Effects of the non-indigenous mud crab *Rhithropanopeus harrisii* on the benthic communities in the northern Baltic Sea

Katariina Riipinen

Master's Thesis

University of Turku
Department of Biology
2.9.2021

UNIVERSITY OF TURKU
Department of Biology

RIIPINEN, KATARIINA:　　　　Effects of the non-indigenous mud crab
Rhithropanopeus harrisii on the benthic
communities in the northern Baltic Sea

Master's thesis, 50 pp., 2 appendices
Ecology
September 2021

The characteristics of the Baltic Sea make it especially vulnerable to non-indigenous species. *Rhithropanopeus harrisii* is a novel mud crab species in the northern Baltic Sea, where no native crab species exist. To determine the effects of *R. harrisii* invasion stage on the invertebrate community composition, six sites were selected in the Finnish Archipelago Sea, representing communities where *R. harrisii* was established, recently invaded communities, and uninvaded communities. Communities were sampled using a benthic grab in May, July, and September, and with non-catching habitat traps deployed from July to September. Communities where *R. harrisii* was established significantly differed from those with no *R. harrisii* in the benthic grab data, and recently invaded communities from the uninvaded in the habitat trap data, although the communities also differed from each other within invasion stage. Community composition was also explained by environmental factors, such as distance from the initial invasion centre, *Fucus vesiculosus* coverage, and site openness. Taxa contributing the most to community differences were *Hydrobia* spp., *Theodoxus fluviatilis*, *Cerastoderma/Parvicardium*, *Mytilus trossulus*, *Macoma balthica*, *Corophium volutator* and other amphipod species, and chironomid larvae. Most of these species tended to be less abundant in the presence of *R. harrisii*, many of them significantly. Diversity was significantly higher in the uninvaded communities compared to those where *R. harrisii* was established in the habitat trap data, but not in the benthic grab data. Although community composition is affected also by abiotic differences, the results show a clear shift in the invertebrate community composition following *R. harrisii* invasion.

Itämeren erityispiirteet tekevät siitä herkän vieraslajien vaikutuksille. Liejutaskurapu *Rhithropanopeus harrisii* on uusi vieraslaji pohjoisella Itämerellä, missä ei ole lainkaan alkuperäisiä taskurapulajeja. Liejutaskuravun leviämisvaiheen vaikutuksia pohjaeläinyhteisöihin selvitettiin keräämällä näytteitä kuudelta tutkimuskohteelta Saaristomerellä. Valitut kohteet edustivat yhteisöjä, joissa liejutaskurapu on vakiintunut; yhteisöjä, joihin se on saapunut vastikään; ja yhteisöjä, joissa rapuja ei ollut. Näytteet kerättiin pohjanoutimella touko-, heinä- ja syyskuussa sekä ei-pyytävillä habitaattimerroilla, jotka laskettiin heinäkuussa ja nostettiin syyskuussa. Yhteisöt, joissa liejutaskurapu oli vakiintunut, erosivat noudinaineistossa yhteisöistä, joissa rapuja ei ole. Merta-aineistossa viimeaikaisen leviämisvaiheen yhteisöt erosivat yhteisöistä, joissa rapuja ei ollut. Tutkimuskohteiden eliöyhteisöt kuitenkin erosivat toisistaan myös leviämisvaiheen sisällä. Myös ympäristötekijät, kuten etäisyys alkuperäisestä leviämiskeskuksesta, rakkohaurun *Fucus vesiculosus* peittävyys ja kohteen avoimuus selittivät yhteisöjen rakennetta. Eliöyhteisöjen rakenne-eroja liejutaskuravun leviämisvaiheiden välillä selittivät eristyisesti erot sukkulakotiloiden *Hydrobia* spp., leväkotilon *Theodoxus fluviatilis*, sydänsimpukoiden *Cerastoderma*/*Parvicardium,* sinisimpukan *Mytilus trossulus*, liejusimpukan *Macoma balthica*, liejukatkan *Corophium volutator*, muiden katkalajien ja surviaissääsken toukkien runsaudessa. Useimmat näistä lajeista tai ryhmistä olivat harvalukuisempia yhteisöissä, joissa liejutaskurapu oli vakiintunut, monet tilastollisesti merkitsevästi. Yhteisöissä, joissa liejutaskurapu oli vakiintunut, monimuotoisuus oli merta-aineistossa merkitsevästi alhaisempi kuin yhteisöissä, joissa rapuja ei ollut. Noudinaineistossa monimuotoisuudessa ei ollut eroa leviämisvaiheiden välillä. Vaikka ympäristötekijät vaikuttavat yhteisön rakenteeseen, tulokset osoittavat, että pohjaeläinyhteisöjen rakenteessa tapahtuu merkittäviä muutoksia liejutaskuravun leviämisen ja runsastumisen myötä.

TABLE OF CONTENTS

1   INTRODUCTION

1.1   *The Baltic Sea*

The Baltic Sea is the largest brackish water basin in the world (Harff et al. 2011; Snoeijs-Leijonmalm and Andrén 2017). It is a geologically young sea, and the current shape has formed during and after the last glaciation period (Harff et al. 2011). It is also quite shallow, on average some 55 meters deep (Snoeijs-Leijonmalm and Andrén 2017; Jakobsson et al. 2019), and only 23 meters in the Archipelago Sea on the southwestern coast of Finland, in the northern Baltic Sea (Tolvanen and Suominen 2005). Its seafloor is uneven and the shoreline complex, especially in the north (Jakobsson et al. 2019). Shallow inlets, gulfs, and lagoons, as well as varied bottom structure and different substrates provide geodiversity in the Baltic Sea (Kaskela and Kotilainen 2017).

In addition to the geological complexity, the Baltic Sea is characterised by gradients and zonation. Salinity decreases from ca. 30 PSU at the Danish straits to 1–2 PSU in the Gulf of Finland and the northernmost part in the Bothnian Bay (Snoeijs-Leijonmalm and Andrén 2017). The Baltic Sea ranges from 53° N to 65° N latitude, over some 1300 kilometres. Over this range, climatic gradient significantly impacts the conditions, with a surface water temperature difference between the southern and northern Baltic Sea around 4–5 °C in summer and winter (Snoeijs-Leijonmalm and Andrén 2017). Temperature also affects sea ice formation. The northern Baltic Sea typically has an ice cover from December to April (Tolvanen and Suominen 2005; Snoeijs-Leijonmalm and Andrén 2017) but the period of ice coverage has been shortening due to climate change (Tolvanen and Suominen 2005) and will likely continue to do so (Snoeijs-Leijonmalm and Andrén 2017). Climate change also affects summer surface water temperature, and salinity via increased precipitation and freshwater inflow from the drainage area (Andersson et al. 2015).

The Baltic Sea drainage area is some four times the size of the sea basin (Snoeijs-Leijonmalm and Andrén 2017). With ca. 85 million people inhabiting the area, human impact on the Baltic Sea ecosystems is strong. Agriculture is a major source of nutrient runoff and eutrophication especially in the southern Baltic Sea (Snoeijs-Leijonmalm and Andrén 2017; HELCOM 2018a). In the northern Baltic Sea, the last remaining nutrient

pollution hotspot is in the Finnish Archipelago Sea (HELCOM 2021). The Baltic Sea is also very heavily trafficked. Most of the traffic are cargo ships, with 28 % arriving from outside the Baltic Sea (HELCOM 2018b). Up to 15 % of the world's marine cargo sails on the Baltic Sea (Baltic LINes 2016). Furthermore, recreational boating is very popular in the area, and there are hundreds of marinas with intense traffic along the Baltic Sea coast (Liljeberg 2016).

1.1.1 Communities in the Baltic Sea

The geographical location, geological features and age, and gradients all define the communities in the northern Baltic Sea. In terrestrial ecosystems, biodiversity decreases towards higher latitudes (Gillison 2018; Stevens and Tello 2018; Stevens et al. 2019). In marine ecosystems, overall diversity also decreases towards higher latitudes, but with deep-sea diversity hot spots (Valentine and Jablonski 2015) and higher macroalgal diversity as well as higher primary production at higher latitudes (Kerswell 2006; Chavez et al. 2011; Valentine and Jablonski 2015). In the Baltic Sea, diversity on the open waters decreases towards the coast of Finland (toward higher latitudes) (Bonsdorff 2006). Diversity is, however, notably higher in the shallow waters near coastline and in the archipelago with higher geological complexity and varied bottom substrates (Bonsdorff 2006).

For bottom-dwelling animals over the size of 0.5–1 mm, i.e. macrozoobenthos, salinity is likely the most important factor in explaining the biodiversity gradient in the Baltic Sea (Zettler et al. 2014). The highest number of species, most of them marine, is found at the highest salinity in the Kattegat (1161 species), and the number decreases towards northern Baltic Proper and the Åland Sea (71–84 species) (Zettler et al. 2014). In the Bothnian Bay, the number of species is slightly higher (135 species), and most of them are freshwater species. The number of species in the Gulf of Finland does not follow the salinity-diversity gradient, with nearly 500 species, although over 400 of them are of freshwater origin (Zettler et al. 2014). The number of freshwater species increases near shore, in shallow waters with river inflow (Bonsdorff 2006; Zettler et al. 2014). Overall, the species in the Baltic Sea are mostly remnants of different post-glacial stages, marine species spread out from the North Atlantic, and introduced by human action (Leppäkoski et al. 2002; Snoeijs-Leijonmalm 2017). Many of both marine and freshwater species are,

though adapted to the brackish water environment, at the edge of their salinity tolerance (Snoeijs-Leijonmalm 2017).

Low diversity in the Baltic Sea is not necessarily due to low species richness, but low evenness of species abundance (Snoeijs-Leijonmalm 2017). Food webs are typically simple and are built on few highly abundant species. However, despite the low diversity and simple food webs, the Baltic Sea is as productive as more diverse systems (Snoeijs-Leijonmalm 2017). Productivity is dependent on the dominant macroscopic species and more diverse phytoplankton species (Snoeijs-Leijonmalm 2017).

Communities are characterised by the few dominant, habitat-forming species: algae *Fucus vesiculosus*, *Furcellaria lumbricalis*, and *Cladophora glomerata*, blue mussel *Mytilus trossulus,* and common eelgrass *Zostera marina* (Snoeijs-Leijonmalm 2017). On the shallow, soft-sediment shores of the northern Baltic Sea, the common reed *Phragmites australis* is also a major habitat-forming species (Ikonen and Hagelberg 2007).

Macroalgae and blue mussel form belts in the rocky bottoms of the northern Baltic Sea. On the Finnish coast, the uppermost hard-substrate zone is occupied by green filamentous algae, dominantly *Cladophora* with varying densities and combinations of other species (Kiirikki 1996). Below green algae, brown alga *Fucus vesiculosus* is the dominant species, and below the *Fucus* belt, red algae, such as *Furcellaria* occupy the substrate (Kiirikki 1996). Finally, blue mussel *Mytilus trossulus* forms dense beds where there is not enough light for algal growth. Zonation is caused by light permeation, winter ice cover, and irregular sea-level changes, as well as exposure to waves affecting all three factors (Kiirikki 1996). In the coastal environments of the Baltic Sea, light reaches to ca. 5 metres depth, limiting photosynthesis to near surface (Snoeijs-Leijonmalm and Andrén 2017). Ice cover, especially pack ice formation, and sea-level changes, conversely, limit perennial algal growth to deeper below surface, by scraping the attached algae off rocks, and causing desiccation when the water is temporarily lower (Kiirikki 1996).

On soft-sediment bottoms, *Zostera* eelgrass forms wide meadows on sand and mixed substrates and supports diverse invertebrate communities (Kautsky et al. 2017). *Phragmites australis* grows semiaquatic on the shoreline, forming dense reed belts. It is very common on the Finnish coasts of the northern Baltic Sea, and can overgrow other

vegetation types on the shore (Ikonen and Hagelberg 2007). Although reed belts provide habitat for a variety of animals (Long et al. 2011), and spawning areas for species of fish (Kallasvuo et al. 2011), there are attempts to control their abundance (Ikonen and Hagelberg 2007).

Fucus vesiculosus, *Zostera marina*, and *Mytilus trossulus* are all keystone species in the Baltic Sea. They provide shelter and food, and house diverse communities of macroscopic as well as epiphytic flora, invertebrates, and fish (Kautsky et al. 2017; Snoeijs-Leijonmalm 2017). However, with only a few key species, the Baltic Sea ecosystems are especially vulnerable to human influence. Nutrient loading, hazardous substances, and fishing (Korpinen et al. 2012), as well as climate change and non-indigenous species (Andersson et al. 2015) exert considerable pressure on the whole Baltic Sea area.

1.2 Non-indigenous species

Non-indigenous species are globally considered the biggest threat to biodiversity after habitat loss and fragmentation (Wilcove et al. 1998; Niemivuo-Lahti 2012). Species are introduced outside their native range and over dispersal barriers via human actions, either accidentally or on purpose, with traffic, through artificial corridors, and for trade purposes (Molnar et al. 2008; Niemivuo-Lahti 2012; Geburzi and McCarthy 2018). In marine environments, the most important vector in spreading non-indigenous species is shipping; species are transported on ship hulls and in ballast water with increasing intensity (Ruiz et al. 1997; Bax et al. 2003). Canals, such as the Suez Canal connecting the Mediterranean Sea to the Red Sea and the Indian Ocean, are not vectors as such, but pathways for introductions (Geburzi and McCarthy 2018). Aquaculture, aquarium trade, and deliberate stocking are other major sources of invaders (Padilla and Williams 2004). Examples of species spread via aquaculture and aquarium trade include some highly successful invaders, such as the water hyacinth *Eichhornia crassipes*, the "killer alga" *Caulerpa taxifolia* (Padilla and Williams 2004), the red lionfish *Pterois volitans* (Albins and Hixon 2013), and the Pacific oyster *Magallana gigas* (Reise et al. 2017; McAfee and Connell 2021).

Successful invasions may require multiple introduction events, and not all introduced species become established. A small proportion of those introduced are able to form

sustained populations, and of those established, another small proportion may impact native communities (Williamson and Fitter 1996; Bax et al. 2003; Geburzi and McCarthy 2018). To become established, non-indigenous species have to survive transport and be able to reproduce in the new environment with its abiotic conditions and existing biotic interactions.

Marine coastal ecosystems are among the most invaded environments (Ruiz et al. 1997; Geburzi and McCarthy 2018). Ballast water is taken in at harbour, at bays and estuaries, and released in more or less similar environmental conditions (e.g. salinity, temperature), meaning transported species are often viable upon introduction (Ruiz et al. 1997; Paavola et al. 2005), although abiotic factors significantly limit non-indigenous species' establishment (Dethier and Hacker 2005; Kelley 2014).

Successful invaders are usually characterised by high tolerance to environmental conditions such as temperature, and salinity in aquatic environments (Sakai et al. 2001). They generally have broad diets, rapid dispersal, fast growth, early maturity, high reproductive potential, and short generation time, i.e. r-selected life-history strategy, or the ability to switch between strategies (Sakai et al. 2001). In marine ecosystems, planktonic larval stage also aids in spread, especially locally after introduction (Geburzi and McCarthy 2018), but planktonic larvae are also transported long-distance in ballast waters (Ruiz et al. 1997; Hänfling et al. 2011).

After initial introduction to suitable environment, biotic interactions in the recipient community also impact establishment success. The biotic resistance hypothesis (BRH) states that the biotic resistance of recipient native community reduces the number of successful invaders (Levine et al. 2004). Although it is unlikely that biotic interactions or diversity would completely prevent invasions (Levine et al. 2004), diversity reduces invasion success (Stachowicz et al. 2002; Levine et al. 2004). Communities with low species or functional richness also have more vacant niches that non-indigenous species can occupy (Paavola et al. 2005).

In the new environments, non-indigenous species may benefit from fewer predators, parasites, or pathogens (Roy et al. 2011). For example, the probability of a parasite or pathogen arriving with the introduced host species is low, as infected individuals of the

host species may not survive transport due to decreased viability (Roy et al. 2011). The host species density, species assemblage, or the abiotic conditions in the new environment may also not be suitable for the parasite or pathogen (Roy et al. 2011). Furthermore, predators in the introduced range may be naïve to new species, i.e. they may not recognise the species as suitable prey or may not be able to utilise appropriate predation strategy (Sih et al. 2010).

This escape from enemies, or the enemy release hypothesis (ERH) may explain the success of non-indigenous species both in terms of establishment and subsequent spread, if predators or parasites in the new environment do not control the population growth of the non-indigenous species (Torchin et al. 2001; Keane and Crawley 2002; Sih et al. 2010; Roy et al. 2011). However, there is evidence both for and against the ERH, and whether or not invasion success can be directly linked to reduced enemies has not been thoroughly examined (Colautti et al. 2004; Roy et al. 2011). All non-indigenous species are released from at least some natural enemies in transport, but also gain new ones in introduction (Colautti et al. 2004). Gaining new enemies is also related to the BRH, where competition with native species may reduce invasion success (Levine et al. 2004). Also, parasites can be, and sometimes are, introduced with non-indigenous species, such as in the case of the American crayfish *Pacifastacus leniusculus* (Roy et al. 2011). The fungal parasite spread by *P. leniusculus* in Europe has reduced native crayfish populations (Niemivuo-Lahti 2012). Conversely, the European shore crab *Carcinus maenas*, non-indigenous in North America, is able to reach a larger body size and biomass in its introduced range in the absence of a parasite (Torchin et al. 2001). In the Baltic Sea, the non-indigenous round goby *Neogobius melanostomus* similarly grows larger and has a reduced parasite load (Kornis et al. 2012; Herlevi et al. 2017).

Another hypothesis explaining the success of non-indigenous species, related to the ERH, is the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995). If the introduced species is well-defended against its native enemies and is released from all or some of them in the new environment, it may be able to allocate resources previously used in defence to population growth (Roy et al. 2011). As with the ERH, there are conflicting results for the EICA hypothesis, and ultimate mechanisms are likely more complex (Colautti et al. 2004; Roy et al. 2011).

