was used per aquarium. The design of the experiment followed Underwood and Clarke (2005) and others (Manly, 2006; Underwood and Clarke, 2006, 2007; Taplin, 2007). To quantify the feeding behaviour of round goby under conditions resembling the field conditions *i.e.*, prey taxa had different initial densities, the relative consumption of prey taxa according to Taplin (2007: 117) was calculated. First, relative consumptions of each prey in relation to the total amount of all consumed taxa were calculated under no choice (high density) conditions. Second, relative consumptions of each prey in relation to the total amount of all consumed taxa were calculated under condition where the predator could choose among prey taxa. To assess prey preference, the above consumption rates were compared. In addition, a density treatment was added, to investigate density-dependent predation. The treatments had 6 replicates. All 11 treatments, altogether 64 trials, were run for 16h. A control experiment without round goby was made, with nil mortality of any prey.

2.3 Statistical methods

Statistical analyses

Two-way ANOVA (Girden, 1992) was used to investigate the effect of the mud crab and nutrient level on the total biomass and richness of benthic invertebrates in the experimental mesocosms (**III**). Similar to the above, Post-hoc Bonferroni tests were used to test which treatment levels were statistically different from each other. SIMPER analysis (Clarke and Warwick, 2001) provided the percent contribution of invertebrate species to the observed difference in community composition between mesocosms with and without mud crabs.

To assess the interactive effects of round goby and the mud carb on benthic communities PERMANOVA analysis was used (**II**). PERMANOVA does not assume the data to have any specific distributions (Anderson, 2005). As a resemblance matrix Bray-Curtis similarity was used. Significance tests were done using F-tests based on sequential sums of squares from permutation of residuals under a reduced model, as this technique had the best power while still controlling type I errors (Anderson and Ter Braak, 2003). SIMPER tests were used to assess which invertebrate species contributed most to the differences in predation rates among factor levels. For the first analysis, a resemblance matrix was calculated based on all species abundance in the community. For the second analysis, resemblance matrices were calculated for each prey taxon separately. To investigate which treatment levels were significantly different, pair-wise comparisons among all pairs of levels of given factors of interest were obtained by using a pseudo-t statistic, a multivariate analogue of the univariate t statistic. Later the results were visualized using non-metric multidimensional scaling (MDS) plots reflecting differences among treatment levels in terms of post-experimental prey communities (Borg and Groenen, 2005).

PERMANOVA and PERMANCOVA analyses were used to investigate the feeding preference and prey consumption rates of the round goby under different prey densities (**I**). In case the effect of covariate (fish length) was not statistically significant, only the results of the PERMANOVA analyses were reported. Differences between the treatment levels were investigated with Post hoc Bonferroni tests.

In order to test how the coastal ecosystem responded to mud crabs (**III**), we performed linear regression analyses of the relationships between nutrient load, water nutrient concentration, phytoplankton biomass (chlorophyll a) as well as richness and biomass of benthic invertebrates separately before and after the establishment of mud crab. SIMPER analysis provided us the percent contribution of invertebrate species to the observed change in community composition in the crab infested area.

CCA analysis was used to test relationships between the multivariate structure of data comprising all diet variables biomass (wet weight) and the structure of data including all environmental variables (**V**). The CCA analysis was run using the vegan R package (Oksanen et al., 2013). The environmental variables included temperature, wind-speed, soft sediment percentage, macrophyte coverage, round goby density, and perch total length. Statistical significance of the relationships between environmental variables and perch diet in CCA ordination was tested using the permutation test (n = 9999) included in the package vegan.

Modelling

As the available data on round goby show only the occurrence of the species and confirmed absences were unavailable, we used the MaxEnt modelling technique (**IV**). MaxEnt is a machine learning algorithm for modelling species distributions from presence-only species records. MaxEnt's predictive performance is consistently competitive with the highest performing methods. Since becoming available in 2004, it has been utilized extensively for finding correlates of species occurrences, mapping current distributions, and predicting future occurrences across many ecological, evolutionary, conservation and biosecurity applications (Elith et al., 2006, 2011). In the MaxEnt models each environmental variable contribution on the probability of occurrence of round goby in the Baltic Sea range was explored. The jack-knife test evaluates how each variable contributes to the "gain" of the MaxEnt's model (*i.e.*, improvement in penalized average log likelihood compared to null model).

Boosted Regression Tree (BRT) modelling was used to analyse relationships between perch feeding and environmental heterogeneity (**V**). BRT analyses were performed in the gbm package (R Core Team, 2015) of R Studio. Three BRT models were developed: Initiation of feeding (Model 1), total diet quantity (Model 2), and round goby quantity (Model 3). Model 1 tested if environmental heterogeneity influenced the presence or absence of any identified or unidentified food item in the gut of all perch (*i.e.*, overall initiation of feeding). Model 2 tested the relationship of the environment with the sum (wet weights) of all food types in stomachs of fed fish (excluding fish with unidentified digested mass in their stomachs). Model 3 tested the environment/gut-content relationship including only weights of round goby in fed fish. Prior to modelling, the Pearson correlation analysis between all environmental variables was run to avoid situations of including highly correlated variables into the modelling. The correlation analysis showed that most variables were only weakly intercorrelated ($r < 0.1$). In fitting a BRT, the learning rate and the tree complexity must be specified. Following the suggestions by Elith et al., 2008, the model tree complexity was kept at 5 for all models, and the learning rate was set at either 0.1 or 0.01 depending on which produced the best correlation mean. It was also checked that the final models had more than 1000 trees. Nevertheless, a selection of model parameters had only marginal impact on model performance with optimal models improving predictions less than 1%. Model performance was evaluated using the cross-validation statistics calculated during model fitting (Hastie et al., 2009). The BRT models allowed the environmental variables that were most strongly associated with gut contents to be determined and ranked according to their relative contribution in the model. Standardised functional-form relationships were plotted to visualise relationships between gut content variables and each predictor variable, while all other variables are held at their means. Biotic variables of round goby densities and lengths of perch were included in the models together with the abiotic environmental variables.

SCAM models were used to investigate the relationship between prey species (*Mytilus trossulus* or *Macoma balthica*) and key environmental variables before the round goby invasion for years prior to round goby invasion (**VI**). SCAMs are a variant of GAM that allow for the general shape of the relationship between explanatory and predictive variables to be pre-selected (Pya and Wood, 2015). The relationships were chosen based on visual examination of the data and theoretical expectation (**VI**). These models were then run on the complete data to predict the biomass of the prey species. The residuals of these predictive models served as the deviation of the realized biomass and the biomass predicted after removal of environmental effects. Negative residuals indicate greater prey biomass than observed in field sampling. A series of negative residuals associated with the elevated density of round goby suggests elevated predation of *M. trossulus* or *M. balthica* by the NIS round goby. Prey species biomass values were square root transformed prior to modelling to reduce data skewedness and the effect of extreme values in the models. To increase normality distribution in *M. trossulus* dataset, depth and perennial plant biomass was log-transformed. Spearman rank correlation test with bootstrapping (R=1000) was done between the residuals and the round goby biomass for each station. To investigate potential lags in prey biomass response to the invasion of round goby, up to 4 years of yearly lags were investigated in each station. Median and MAD was calculated based on the bootstrapped Spearman rho values. For each station a lag or no lag with the highest median Spearman correlation rho was chosen.

