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The effects of a novel invasive predator (*Rhithropanopeus harrisii*) on rocky littoral invertebrate community in the Northern Baltic

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Human facilitated introductions of invasive species into aquatic systems on a global scale result in major environmental and economic losses. Many contemporary examples have shown that invasive species have the ability to drive native population to extinction. Invasive predators can cause major disturbances to native communities through either direct (competition, predation) or indirect (interaction chains or interaction modification) means. In the Northern Baltic Sea, prior studies have suggested that a novel invasive decapod, *Rhithropanopeus harrisii,* can drastically reduce important mesoherbivore densities in rocky littoral habitats. In this thesis, I investigated changes in invertebrate communities exposed to *R. harrisii* in *Fucus vesiculosus* dominated shores. I compared community structures and the abundance of affected species across sites with different durations of crab exposure. Results suggested that *R. harrisii* can quickly decimate much of the native mesoherbivore community. In their place, densities of filter feeders and bivalves increased. Even sites with long co-existence with the crab did not show signs of recovery, possibly due to delayed prey antipredatory responses or a more persistent regime shift enforced by the crab. I argue that the changes to invertebrate communities and release from top-down control for macrophytes can likely worsen growth conditions for slow-growing perennial algae and exacerbate eutrophication-like effects as a result of reduced herbivory.

Key Words: community ecology, aquatic ecology, invasive species, Baltic Sea

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1 Introduction

1.1 Invasive species in aquatic systems

Invasive species are defined as non-indigenous species, that pose a threat to native ecosystems, habitats or species (Convention on Biological Diversity (CBD), 2008). While the dispersal of species to new areas is a completely natural phenomenon, the rate and expanse, and therefore possible threats of introductions have been greatly accelerated by human activity. Compared to the natural spread through dispersal, species invasions are by definition human mediated and the number of new invasions has been increasing rapidly in modern times (Carlton, 2000). Species invasions are a prominent global issue both environmentally and economically (Blackburn et al., 2019; Cuthbert et al., 2021; Mollot et al., 2017).

Invasions progress through four distinct phases: (1) transport out of a native area, (2) introduction to a new habitat, (3) establishment of a self-sufficient population in an introduced habitat, and (4) spread and expansion from the newly invaded area (Papacostas et al., 2017). All of these steps pose challenges for potential invaders that they must overcome to permanently settle in new regions. Therefore, successful invaders are not a random sample of available species but instead share characteristics that make them successful in reaching, settling and surviving alien environments. Qualities such as fast reproduction and growth, high tolerance to environmental stressors and a generalist feeding strategy are common among successful invaders. (Papacostas et al., 2017).

The framework for invasion ecology and invader interactions has been built on a multitude of ecological theories like the enemy release (Liu & Stiling, 2006) and novel weapons (Callaway & Ridenour, 2004) hypotheses that predict invasion success through biotic interactions or theories considering invader characteristics such as the ideal weed hypothesis (Elton, 1958). A review by Catford et al. (2009) gathered and described 29 hypotheses explaining invasion success and invader characteristics and condensed them into a framework consisting of three distinct drivers: propagule pressure (P), abiotic characteristics of the invaded environment (A), and the characteristics of native communities or invading species (biotic characteristics; B). They concluded that for a successful invasion to occur, there has to be a sufficient number of introductions into a habitat that is environmentally appropriate and with biotic interactions that allow establishment and possible spread. These drivers are not fixed, but their strength and relationship changes in time and space.

The negative interactions among native and invasive species as well as the traits of invasive species in aquatic environments have been extensively studied (Papacostas et al., 2017). The systematic review by Papacostas et al. (2017) outlined two major negative interactions: competition and consumer pressure. They found that in aquatic environments, many invasive species succeeded by filling new functional niches therefore limiting competition with existing species. Based on their review, functional diversity of the native system acts as a more reliable measure for resilience against invasion than traditional species diversity.