Increased resource availability can boost the effects of enemy release of both the ERH and the EICA hypothesis (Blumenthal 2006). However, resource availability also increases invasion success directly. Invading, like all species, need access to resources to survive, and "fluctuating resources", or increase in limiting resources can facilitate the increase of species that utilise it (Davis et al. 2000). Resource availability hypotheses have been studied especially with respect to plant invasions (Davis et al. 2000; Blumenthal 2006), but they can likely also be applied to invasions by animal species to some extent. In a manner, species invasions can also contribute to increased resources for the invading animal species. If native prey species lack evolutionary history and therefore anti-predator behaviours towards a novel predator, they can be more readily consumed by the non-indigenous species than by native predators, i.e. there is more available prey for the non-indigenous species (Cox and Lima 2006; Sih et al. 2010). Prey naivety, the lack of anti-predator behaviours towards non-indigenous predators, therefore also improves invasion success.

Overall, there are several hypotheses about invasion success that can be divided into groups, or concept clusters (Enders et al. 2020). Biotic interactions, resource availability, eco-evolutionary Darwin's cluster, propagule cluster, and trait cluster all explain different aspects of invasion success and are connected both within and between groups (Enders et al. 2020). Multiple aspects and both biotic and abiotic conditions likely all play a role in invasion success and the impact of invaders (Colautti et al. 2004; Enders et al. 2020).

Once established, non-indigenous species can alter the abiotic conditions and impact the communities and ecosystem functions in the new environments (Vitousek et al. 1997; Ruiz et al. 1997; Leppäkoski et al. 2002; Bax et al. 2003; Molnar et al. 2008; Geburzi and McCarthy 2018; Guy-Haim et al. 2018). Non-indigenous species can function as so-called ecosystem engineers by providing structure and shelter and by increasing nutrient fluxes and sedimentation, as well as decreasing primary production (Guy-Haim et al. 2018), but they may also provide ecosystem services, such as improved oxygenation by bioturbation (Norkko et al. 2012). Community-level impacts are mediated via biotic interactions. Non-indigenous species can compete with (Thomsen et al. 2014) and increase predation pressure on native species (Rilov 2009). The strongest impacts are caused by completely novel species due to prey naivety (Ricciardi and Atkinson 2004; Cox and Lima 2006; Sih et al. 2010; Anton et al. 2016). The effects of non-indigenous

species can be direct or indirect, such as trophic cascades (Lau 2013), and non-indigenous species can also change existing community-regulating cascades (Kimbro et al. 2010). Successful invaders may facilitate further invasions and cause ecosystem-wide changes, leading to a so-called "invasional meltdown" (Bax et al. 2003). Effects of non-indigenous species are, however, context-specific (Rilov 2009; Nurkse et al. 2018); the same species are not necessarily harmful everywhere but rather, impacts are dependent on the recipient community (Ricciardi and Kipp 2008).

In addition to the ecological effects, there are welfare implications of the changes caused by non-indigenous species in nature (Bax et al. 2003), and often major economic harm (Vitousek et al. 1997; Ruiz et al. 1997; Bax et al. 2003). For example, bivalves *Dreissena polymorpha* and *Mytilopsis leucophaeta* can obstruct cooling water pipes, and fouling organisms on ships and boats increase fuel consumption due to increased friction (Niemivuo-Lahti 2012). Management and eradication of non-indigenous species is often labour-intensive and costly, and in aquatic environments usually impossible.

1.2.1   Non-indigenous species in the Baltic Sea

Currently, 224 non-indigenous species have been detected in the Baltic Sea (AquaNIS Editorial Board 2015). Among them, at least 78 have been able to establish stable populations (Ojaveer et al. 2017), although given the rise in the number of observed species in recent years (from 132 species in 2016 to 224 in 2021; AquaNIS Editorial Board 2015; Ojaveer et al. 2017), the number of those established is likely higher.

The most common sources of species introductions to the Baltic Sea are the Northeast Atlantic (53 species), the Ponto-Caspian region (26 species), and the North Sea (26 species) (AquaNIS Editorial Board 2015). Introductions are often successful as salinity in the brackish water bays and estuaries of the Atlantic, and in the Black Sea and Caspian Sea, is similar to the Baltic. Brackish water, therefore, does not "protect" the Baltic Sea from non-indigenous species (Leppäkoski et al. 2002; Paavola et al. 2005). The North Sea is a source of introductions due to close connection via the Danish straits and the Kiel Canal, and the Baltic Sea is also connected to the Ponto-Caspian region via rivers and canals (Olenin et al. 2017). Most of the introductions are associated with shipping and deliberate stocking, but natural spread for example from neighbouring invaded areas and

via canals is a significant pathway (Ojaveer et al. 2017). Species are also spread locally via recreational boating (for example Peters et al. 2019).

The number of non-indigenous species in the Baltic Sea is the highest in the Gulf of Finland and in the Vistula and the Szczecin Lagoon, and is negatively correlated with benthic biodiversity (Zettler et al. 2014). As communities of low native diversity and simple food webs, such as the macrozoobenthic communities of the Baltic Sea, are considered more susceptible to non-indigenous species, species arriving to the Baltic Sea often find vacant niche space (Paavola et al. 2005; Olenin et al. 2017). This way, non-indigenous species can increase functional diversity, as for example the gastropod *Potamopyrgus antipodarum*, zebra mussel *Dreissena polymorpha*, polychaetes *Marenzelleria* spp., and decapods *Rhithropanopeus harrisii* and *Eriocheir sinensis* in the Baltic Sea: *P. antipodarum* is a surface deposit feeder on soft bottoms with no native *Hydrobia* spp. snails, *D. polymorpha* a filter feeder in salinities lower than the blue mussel *Mytilus trossulus* tolerates (Paavola et al. 2005), *Marenzelleria* spp. bioturbate deeper sediment than the native species and can improve bottom oxygen condition (Norkko et al. 2012), and *R. harrisii* and *E. sinensis* are predators and scavengers in shallow, low-salinity areas where no native crab species exist (Olenin and Leppäkoski 1999). However, increased functional diversity does not imply that the species cannot have also negative effects (Olenin et al. 2017).

Most of the widespread non-indigenous species in the Baltic Sea have community impacts (Ojaveer and Kotta 2015). For example, the cladoceran *Cercopagis pengoi* has decreased the populations of native zooplankton via predation and competition, and also causes economic harm by biofouling fishing gear (Olenin et al. 2017). The impacts of non-indigenous species can also be amplified by their interactions with other non-indigenous species (Ojaveer and Kotta 2015). The round goby *Neogobius melanostomus* and the North American mud crab *Rhithropanopeus harrisii* are expected to have higher predation impacts when both are present (Ojaveer and Kotta 2015).

The effects of *R. harrisii* on the structure of the native benthic communities in the northern Baltic Sea are studied in this thesis. *R. harrisii* was first observed in Europe already in 1874 in the Netherlands, and in the Baltic Sea in 1936 (Schubert 1936). Its high tolerance to environmental conditions, high fecundity, and diverse diet have made it a

very successful invader. In the northern Baltic Sea, *R. harrisii* has been able to fill a vacant niche on the shallow coastal waters (Olenin and Leppäkoski 1999; Paavola et al. 2005), and only a few years after the first observations in the area, an increase in their abundance was found to coincide with a change in the structure and a decrease in diversity of the *Fucus*-associated community (Jormalainen et al. 2016) and a decrease in sand bottom invertebrate biomass and species richness (Kotta et al. 2018).

1.3   Objectives

The non-indigenous North American mud crab *Rhithropanopeus harrisii* is a relatively recent invader in the Finnish coastal waters, in the northern Baltic Sea. As there are no native crab species in the area, this novel predator has a high potential of affecting local communities. Indeed, some impacts have already been documented. Therefore, the main objectives of this thesis were to determine:

1) does the presence of *R. harrisii* change the diversity and composition of benthic invertebrate communities in the northern Baltic Sea, and
2) do such changes vary with the abundance of *R. harrisii* at different invasion stages, site location, or other abiotic factors.

2   MATERIAL AND METHODS

2.1   Study species

Rhithropanopeus harrisii is a North American mud crab species that was first found in Finland in the Archipelago Sea, in Naantali, in 2009 (Karhilahti 2010). Since the first observation, it has spread in the Archipelago Sea, and more recently reached the Gulf of Finland at the southernmost tip of Finland, in Hanko, and spread northward up to near Rauma, and to the Åland Islands west of the Archipelago Sea (Appendix I). Its native distribution range reaches from the Gulf of Mexico to the Gulf of St. Lawrence in Canada on the Atlantic coast of North America (Williams 1984). Including the Baltic Sea, it has spread to eight seas, in two oceans, in over 20 countries on four, possibly five continents (Roche 2021), and to inland freshwater reservoirs (Roche and Torchin 2007).

R. harrisii can tolerate salinities between 0.5 and 40 PSU and has also been found to be able to reproduce in freshwater (Turoboyski 1973; Roche and Torchin 2007; Boyle et al. 2010). Its temperature tolerance range is similarly high: *R. harrisii* can survive temperatures below 1 °C and over 35 °C (Turoboyski 1973). Therefore, neither salinity nor temperature limit its occurrence in the northern Baltic Sea.

In its native range, *R. harrisii* occupy a variety of shelter-offering habitats, such as oyster reefs, and bottoms with vegetation and debris (Fowler et al. 2013). In the introduced range, *R. harrisii* are found, similarly, in habitats that provide some kind of shelter: on mud and sand bottoms with rocks and shells, pieces of wood, and decaying vegetation (Turoboyski 1973; Roche and Torchin 2007; Fowler et al. 2013). In the northern Baltic Sea, it has been found among and inside pieces of the reed *Phragmites australis*, on exposed rocky bottoms, and inhabiting stands of *Fucus vesiculosus* (Fowler et al. 2013). Laboratory experiments have also shown that *R. harrisii* prefer shelter-offering habitat structure over food availability (Aarnio et al. 2015; Nurkse et al. 2015; Riipinen et al. 2017).

In the southern Baltic Sea, in Poland, *R. harrisii* diet consists mainly of detritus, with some animals (polychaets, amphipods, copepods, insects, and gastropods, as well as blue mussel *Mytilus trossulus* and zebra mussel *Dreissena polymorpha*) and algae (*Cladophora* sp. and *Enteromorpha* sp.) (Turoboyski 1973; Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009). In the northern Baltic Sea, in the Finnish Archipelago Sea, *R. harrisii* prefer isopods and amphipods, and blue mussel *M. trossulus* based on laboratory experiments (Forsström et al. 2015). All are common in the *Fucus* habitat, and *M. trossulus* also form dense beds below the algal zones on the rocky shores. Stable isotope analyses place large *R. harrisii* individuals among secondary consumers, whereas the trophic position of smaller individuals is primary consumer (Aarnio et al. 2015). In the Sea of Azov, the trophic position of *R. harrisii* is predator or scavenger, similar to larger individuals in Finland, though no size distinction was made in the latter study (Zalota et al. 2017).

2.2   Study sites

To determine the effects of *R. harrisii* on the benthic communities in the northern Baltic Sea, six sites in the Finnish Archipelago Sea were selected based on previous records of *R. harrisii* presence and abundance (FinBIF 2021 (in 2013, Finnish Game and Fisheries Research Institute); see Appendix I for map of observations). Sites were chosen so that there were two sites where *R. harrisii* was known to be abundant and established (Lapila and Lammasluoto), two sites with some observations, indicating moderate abundance or recent invasion (Korpinkarit and Gyttja viken), and finally, two sites with no previous *R. harrisii* observations (Houtskär and Konungsskär).

All sites were quite sheltered, locations ranging from the inner archipelago near mainland to outer archipelago. At two of the sites (Lapila and Gyttja viken) there was no *Fucus* present. In Houtskär, *Fucus* was floating near the bottom. Reed was present at all sites. The sites were located at (Figure 1):

- Lapila, Naantali (60° 23' 53,062" N 22° 2' 36,168" E): Established invasion stage. Shallow inlet near mainland and harbour, sheltered from fairway. Soft sediment mud bottom, no *Fucus*. *Phragmites* reeds growing at around 1 m depth.

- Lammasluoto, Parainen (60° 13' 58,084" N 21° 56' 50,126" E): Established invasion stage. Rocky shore with *Fucus* attached to rocks on one side, soft sediment bottom on the other with *Phragmites* reed growing quite deep; off regular small ferry route.

- Korpinkarit, Parainen (60° 16' 53,150" N 21° 50' 21,352" E): Recent invasion stage. Rocky shore and soft sediment sand bottom at narrow pass between two islands. Reeds growing rather shallow, 0.5-1 m, *Fucus* from 1.5 m.

- Gyttja viken, Parainen (60° 9' 36,463" N 22° 3' 9,582" E): Recent invasion stage. Soft sediment bottom on the south side of one of the main islands. No *Fucus* except some floating among the reeds.

- Houtskär, Parainen (60° 13' 31,624" N 21° 22' 21,468" E): Uninvaded. Near guest harbour, next to boat shed. *Fucus* floating on the bottom and loosely attached to small rocks. Reed growing at around 0.5 m deep.

- Konungsskär, Parainen (60° 3' 52,286" N 21° 34' 53,808" E): Uninvaded. Very shallow and sheltered in the outer archipelago. Maximum depth 1.3 m, reed

growing at 0.5 m depth. Very clear water, *Fucus*, and plenty of filamentous algae. Located in the Archipelago National Park and Natura 2000 protected area (research permit MH 2552/2013).
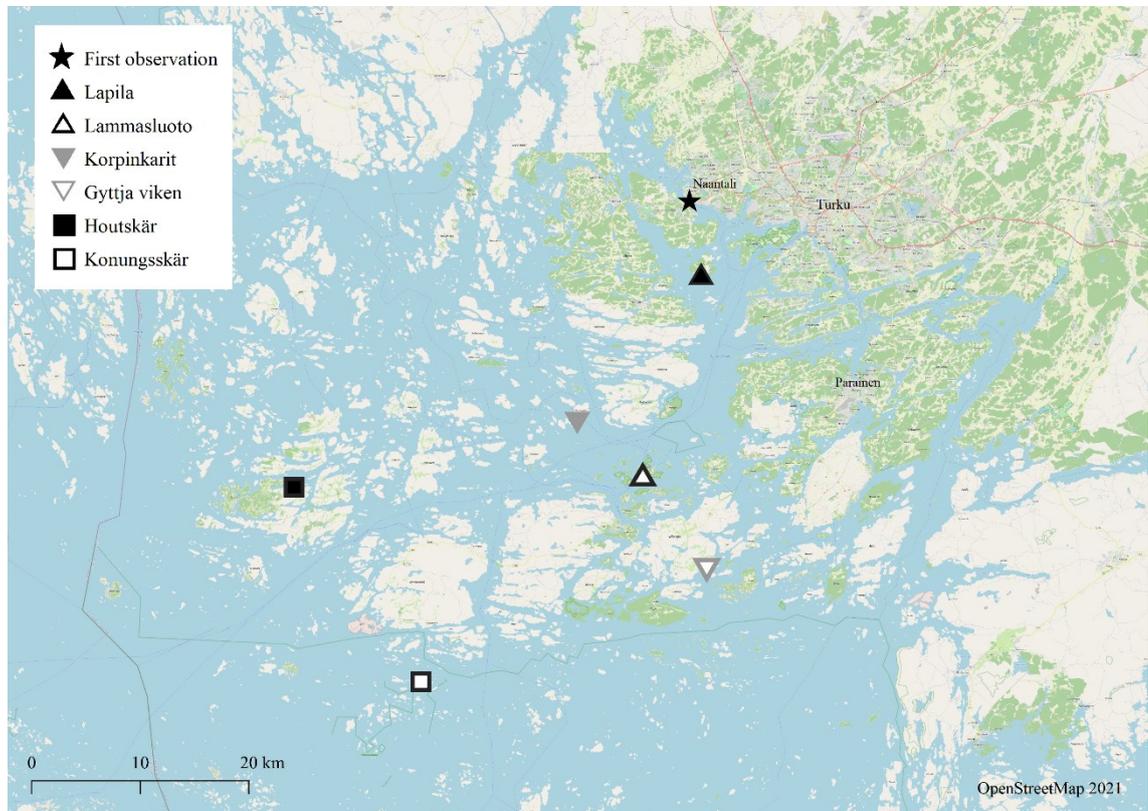
Figure 1. Site locations in the Archipelago Sea, in the southwestern Finland. Black triangles indicate established invasion stage, grey inverted triangles recent invasion stage, and squares the uninvaded sites. Star denotes the location of the first observation in Naantali.

2.3 Field sampling and sample processing

Three replicate benthic grab samples were collected from each site three times in 2013, in May, July, and September. Benthos was sampled using a Mini Petersen grab (surface area 14 cm x 23 cm; Fig. 2) so that one replicate sample was taken near *Fucus* or rocky bottom (where *Fucus* was present), one near *Phragmites* reeds, and one between the two vegetated habitats or on open bottom.

Three non-catching habitat traps were also placed at each site, to estimate the abundance of *R. harrisii*. Habitat traps were taken to the sites in July and checked in September, after being in the water for two months. Similar traps have also been used previously in *R. harrisii* abundance estimation (Fowler et al. 2013; Forsström et al. 2018; Outinen et al. 2019; Fig. 2).

Figure 2. Mini Petersen grab and a type of non-catching habitat trap used in the sampling.

Benthic samples were sifted with a 1 mm sieve after sampling to collect only macroscopic fauna. Samples were preserved in 70 % ethanol in glass jars, and dyed with Rose Bengal. Fauna in the habitat traps was sifted with a 500 μm sieve and preserved in 70 % ethanol.

Fauna in the samples were identified to species level when possible, or to family or other higher taxon. All individuals were counted, or when the abundance was very high, total number was estimated based on subsampling. *R. harrisii* individuals were counted, measured (in mm, carapace width, CW) with calipers, and sexed based on abdomen width when possible (male, female; Fig. 3). When the sex of a very small crab was not possible to determine by abdomen width, it was marked down as juvenile. The number of egg-carrying females was also counted.

Figure 3. *Rhithropanopeus harrisii* A) male and B) female. Sex is determined by abdomen width, and size measured from the carapace width C), marked with a red line.

Average depth, bottom substrate, cover percentage of *Fucus vesiculosus*, and reed *Phragmites australis* shoot density were estimated in the field, and salinity, temperature, and Secchi depth measured at each site.