3. RESULTS AND DISCUSSION

Experimental studies

Experimental studies in this thesis revealed many previously unknown behavioural patterns for the novel species in the north-eastern Baltic Sea area. The round goby proved to be a generalist feeder with no significant prey preference in the studied native invertebrate community (**I**), rejecting the first hypothesis that the round goby has preference towards native bivalves. The observed generalist feeding strategy allows the novel predator to switch to other prey taxa when the dominant prey biomass is reduced, thus impacting a broad range of taxa and the functions they perform in the community (Volterra 1928, Schreiber 1997). High consumption rates of native invertebrates by the invasive fish were observed under laboratory conditions (**I**). Compared to other invaded areas, the observed consumption rates were much higher (Ray and Corkum, 1997; Diggins et al., 2002), indicating severe impacts of the round goby to the benthic communities. Considering the feeding activity observed in the lab, the goby can consume an average invertebrate biomass (Kotta et al., 2009) in 10 days. In field conditions consumption rates are usually lower, due to competition, environmental conditions, reproductive behaviour, and predator avoidance behaviour. The investigated area is very heterogenic (Martin et al., 2013), creating patches of communities, which increases foraging time and provides more refuges for prey. However, the observed prey consumption rates are still high enough to indicate substantial predation rates in field conditions and potential impact on the community, concurring with the second hypothesis that the novel species consumption rates of native species affect benthic communities.

So far, no viable crab populations have established itself in the north-eastern Baltic Sea zoobenthos, since previously only a small non-reproducing population of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards, 1853) have been observed (Ojaveer et al., 2007). Thus, the arrival of a reproducing and burrowing crab to a previously unoccupied niche has the potential to change the whole community functioning due to its effect on both the biotic and abiotic environment. The effect of the crabs in soft-bottom community was first tested through a field experiment (**III**), which showed the Harris mud crab to be able to affect both the biomass and species richness of benthic invertebrate communities, with 61% and 35% decreases, respectively (Figure 4), concurring with the second hypothesis. These benthic communities are usually regulated by bottom-up processes *e.g.*, nutrient availability. Climate change scenarios predict an increase of riverine nutrient inflow to the Baltic Sea, thus an increase in bottom-up forcing. It was therefore necessary to assess experimentally the interactive effects of the presence of crab and nutrient enrichment on benthic communities. The mesocosm experiment (**III**) showed that top-down effects induced by the crab are likely stronger than nutrient loading (Figure 5), suggesting the crab to have sustained effects on the whole community.

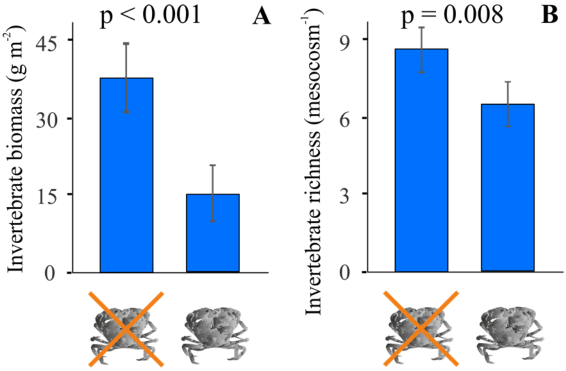

Figure 4. Results of the two-way ANOVA on the effect of mud crab on the total biomass (A) and richness (B) of benthic invertebrates in mesocosms. Vertical bars denote 95% confidence intervals. The other main effect (background nutrient level) and the interaction term (crab × nutrient level) were not significant at $p < 0.05$. (**III**)

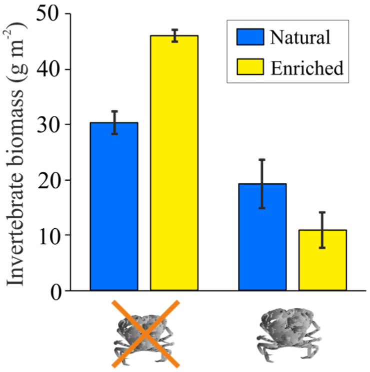

Figure 5. The mud crab effect on inveretebrate biomass in different nutrient levels. (**III**)

Considering the high number of species arriving in the Baltic Sea annually, there is a need to assess interactive effects of species with a potential areal overlap for the ecosystem. Experiments including multiple invasive species are rare, especially with invasive species (Liversage et al., 2021). The two invaders, the Harris mud crab and the round goby, are both benthic predators occupying similar habitats and preying on similar species. Moreover, the goby can potentially prey on the different life-stages of the crab and the crab could prey on juveniles and eggs of the goby. A laboratory experiment showed that despite the substantial size difference, the round goby did not prey on the adult mud crabs (**II**). In the overlapping distribution area (**III**, **IV**), only rare sightings of mud crabs in round goby diet have been recorded (EMI database, 2012–2016). As the abundance of the round goby is rapidly increasing in the area, potential food limitation might increase the goby's affinity towards the low dietary value crab (Wiszniewska et al., 1998). In other invaded areas, the round goby crushes larger bivalve prey (Ray and Corkum, 1997). However, a gape limitation could occur with larger crab individuals, due to a stronger carapace than other invertebrates in the area. So far, larger predators such as *Perca fluviatilis* and *Myoxocephalus quadricornis* (Linnaeus, 1758) have not been shown to consume small mud crabs (Puntila-Dodd et al., 2019), but such size-specific predation should be further investigated. It is not unlikely that elevated consumption of juvenile mud crabs by larger predators might control the population of mud crab in the future. Similarly, the mud crab's ability to eat goby's eggs needs further investigation.

The effects of multiple predators on native communities are modulated by many factors, such as variations in foraging behaviour, surrounding habitat complexity, and overlap in foraging area (Sih et al., 1998). The invasive predators have the potential to modify each other's feeding behaviour (Marentette and Balshine, 2012), causing their interactive effects on benthic communities to differ from separate effects. The conducted laboratory experiment (**II**) showed that the two predators have mainly independent effects on the prey communities, with the exception of the round goby reducing the consumption of the bivalve *Macoma balthica* by the mud crab. Such reduced activity in the presence of predatory cues are known for other species (Jackson, 2015) and allows speculations that in field conditions the presence of the round goby reduces the consumption rates of the mud crabs and additive consumption rates are unlikely. However, the reduced predatory pressure on prey will be compensated by the ability of round goby to consume high amounts of native invertebrates, since they consume similar prey (**I**).

Field studies

Both experimental studies and field observations showed that the mud crab and the round goby were key benthic predators in the invaded range (**III**, **VI**), causing significant changes in the ecosystem and acting as valuable prey for the European perch (**V**). The invasive species demonstrated a substantial large-scale and long-term change in the food web, with previously primarily bottom-up regulated communities facing strong top-down control effects (**III**, **VI**). These effects have the potential to spread to upper (**V**) and lower trophic levels (**III**) through trophic cascades.

The consumption rates of the round goby were high, both under laboratory (**I**) and field conditions (**VI**) with a substantial decline in 30% of the studied populations of the native bivalves attributed to round goby predation (Figure 6), confirming the third hypothesis that the studied novel species reduce in long-term benthic community biomass. Such a substantial decrease in the biomass of bivalve species will likely lead to a large-scale reduction of water transparency and decreased benthic production. However, some areas were less affected by the round goby. Invasion ecology predicts that some communities are more resistant to invasion effects (González-Moreno et al., 2013; Beaury et al., 2020) and in our study (**VI**) the effects of round goby were systematically milder in high productivity areas. High productivity areas have more phytoplankton food for the bivalves allowing the communities to better recover from the predation of round goby (Beukema et al., 1977; Kotta et al., 2015). In addition, high productivity areas usually have high biomass of alternative food sources (*e.g.*, amphipods, isopods, snails, other bivalves) for the generalist predator (**I**) to prey on, further reducing the predation pressure of round goby on the bivalve populations. A similar pattern is known for herbivores with strong top-down effects mostly observed in low-productivity systems (Burkepile and Hay, 2006). This suggests that impacts of any non-indigenous species should be assessed in the context of important ecosystem processes, as these processes define the flows of matter and energy, thereby setting the realized consequences of the invasion in a given ecosystem.