2.4   Statistical analyses

2.4.1   Data processing

Benthic grab data and habitat trap data were analysed separately. In the benthic grab data, one replicate sample from Korpinkarit May sampling was missing. In the habitat trap data, the samples were collected in September. Two replicate samples, one from Lammasluoto and the other from Konungsskär, were also missing from the September habitat trap data (traps lost during sampling).

Some groups, where only few individuals were identified to species level, were pooled to higher taxon (e.g. insect larvae, oligochaetes, most amphipods, and some gastropods and fish). Bivalves without a shell were only marked down as Bivalvia and were removed from the data to avoid skewing the number of species and to make sure no individuals were counted twice. These amounted to ca. 2 % of all bivalve individuals. *R. harrisii* were removed from both data and analysed separately.

Distance from the initial invasion centre, and distance (fetch length) to the farthest and nearest shore were measured from the Finnish Environmental Institute map service (KARPALO). Distance from the initial invasion centre was measured from mainland, from the Port of Naantali. Fetch is commonly used as a measure of openness and exposure to waves, and is defined as the length of water over which wind can blow without obstruction (Tolvanen and Suominen 2005; Burrows et al. 2008). Distance (or fetch length) to both farthest and nearest shore were then measured as the longest and shortest distance, respectively, from the sampling site to shore over open water (nearest not including the shore where the site was located). Bottom substrate was transformed to a numerical value for the sake of the analyses, using the largest grain size (in mm, based on ISO 14688 soil fractions) of the dominant bottom substrate of each sample (for example, sand, grain size >0.063–2 mm, was then given the value of 2).

2.4.2   Crab population demographics

R. harrisii abundance as well as size and sex distribution was analysed from the September habitat trap data using SAS 9.4 (SAS Institute Inc. 2021). P-value of 0.05 was

used to determine statistical significance, with Bonferroni correction for multiple comparisons. Differences in *R. harrisii* abundance and size distribution between invasion stages were analysed using Kruskal-Wallis test, and pairwise differences between and within invasion stages using Mann-Whitney U test. The proportion of male and female, and adult and juvenile crabs was analysed using χ^2 test of equal proportions. Crab density estimate (crabs/m^2) was calculated from the benthic grab data as average number of crabs at each site divided by the surface area of the grab.

2.4.3 Community resemblance

The effect of *R. harrisii* invasion stage and environmental factors on community resemblance was analysed using multivariate analyses in PRIMER 7 and PERMANOVA+ (PRIMER-e (Quest Research Limited 2021)). P-value of 0.05 was used to determine statistical significance.

First, both species abundance data was square root transformed to reduce the effect of the most abundant species (Clarke and Gorley 2015). A resemblance matrix was created using the standard Bray-Curtis similarity measure, and presented visually with non-metric multi-dimensional scaling (nMDS).

The species contributing the most to between crab invasion stage differences based on Bray-Curtis similarities were determined using one-way similarity percentage (SIMPER) analysis with low-contribution cut-off at 50 %.

The effect of crab invasion stage on the community resemblance was tested using permutational multivariate analyses of variance (PERMANOVA). Crab invasion stage, and sampling month and their interaction for benthic grab data, were used as explanatory factors, and site nested in invasion stage as a random factor to account for natural variation between the sites. Pairwise differences between crab invasion stages were determined using post-hoc t-tests (Anderson et al. 2008). Analysis was set to run 9999 permutations.

The effect of environmental factors on the community resemblance was analysed using principal component analysis (PCA) and biota-environment matching (BEST test in

PRIMER 7). First, the environmental factors were normalised due to different data units and scales (Clarke and Gorley 2015). The PCA was set to run 5 principal components (eigenvalues) and include 9 environmental factors (eigenvectors) for the benthic grab data and habitat trap data separately. The environmental factors were distance from the initial invasion centre, distance to farthest shore, distance to nearest shore, *Fucus* coverage, reed shoot density, depth, Secchi depth, salinity, and bottom substrate for the benthic grab data, and distance from invasion centre, distance to farthest shore, distance to nearest shore, *Fucus* coverage, reed shoot density, depth, Secchi depth, salinity, and water temperature in September for the habitat trap data. In the biota-environment matching, Spearman rank correlation was used to match the environmental factors with the community resemblance (Bray-Curtis similarity). Statistical significance was determined using a permutational test set to run 999 permutations. Here, the same factors as in the PCA were used, with crab abundance (number of crabs per trap in the September habitat trap data) added as a factor in a second run to further test the crabs' effect on the community resemblance.

2.4.4 The effect of crab invasion stage on individual species and diversity

The effect of *R. harrisii* invasion stage on the species diversity (diversity index) and on those individual species that contributed the most to between invasion stage community differences was analysed using generalized linear mixed models (GLMM) in SAS 9.4 (SAS Institute Inc. 2021). Pairwise differences between classes of explanatory factors were determined using Tukey's test. A P-value of 0.05 was used to determine statistical significance. Model fit was estimated using Akaike information criterion for small sample size (AICc).

To determine the effect of crab invasion stage on the contributing species' abundances, the number of individuals for each species separately was used as a response variable. Crab invasion stage, and sampling month for the benthic grab data, were used as explanatory factors, and site nested in invasion stage as a random factor. Negative binomial error distribution was used for count data, determined visually from the model residuals and based on model fit. Interaction between invasion stage and sampling month was left out of the final models as it decreased model fit. *Theodoxus fluviatilis* was not one of the contributing species in the benthic grab data but it was included in the analyses

as an otherwise interesting species, abundant in the habitat trap data. In the habitat trap data, there were no *Hydrobia* spp. and chironomid individuals in the established invasion stage sites, and Tukey's pairwise test could not be used. Instead, pairwise differences between invasion stages were determined using Mann-Whitney U test. P-values were Bonferroni-corrected for multiple comparisons.

Shannon's diversity index for each sample was calculated in PRIMER 7 for both benthic grab data and habitat trap data. The effect of crab invasion stage on the species diversity was analysed using the diversity index as a response variable, with normally distributed errors. Invasion stage, and sampling month for the benthic grab data, were used as explanatory factors, and site nested in invasion stage as a random factor. Interaction between invasion stage and sampling month was left out of the final model as it decreased model fit.

3   RESULTS

3.1   *Crab population demographics*

There were altogether 17 *R. harrisii* individuals in the benthic grab data and 129 individuals in the habitat traps. Crab abundances significantly differed between crab invasion stages in the Kruskal-Wallis test of the habitat trap data (N=16, χ^2=13.77, DF=2, P<0.0001). Crab abundance followed the expected abundance at different invasion stages: abundance was the highest at established sites, moderate at recently invaded sites, and there were no crabs at the uninvaded sites (Fig. 4). Abundances differed from each other between all pairs of invasion stage and did not differ within crab invasion stage in the Mann-Whitney U test.
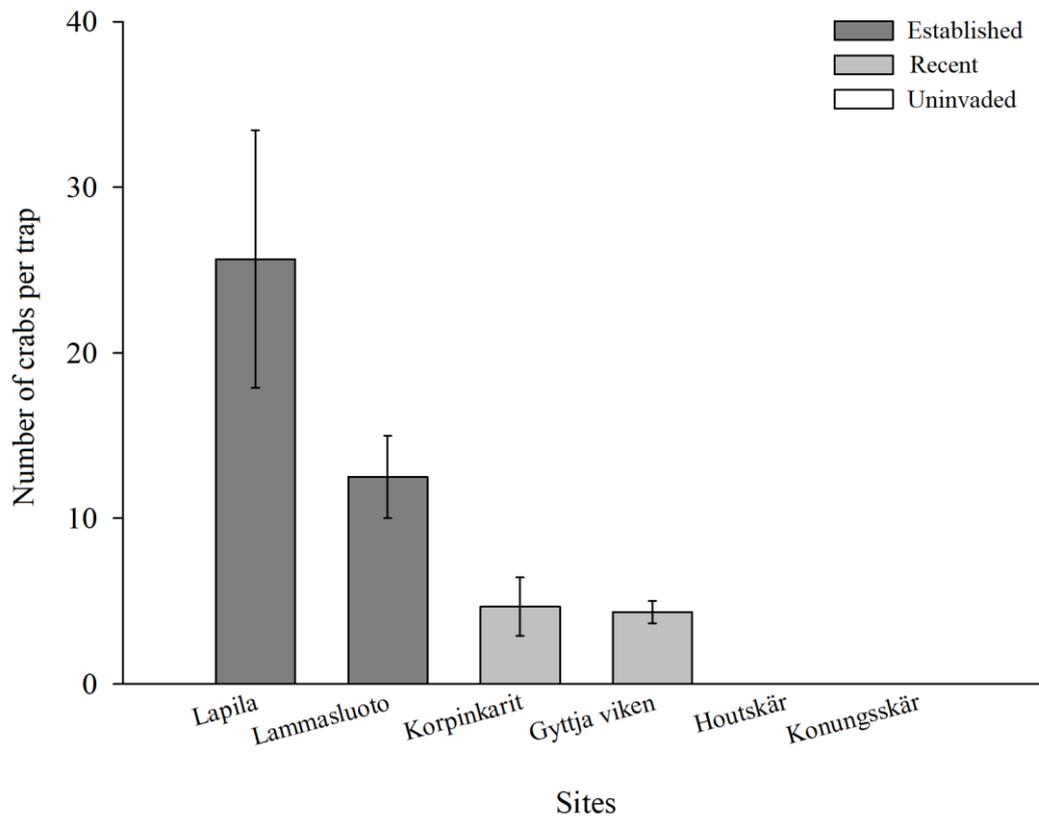
Figure 4. The number of crabs (mean ± SE) per trap at each site in the habitat trap data in September. The number of crabs differed between but not within invasion stage.

Crab size distribution in September in the habitat trap data did not differ between the established and recent invasion stage communities in the Mann-Whitney U test (N=129, Z=1.63, P=0.10). The average crab size at the established sites was 5.67 ± 0.48 mm CW, and 7.53 ± 1.04 mm CW at recently invaded sites. Crab size did, however, differ between the two established sites (N=102, Z=4.58, P<0.0001), with average crab size in Lapila 4.50 ± 0.47 mm CW and in Lammasluoto 9.29 ± 1.07 mm CW, but not between the two recently invaded sites (N=27, Z= -0.68, P=0.50; average size at Korpinkarit 8.21 ± 1.53 mm CW, and at Gyttja viken 6.79 ± 1.43 mm CW). The largest crab was 20.2 mm CW and the smallest 1.4 mm CW.

The proportion of male and female crabs differed from equal distribution (N=66, χ^2=7.33, DF=1, P=0.0068), whereas the proportion of juvenile and adult crabs did not (N=129, χ^2=0.07, DF=1, P=0.79). 51 % of the crabs were adults, and 67 % of the adult crabs were male and 33 % female. The size of the juvenile crabs varied between 1.4 and 5.6 mm CW. There were no egg-carrying females in the September habitat trap data.

In the benthic grab data, the mean number of crabs per sample did not differ between invasion stage (N=53, χ^2=4.17, DF=2, P=0.15), with no crabs at uninvaded sites, 0.5 ± 0.26 crabs per sample at established sites and 0.47 ± 0.29 crabs per sample at recently invaded sites. With all samples from the invaded sites then pooled together, there were on average 15.08 (9.20–20.97) crabs/m^2. However, with only a few individuals in the grab samples, density is a very rough estimate.

3.2 Community resemblance

There were altogether 26 species and 7705 individuals in the benthic grab data, and 32 species and 2792 individuals in the habitat trap data (September only) (Fig. 5; Appendix II). *Hydrobia* spp. (Gastropoda) was the most common taxon, with a total of 4693 individuals in the benthic grab data. The most common species in the habitat trap data was the gastropod *Theodoxus fluviatilis* with 670 individuals. The highest number of species and individuals were found at the uninvaded sites in Konungsskär and Houtskär in both benthic grab data and habitat trap data (Appendix II). The number of species and individuals was the lowest at the established invasion stage sites in Lapila and Lammasluoto (Appendix II).

A   Benthic grab data

20
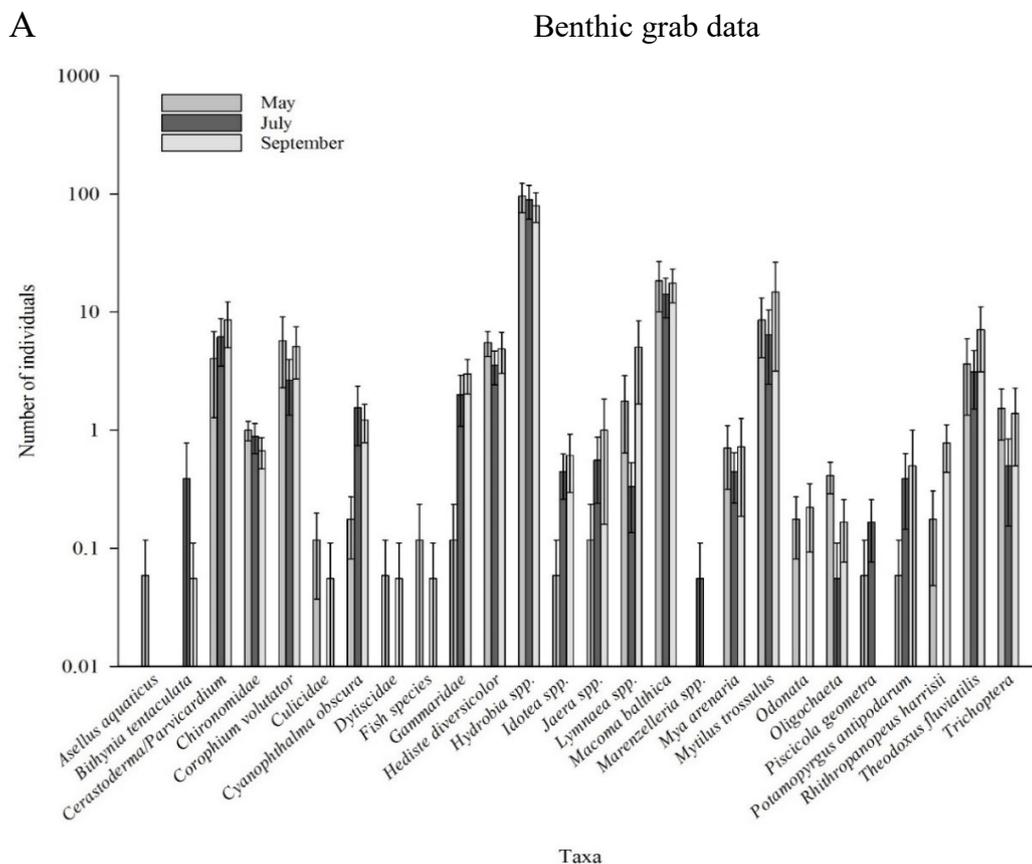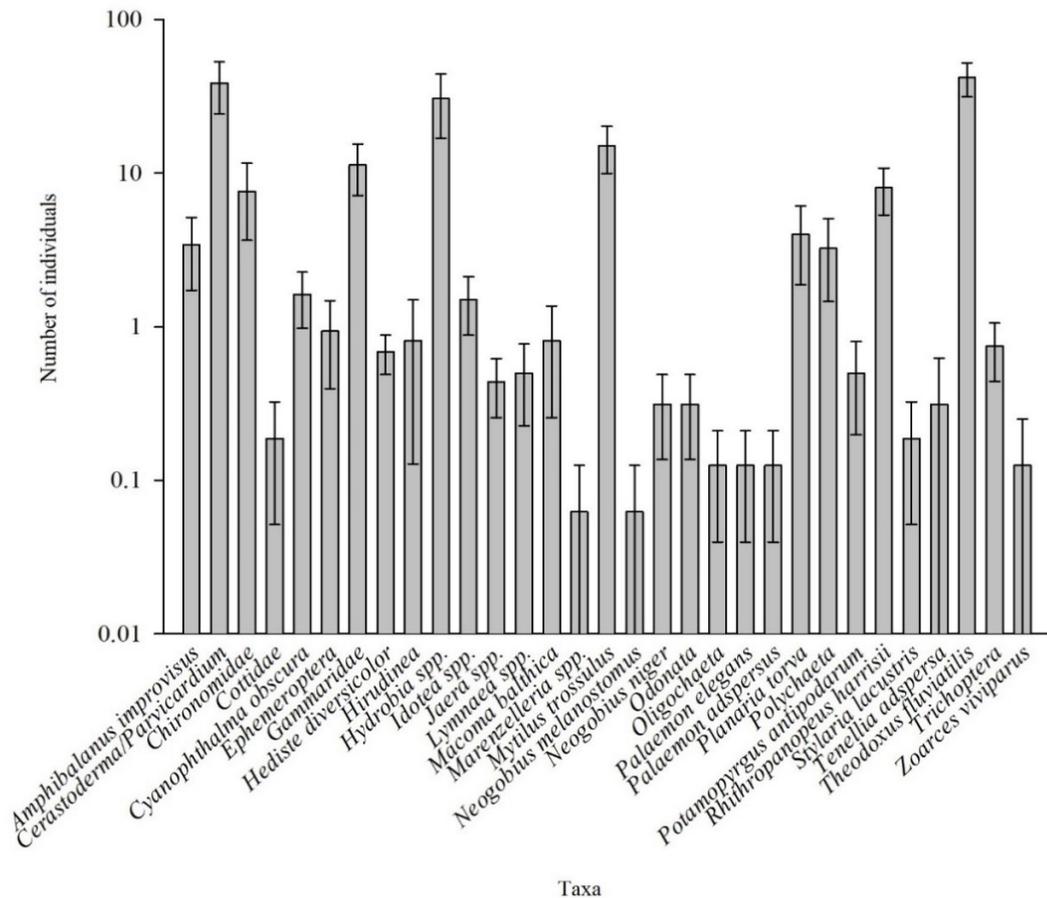
B   Habitat trap data

Figure 5. The number of individuals (mean ± SE) per sample in A) the benthic grab data, by sampling month, and B) the habitat trap data (September only), on logarithmic scale.

In the benthic grab data, the species contributing the most to between invasion stage community differences in the SIMPER analysis was *Hydrobia* spp. (Table 1). In the habitat trap data, the highest contributing species were *Hydrobia* spp. and *Theodoxus fluviatilis* (Table 1). Highest contributing species were also among the most common species in both data (Fig. 5).