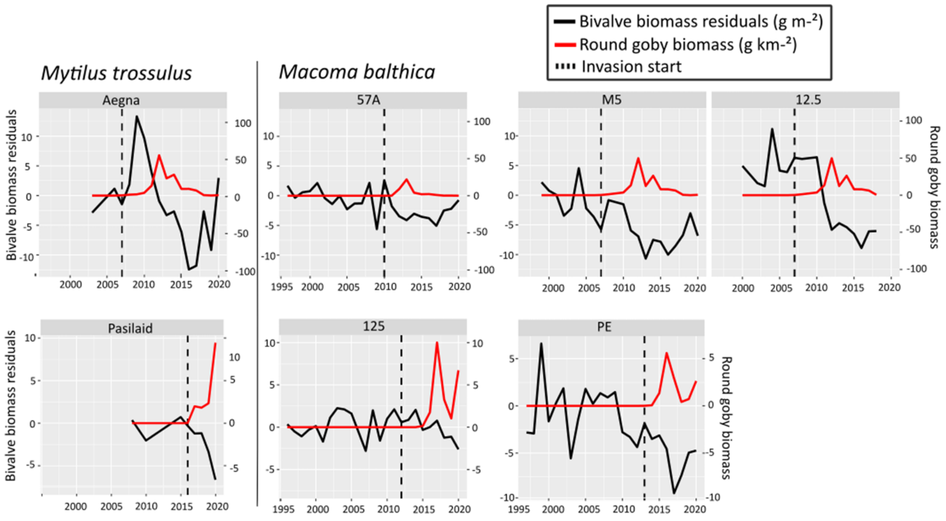

Figure 6. Stations with significant correlation ($p<0.05$) between annual biomass residuals (observed – predicted biomass) of bivalve species (black) (g dw m^{-2}) and round goby (red) (annual kg km^{-2}). Dashed vertical line indicates start of round goby invasion in each station. (**VI**)

In some systems, invasive species can alter communities with a time lag (Catford et al., 2019). Such time lags also vary depending on the characteristics of newly-invaded habitats and invaders (Thorlacius and Brodin, 2018). So far, field study results (**VI**) show up to 3 years lag and considering the short invasion history in several areas, those lags could be even longer. This concurs with other invaded areas, where the presence of NIS has likely been too short to exhibit any effect (Kornis et al., 2013). During the five-year invasion time in large *M. trossulus* reefs on the open coast of western Estonia, lower maximum *M. trossulus* biomass values (from 405.1 to 230.7 g dry weight m^{-2}) have already been recorded, allowing speculation that given enough time round goby will likely significantly affect all communities it invades.

When assessing invasion impacts, the recovery of impacted community after the invaders initial boom should be considered. Examples of community total recovery after invasion are rare (Case et al., 2016; Maclean et al., 2018). Prey population recovery was observed in some stations, in some of them the decrease continued after partial recovery peak (Figure 7; Stations Kõiguste and Eru). These recoveries show that in some areas the observed decline is not linear and non-linear analysis should be applied in the future, to better describe the novel predator-prey dynamics. Recoveries are facilitated by high productivity in the area (as discussed above) or potential alternative food resource in adjacent areas. Recent studies have shown the goby to be able to move several kilometres daily (Christoffersen et al., 2019, Nõomaa et al., unpublished), buffering the predation impact on one community. Since recovery of bivalve populations to previous biomass levels was only observed in a few stations (Figure 8; Station K21), substantially lower population sizes in our coastal waters will affect the ecosystem's ability to act as a natural filter to mitigate eutrophication effects.

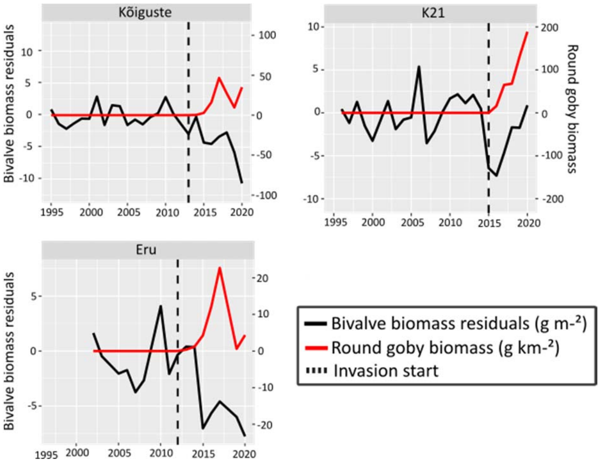

Figure 7. Annual biomass residuals (observed – predicted) in bivalve species (black) (g dw m^{-2}) and round goby (red) (annual kg km^{-2}) at stations where biomass recovery was observed. Dashed vertical line indicates start of round goby invasion in each station. (**IV**)

Like the round goby, the invasive Harris mud crab significantly affected benthic communities under field (**III**) and experimental conditions (**II**, **III**). Prior to the invasion, annual nutrient loads to the Gulf of Riga and the biomass of invertebrate communities were strongly correlated (Figure 8). The arrival of the mud crab substantially weakened the relationship, increasing the effect of top-down pressure on the community enough to overcome nutrient loading caused by bottom-up effects (Figure 8), concurring with the third hypothesis. Interestingly, these changes were also manifested in the pelagic environment characterized by higher inorganic nutrient availability and more intense phytoplankton blooms in pelagic system (**III**) (Figure 9). This marks a significant regime shift in the whole ecosystem with substantially increased top-down effects reaching to other trophic levels. Such shifts have only rarely been described in the past (Österblom et al., 2007; Graham et al., 2013; Filbee-Dexter and Scheibling, 2014) and their investigations require extensive data from the whole trophic food web. Some of them show irreversible effects on the ecosystem (Österblom et al., 2007; Wernberg et al., 2016), where ecosystems reach a new level of "stability" which might not deliver all ecosystem services that the previous state provided (*e.g.*, water purification, valuable fish communities). For example, the Baltic Sea cod population underwent a massive decrease due to overfishing and has been unable to recover due to changes in the environment cascaded to other trophic levels (Casini et al., 2009).

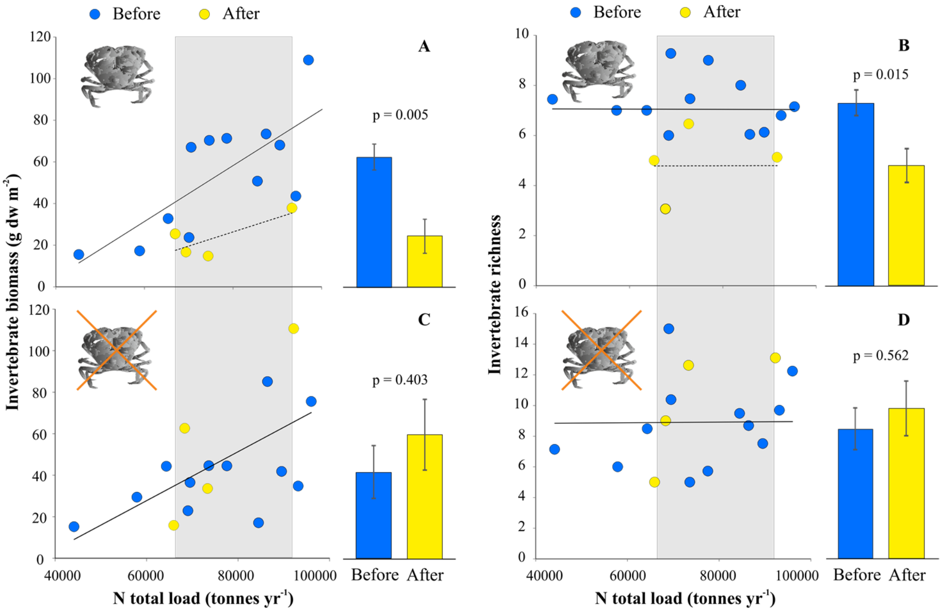

Figure 8. Relationship between annual nitrogen load, total biomass and richness of benthic invertebrates on soft bottom habitat before and after crab invasion in crab-infested (A, B) and control areas (C, D). Fitted lines highlight the slope of the linear regressions. Grey area shows the nutrient load values after crab invasion and this range was used to compare changes in the biota. Vertical bars denote 95% confidence intervals. (**III**)

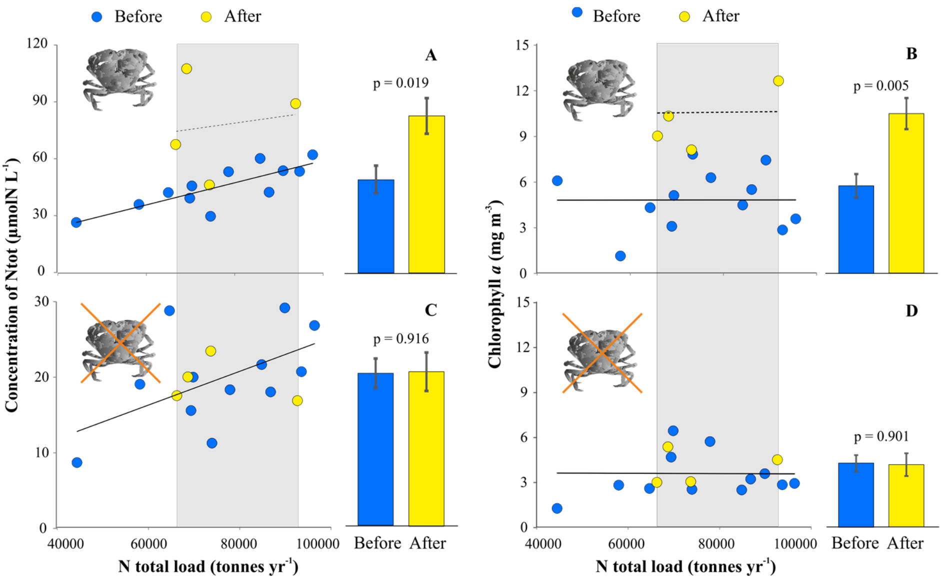

Figure 9. Relationship between annual nitrogen load, concentration of total nitrogen and chlorophyll a in seawater in pelagic habitat before and after crab invasion in crab-infested (A, B) and control areas (C, D). Fitted lines highlight the slope of the linear regressions. Grey area shows the nutrient load values after crab invasion and this range was used to compare changes in nutrient concentrations and the biota. Vertical bars denote 95% confidence intervals. (**III**)

Besides actively modifying infested communities, the novel species can be considered valuable food for native predators. Contrary to the low-energy value crab with some occurrences recorded in predatory fish diets so far (Filuk and Żmudziński, 1965; Bacevičius and Gasiūnaitė, 2008; Puntila-Dodd et al., 2019), the slow-moving benthic round goby has become an important component in the diet of many species (Almqvist et al., 2010; Oesterwind et al., 2017). Similar to other areas (Madenjian et al., 2011; Crane and Einhouse, 2016), the round goby has been successfully integrated into food webs and is currently a dominant component of perch diet in some Estonian coastal areas (**V**). In all investigated areas, the round goby dominated the diet (over 50%). The overall feeding of perch was explained mostly by temperature, wind-speed, and fish size (Figure 10). In general, bigger fish at higher temperatures, up to a certain wind-speed level, are more fed but prey abundance had no significant effect on feeding rates of perch. Similar to other areas, the feeding behaviour of perch is influenced mainly by environmental heterogeneity in space and time (Persson, 1986; Diehl, 1988; Nelson and Bonsdorff, 1990; Pekcan-Hekim and Lappalainen, 2006). The metabolism and activity of predatory fish is likely influenced by surrounding temperature (Kieffer et al., 1994; Payne et al., 2018). In the occurrence of suitable temperature to initiate feeding, diet composition is significantly affected by all other variables (**V**), with perch size as the most important factor describing the overall amount and predation rates on the round goby (Figure 11, 12). Since larger perch individuals consumed more round goby (Figure 11, 12), sustainable perch stock management (Pukk et al., 2013) could increase average size and thus increase predation pressure on the round goby. Predation pressure on the round goby is weaker at high wind speed (Figure 12), especially in soft-sediment areas, where strong winds reduce prey visibility and predation success (Pekcan-Hekim and Lappalainen, 2006). In addition, high macrophyte cover provides refuges from predation for the round goby (**V**). This suggest that in some habitat types the round goby has lower predation pressure from perch (Diehl, 1988; Nelson and Bonsdorff, 1990).

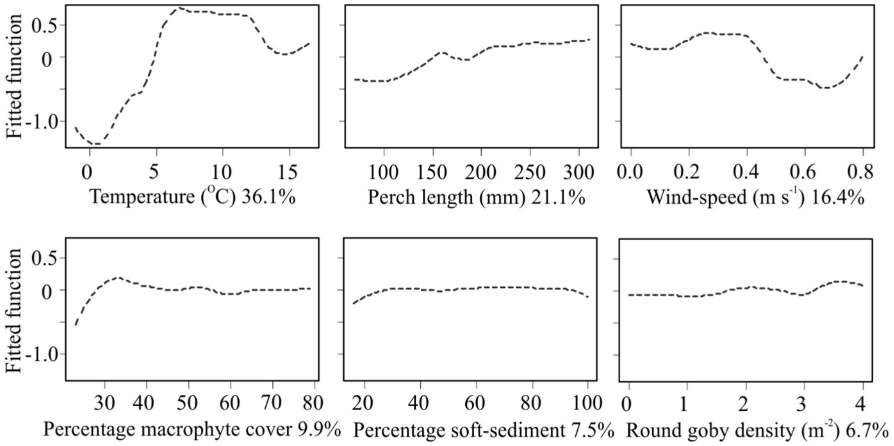

Figure 10. Standardised functional-form relationships from BRT (presence or absence of food in perch stomachs). Relationships were assessed for the environmental variables (a) minimum air temperatures that occurred within the five days prior to sampling events, (b) lengths of perch, (c) maximum windspeeds that occurred within the five days prior to sampling, (d) percentage of the benthos covered in macrophytes, (e) percentage soft-sediment and (f) densities in the environment of round goby. The Location variable did not explain considerable levels of variation in any of the models and is not graphed in this or subsequent figures. (**V**)

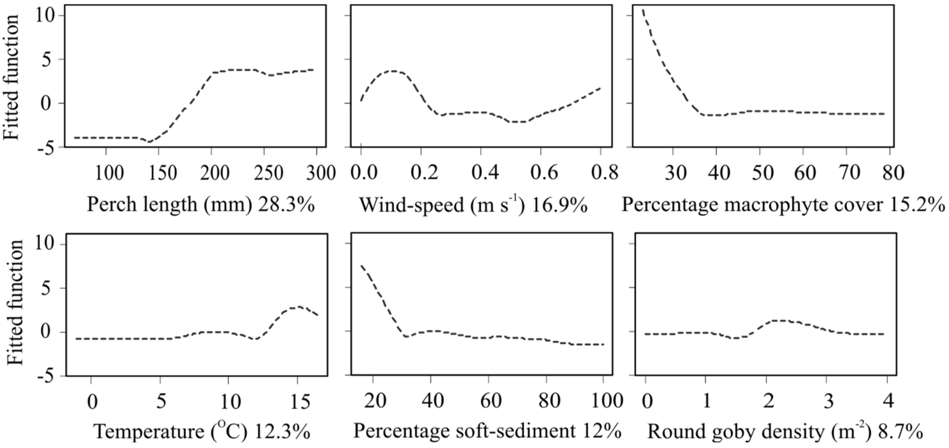

Figure 11. Standardised functional-form relationships between wet-weights of total stomach contents of perch and environmental variables. (**V**)