Table 1. The species contributing a cumulative 50 % to between invasion stages differences in A) the benthic grab data and B) habitat trap data. Average abundance is based on the number of individuals per sample in the square root transformed data.

A	Benthic grab data		
Species	**Average abundance**		**Contribution-%**
	Established	Uninvaded	
Hydrobia spp.	4.11	12.68	28.57
Macoma balthica	1.76	5.36	12.14
Mytilus trossulus	0.88	3.01	9.40
	Established	Recent	

21

Hydrobia spp.	4.11	6.28	23.26
Macoma balthica	1.76	2.13	10.33
Corophium volutator	0.30	1.43	8.96
Cerastoderma/Parvicardium	0.62	1.62	8.11
	Recent	Uninvaded	
Hydrobia spp.	6.28	12.68	24.18
Macoma balthica	2.13	5.36	12.41
Mytilus trossulus	1.14	3.01	9.13
Cerastoderma/Parvicardium	1.62	2.67	7.40
B	Habitat trap data		
	Established	Uninvaded	
Hydrobia spp.	0.00	9.38	16.94
Theodoxus fluviatilis	1.38	9.28	14.19
Cerastoderma/Parvicardium	2.02	7.60	9.78
Chironomidae	0.00	4.38	7.84
Mytilus trossulus	0.81	4.14	6.58
	Established	Recent	
Theodoxus fluviatilis	1.38	5.64	22.58
Cerastoderma/Parvicardium	2.02	5.27	18.91
Mytilus trossulus	0.81	3.42	13.66
	Recent	Uninvaded	
Hydrobia spp.	1.11	9.38	17.93
Cerastoderma/Parvicardium	5.27	7.60	8.66
Chironomidae	0.62	4.38	8.02
Theodoxus fluviatilis	5.64	9.28	7.80
Mytilus trossulus	3.42	4.14	6.71
Amphipoda	1.83	4.70	6.54

In the non-metric MDS of the benthic grab data, the established and uninvaded communities presented as separate and recently invaded overlapped with both, which was also supported by statistical testing (Fig. 6; Table 2). The stress of 0.19 was, however, quite high and therefore, the two-dimensional representation is not entirely accurate. Adding a third dimension lowered the stress to 0.13. In the habitat trap data, the communities presented more separate from each other, with recently invaded communities between the established and uninvaded, and little to no overlap (Fig. 6). The established and uninvaded communities seemed less similar than the uninvaded and recently invaded communities, contrary to the results of statistical testing (Fig. 6; Table 2).

A Benthic grab data
Community resemblance (nMDS)

Invasion stage
▲ Established
▼ Recent
□ Uninvaded

2D Stress: 0,19

Transformation: Square root
Resemblance: Bray-Curtis similarity

B Habitat trap data
Community resemblance (nMDS)

Transformation: Square root
Resemblance: Bray-Curtis similarity

Invasion stage
▲ Established
▼ Recent
□ Uninvaded

2D Stress: 0,07
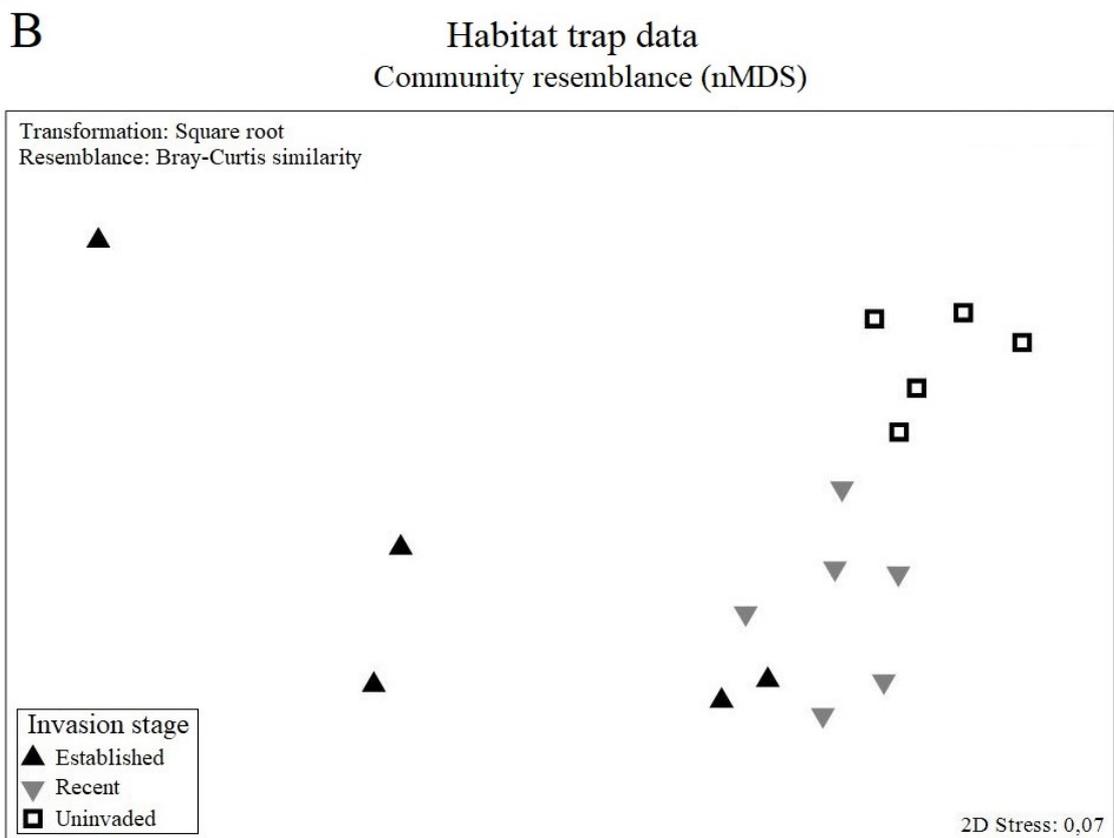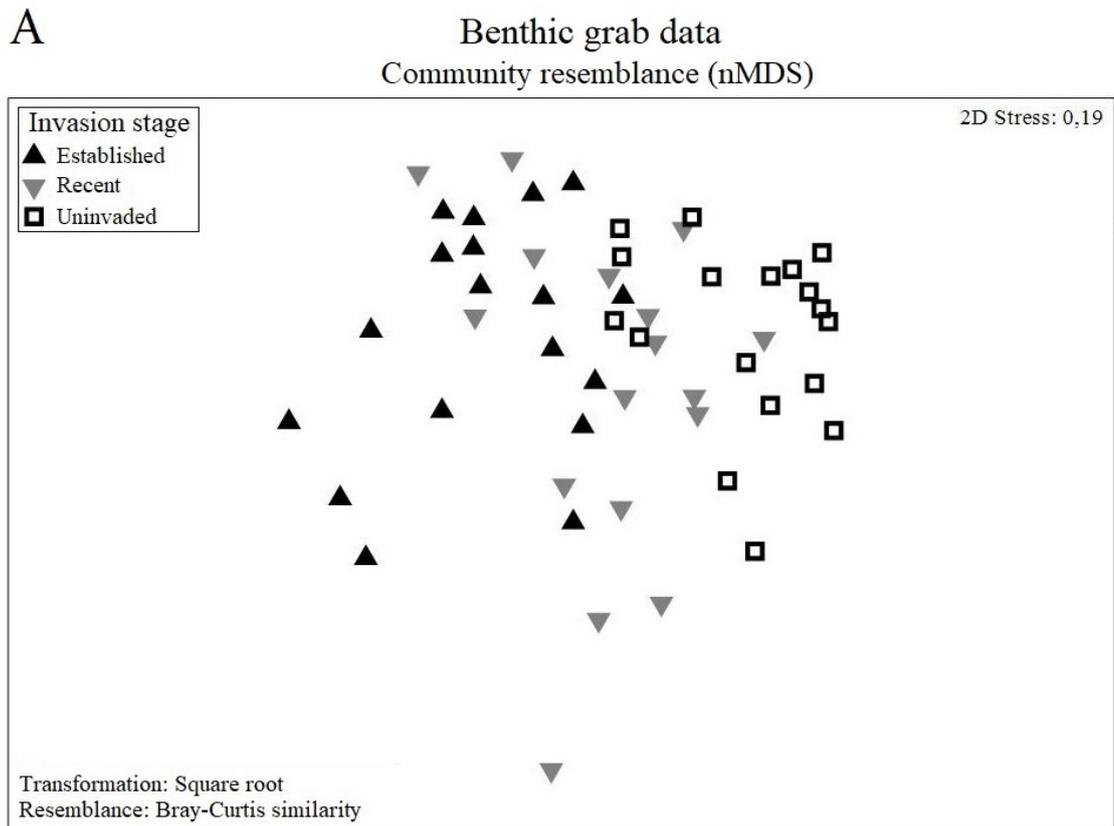
Figure 6. Community resemblance as non-metric multidimensional scaling for A) the benthic grab data and B) habitat trap data. Each data point is one sample; in the habitat trap data (B) only

September samples are used. Resemblance is based on Bray-Curtis similarity measure. Shorter distance between samples indicates similarity.

There were differences in community composition between crab invasion stages in both the benthic grab data and the habitat trap data in statistical testing. In the benthic grab data, there was non-significant indication of the effect of crab invasion stage on the community resemblance as a whole, and the established invasion stage communities significantly differed from the uninvaded communities (Table 2). In the habitat trap data, crab invasion stage had a significant effect on the community resemblance as a whole. Recently invaded communities significantly differed from the uninvaded communities, and there was non-significant indication also for difference between established and uninvaded communities (Table 2). Sampling month, or interactions between month and invasion stage or month and site had no effect on the community resemblance (Table 2). Site nested in invasion stage as a random factor did, however, significantly explain within and between invasion stage community differences (Table 2).

Table 2. The effect of crab invasion stage, sampling month, site as a random factor nested in invasion stage, and interactions on the community resemblance in the benthic grab data (A), and crab invasion stage, site as a random factor nested in invasion stage, and their interaction in the habitat trap data (B). Bolded and italicised P-value indicates statistical significance, italicised indicates a trend. When the number of unique permutations (Perms) is low, Monte-Carlo P-values (P(MC)) should be looked at instead of permutational P-values (P(perm)). Statistical significance is indicated for the correct P-value.

A	Benthic grab data (May-September)				
Factor	**DF**	**Pseudo-F**	**P(perm)**	**P(MC)**	**Perms**
Invasion stage	2, 3	2.1556	0.0244	*0.0756*	45
Month	2, 6.03	1.3282	0.2630	0.2481	9948
Invasion stage x Month	4, 6.01	0.784	0.6934	0.7268	9928
Site (Invasion stage)	3, 35	3.3043	***0.0001***	0.0002	9921
Site (Invasion stage) x Month	6, 35	1.1444	0.2686	0.2717	9871

PAIRWISE TESTS for factor Invasion stage

Groups	**DF**	**t**	**P(perm)**	**P(MC)**	**Perms**
Established, Recent	2	1.1564	0.1633	0.3311	6
Established, Uninvaded	2	2.1019	0.3287	***0.0253***	3
Recent, Uninvaded	2	1.1144	0.1702	0.3637	6

PAIRWISE TESTS for random factor Site (Invasion stage)

Groups	**DF**	**t**	**P(perm)**	**P(MC)**	**Perms**
Established	12	1.2936	0.1776	0.1871	9955
Recent	11	2.0624	***0.0060***	0.0122	9956
Uninvaded	12	2.0384	***0.0023***	0.0093	9938

B	Habitat trap data (September only)				
Factor	**DF**	**Pseudo-F**	**P(perm)**	**P(MC)**	**Perms**
Invasion stage	2, 3.02	3.0427	0.0418	***0.0297***	45
Site (Invasion stage)	3, 10	1.9967	***0.0045***	0.0307	9902

PAIRWISE TESTS for factor Invasion stage

Groups	**DF**	**t**	**P(perm)**	**P(MC)**	**Perms**
Established, Recent	2.02	1.3018	0.1645	0.2424	6
Established, Uninvaded	2	1.8399	0.3342	*0.0650*	3
Recent, Uninvaded	2.04	2.5102	0.1657	***0.0124***	6

PAIRWISE TESTS for random factor Site (Invasion stage)

Groups	**DF**	**t**	**P(perm)**	**P(MC)**	**Perms**
Established	3	1.5830	0.1024	0.1365	10
Recent	4	1.0093	0.3973	0.4187	10
Uninvaded	3	1.2724	0.0975	0.2452	10

In the PCA, the five principal components explained 89.7 % of the variation and the first two a cumulative 60.6 % in the benthic grab data (Fig. 7). In the habitat trap data, the five principal components explained 97.8 % and the first two 67.7 % of the variation (Fig. 7).
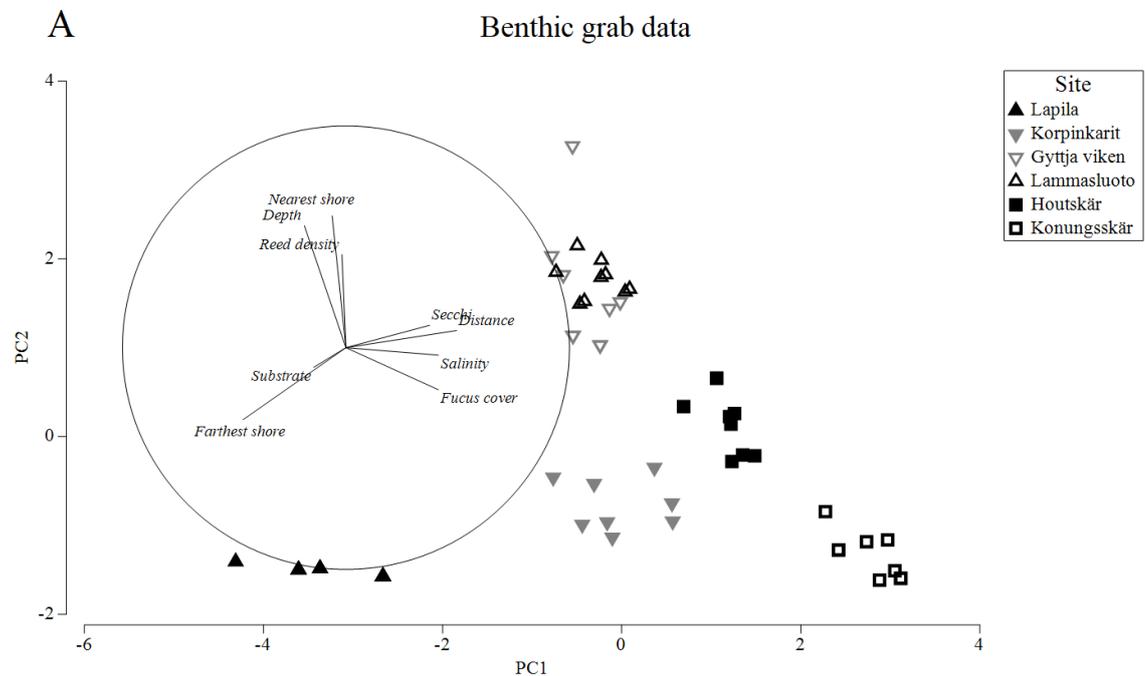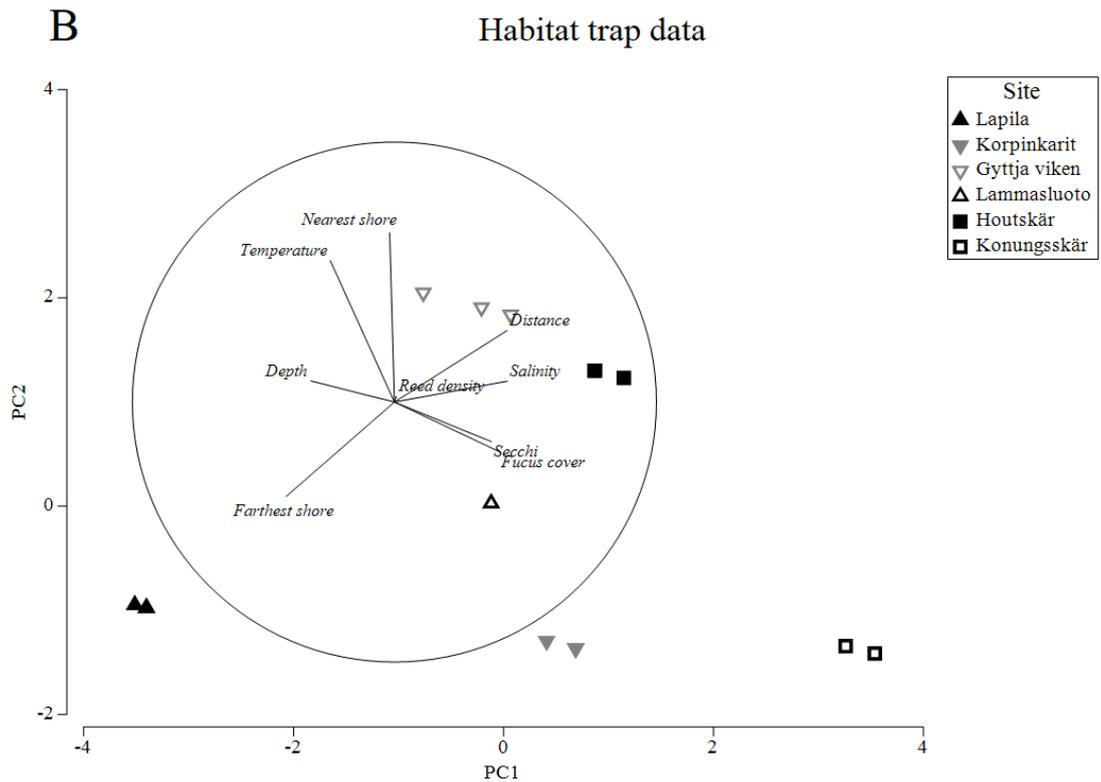
Figure 7. Principal component analysis of A) the benthic grab data and B) habitat trap data. Vector direction indicates the line on which sites are placed in relation to the environmental factor. Sites are fitted on the first two principal component axis explaining A) 60.6 % of the variation in the benthic grab data and B) 67.7 % in the habitat trap data.