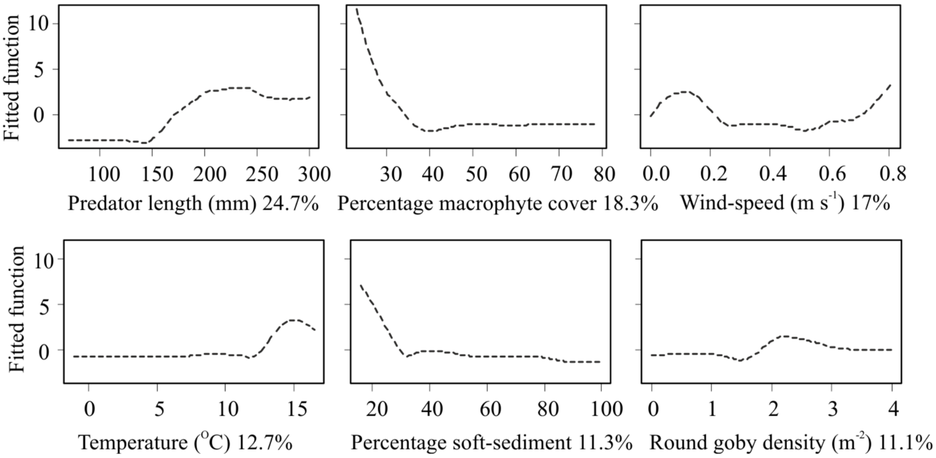

Figure 12. Standardised functional-form relationships between wet-weights of round goby in perch stomachs and environmental variables. (**V**)

The density of the round goby did not substantially increase the overall feeding of perch, or the amount of round goby consumed by perch (Figure 12), rejecting the fourth hypothesis that the density of round goby defines the feeding rates of larger predatory fish. Thus, it is unlikely that perch population is able to control round goby abundance at this point. However, the invasion of the round goby in some regions of the Baltic Sea is still at boom phase and perch potentially reached a level of saturation (Bochdansky et al., 2005). In areas with longer invasion, such predatory control has been already documented (Madenjian et al., 2011). In addition, the round goby could be valuable prey for other coastal fish in the area.

So far, the overall coastal predatory fish abundance in the north-eastern Baltic Sea area is considered low (Ojaveer, 1999; Järv et al., 2016). In the future, warmer climate, habitat restoration efforts, and reduced fishing pressure could lead to larger coastal fish populations able to control round goby abundance (Nilsson et al., 2004).

Distribution of the invaders in the study area

Establishing distribution maps and estimating how environmental conditions influence the species distribution potential is essential for estimating the current and potential impact of invasive species. The invasion of round goby in the Baltic Sea was documented in several publications but the overall speed of this invasion and occurrence in different sub-basins was poorly documented. To assess the prevalence of round goby in the Baltic Sea ecosystem, its distribution map was collated using all available evidence (**IV**). The map showed that the round goby achieved pan-Baltic distribution within 25 years (1990–2014) (Figure 2), indicating that the overall distribution speed in the Baltic Sea has been slower than in other invaded areas (*e.g.,* Great Lakes of North America) (Kornis et al., 2012). Modelling of main ecological variables that potentially modulate its distribution (**IV**) indicated that the occurrence of round goby is related primarily to local hydrological conditions and higher probability of occurrence is related to the proximity of large cargo ports, indicating that maritime shipping is likely the main factor driving the invasion of round goby. It can be concluded that anthropogenic factors together with natural environmental conditions (*e.g.,* wave exposure, salinity, temperature) are responsible for the spread of round goby, thus confirming the fifth hypothesis that local abiotic conditions along with anthropogenic effects are shaping the distribution patterns of the round goby. So far, factors contributing to increasing abundances of the round goby are yet to be investigated. In the Estonian coastal sea, after first observation in Pärnu Bay in 2002 and Gulf of Finland in 2005, the species did not rapidly increase population size until 2012 and 2009, respectively (**VI**). To date the species has established a large population in the Estonian coastal sea with local fishermen catching large amounts in the entire coastal sea annually (**VI**). The species abundance appears to follow the boom and bust pattern, similar to the mud crab's behaviour in Finland (Forsström et al., 2018).

There is a lack of observational data for the Harris mud crab in different areas of the Baltic Sea, and consequently it is not possible to produce an accurate pan-Baltic map of its distribution (Bacevičius and Gasiūnaitė, 2008; Czerniejewski, 2009; Fowler et al., 2013; Hegele-Drywa and Normant, 2014; Lehtiniemi et al., 2020). In paper **III** the distribution and abundance of mud crabs were assessed using artificial collectors in the Gulf of Riga (Figure 13). Already a year after their initial discovery in Pärnu Bay, the mud crab had established a stable population in Pärnu Bay and abundances between 1–3.2 individuals per artificial collector were recorded. By 2015, the abundance increased to an average of 8 individuals per collector (with a local maximum of 43 individuals per collector) and extended their distribution more than 40 kilometres from the initial site of discovery. Based on the initial rapid dispersal, it was expected that the species will resume their range expansion outside Pärnu Bay and the Gulf of Riga. In general, the invasion has been slower than expected – by 2022 only very rare findings of mud crab have occurred in the Gulf of Finland and Matsalu Bay, with new reproductive populations observed only in two locations in the Gulf of Riga *e.g.*, west of Island of Kihnu and near Matsi (Nõomaa et al., unpublished). Contrary to the Estonian coastal sea, in Finland the species has continued expanding its distribution range (Forsström et al., 2018) after initial invasion in 2009 (Fowler et al., 2013), indicating possibly differences in the genetic background of the sub-population (Forsström et al., 2017). Factors responsible for the species dispersal in different invaded areas and subpopulation differences in community impacts needs further research.