In the biota-environment matching, the individual factors correlating the most with community resemblance were distance from invasion centre and *Fucus* coverage in the benthic grab data (Table 3), and distance from invasion centre and distance to farthest shore in the habitat trap data (Table 3). The highest correlating combination of factors, i.e. the combination of environmental factors explaining the most of the community resemblance, was distance from invasion centre, distance to nearest shore, *Fucus* coverage, reed shoot density, depth, and Secchi depth in the benthic grab data (Table 3; P=0.001). In the habitat trap data, the highest correlating combination was distance from invasion centre, distance to farthest shore, *Fucus* coverage, depth, and Secchi depth (Table 3; P=0.001). When crab abundance in the September habitat trap data was added as a factor in the analyses, it was among the highest correlating factors in both benthic grab data and habitat trap data, and was included in all the highest correlating combinations of factors (Table 3; benthic grab data P=0.002, habitat trap data P=0.001).

Table 3. Individual environmental factors' and their combinations' correlation with community resemblance in A) the benthic grab data and B) habitat trap data. Crab abundance (mean number of crabs per sample in the September habitat trap data) was added as a factor in the analyses in a second run to further test the crabs' effect on community resemblance. Resemblance is based on Bray-Curtis similarity.

A Benthic grab data (May-September)		B Habitat trap data (September only)	
Factor	**ρ**	**Factor**	**ρ**
Distance from invasion centre	0.220	Distance from invasion centre	0.692
Fucus coverage	0.216	Distance to farthest shore	0.681
Salinity	0.168	Salinity	0.505
Secchi depth	0.159	Secchi depth	0.466
Distance to farthest shore	0.149	*Fucus* coverage	0.355
Distance to nearest shore	0.147	Depth	0.279
Reed shoot density	0.084	Distance to nearest shore	0.231
Depth	0.069	Reed shoot density	0.015
Bottom substrate	-0.045	Temperature	-0.113
Crab abundance	0.230	Crab abundance	0.770

A Benthic grab data (May-September)	
Combination	**ρ**
Distance from invasion centre, distance to nearest shore, *Fucus* coverage, reed shoot density, depth, Secchi depth	0.293
Distance from invasion centre, *Fucus* coverage, reed shoot density, depth, Secchi depth	0.292
Distance from invasion centre, distance to farthest shore, distance to nearest shore, *Fucus* coverage, reed shoot density, depth	0.292
Distance from invasion centre, distance to nearest shore, *Fucus* coverage, reed shoot density, depth, crab abundance	0.311
Distance from invasion centre, distance to nearest shore, *Fucus* coverage, reed shoot density, depth, Secchi depth, crab abundance	0.310
Distance to nearest shore, *Fucus* coverage, reed shoot density, depth, Secchi depth, crab abundance	0.307

B Habitat trap data (September only)	
Combination	**ρ**
Distance from invasion centre, distance to farthest shore, *Fucus* coverage, depth, Secchi depth	0.777
Distance from invasion centre, distance to farthest shore, *Fucus* coverage, depth, Secchi depth, salinity	0.772
Distance from invasion centre, distance to farthest shore, *Fucus* coverage, Secchi depth	0.768
Distance from invasion centre, distance to farthest shore, *Fucus* coverage, crab abundance	0.813
Distance from invasion centre, crab abundance	0.810
Distance from invasion centre, distance to farthest shore, *Fucus* coverage, depth, Secchi depth, salinity, crab abundance	0.806

3.3 The effect of crab invasion stage on individual species and diversity

R. harrisii invasion stage had an effect on some of the contributing species' abundances in the GLMM, but not all of them (Table 4; for the species, see Table 1). In the benthic grab data, the number of *Hydrobia* gastropods, *Cerastoderma/Parvicardium* bivalves, and *Theodoxus* gastropods was significantly lower in the established crab invasion stage communities compared to the uninvaded (Fig. 8). There was no significant difference in the number of bivalves *Mytilus trossulus* and *Macoma balthica* or the amphipod *Corophium volutator* between the invasion stages (Table 4).
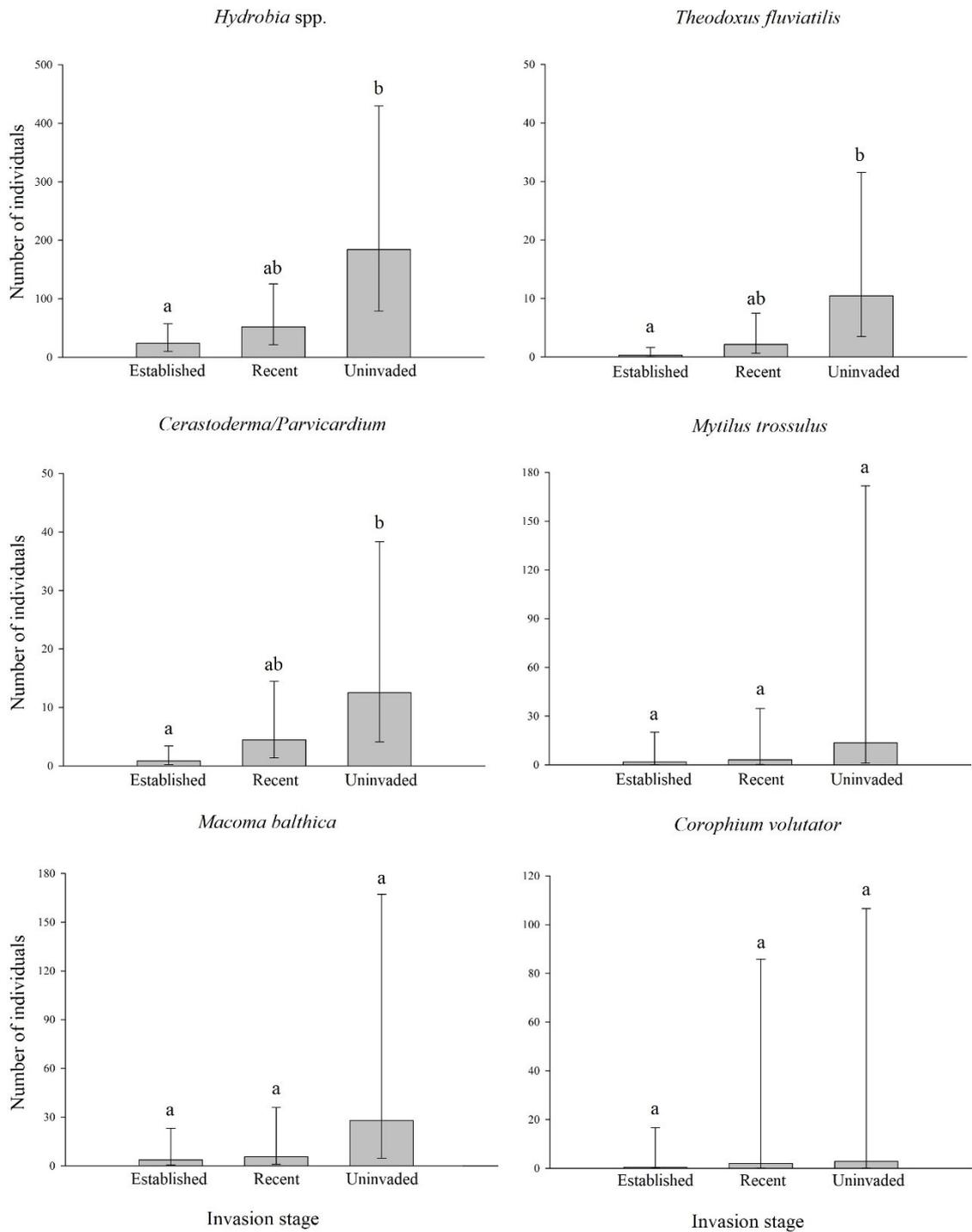
Figure 8. The effect of crab invasion stage on the abundance (mean ± 95 % CL) of the species contributing a cumulative 50 % to between invasion stage community differences in the benthic grab data. Different letters denote significant differences.

In the habitat trap data, the number of *Hydrobia* gastropods and chironomid larvae was significantly lower in both the established and recent invasion stage communities compared to the uninvaded (Fig. 9). Both *Hydrobia* and chironomids were completely missing from the established invasion stage communities. There was also non-significant indication for a lower abundance of *Theodoxus* gastropods and amphipods in the

established invasion stage communities compared to the uninvaded (Table 4). There was no difference in the number of bivalves *Cerastoderma/Parvicardium* and *Mytilus trossulus* between the invasion stages (Table 4).
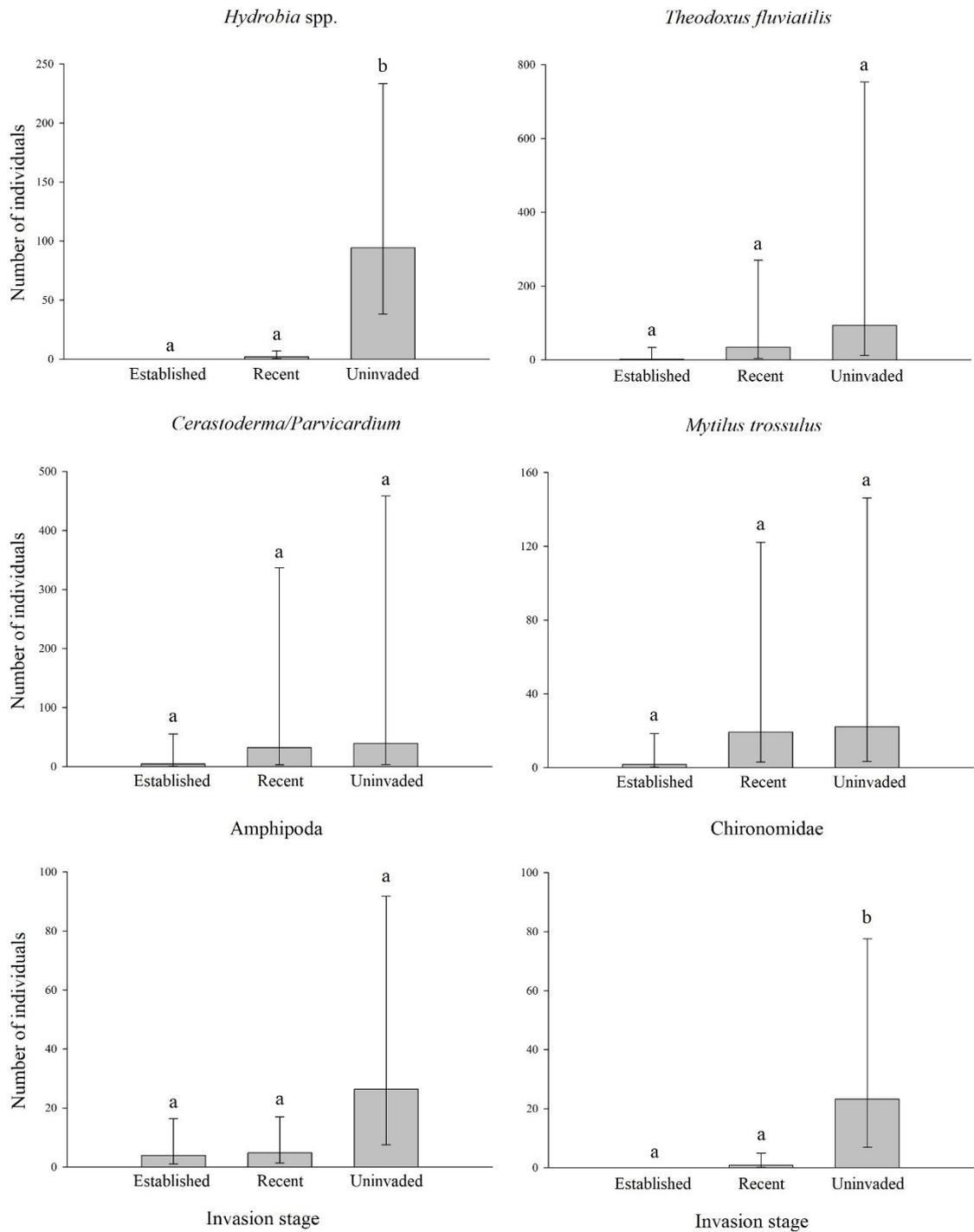

Figure 9. The effect of crab invasion stage on the abundance (mean ± 95 % CL) of the species contributing a cumulative 50 % to between invasion stage community differences in the habitat trap data. Different letters denote significant differences.

30

Sampling month had no effect on the abundance of contributing species in the benthic grab data (Table 4). Site nested in invasion stage as a random factor significantly explained between invasion stage variation for *Macoma balthica* in the benthic grab data, and for *Theodoxus fluviatilis* in the habitat trap data.

Table 4. The effect of A) crab invasion stage and sampling month on the abundance of the species contributing a cumulative 50 % to between invasion stage community differences in the benthic grab data, and B) the effect of crab invasion stage in the habitat trap data. Bolded and italicised P-value indicates statistical significance, italicised indicates a trend.

A	Benthic grab data			
Species	**Factor**	**DF**	**F**	**P**
Hydrobia spp.	Invasion stage	2, 3	14.70	***0.0282***
	Month	2, 45	0.00	0.9959
Macoma balthica	Invasion stage	2, 3	3.51	0.1637
	Month	2, 45	0.85	0.4349
Mytilus trossulus	Invasion stage	2, 3	1.76	0.3123
	Month	2, 45	0.31	0.7347
Cerastoderma/Parvicardium	Invasion stage	2, 3	11.34	***0.0399***
	Month	2, 45	2.21	0.1219
Corophium volutator	Invasion stage	2, 3	0.78	0.5353
	Month	2, 45	1.08	0.3473
Theodoxus fluviatilis	Invasion stage	2, 3	15.87	***0.0254***
	Month	2, 45	1.3	0.2826

B	Habitat trap data			
Species	**Factor**	**DF**	**F**	**P**
Hydrobia spp.	Invasion stage	2, 3	32.76	***0.0092***
Theodoxus fluviatilis	Invasion stage	2, 3	6.13	*0.0871*
Cerastoderma/Parvicardium	Invasion stage	2, 3	2.41	0.2373
Chironomidae	Invasion stage	2, 3	12.64	***0.0346***
Mytilus trossulus	Invasion stage	2, 3	4.18	0.1356
Amphipoda	Invasion stage	2, 3	6.66	*0.0788*

Species diversity measured as Shannon's diversity index did not differ between the invasion stages in the benthic grab data (N=53, $F_{2,3}$=4.05, P=0.1405). In the habitat trap data, invasion stage had a significant effect on the species diversity (N=16, $F_{2,3}$=12.65, P=0.0345). Diversity was higher in the uninvaded communities compared to established invasion stage communities, and there was also statistically non-significant indication of higher diversity in the uninvaded communities compared to recently invaded in the habitat trap data (Fig.10). Diversity did not differ between sampling months in the benthic

grab data (N=53, $F_{2, 45}$=1.12, P=0.3351). Site as a random factor nested in invasion stage had no effect on diversity.
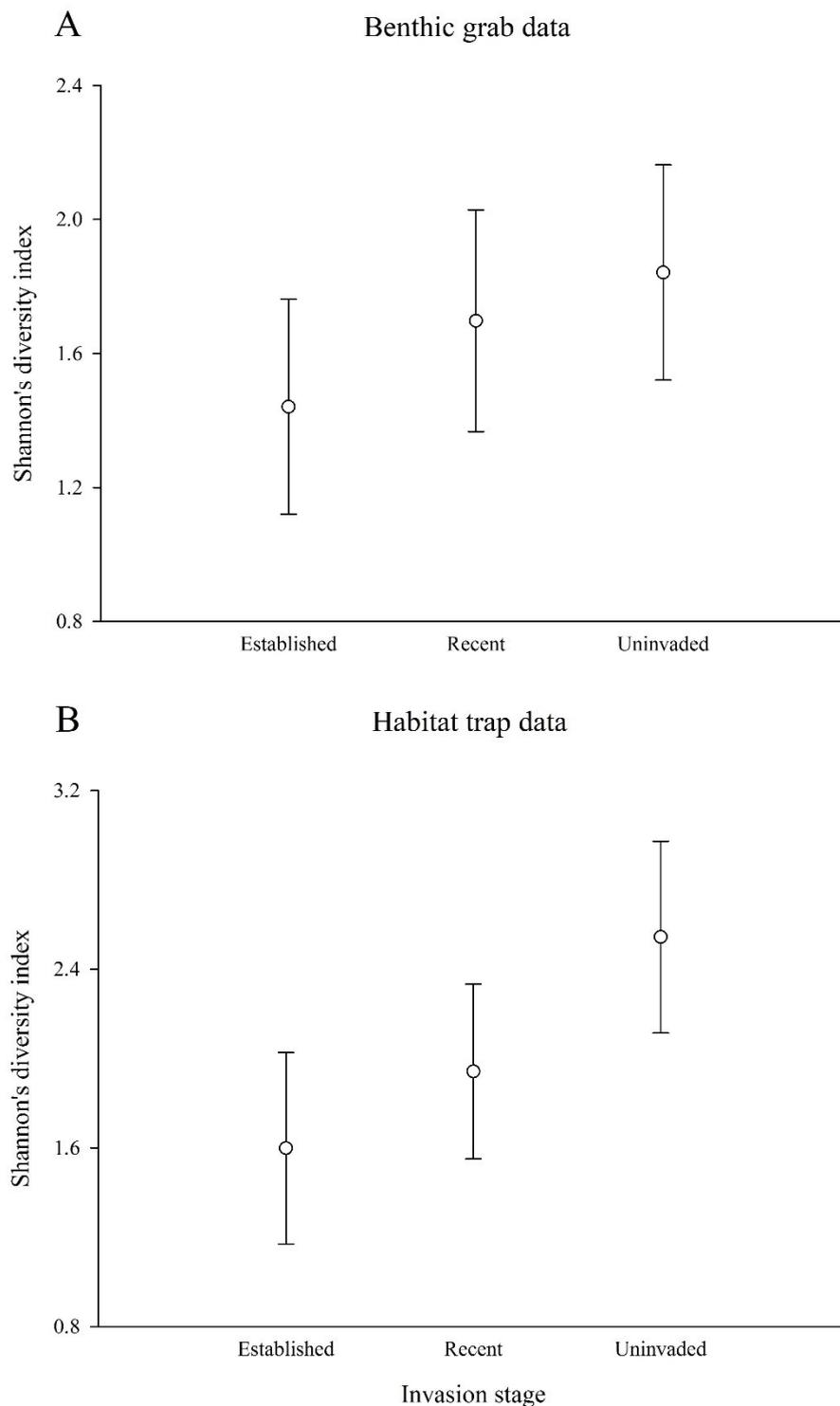
Figure 10. The effect of crab invasion stage on diversity measured as Shannon's diversity index (mean ± 95 % CL) in A) the benthic grab data, and B) habitat trap data. Diversity index is based on square root transformed data. In the habitat trap data (B), diversity is significantly lower in the established invasion stage communities than in the uninvaded communities. In the benthic grab data (A), diversity did not differ between invasion stage.