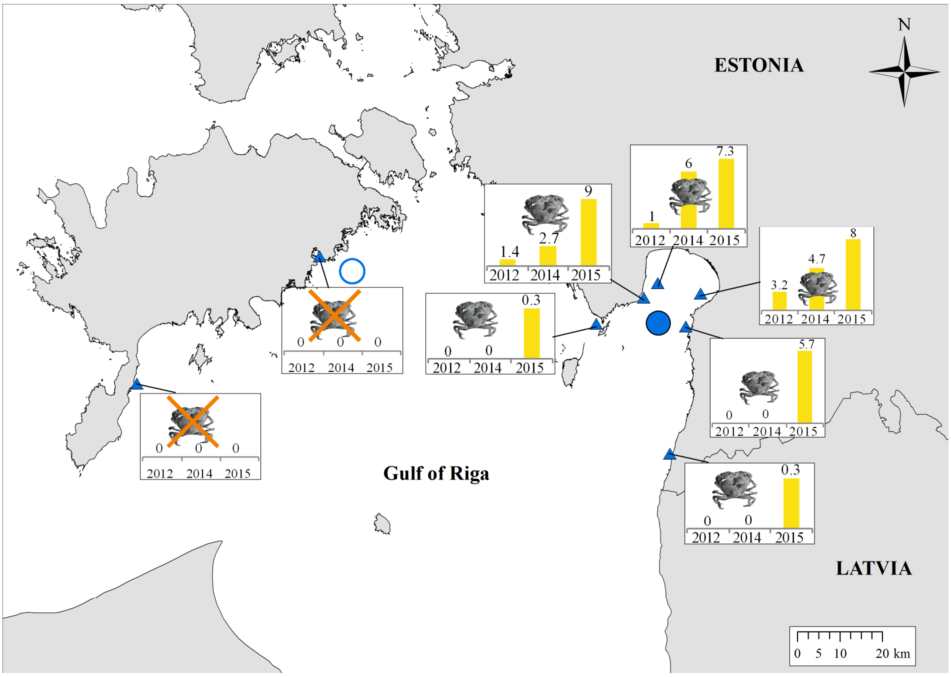

Figure 13. Harris mud crab abundance patterns in Gulf of Riga mud crab monitoring stations from 2012 to 2015. Bar charts represent annual average count at each station (adult individuals per artificial collector, covering a 0.05 m^2 surface area). Filled circle (Pärnu Bay) indicates the sampling polygon of soft bottom and pelagic habitats of the impacted area with high mud crab density and empty circle (Gulf of Riga) the control polygon with no known record of the crab, respectively. (**III**)

Conclusions

The thesis shows that novel benthic predators are severely impacting native benthic invertebrate communities and their effects are proliferating throughout the ecosystem via trophic cascades. The main conclusions of the thesis are:

i. In the north-eastern Baltic Sea, both the round goby and the Harris mud crab are changing biomass and species richness of benthic communities, with their induced top-down pressure being stronger than environmental change induced bottom-up effects.

ii. Both experimental evidence and field data demonstrate that the round goby substantially consumes native bivalves, reducing their ability to sufficiently filter water and mitigate eutrophication effects.

iii. Effects of the predation of crabs on native bivalves are cascading though the ecosystem, with elevated nutrient levels causing changes in the pelagic environment.

iv. The round goby is valuable prey for native coastal fishes. To date, one of the most abundant predators in the coastal area, European perch, feeds predominantly on round goby. However, its overall feeding rate is regulated mainly by other environmental conditions than the abundance of round goby. Thus, it can be concluded that so far, the round goby population lacks sufficient predatory control.

v. The range expansion speed of the round goby and the Harris mud crab differs between invaded areas. The distribution of round goby at the Baltic Sea scale is much slower than in the Great Lakes of North America and affected mainly by the proximity of large ports and local hydrological conditions. The documented slow spread of the mud crab in the Estonian coastal area (in contrast to Finnish waters) may be due to differences in genetic background of different invasion events and such genetically induced behavioural traits needs further investigations.

SUMMARY

Globally increasing numbers of invasive species is creating opportunities for novel species to arrive to habitats where they can significantly change native ecosystem functioning. Already there are some striking observations showing that alien species dominated communities cannot provide all functions of the native communities. Understanding invasion effects on native communities requires knowledge of different aspects of the invasive species and how species act in their new environment.

In this thesis large knowledge gaps were addressed – distribution, feeding ecology, separate and interactive effects on benthic communities for the round goby *(Neogobius melanostomus)* and the Harris mud crab *(Rhithropanopeus harrisii)*. First, the invasive species potential role in newly invaded communities were assessed with manipulative experiments (**I**, **II**, **III**), where the species diet and native prey preference in local benthic communities were explored. Both separate and interactive effects were assessed. Secondly, impact and role in communities in the field were assessed (**III**, **IV**, **VI**) by looking at long-term patterns in benthic communities and in the food web (**V**). In addition, species distributions and abundance patterns were described (**III**, **IV**) to study potential impact magnitude.

Experimental studies prevailed both invasive species to be able to consume high amounts of most dominant benthic invertebrate species in the north-eastern Baltic Sea area. Round goby proved to be a generalist feeder with high consumption rates indicating the species ability to significantly reduce the biomass of benthic communities. Similarly, the mud crab was able to decrease invertebrate community biomass and species richness and the predation pressure was stronger than bottom-up forces from potential climate change induced nutrient enrichment. Although no interactive effects of the two benthic predators to benthic communities were observed, the presence of the round goby decreased predation pressure of the mud crab on the bivalve *Macoma balthica*, suggesting that in field conditions biotic interactions reduce the consumption rates of the novel predator. Still, even with lower consumption rates, both species consumption rates were high enough to suggest large-scale impacts in benthic communities.

The impacts of novel species in native communities were evident in long-term benthic community trends. The round goby has caused a drastic decline of bivalve abundance in the Estonian coastal sea. Throughout the whole coastline, the biomass of *Mytilus trossulus* and *M. balthica* has declined 38% and 23%, respectively. So far, the round goby invasion has been shown to be the reason in over 30% of the investigated stations. Given enough time the round goby has the potential to impact all areas, however some areas could have stronger resistance to the invasion. This severe decline in benthic bivalve biomass is expected to have serious consequences in the ecosystem with reduced water transparency and increased eutrophication effects. The Harris mud crab has reduced the biomass and species richness in benthic vertebrate communities when observed in changing environmental conditions. The decline in benthic biomass caused nutrient concentrations to double and lead to a two-fold increase in the chlorophyll a concentration in the seawater. This indicates the mud crab predation caused a regime shift with previously bottom-up regulated system facing changes from top-down forcing that proliferate though trophic levels via trophic cascades.

The round goby also has been shown to be an important prey object for native coastal predatory fish. For one of the most important coastal predatory fish, the European perch, the round goby is becoming the dominant prey object in their diet. However, modelling suggested that the overall feeding of the perch is related to suitable environmental conditions and round goby abundance did not play a significant role. Thus, so far, the predation pressure is not controlling the abundance of round goby. If sufficient improvement in coastal fisheries management (*e.g.*, reduced fishing pressure, habitat and spawning area restoration) is done, the populations could exhibit significant predation pressure on the round goby.

The thesis gives an overview of the invader's distribution and abundance patterns. The round goby has achieved pan-Baltic distribution with occurrences in all major sub-basins. The main factors describing the distribution are local abiotic hydrological conditions (*e.g.,* wave exposure, salinity, temperature) and higher probability of occurrence is related to the proximity of large cargo ports, suggesting that maritime shipping is likely the main factor driving round goby invasion. The abundance is in fluctuation throughout the coastline and in many areas coastal fishermen are landing large amounts annually. The mud crab distribution and annual abundance patters in the Gulf of Riga show the species initial dispersal to be fast with large populations established in a couple of years in Pärnu Bay. However, range expansion to the rest of the Estonian coastal sea has been much slower with rare sightings in some areas and a few new viable populations only in the proximity of Pärnu Bay by 2022. This suggests sub-population differences between other invaded areas in the Baltic Sea.

In conclusion the novel predators are a serious threat for the Baltic Sea benthic community functioning. The significantly increased top-down pressure is already showing cascading effect to the whole ecosystems in some areas and given enough time the species have the potential to spread and severely impact most coastal ecosystems. The ability of species to affect the ecosystems both as predators and as prey, is suggesting changes in most ecosystem levels, thus creating a profound need to consider invasive species role in marine ecosystems management and protection.

SUMMARY IN ESTONIAN

Invasiivsete liikide roll riimveeliste põhjakoosluste struktuuri ja biomassi muutustes

Globaalselt suurenev võõrliikide arv maismaa ja vee ökosüsteemides on tekitanud vajaduse uurida, milline on selliste invasiivsete liikide mõju uutes elupaikades. Üle maailma on juba näiteid, kuidas võõrliikide lisandumine muudab kogu ökosüsteemi toimimist ja uus võõrliikidest koosnev kooslus ei suuda pakkuda kõiki ökosüsteemi toimimiseks vajalikke funktsioone.

Läänemeres on tänaseks registreeritud 220 võõrliiki ning paljud neist on juba oluliselt mõjutamas mere ökosüsteeme. Erinevalt teistest meredest on Läänemeri liigivaene ja paljud funktsioonid on tagatud vaid üksikute liikide poolt. Veelgi enam, Läänemere keskkonda kujundab ümber eutrofeerumine, elupaikade hävimine, merereostus ja kliimamuutused (nt. soolsuse vähenemine, vee temperatuuri hüppeline suurenemine jne). Seetõttu on Läänemeri võrdlemisi vastuvõtlik uutele liikidele ja siia saabunud uued liigid loovad arvukid ja elujõulisi populatsioone, mis suudavad olulisel määral ümber kujundada kohalikke ökosüsteeme.

Tänini on läbi viidud väga vähe pikaajalisi võõrliikide mõjude uuringuid. Tihti hinnatakse võõrliikide mõju eksperthinnangute kaudu või lühiajaliste katsetega, mis ei pruugi aga adekvaatselt näidata võõrliikide pikaajalist mõju ökosüsteemidele. Võõrliikide mõjude uuringute üheks kitsaskohaks on ka invasioonile eelnenud ajal eesmärgipäraselt kogutud andmete puudumine. Samuti tuleb ökosüsteemi muutuste hindamisel arvestada keskkonnategurite pikaajaliste trendidega, et paremini mõista võõrliikide rolli muutustes.

Selleks, et selgitada välja võõrliikide invasiooni mõju kohalikule ökosüsteemile, on vaja teada, kuidas võõrliigid uues elupaigas käituvad. Käesolevas doktoritöös käsitletakse olulisi teadmiste lünki ümarmudila (*Neogobius melanostomus*) ja hariliku rändkrabi (*Rhithropanopeus harrisii*) levikus, toitumises ja liikide mõjus kohalikule ökosüsteemile. Esmalt hinnati manipulatiivsete katsete abil liikide rolli uues elupaigas (**I**, **II**, **III**). Katsete käigus uuriti võõrliikide toidueelistusi ning nende eraldi- ja koosmõju kohalikele põhjakooslustele. Teiseks hinnati võõrliikide mõju ökosüsteemile looduslikes tingimustes (**III**, **IV**, **VI**) modelleerides põhjakoosluste pikaajalisi trende muutuvas merekeskkonnas ja hinnates ümarmudila rolli saakloomana (**V**). Lisaks kirjeldati antud võõrliikide levikut ja arvukuse trende (**III**, **IV**), et hinnata mõju võimalikku ulatust.

Töö käigus läbi viidud eksperimentaalsed uuringud näitasid, et ümarmudil ja rändkrabi on võimelised sööma väga suurtes kogustes Läänemere kirdeosa põhjakooslustes domineerivaid selgrootuid loomi. Toitumisstrateegialt osutus ümarmudil generalistiks ehk mitteselektiivseks kiskjaks, kes suudab toitumise kaudu põhjustada põhjakooslustes püsivaid muutusi. Kui laboratoorsetes uuringutes ette antud toidukogused oleksid samaväärsed ka looduskeskkonnas ning ümarmudil asustaks kõiki merealasid, hävitaks võõrliik kogu Läänemere selgrootute koosluse vähem kui kahe nädalaga. Sarnaselt vähendas harilik rändkrabi eksperimendi käigus oluliselt selgrootute koosluste biomassi ja liigirikkust. Krabi kisklussurve oli tugevam kui näiteks kliimamuutuste kaudu toitainete sissevoolu suurenemisest tingitud sekundaarne biomassi juurdekasv. Kuigi kahe liigi koosmõju ei erinenud suures plaanis võõrliikide eraldimõjudest, vähendas ümarmudil mõningal määral hariliku rändkrabi toitumist balti lamekarbist (*Macoma balthica*). Sellest võime järeldada, et looduslikes tingimustes võivad liikidevahelised interaktsioonid mõneti vähendada võõrliikide mõju ümbritsevale keskkonnale.

Lisaks kirjeldati doktoritöös võõrliikide pikaajalist mõju põhjakoosluste biomassi trendidele. Ümarmudil on põhjustanud karbipopulatsioonide järsu vähenemise Eesti rannikumeres. Keskmiselt on kogu rannikumeres söödava rannakarbi (*Mytilus trossulus*) biomass langenud 38% ja balti lamekarbi biomass langenud 23%. Üle 30% rannikumere seirejaamades on karpide biomassi languse põhjuseks ümarmudila invasioon ning ümarmudila levila laienemisel see protsent kasvab. Pikemas perspektiivis mõjutab ümarmudil Eesti rannikumeres tõenäoliselt kõiki piirkondi, ent mõne piirkonna kooslused võivad ümarmudila kisklussurvet paremini taluda. Andmeanalüüsid näitasid, et sellisteks piirkondadeks võivad olla suure liigirikkuse või produktiivsusega elupaigad. Laialdane karbipopulatsioonide vähenemine mõjutab kogu ökosüsteemi toimimist – merevee läbipaistvus väheneb ja intensiivistuvad eutrofeerumise ilmingud.

Sarnaselt ümarmudilaga on ka harilik rändkrabi looduslikes põhjaloomastike kooslustes olulisel määral vähendanud kohalike selgrootute liigirikkust ja biomassi. Põhjakoosluste biomassi oluline kahanemine põhjustas toitainete kontsentratsiooni tõusu merevees, mis omakorda põhjustas veesambas vetikaõitsenguid. Kui varasemalt mõjutasid meie rannikumere kooslusi peamiselt eluta keskkonnas toimuvad muutused (näiteks toitainete ja valguse määras), siis peale võõrliikide saabumist on kisklussurve muutumas üheks olulisemaks kooslusi kujundavaks protsessiks. Selline muutus on põhjustanud rannikumeres olulise režiiminihke, mille käigus madalamatel troofilistel tasemetel toimunud muutused levivad kaskaadidena ka teistele tasanditele mõjutades ka selliseid elupaiku (pelagiaali), mida võõrliigid ise ei asusta.

Eesti rannikumere ökosüsteemis on ümarmudil muutunud oluliseks toiduobjektiks kohalikele rannikukaladele. Doktoritöö käigus näidati, et mitmes piirkonnas on ümarmudil ühe meie rannikumere tähtsaima püügikala, ahvena (*Perca fluviatilis*) toidus juba domineeriv komponent. Modelleerimine näitas, et hetkel sõltub ahvena üldine toitumus sobivatest keskkonnatingimustest ja ümarmudila arvukus seda olulisel määral ei mõjutanud. Seega võib eeldada, et praegu ei suuda suuremate kalade kisklussurve ümarmudila arvukust kontrollida. Jätkusuutliku kalapopulatsioonide majandamise korral (nt püügisurve vähendamine, edukas elupaikade ja kudealade taastamine) võivad suurenenud rannikukalade populatsioonid hakata ümarmudila arvukust oluliselt kontrollima.