4   DISCUSSION

R. harrisii abundance at different invasion stages followed what was expected prior to sampling: abundance was the highest at the established invasion stage sites, moderate at recently invaded sites, and there were no *R. harrisii* at the uninvaded sites. Most *R. harrisii* individuals were collected in Lapila, although there was no statistical difference between the abundance in Lapila and Lammasluoto. The mean number of *R. harrisii* in Lapila in this study (25.67 individuals per trap) was similar to that observed in 2011–2016 (28 individuals per trap; Forsström et al. 2018). Similar habitat traps were used in both studies, and consistent results show that the habitat traps are well suited for this kind of sampling.

There was no difference in *R. harrisii* size between the invasion stages. However, between the two established invasion stage sites, *R. harrisii* were on average smaller in Lapila than in Lammasluoto. Overall, there was no difference between the number of adult and juvenile *R. harrisii*. However, in Lapila, unlike the other sites, there were more juvenile than adult *R. harrisii*, which likely explains the size difference there. There were fewer female than male *R. harrisii*, and no ovigerous (egg-carrying) females. *R. harrisii* size and sex were analysed from the habitat trap data from September, at the end of the reproductive period (Turoboyski 1973). In autumn, the number of juvenile (or young-of-the-year) *R. harrisii* is likely higher than in summer, and the number of ovigerous females lower. Some ovigerous females have, however, been found in September and October in the Finnish Archipelago Sea (Fowler et al. 2013) and in Poland, in the Gulf of Gdansk (Hegele-Drywa et al. 2014). A high abundance of juveniles, and lower abundance of female than male *R. harrisii* in autumn has also been previously observed in the Archipelago Sea (Forsström et al. 2018). Reproductive effort may cause higher mortality of females after brooding, and the lower number of female *R. harrisii* could also be explained by different habitat preference between summer and autumn (Forsström et al. 2018). Differences in habitat preference between ovigerous females, and males and non-ovigerous females have been observed in other crab species (Stone and O'Clair 2001; Benetti et al. 2007; Luppi et al. 2013). In the Gulf of Gdansk, the overall male-female ratio is also slightly towards male (Hegele-Drywa et al. 2014), and close to 50 % female in the Archipelago Sea (Forsström et al. 2018).

There was no difference in *R. harrisii* abundance between the invasion stages in the benthic grab data. Only 17 individuals were found in altogether 35 samples taken from the invaded sites. Average density, then, on the invaded sites was 15 crabs/m^2, but with only a few individuals in the samples and no statistical difference from the uninvaded sites, density here is an unreliable estimate. It does, however, give indication as to how high, at least, *R. harrisii* density in the sampled communities is.

R. harrisii density also varies among habitat types in the area. In the Archipelago Sea, densities of up to an average of 75 individuals/m^2 have been measured in *Phragmites australis* reeds, whereas no crabs were found on open mud bottom (Sjöroos 2016). Here, however, the highest abundance of *R. harrisii* was found in Lapila, where the sampled habitat at the site is mostly open mud bottom. Abundance is counted from the habitat trap data, whereas density is calculated from the number of *R. harrisii* on the surface area of the benthic grab. As the habitat traps provide additional structure and shelter on the open bottom, they can attract *R. harrisii* and other animals from a larger area, and therefore, absolute density and relative abundance cannot be compared. The habitat traps may be especially interesting on bottoms with less natural structure, *Fucus vesiculosus* for example. Here, there was no *F. vesiculosus* in Lapila or Gyttja viken.

The studied communities differed between *R. harrisii* invasion stages. In the benthic grab data, the results show indication, though non-significant, that invasion stage had an effect on the overall community composition, and the communities, where *R. harrisii* was established, differed from the uninvaded communities. In the habitat trap data, invasion stage affected the community composition as a whole, and the recently invaded communities differed from the communities with no *R. harrisii*. There was also indication for difference between the established invasion stage communities and the uninvaded communities.

Diversity in the habitat trap data was significantly higher in the uninvaded communities compared to the established invasion stage communities, and there was also indication for higher diversity in the uninvaded communities than in the recently invaded. In the benthic grab data, diversity did not differ between *R. harrisii* invasion stages. Therefore, the communities in the benthic grab data are not different in terms of diversity, but rather, differ in the community structure. The different results between the habitat trap data and

the benthic grab data may also be due to sampling method. The habitat traps attract more mobile animals and are especially efficient in collecting *R. harrisii*. It is likely that *R. harrisii* prey on the species in the habitat traps and therefore differences in the habitat trap data can be more prominent. The lack of difference in diversity in the benthic grab data can likewise be explained by habitat and prey preference. If *R. harrisii* prefer to feed elsewhere, for example in the stands of *F. vesiculosus* (Fowler et al. 2013; Aarnio et al. 2015; Nurkse et al. 2015; Jormalainen et al. 2016) instead of on open bottom searching for buried prey, bottom-dwelling animals may not be impacted.

Differences in the community composition could also be seen in the abundance of some of the species contributing to between invasion stage differences, though not all of them. In the benthic grab data, the abundance of *Hydrobia* spp. and *Theodoxus fluviatilis* gastropods, and *Cerastoderma/Parvicardium* bivalves was significantly lower in the established invasion stage communities than in the uninvaded communities. There was no difference in their abundance between the recently invaded and uninvaded communities, or the established and recently invaded communities. In the habitat trap data, *Hydrobia* spp. and Chironomidae larvae were significantly less abundant in both the established invasion stage communities and recently invaded communities compared to the uninvaded communities. Their abundances did not differ between the established invasion stage and recently invaded communities. There was also non-significant indication of lower abundance of *T. fluviatilis* and amphipods in the established invasion stage communities than in the uninvaded communities.

The effect of *R. harrisii* invasion on the species' abundances is most likely due to predation. *R. harrisii* is an opportunistic predator, and even though the particular species it has favoured as prey in laboratory experiments (Forsström et al. 2015) were not among the contributing species in this study, the contributing species belong in groups that have been found in *R. harrisii* stomach content analyses (Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009). If prey species do not recognise *R. harrisii* as a predator and do not present anti-predator behaviours, such as predator avoidance (Cox and Lima 2006; Sih et al. 2010; Anton et al. 2016), they are likely an easy catch for it. In the northern Baltic Sea, for example, the isopod *Idotea balthica* do not exhibit antipredator response to *R. harrisii* (Yli-Renko et al., submitted ms), and further, have been observed climbing on the crabs in laboratory experiments (personal observation;

Puntila-Dodd et al., unpublished data). Although *R. harrisii* has been speculated not to be a very efficient predator (Hegele-Drywa and Normant 2009), it reacts to the scent of food and begins searching for it (Kidawa et al. 2004). *R. harrisii* do also catch mobile prey, at least in laboratory setting (Forsström et al. 2015).

However, predator avoidance can also be another explanation for the decreased abundance of some species in the presence of *R. harrisii*. The abundance of *T. fluviatilis* snails has been found to decrease with increasing *R. harrisii* also in other studies (Forsström et al. 2015; Jormalainen et al. 2016), and in laboratory settings, *T. fluviatilis* have a tendency to escape from aquaria with *R. harrisii* present (Forsström et al. 2015; Puntila-Dodd et al., unpublished data).

Out of the three bivalve species among the species contributing the most to community differences, only the abundance of the species pair *Cerastoderma/Parvicardium* was affected by *R. harrisii* invasion stage. This is somewhat confusing, as shell size and thickness are factors that limit the predation on hard-shelled animals due to prey handling cost and risk of claw damage (Juanes 1992), and both *Mytilus trossulus* and *Macoma balthica* seem to have thinner, softer shells than *Cerastoderma/Parvicardium*. One possible explanation, at least for *M. trossulus* is its low abundance also at the uninvaded site in Konungsskär. The sampling site at Konungsskär, although located in the outer archipelago, is very sheltered and shallow with seemingly little current between the two islands, and as such, it may not be suitable habitat for *M. trossulus*. Because of this, possible predation effects towards *M. trossulus* may not be apparent in statistical testing, even though *M. trossulus* would be suitable prey for *R. harrisii*. *M. balthica* on the other hand, may not be preferred prey, if *R. harrisii* do not primarily search for food buried in the sediment. However, there were crushed and eaten *Cerastoderma/Parvicardium* bivalves in the habitat trap samples, and the same was not noted for the other bivalve species.

Site nested in invasion stage was used as a random factor in the analyses to account for natural variation between the sites. Site was significant in explaining overall community differences in both data, and differences between the established invasion stage sites and recently invaded sites in the benthic grab data. Site also significantly explained differences in the abundance of some of the contributing species, but not diversity. The

sites were different not only in terms of *R. harrisii* invasion stage, but also for example in their location in the inner to outer archipelago and habitat characteristics at site. Community composition was explained by environmental factors, especially distance from the initial invasion centre. The uninvaded sites were also the farthest from the invasion centre, and therefore *R. harrisii* invasion stage and distance from invasion centre are correlated. However, adding *R. harrisii* abundance as an environmental factor to the biota-environment matching model, with distance from the invasion centre already included, resulted in a higher correlation between community composition and the environmental factors.

In addition to distance from the initial invasion centre, other environmental factors that explained the community composition were *F. vesiculosus* coverage, *Phragmites australis* shoot density*,* and depth, all included in the highest correlating combinations of factors in the benthic grab data. In the habitat trap data, distance to farthest shore, *F. vesiculosus* coverage, and Secchi depth were similarly included in the highest correlating combinations of factors. The importance of *F. vesiculosus* to community composition can therefore be seen in both data, and regardless of the size of the correlation coefficient, communities in similar habitats are more similar to each other. The environmental factors were overall more highly correlated with community composition in the habitat trap data. However, with the samples collected only in September compared to the three sampling occasions and higher temporal variation in the benthic grab data, the effect of the environmental factors cannot be compared between data.

Communities in the Archipelago Sea can be characterised by their position in the land-sea ratio based archipelago zones with zone-typical species (Bonsdorff et al. 2003; Perus and Bonsdorff 2003; O'Brien et al. 2004). Here, Lapila is located in the inner, and Konungsskär in the outer archipelago, with most sites in the middle archipelago (sensu Jaatinen 1960). The species found in the outer archipelago and the farthest from mainland (or initial invasion centre) in this study do not match those typically found in the outer archipelago (Appendix II; Bonsdorff et al. 2003; O'Brien et al. 2004). Previous studies have, however, typically sampled deep bottoms, whereas here all the sites were very shallow and sheltered. Depth and exposure are considered more significant in explaining species assemblages than the traditional geographical zonation (O'Brien et al. 2004; Burrows et al. 2008). In this study, the shortest and longest fetch lengths (distance to the

nearest and farthest shore, respectively) were used to indicate site openness and exposure, and both measures were the smallest in Konungsskär in the outer archipelago, whereas the longest fetch length was measured from Lapila in the inner archipelago.

Community composition, diversity, or the abundance of contributing species did not differ between sampling months in the benthic grab data. Seasonal variation could probably be seen in the size distribution of *R. harrisii* or other species, with individual growth and species-specific reproductive patterns, if measured. Otherwise, temporal variation would likely be observed with continued sampling. Species abundances can fluctuate quite a lot between years, and observations made over a single year may not necessarily be adequate to show invasion effects (Kindlmann et al. 2011). However, with growing evidence to support changes coinciding with increasing *R. harrisii* abundance and spread over multiple years, and comparisons between invaded and uninvaded communities, it is very likely that the observed changes are driven by *R. harrisii*. Decapods are also one the most successful groups of non-indigenous species, with major impacts on communities (Hänfling et al. 2011).

In addition to the direct effects of *R. harrisii* observed both here and previously (Jormalainen et al. 2016; Kotta et al. 2018; Lokko et al. 2018), *R. harrisii* may have indirect effects on the communities. Cascading effects in the *F. vesiculosus* communities could likely be mediated by the reduction in the abundance of *Theodoxus fluviatilis*. *T. fluviatilis* are grazers on the epiphytic algae growing on *F. vesiculosus* (Honkanen and Jormalainen 2005; Råberg and Kautsky 2008). Epiphytic algae are harmful to the growth and reproduction of *F. vesiculosus* (Honkanen and Jormalainen 2005; Korpinen et al. 2007), and therefore, the decreased abundance of *T. fluviatilis* due to predation by or avoidance of *R. harrisii* could have larger scale impacts on the *F. vesiculosus* communities. However, though not among the contributing species here, *R. harrisii* also prey on the isopods *Idotea* spp. (Forsström et al. 2015; Jormalainen et al. 2016) that, in turn, feed directly on *F. vesiculosus* (Råberg and Kautsky 2008). High abundances of *Idotea* spp. in the autumn can defoliate entire stands of *F. vesiculosus* (Haavisto and Jormalainen 2014), and a reduction in their number could also benefit *F. vesiculosus*, but affect their native predators. *R. harrisii* have also been found in eelgrass *Zostera marina* meadows (Gagnon and Boström 2016), and on hard-bottom *M. trossulus* beds (Puntila-Dodd et al., submitted ms), meaning more impacts can likely be expected.

As *R. harrisii* has established itself in the northern Baltic Sea, it has become integrated in the native species diet. In the Archipelago Sea, the four-horned sculpin *Myoxocephalus quadricornis*, and perch *Perca fluviatilis* and roach *Rutilus rutilus* to lesser extent, (Puntila-Dodd et al. 2019), as well as some seabirds (Forsström et al. 2015) have been found to consume *R. harrisii*. After the initial rapid increase in the number of *R. harrisii* in the area, its abundance seems to have reached a stable lower level, indicating top-down control by new native predators (Forsström et al. 2018).

In conclusion, the results show a significant shift in the benthic invertebrate community composition with advancing *R. harrisii* invasion. The decrease in the abundance of specific native species also has implications for further-reaching cascading effects on the habitat-forming key species in the northern Baltic Sea. With continuing spread to new areas and habitats, further assessment of the impacts of *R. harrisii* is needed. The current study provides a reference point for future research in the expanding range and is the first revealing community-level changes in different stages of *R. harrisii* invasion.

ACKNOWLEDGEMENTS

REFERENCES

Aarnio K, Törnroos A, Björklund C, Bonsdorff E (2015) Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea. Aquatic Invasions 10: 399–413. doi: 10.3391/ai.2015.10.4.04

Albins MA, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. Environmental Biology of Fishes 96: 1151–1157. doi: 10.1007/s10641-011-9795-1

Anderson MJ, Gorley RN, Clarke KR (2008) *PERMANOVA+ for PRIMER: Guide to software and statistical methods*. PRIMER-E, Plymouth.

Andersson A, Meier HEM, Ripszam M, Rowe O, Wikner J, Haglund P, Eilola K, Legrand C, Figueroa D, Paczkowska J, Lindehoff E, Tysklind M, Elmgren R (2015) Projected future climate change and Baltic Sea ecosystem management. Ambio 44: S345–S356. doi: 10.1007/s13280-015-0654-8

Anton A, Cure K, Layman CA, Puntila R, Simpson MS, Bruno JF (2016) Prey naiveté to invasive lionfish *Pterois volitans* on Caribbean coral reefs. Marine Ecology Progress Series 544: 257–269. doi: 10.3354/meps11553

AquaNIS Editorial Board (2015) Information system on aquatic non-indigenous and cryptogenic species. Version 2.36+ <http://www.corpi.ku.lt/databases/aquanis> [Accessed 31.7.2021]

Baltic LINes (2016) Shipping in the Baltic Sea – past, present and future developments relevant for maritime spatial planning. Project Report I.

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. Marine Policy 27: 313–323. doi: 10.1016/S0308-597X(03)00041-1

Benetti AS, Negreiros-Fronsozo ML, Costa TM (2007) Population and reproductive biology of the crab *Uca burgersi* (Crustacea: Ocypodidae) in three subtropical mangrove forests. Revista de Biología Tropical 55: S55–S70. doi: 10.15517/rbt.v55i0.5806

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83: 887–889.

Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasions. Ecology Letters 9: 887–895. doi: 10.1111/j.1461-0248. 2006.00934.x

Bonsdorff E, Laine AO, Hänninen J, Vuorinen I, Norkko A (2003) Zoobenthos of the outer archipelago waters (N. Baltic Sea) – the importance of local conditions for spatial distribution patterns. Boreal Environmental Research 8: 135–145.

Bonsdorff E (2006) Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. Journal of Experimental Marine Biology and Ecology 330: 383–391. doi: 10.1016/j.jembe.2005.12.041

Boyle T Jr, Keith D, Pfau R (2010) Occurrence, reproduction, and population genetics of the estuarine mud crab, *Rhithropanopeus harrisii* (Gould) (Decapoda, Panopidae) in Texas freshwater reservoirs. Crustaceana 83: 493–505. doi: 10.1163/ 001121610X492148

Burrows MT, Harvey R, Robb L (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. Marine Ecology Progress Series 353: 1–12. doi: 10.3354/meps07284

Chavez FP, Messié M, Pennington JT (2011) Marine primary production in relation to climate variability and change. Annual Review of Marine Science 3: 227–260. doi: 10.1146/annurev.marine.010908.163917

Clarke KR, Gorley RN (2015) *PRIMER v7: User Manual/Tutorial*. PRIMER-E, Plymouth.