Doktoritöös antakse ka ülevaade võõrliikide levikumustritest ja populatsiooni arvukusest. Ümarmudila levik ulatus 2016. aastaks kõikidesse Läänemere suurematesse alambasseinidesse. Ümarmudila levikut kirjeldavad peamiselt mereala eluta keskkond ja hüdroloogilised tingimused (sh avatus lainetele, vee soolsus ja temperatuur). Suurem ümarmudila esinemise tõenäosus on seotud ka suuremate kaubasadamate lähedusega, viidates laevandusele kui põhilisele ümarmudila levitajale. Ümarmudila populatsiooni suurus kõigub kogu Eesti rannikumeres ja selget stabiilsust pole veel saavutatud. Paljudes Läänemere piirkondades, nt Liivi lahes, püüavad rannakalurid igal aastal märkimisväärse koguse ümarmudilat. Hariliku rändkrabi ilmumisel Pärnu lahte levis liik kiiresti ning arvukused kasvasid järgneva nelja aasta jooksul mitu korda. Mujal Eesti rannikumeres on hariliku rändkrabi levik olnud oluliselt aeglasem. 2022. aastaks on Liivi lahte tekkinud ainult üksikud uued elujõulised krabiasurkonnad. Veelgi aeglasem hariliku rändkrabi levik Soome lahes viitab krabi alampopulatsioonide geneetilistele erinevustele.

Doktoritööst võime järeldada, et võõrliigid kujutavad tõsist ohtu Läänemere ökosüsteemidele. Oluliselt suurenenud kisklussurve karbipopulatsioonidele on mõnes piirkonnas juba avaldunud mõjudena toiduvõrgustiku teistel troofsetel tasemetel ning elupaikades, mida võõrliigid ise ei asusta. Pikemas perspektiivis suudavad ümarmudil ja harilik rändkrabi oluliselt ümber kujundada rannikumere kooslusi kõikjal Eesti rannikumeres. Uuritud liigid suudavad mõjutada ökosüsteeme nii kiskjate kui ka saakloomadena. Sellised laialdased mõjud võivad oluliselt muuta kogu ökosüsteemi toimimist ja seisundit. Seega on oluline arvestada võõrliikidega ökosüsteemide keskkonnaseisundi parandamisel ja rannikumere majandamisel.

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PUBLICATIONS

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Education

2014 –…	University of Tartu, Doctoral studies in Hydrobiology
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Professional career

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Scientific publications

Nõomaa, K.; Kotta, J.; Szava-Kovats, R.; Herkül, K.; Hubel, K.; Eschbaum, R.; Vetemaa, M. (2022). Novel fish predator causes sustained changes in its prey populations. Frontiers in Marine Science, 9, 849878. DOI: 10.3389/fmars.2022.849878.

Behrens, Jane W.; Ryberg, Marie P.; Einberg, Heli; Eschbaum, Redik; Florin, Ann-Britt; Grygiel, Wlodzimierz; Herrmann, Jens Peter; Huwer, Bastian; Hussy, Karin; Knospina, Elina; **Nõomaa, Kristiina**; Oesterwind, Daniel; Polte, Patrick; Smolinski, Szymon; Ustups, Didzis; van Deurs, Mikael; Ojaveer, Henn (2022). Seasonal depth distribution and thermal experience of the non-indigenous round goby *Neogobius melanostomus* in the Baltic Sea: implications to key trophic relations. Biological Invasions, 24, 527−541. DOI: 10.1007/s10530-021-02662-w.

Liversage, K.; Kotta, J.; Kuprijanov, I.; Rätsep, M.; **Nõomaa, K.** (2021). A trophic cascade facilitates native habitat providers within assemblages of multiple invasive marine species. Ecosphere, 12 (6), e03621. DOI: 10.1002/ecs2.3621.

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Liversage, Kiran; **Nurkse, Kristiina**; Kotta, Jonne; Järv, Leili (2017). Environmental heterogeneity associated with European perch *(Perca fluviatilis)* predation on invasive round goby (Neogobius melanostomus). Marine Environmental Research, 132, 132−139. DOI: 10.1016/j.marenvres.2017.10.017.

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Kotta, J.; **Nurkse, K.**; Puntila, R.; Ojaveer, H. (2016). Shipping and natural environmental conditions determine the distribution of the invasive non-indigenous round goby *Neogobius melanostomus* in a regional sea. Estuarine, Coastal and Shelf Science, 169, 15−24.

Awards and scholarships

2015 Doctoral School of Earth Sciences and Ecology, travelling scholarship to Umea, Sweden.

Conference presentations

Oral presentation: “Novel fish predator causes sustained changes in its prey populations”. In: 12th International Conference on Biological Invasions, Neobiota, 12–16 September 2022, Tartu, Estonia.

Oral presentation: “Separate and interactive effects of non-indigenous species on native communities: the two aggressive novel benthic predators in the Baltic Sea”. In: 51st European Marine Biology Symposium, 26–30 September 2016, Rhodes, Greece.

Oral presentation: "Invasive epibenthic predators' impact on benthic communities functioning". In: 10th Baltic Sea Science Congress, 15–19 June 2015, Riga, Latvia.

Oral presentation: "Highlights of the recent round goby research in Estonia". In: "The goby meeting 2015", 24–27 February 2015, Umea, Sweden.

Additional coursework

BONUS BIO-C3/INSPIRE/COCOA/BAMBI 2016 Summer School: Modelling Biodiversity for Sustainable Use of Baltic Sea Living Resources, Søminnestationen, Holbæk, Denmark, August 21–27, 2016.

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Nõomaa, K.; Kotta, J.; Szava-Kovats, R.; Herkül, K.; Hubel, K.; Eschbaum, R.; Vetemaa, M. (2022). Novel fish predator causes sustained changes in its prey populations. Frontiers in Marine Science, 9, 849878. DOI: 10.3389/fmars.2022.849878.

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Saadud uurimistoetused

2015 Doctoral School of Earth Sciences and Ecology, travelling scholarship to Umea, Sweden.

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Suuline ettekanne: “Novel fish predator causes sustained changes in its prey populations”. In: 12th International Conference on Biological Invasions, Neobiota, 12–16 September 2022, Tartu, Estonia.

Suuline ettekanne: “Separate and interactive effects of non-indigenous species on native communities: the two aggressive novel benthic predators in the Baltic Sea”. In: 51st European Marine Biology Symposium, 26–30 September 2016, Rhodes, Greece.

Suuline ettekanne: “Invasive epibenthic predators’ impact on benthic communities functioning”. In: 10th Baltic Sea Science Congress, 15–19 June 2015, Riga, Latvia.

Suuline ettekanne: “Highlights of the recent round goby research in Estonia”. In: “The goby meeting 2015”, 24–27 February 2015, Umea, Sweden.

Täiendõpe

BONUS BIO-C3/INSPIRE/COCOA/BAMBI 2016 Suvekool: Modelling Biodiversity for Sustainable Use of Baltic Sea Living Resources, Søminnestationen, Holbæk, Denmark, August 21–27, 2016.

BONUS BIO-C3/BAMBI/INSPIRE Suvekool “The Baltic Sea: a model for the global future ocean?”, Glücksburg, Germany, 5–11 July 2015

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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23. **Maido Remm**. Human papillomavirus type 18: replication, transformation and gene expression. Tartu, 1997, 117 p.
24. **Tiiu Kull**. Population dynamics in *Cypripedium calceolus* L. Tartu, 1997, 124 p.
25. **Kalle Olli**. Evolutionary life-strategies of autotrophic planktonic microorganisms in the Baltic Sea. Tartu, 1997, 180 p.
26. **Meelis Pärtel**. Species diversity and community dynamics in calcareous grassland communities in Western Estonia. Tartu, 1997, 124 p.
27. **Malle Leht**. The Genus *Potentilla* L. in Estonia, Latvia and Lithuania: distribution, morphology and taxonomy. Tartu, 1997, 186 p.
28. **Tanel Tenson**. Ribosomes, peptides and antibiotic resistance. Tartu, 1997, 80 p.
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