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721–733. doi: 10.1111/j.1461-0248.2004.00616.x

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends in Ecology and Evolution 21: 674–680. doi: 10.1016/j.tree.2006.07.011

Czerniejewski P, Rybczyk A (2008) Body weight, morphometry, and diet of the mud crab, *Rhithropanopeus harrisii tridentatus* (Maitland, 1874) in the Odra estuary, Poland. Crustaceana 81: 1289–1299. doi: 10.1163/156854008X369483

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invisibility. Journal of Ecology 88: 528–534. doi: 10.1046/j.1365-2745.2000.00473.x

Dethier MN, Hacker SD (2005) Physical factors vs. biotic resistance in controlling the

invasion of an estuarine marsh grass. Ecological Applications 15: 1273–1283. doi: 10.1890/04-0505

Enders M, Havemann F, Ruland F, Bernard-Verdier M, Catford JA, Gomez-Aparicio L, Haider S, Heger T, Kueffer C, Kühn I, Meyerson LA, Musseau C, Novoa A, Ricciardi A, Sagouis A, Schittko C, Strayer DL, Vilà M, Essl F, Hulme PE, van Kleunen M, Kumschick S, Lockwood JL, Mabey AL, McGeoch MA, Palma E, Pyšek P, Saul W-C, Yannelli FA, Jeschke JM (2020) A conceptual map of invasion biology: integrating hypotheses into a consensus network. Global Ecology and Biogeography 29: 978–991. doi: 10.1111/geb.13082

FinBIF (2021) *Rhithropanopeus harrisii*. <http://tun.fi/HBF.54813> [Accessed 31.7.2021]

Forsström T, Fowler AE, Manninen I, Vesakoski O (2015) An introduced species meets the local fauna: predatory behavior of the crab *Rhithropanopeus harrisii* in the Northern Baltic Sea. Biological Invasions 17: 2729–2741. doi: 10.1007/s10530-015-0909-0

Forsström T, Vesakoski O, Riipinen K, Fowler AE (2018) Post-invasion demography and persistence of a novel functional species in an estuarine system. Biological Invasions 20: 3331–3345. doi: 10.1007/s10530-018-1777-1

Fowler AE, Forsström T, von Numers M, Vesakoski O (2013) The North American mud crab *Rhithropanopeus harrisii* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. Aquatic Invasions 8: 89–96. doi: 10.3391/ai.2013.8.1.10

Gagnon K, Boström C (2016) Habitat expansion of the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea: potential consequences for the eelgrass food web. BioInvasions Records 5: 101–106. doi:10.3391/bir.2016.5.2.07

Geburzi JC, McCarthy ML (2018) How do they do it? – Understanding the success of marine invasive species. In: *YOUMARES 8 – Oceans Across Boundaries: Learning from each other* (Jungblut S, Liebich V, Bode M, eds.), pp. 109–124. Springer, Cham. doi: 10.1007/978-3-319-93284-2_8

Gillison AN (2018) Latitudinal variation in plant functional types. In: *Geographical changes in vegetation and plant functional studies* (Greller AM, Fujiwara K, Pedrotti F, eds.), pp. 21–57. Springer, Cham. doi: 10.1007/978-3-319-68738-4_2

Guy-Haim T, Lyons DA, Kotta J, Ojaveer H, Queirós AM, Chatzinikolaou E, Arvanitidis C, Como S, Magni P, Blight AJ, Orav-Kotta H, Somerfield PJ, Crowe TP, Rilov G

(2018) Diverse effects on invasive ecosystem engineers on marine biodiversity and ecosystem functions: a global review and meta-analysis. Global Change Biology 24: 906–924. doi: 10.1111/gcb.14007

Haavisto F, Jormalainen V (2014) Seasonality elicits herbivores' escape from trophic control and favors induced resistance in a temperate macroalgae. Ecology 95: 3035–3045. doi: 10.1890/13-2387.1

Harff J, Björck S, Hoth P (2011) The Baltic Sea basin: Introduction. In: *The Baltic Sea Basin* (Harff J, Björck S, Hoth P, eds.), pp. 3–9. Springer, Heidelberg, Dordrecht, London, New York. doi: 10.1007/978-3-642-17220-5_1

Hegele-Drywa J, Normant M (2009) Feeding ecology of the American crab *Rhithropanopeus harrisii* (Crustacea, Decapoda) in the coastal waters of the Baltic Sea. Oceanologia 51:361–375. doi: 10.5697/oc.51-3.361

Hegele-Drywa J, Normant M, Szwarc B, Podluska A (2014) Population structure, morphometry and individual condition of the non-native crab *Rhithropanopeus harrisii* (Gould, 1841), a recent coloniser of the Gulf of Gdansk (southern Baltic Sea). Oceanologia 56: 805–824. doi: 10.5697/oc.56-4.805

HELCOM (2018a) State of the Baltic Sea – second HELCOM holistic assessment 2011-2016. Baltic Sea Environment Proceedings 155. Helsinki Commission, Helsinki.

HELCOM (2018b) HELCOM Assessment on maritime activities in the Baltic Sea 2018. Baltic Sea Environment Proceedings 152. Helsinki Commission, Helsinki.

HELCOM (2021) HELCOM Hot Spots. <https://helcom.fi/action-areas/industrial-municipal-releases/helcom-hot-spots> [Accessed 18.8.2021]

Herlevi H, Puntila R, Kuosa H, Hagerholm H-P (2017) Infection rates and prevalence of metazoan parasites of the non-native round goby (*Neogobius melanostomus*) in the Baltic Sea. Hydrobiology 792: 265–282. doi: 10.1007/s10750-016-3062-6

Honkanen T, Jormalainen V (2005) Genotypic variation in tolerance and resistance to fouling in the brown alga *Fucus vesiculosus*. Oecologia 144: 196–205. doi: 10.1007/s00442-005-0053-0

Hänfling B, Edwards F, Gherardi F (2011) Invasive alien Crustacea: dispersal, establishment, impact and control. BioControl 56: 573–595. doi: 10.1007/s10526-011-9380-8

Ikonen I, Hagelberg E (2007) *Read up on reed!* Southwest Finland Regional Environment Centre, Turku.

Jaatinen S (1960) Geografiska regioner. In: *Atlas över Skärgårds-Finland* (Smeds H, ed.), map 15. Nordenskiöld samfundet i Finland, Helsinki. (Referenced in: O'Brien K, Hänninen J, Kanerva T, Metsärinne L, Vuorinen I (2003) Macrozoobenthic zonation in relation to major environmental factors across the Archipelago Sea, northern Baltic Sea. Boreal Environment Research 8: 159–170.)

Jakobsson M, Stranne C, O'Regan M, Greenwood SL, Gustafsson B, Humborg C, Weidner E (2019) Bathymetric properties of the Baltic Sea. Ocean Science 15: 905–924. doi: 10.5194/os-15-905-2019

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. Biological Invasions 18: 1409–1419. doi:10.1007/s10530-016-1090-9

Juanes F (1992) Why do decapod crustaceans prefer small-sized molluscan prey? Marine Ecology Progress Series 87: 239–249. doi: 10.3354/MEPS087239

Kallasvuo M, Lappalainen A, Urho L (2011) Coastal reed belts as fish reproduction habitats. Boreal Environment Research 16: 1–14. doi: 10.1016/j.ecss.2018.02.014

Karhilahti A (2010) Taskurapu tarttui pyydykseen. Suomen Luonto 4: 12–13.

Kaskela AM, Kotilainen AT (2017) Seabed geodiversity in a glaciated shelf area, the Baltic Sea. Geomorphology 295: 419–435. doi: 10.1016/j.geomorph.2017.07.014

Kautsky H, Martin G, Snoeijs-Leijonmalm P (2017) The phytobenthic zone. In: *The Biological oceanography of the Baltic Sea* (Snoeijs-Leijonmalm P, Schubert H, Radziejewska T, eds.), pp. 387–455. Springer, Dordrecht. doi: 10.1007/978-94-007-0668-2_11

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164–170. doi:10.1016/S0169-5347(02)02499-0

Kelley AL (2014) The role of thermal physiology plays in species invasion. Conservation Physiology 2: 1–14. doi: 10.1093/conphys/cou045

Kerswell AP (2006) Global biodiversity patterns of benthic marine algae. Ecology 87: 2479-2488. doi: 10.1890/0012-9658(2006)87[2479:GBPOBM]2.0.CO;2

Kidawa A, Markowska M, Rakusa-Suszczewski S (2004) Chemosensory behaviour in the mud crab, *Rhithropanopeus harrisii tridentatus* from Martwa Wisla Estuary (Gdansk Bay, Baltic Sea). Crustaceana 77: 897–908. doi: 10.1163/1568540042781711

Kiirikki M (1996) Mechanisms affecting macroalgal zonation in the northern Baltic Sea. European Journal of Phycology 31: 225–232. doi: 10.1080/09670269600651421

Kimbro DL, Grosholz E, Baukus AJ, Nesbitt NJ, Travis NM, Attoe S, Coleman-Hulbert
C (2010) Invasive species cause large-scale loss of native California oyster habitat
by disrupting trophic cascades. Oecologia 160: 563–575. doi: 10.1007/s00442-009-1322-0

Kindlmann P, Ameixa OMCC, Dixon AFG (2011) Ecological effects of invasive alien
species on native communities, with particular emphasis on the interactions between
aphids and ladybirds. BioControl 56: 469–476. doi: 10.1007/s10526-011-9384-4

Kornis MS, Mercado-Silva N, Vander Sanden MJ (2012) Twenty years of invasion: a
review of round goby *Neogobius melanostomus* biology, spread and ecological
implications. Journal of Fish Biology 80: 235–285. doi: 10.1111/j.1095-8649.2011.03157.x

Korpinen S, Jormalainen V, Honkanen T (2007) Effects of nutrients, herbivory, and depth
on the macroalgal community along a depth gradient. Journal of Experimental
Marine Biology and Ecology 88: 839–852. doi: 10.1890/05-0144

Korpinen S, Meski L, Andersen JH, Laamanen M (2012) Human pressures and their
potential impact on the Baltic Sea ecosystem. Ecological Indicators 15: 105–114. doi:
10.1016/j.ecolind.2011.09.023

Kotta J, Wernberg T, Jänes H, Nurkse K, Pärnoja M, Orav-Kotta H (2018) Novel crab
predator causes marine ecosystem regime shift. Scientific Reports 8: 4956. doi:
10.1038/s41598-018-23282-w

Lau JA (2013) Trophic consequences of a biological invasion: do plant invasions increase
predator abundance? Oikos 122: 474–480. doi: 10.1111/j.1600-0706.2012.20774.x

Leppäkoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S, Panov V (2002) The Baltic
– a sea of invaders. Canadian Journal of Fisheries and Aquatic Sciences 59: 1175–1188. doi:10.1139/f02-089

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic
plant invasions. Ecology Letters 7: 975–989. doi: 10.1111/j.1461-0248.2004.00657.x

Liljeberg M (2016) Spatial distribution of leisure boats in the Baltic Sea region. IVL
Swedish Research Institute, Stockholm.

Lokko K, Kotta J, Orav-Kotta H, Nurkse K, Pärnoja M (2018) Introduction of a
functionally novel consumer to a low diversity system: effects of the mud crab
Rhithropanopeus harrisii on meiobenthos. Estuarine, Coastal and Shelf Science 201:
132–139. doi: 10.1016/j.ecss.2015.11.017

Long WC, Grow JN, Majoris JE, Hines AH (2011) Effects of anthropogenic shoreline hardening and invasion by *Phragmites australis* on habitat quality for juvenile blue crabs (*Callinectes sapidus*). Journal of Experimental Marine Biology and Ecology 409: 215–222. doi: 10.1016/j.jembe.2011.08.024

Luppi T, Bas C, Méndez Casariego A, Albano M, Lancia J, Kittlein M, Rosenthal A, Farías N, Spivak E, Iribarne O (2013) The influence of habitat, season and tidal regime in the activity of the intertidal crab *Neohelice* (=*Chasmagnathus*) *granulate*. Helgoland Marine Research 67: 1–15. doi: 10.1007/s10152-012-0300-9

McAfee D, Connell SD (2021) The global fall and rise of oyster reefs. Frontiers in Ecology and the Environment 19: 118–125. doi: 10.1002/fee.2291

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6: 485–492. doi: 10.1890/070064

Niemivuo-Lahti J (ed.) (2012) *Finland's national strategy on invasive alien species*. Ministry of Agriculture and Forestry, Helsinki.

Norkko J, Reed DC, Timmermann K, Norkko A, Gustafsson BG, Bonsdorff E, Slomp CP, Carstensen J, Conley DJ (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. Global Change Biology 18: 422–434. doi:10.1111/j.1365-2486.2011.02513x

Nurkse K, Kotta J, Orav-Kotta H, Pärnoja M, Kuprijanov I (2015) Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisii* (Gould) in an invaded ecosystem: the north-eastern Baltic Sea. Estuarine, Coastal and Shelf Science 154: 152–157. doi: 10.1016/j.ecss.2014.12.046

Nurkse K, Kotta J, Rätsep M, Kotta I, 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: 25–31. doi: 10.1017/S0025315417001965

O'Brien K, Hänninen J, Kanerva T, Metsärinne L, Vuorinen I (2003) Macrozoobenthic zonation in relation to major environmental factors across the Archipelago Sea, northern Baltic Sea. Boreal Environment Research 8: 159–170.

Ojaveer H, Olenin S, Narščius A, Florin A-B, Ezhova E, Gollasch S, Jensen KR, Lehtiniemi M, Minchin D, Normant-Saremba M, Strāke S (2017) Dynamics of biological invasions and pathways over time: a case study of a temperate coastal sea. Biological Invasions 19: 799–813. doi: 10.1007/s10530-016-1316-x

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. doi: 10.1007/s10750-014-2080-5

Olenin S, Gollasch S, Lehtiniemi M, Sapota M, Zaiko A (2017) Biological invasions. In: *Biological oceanography of the Baltic Sea* (Snoeijs-Leijonmalm P, Schubert H, Radziejewska T, eds.), pp. 193–232. Springer, Dordrecht. doi: 10.1007/978-94-007-0668-2_5

Olenin S, Leppäkoski E (1999) Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. Hydrobiologia 393: 233–243.

Outinen O, Forsström T, Yli-Rosti J, Vesakoski O, Lehtiniemi M (2019) Monitoring of sessile and mobile epifauna – considerations for non-indigenous species. Marine Pollution Bulletin 141: 332–342. doi: 10.1016/j.marpolbul.2019.02.055

Paavola M, Olenin S, Leppäkoski E (2005) Are invasive species most successful in habitats of low native species richness across European brackish water seas? Estuarine and Coastal Shelf Science 64: 738–750. doi: 10.1016/j.ecss.2005.03.021

Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. Frontiers in Ecology and the Environment 2: 131–138. doi: 10.1890/1540-9295(2004)002[0131:BBWAAO]2.0.CO;2

Perus J, Bonsdorff E (2003) Long-term changes in macrozoobenthos in the Åland archipelago, northern Baltic Sea. Journal of Sea Research 52: 45–56. doi: 10.1016/j.seares.2003.07.004

Peters K, Sink KJ, Robinson TB (2019) Sampling methods and approaches to inform standardized detection of marine alien fouling species on recreational vessels. Journal of Environmental Management 230: 159–167. doi: 10.1016/j.jenvman.2018.09.063

Puntila-Dodd R, Loisa O, Riipinen K, Fowler AE (2019) A taste for aliens: contribution of a novel prey item to native fishes' diet. Biological Invasion 21: 2907–2917. doi: 10.1007/s10530-019-02021-w

Reise K, Buschbaum C, Büttger H, Wegner KM (2017) Invading oysters and native mussels: from hostile takeover to compatible bedfellows. Ecosphere 8: e01949. doi: 10.1002/ecs2.1949

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7: 781–784. doi: 10.1111/j.1461-0248.2004.00642.x

Ricciardi A, Kipp R (2008) Predicting the number of ecologically harmful exotic species in an aquatic system. Diversity and Distributions 14: 374–380. doi: 10.1111/j.1472-4642.2007.00451.x

Riipinen K, Mikkola S, Ahola MK, Aalto MM, Olkinuora A, Vesakoski O (2017) Habitat selection of the mud crab *Rhithropanopeus harrisii* in its newly invaded range. Aquatic Invasions 12: 191–200. doi: 10.3391/ai.2017.12.2.07

Rilov G (2009) Predator-prey interactions of marine invaders. In: Biological Invasions in Marine Ecosystems (Rilov G, Crooks JA, eds.), pp. 261–285. Springer-Verlag, Berlin, Heidelberg. doi: 10.1007/978-3-540-79236-9_15

Roche D (2021) *Rhithropanopeus harrisii.* In: Invasive Species Compendium. CAB International, Wallingford. <https://www.cabi.org/isc/datasheet/66045> [Accessed 12.8.2021]

Roche DG, Torchin ME (2007) Established population of the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould, 1841) (Crustacea: Brachyura: Xanthidae) in the Panama Canal. Aquatic Invasions 2: 155–161. doi: 10.3391/ai.2007.2.3.1

Roy HE, Lawson Handley L-J, Schönrogge K, Poland RL, Purse BV (2011) Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? BioControl 56: 451–468. doi: 10.1007/s10526-011-9349-7

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. American Zoologist 37: 621–632. doi: 10.1093/icb/37.6.621

Råberg S, Kautsky L (2008) Grazer identity is crucial for facilitating growth of the perennial brown alga *Fucus vesiculosus*. Marine Ecology Progress Series 361: 111–118. doi: 10.3354/meps07428

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305–320. doi: 10.1146/annurev.ecolsys.32.081501.114037

Schubert K (1936) *Pilumnopeus tridentatus* Maitland, eine neue Rundkrabbe in Deutschland. Zoologischer Anzeiger 116: 320–323.

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR (2010) Predator-prey naivete, anti-predator behavior, and the ecology of predator invasions. Oikos 119: 610–621. doi:10.1111/j.1600-0706.2009.18039.x

Sjöroos J (2016) Liejutaskuravun (*Rhithropanopeus harrisii*) tiheyden määrittäminen Saaristomeren liejupohjilla. Bachelor's Thesis, University of Turku, Turku.

Snoeijs-Leijonmalm P (2017) Patterns of biodiversity. In: *Biological oceanography of the Baltic Sea* (Snoeijs-Leijonmalm P, Schubert H, Radziejewska T, eds.), pp. 123–191. Springer, Dordrecht. doi: 10.1007/978-94-007-0668-2_4

Snoeijs-Leijonmalm P, Andrén E (2017) Why is the Baltic Sea so special to live in? In: *Biological oceanography of the Baltic Sea* (Snoeijs-Leijonmalm P, Schubert H, Radziejewska T, eds.), pp. 123–191. Springer, Dordrecht. doi: 10.1007/978-94-007-0668-2_2

Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83: 2575–2590. doi: 10.1890/0012-9658(2002)083[2575:BIRAME]2.0.CO;2

Stevens RD, Rowe RJ, Badgley C (2019) Gradients of mammalian biodiversity through space and time. Journal of Mammalogy 100: 1069–1086. doi: 10.1093/jmammal/gyz024

Stevens RD, Tello JS (2018) A latitudinal gradient in dimensionality of biodiversity. Ecography 41: 2016–2026. doi: 10.1111/ecog.03654

Stone RP, O'Clair CE (2001) Seasonal movements and distribution of Dungeness crabs *Cancer magister* in a glacial southeastern Alaska estuary. Marine Ecology Progress Series 214: 167–176. doi: 10.3354/meps214167

Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. Marine Ecology Progress Series 495: 39–47. doi: 10.3354/meps10566

Tolvanen H, Suominen T (2005) Quantification of openness and wave action in archipelago environments. Estuarine, Coastal and Shelf Science 64: 436–446. doi: 10.1016/j.ecss.2005.03.001

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions 3: 333–345. doi: 10.1023/A:1015855019360

Turoboyski K (1973) Biology and ecology of the crab *Rhithropanopeus harrisii* ssp. *tridentatus*. Marine Biology 23: 303–313. doi: 10.1007/BF00389338

Valentine JW, Jablonski D (2015) A twofold role for global energy gradients in marine biodiversity trends. Journal of Biogeography 42: 997–1005. doi: 10.1111/jbi.12515

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant component of human-induced global change. New Zealand Journal of Ecology 21: 1–16.

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United Stated. BioScience 48: 607–615.

Williams AB (1984) *Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida*. Smithsonian Institution, Washington D.C.

Williamson MH, Fitter A (1996) The varying success of invaders. Ecology 77:1661–1666.

Zalota AK, Kolyuchkina GA, Tiunov AV, Biriukov SV, Spiridonov VA (2017) The trophic position of the alien crab *Rhithropanopeus harrisii* (Crustacea Decapoda Panopeidae) in the Taman Bay, Sea of Azov community. Oceanology 57: 322–330. doi: 10.1134/S0001437017020217

Zettler ML, Karlsson A, Kontula T, Gruszka P, Laine AO, Herkül K, Schiele KS, Maximov A, Haldin J (2014) Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data. Helgoland Marine Research 68: 49–57. doi: 10.1007/s10152-013-0368-x

Appendix I
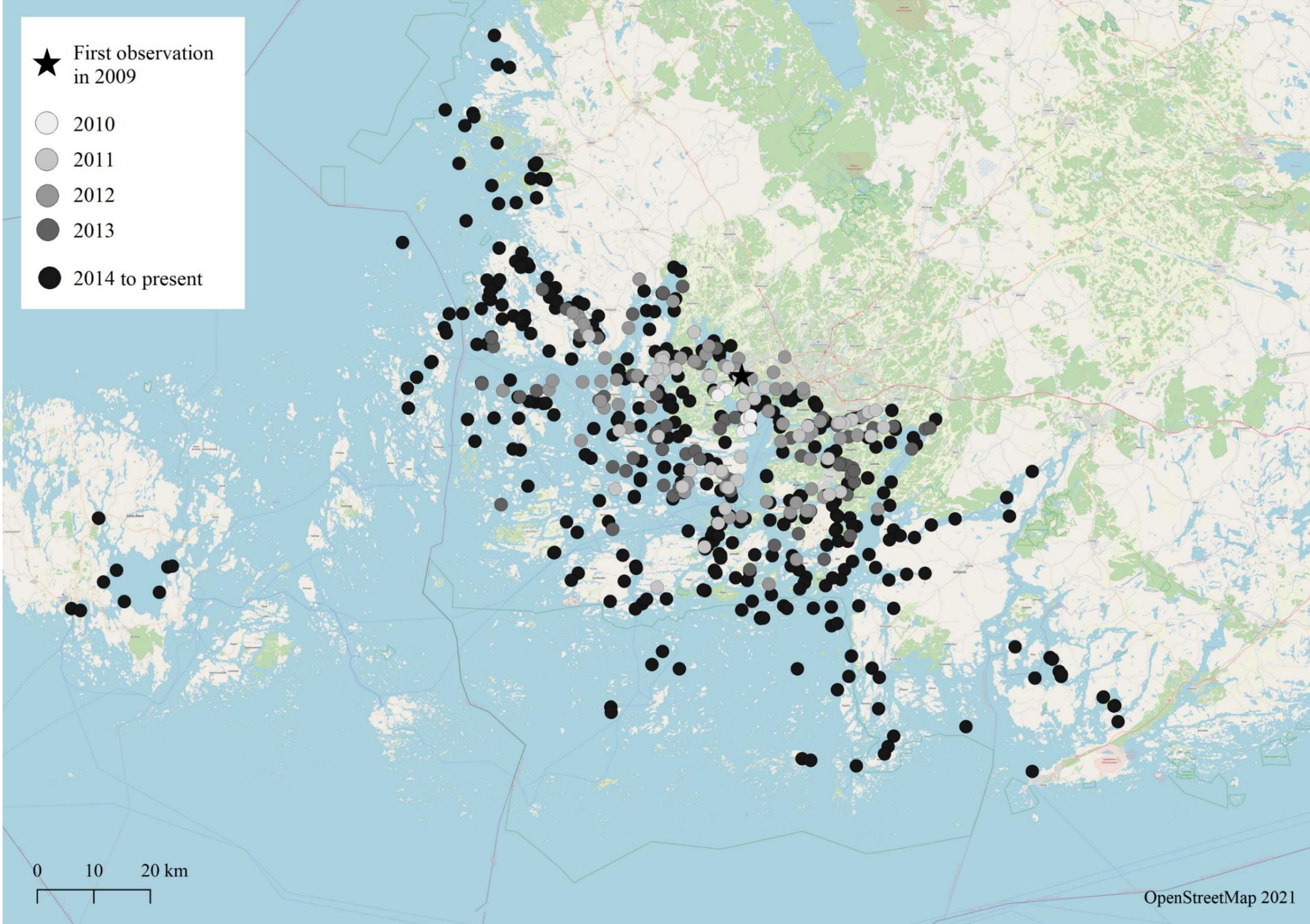
Map of *R. harrisii* observations from the public from the first observation in Naantali in 2009 to July 2021 (FinBIF 2021). Community sampling was done based on observations by 2013.

Appendix II

Mean, minimum, and maximum number of individuals per sample, and standard deviation of the mean at each site in A) the benthic grab data and B) the habitat trap data.

A	Benthic grab data (May-September)			
	Number of individuals			**Standard**
Species	**Mean**	**Minimum**	**Maximum**	**deviation**
Established invasion stage				
Lapila				
Amphipoda	0.22	0	2	0.67
Asellus aquaticus	0.11	0	1	0.33
Cerastoderma/Parvicardium	0.56	0	3	1.01
Chironomidae	Present	-	-	-
Corophium volutator	0.33	0	3	1.00
Fish species	0.11	0	1	0.33
Hediste diversicolor	1.67	0	8	2.69
Hydrobia spp.	29.44	0	73	27.10
Macoma balthica	5.11	1	15	4.78
Mya arenaria	0.11	0	1	0.33
Mytilus trossulus	0.89	0	7	2.32
Oligochaeta	Present	-	-	-
Piscicola geometra	0.11	0	1	0.33
Rhithropanopeus harrisii	0.67	0	4	1.41
Theodoxus fluviatilis	0.33	0	2	0.71
Lammasluoto				
Amphipoda	1.11	0	6	1.96
Cerastoderma/Parvicardium	1.56	0	5	2.01
Chironomidae	Present	-	-	-
Corophium volutator	0.78	0	4	1.56
Cyanophthalma obscura	1.11	0	3	1.27
Hediste diversicolor	4.22	0	9	3.42
Hydrobia spp.	18.11	0	46	15.43
Idotea spp.	0.11	0	1	0.33
Macoma balthica	2.56	0	5	1.81
Mya arenaria	0.67	0	4	1.41
Mytilus trossulus	3.56	0	11	4.36
Oligochaeta	Present	-	-	-
Rhithropanopeus harrisii	0.33	0	2	0.71
Theodoxus fluviatilis	0.22	0	1	0.44

Recent invasion stage

Korpinkarit

Amphipoda	2.38	0	14	4.90
Cerastoderma/Parvicardium	6.13	0	36	12.18
Chironomidae	Present	-	-	-
Corophium volutator	0.25	0	2	0.71
Culicidae	0.13	0	1	0.35
Cyanophthalma obscura	2.38	0	14	4.78
Hediste diversicolor	5.75	1	17	5.26
Hydrobia spp.	79.75	15	181	66.01
Idotea spp.	0.50	0	3	1.07
Jaera spp.	3.00	0	15	5.10
Macoma balthica	14.88	0	44	13.87
Mya arenaria	0.13	0	1	0.35
Mytilus trossulus	5.38	0	17	6.91
Odonata	0.13	0	1	0.35
Oligochaeta	Present	-	-	-
Piscicola geometra	0.13	0	1	0.35
Rhithropanopeus harrisii	0.50	0	3	1.07
Theodoxus fluviatilis	3.13	0	9	3.40
Trichoptera	1.00	0	6	2.14

Gyttja viken

Amphipoda	3.11	0	12	4.14
Cerastoderma/Parvicardium	5.00	0	26	8.34
Chironomidae	Present	-	-	-
Corophium volutator	9.22	0	20	8.07
Cyanophthalma obscura	0.44	0	3	1.01
Hediste diversicolor	0.89	0	3	1.17
Hydrobia spp.	30.11	0	93	35.24
Idotea spp.	0.22	0	2	0.67
Macoma balthica	2.11	0	7	2.71
Marenzelleria spp.	0.11	0	1	0.33
Mytilus trossulus	1.22	0	8	2.59
Odonata	0.11	0	1	0.33
Oligochaeta	Present	-	-	-
Potamopyrgus antipodarum	0.22	0	2	0.67
Rhithropanopeus harrisii	0.44	0	4	1.33
Theodoxus fluviatilis	1.67	0	8	2.50
Trichoptera	2.33	0	15	4.87

Uninvaded

Houtskär				
Amphipoda	2.11	0	12	3.89
Cerastoderma/Parvicardium	20.56	0	60	23.05
Chironomidae	Present	-	-	-
Corophium volutator	0.33	0	2	0.71
Culicidae	0.11	0	1	0.33
Cyanophthalma obscura	0.33	0	2	0.71
Hediste diversicolor	2.89	0	8	3.06
Hydrobia spp.	132.11	12	315	100.27
Idotea spp.	1.00	0	5	1.66
Lymnaea spp.	0.44	0	3	1.01
Macoma balthica	12.11	0	33	11.14
Mya arenaria	1.00	0	9	3.00
Mytilus trossulus	46.56	0	212	68.31
Odonata	0.33	0	2	0.71
Oligochaeta	Present	-	-	-
Piscicola geometra	0.11	0	1	0.33
Theodoxus fluviatilis	15.22	0	69	24.18
Trichoptera	0.44	0	2	0.73
Konungsskär				
Amphipoda	1.56	0	12	3.97
Bithynia tentaculata	0.89	0	7	2.32
Cerastoderma/Parvicardium	4.11	0	12	4.40
Chironomidae	Present	-	-	-
Corophium volutator	15.44	0	50	19.79
Culicidae	0.11	0	1	0.33
Cyanophthalma obscura	1.89	0	7	2.71
Dytiscidae	0.22	0	1	0.44
Fish species	0.22	0	2	0.67
Hediste diversicolor	12.56	4	34	9.61
Hydrobia spp.	240.78	30	380	131.48
Idotea spp.	0.44	0	2	0.73
Jaera spp.	0.67	0	4	1.41
Lymnaea spp.	13.67	0	45	18.32
Macoma balthica	63.22	22	125	34.94
Mya arenaria	1.78	0	6	1.99
Mytilus trossulus	1.78	0	9	2.91
Odonata	0.22	0	1	0.44
Oligochaeta	Present	-	-	-
Piscicola geometra	0.11	0	1	0.33
Potamopyrgus antipodarum	1.67	0	9	3.04
Theodoxus fluviatilis	7.11	0	29	10.94
Trichoptera	3.00	0	11	4.03

B	Habitat trap data (September only)			
	Number of individuals			**Standard**
Species	**Mean**	**Minimum**	**Maximum**	**deviation**
Established invasion stage				
Lapila				
Amphibalanus improvisus	2.00	0	3	1.73
Amphipoda	3.67	1	7	3.06
Cerastoderma/Parvicardium	1.00	0	2	1.00
Idotea spp.	0.67	0	2	1.15
Marenzelleria spp.	0.33	0	1	0.58
Neogobius melanostomus	0.33	0	1	0.58
Neogobius niger	0.33	0	1	0.58
Palaemon elegans	0.33	0	1	0.58
Polychaeta	0.33	0	1	0.58
Rhithropanopeus harrisii	25.67	12	39	13.50
Lammasluoto				
Amphipoda	4.50	3	6	2.12
Cerastoderma/Parvicardium	15.00	12	18	4.24
Cottidae	0.50	0	1	0.71
Hediste diversicolor	1.00	0	2	1.41
Idotea spp.	0.50	0	1	0.71
Mytilus trossulus	4.50	2	7	3.54
Palaemon elegans	0.50	0	1	0.71
Rhithropanopeus harrisii	12.50	10	15	3.54
Theodoxus fluviatilis	12.00	10	14	2.83
Zoarces viviparus	1.00	0	2	1.41
Recent invasion stage				
Korpinkarit				
Amphibalanus improvisus	0.67	0	1	0.58
Amphipoda	4.00	1	10	5.20
Cerastoderma/Parvicardium	35.33	6	64	29.01
Chironomidae	1.00	0	3	1.73
Cyanophthalma obscura	2.00	0	6	3.46
Hediste diversicolor	0.67	0	2	1.15
Hydrobia spp.	4.00	1	7	3.00
Idotea spp.	0.67	0	2	1.15
Jaera spp.	0.33	0	1	0.58
Mytilus trossulus	27.00	0	48	24.56
Neogobius niger	0.67	0	2	1.15
Planaria torva	0.67	0	2	1.15
Polychaeta	0.67	0	2	1.15
Rhithropanopeus harrisii	4.67	2	8	3.06
Theodoxus fluviatilis	35.00	20	58	20.22

Gyttja viken				
Amphibalanus improvisus	4.67	1	11	5.51
Amphipoda	5.67	0	10	5.13
Cerastoderma/Parvicardium	26.33	15	34	10.02
Chironomidae	0.67	0	1	0.58
Hediste diversicolor	0.33	0	1	0.58
Hirudinea	0.33	0	1	0.58
Hydrobia spp.	0.33	0	1	0.58
Macoma balthica	0.33	0	1	0.58
Mytilus trossulus	9.67	2	25	13.28
Odonata	1.00	0	2	1.00
Palaemon adspersus	0.33	0	1	0.58
Rhithropanopeus harrisii	4.33	3	5	1.15
Theodoxus fluviatilis	31.33	17	39	12.42
Trichoptera	0.67	0	1	0.58
Uninvaded				
Houtskär				
Amphibalanus improvisus	10.33	1	27	14.47
Amphipoda	19.33	5	34	14.50
Cerastoderma/Parvicardium	127.67	36	214	89.12
Chironomidae	18.00	6	27	10.82
Cottidae	0.67	0	2	1.15
Cyanophthalma obscura	4.33	2	7	2.52
Ephemeroptera	3.00	0	8	4.36
Hediste diversicolor	1.00	1	1	0.00
Hirudinea	0.33	0	1	0.58
Hydrobia spp.	76.67	37	128	46.61
Idotea spp.	3.67	1	8	3.79
Jaera spp.	1.67	1	2	0.58
Lymnaea spp.	1.67	0	3	1.53
Macoma balthica	1.00	1	1	0.00
Mytilus trossulus	40.00	15	62	23.64
Neogobius niger	0.67	0	2	1.15
Oligochaeta	0.33	0	1	0.58
Palaemon adspersus	0.33	0	1	0.58
Planaria torva	11.67	0	22	11.06
Polychaeta	16.33	9	25	8.08
Potamopyrgus antipodarum	1.33	0	3	1.53
Stylaria lacustris	0.33	0	1	0.58
Theodoxus fluviatilis	85.00	61	120	31.00
Trichoptera	1.67	0	4	2.08

Konungsskär				
Amphibalanus improvisus	1.00	0	2	1.41
Amphipoda	37.00	9	65	39.60
Cerastoderma/Parvicardium	8.50	8	9	0.71
Chironomidae	31.50	4	59	38.89
Cyanophthalma obscura	3.50	1	6	3.54
Ephemeroptera	3.00	2	4	1.41
Hediste diversicolor	1.50	1	2	0.71
Hirudinea	5.50	0	11	7.78
Hydrobia spp.	123.00	62	184	86.27
Idotea spp.	4.00	1	7	4.24
Jaera spp.	0.50	0	1	0.71
Lymnaea spp.	1.50	0	3	2.12
Macoma balthica	4.50	0	9	6.36
Mytilus trossulus	1.50	1	2	0.71
Odonata	1.00	0	2	1.41
Oligochaeta	0.50	0	1	0.71
Planaria torva	13.50	1	26	17.68
Potamopyrgus antipodarum	2.00	0	4	2.83
Stylaria lacustris	1.00	0	2	1.41
Tenellia adspersa	2.50	0	5	3.54
Theodoxus fluviatilis	96.00	52	140	62.23
Trichoptera	2.50	2	3	0.71