Due to the confounding effects of invasive species along with other biotic and abiotic drivers, quantifying the effects of invaders is difficult (Mollot et al., 2017; Thomsen et al., 2014). This complexity is even more evident when looking at community level responses like diversity (Thomsen et al., 2014). However, based on extensive study and reviews, it can be concluded that invasive species can impose serious impacts on whole ecosystems through competition, predation or disease transmission (Blackburn et al., 2019). The same characteristics that allow non-indigenous species to successfully establish also often cause adverse effects for the ecosystems they invade (Blackburn et al., 2019).

Aquatic communities are characterized by strong trophic links, which generally make them susceptible to the effects of invasive species. Distinct trophic levels and strong trophic links in aquatic communities can result in top-down or bottom-up effects that propagate through the food web (Gallardo et al., 2016). A meta-analysis by Gallardo et al. (2016) investigated the effects of aquatic invasive species on resident communities through direct biotic interactions and habitat alteration on a global scale. Based on their analysis, invaders cause a generalized decrease of abundance and diversity in aquatic systems. They found that the effect of successful invaders on native species is highly dependent on the trophic position of the invader and functional group of the resident community. In addition to reducing the abundance, and in some cases diversity, of resident species, invaders also impacted nutrient concentrations and water turbidity.

Many contemporary examples have demonstrated that invasive predators have the ability to drive entire populations and species to extinction (Doherty et al., 2016). In aquatic ecosystems, invasive predators and omnivores can impact benthic invertebrates through competition, predation or habitat alterations. In addition, they can also affect producer communities through grazing (omnivores) or grazer removal (Gallardo et al., 2016). A meta-analysis by Faria et al. (2025), looking at analogous native and invasive predators, concluded that invasive predators often have higher maximum consumption rates and attack rates than their native counterparts, especially in resource-rich environments. They found this effect to be significant particularly in freshwater habitats, where a higher level of isolation between systems increases the potential for naivety between native and alien populations. Differences in consumption and attack rates were also dependent on the taxonomic and functional group of the invader, with mollusk, insect and crustacean invaders showing higher consumption rates relative to their native analogs. Interestingly, the results from Faria et al. (2025) suggested that invaders more closely related to the recipient communities' native populations had considerably higher maximum consumption rates than more distant relatives, most likely due to the more closely related relatives being better "pre-adapted" to taking advantage of available resources. This contradicts some earlier theories that invasion impacts increase with decreased evolutionary co-existence (Anton et al., 2020).

A major factor in invasive predator interactions is the naivety of native prey species and the lack of efficient antipredatory responses (Carthey & Banks, 2014). This results in situations where prey species are unable to recognize and respond to a novel predator (Kondoh, 2006). Predator invasions are often characterized by the so-called boom-and-bust pattern, where after an initial lag time, the invader population quickly explodes, eradicating much of the prey population. After the initial boom, the predator population decreases and prey population increases to more stable levels (Carthey & Banks, 2014; Kondoh, 2006). This pattern has been described as a result of the mismatch between the adaptive behavioral plasticity of predator and prey. Before a novel predator is introduced to a new area, both the predator and prey are naïve to each other. However, as soon as the predator is introduced, it will start gaining experience and adapting to take advantage of the native prey. On the contrary, as long as the predator densities remain low, native prey populations initially have less opportunities to gain experience of the invader. This delay in prey response results in the typical boom-and bust pattern (Kondoh, 2006).

As more and more invasive species are introduced, it is possible for facilitative relationships to form between introduced species. A theory based on facilitative interactions between non-indigenous species has been originally described by Simberloff and Von Holle (1999), which they named the invasional meltdown hypothesis. Based on the theory, an invasional meltdown happens when two or more invasive species synergistically interact, creating a larger impact together than the sum of the impacts of the individual species. Evidence for invasional meltdowns in natural systems is mixed, with many studies indicating that while positive interactions between invasives certainly happen, quantifying their impact can be difficult and they may more often be additive than synergistic by nature (Braga et al., 2018, 2019).

While the majority of research has focused on the negative impacts between invasive species and recipient communities (Papacostas et al., 2017), invasive species can also in some cases benefit invaded areas if newcomers that fill a new niche in an environment act as ecosystem engineers facilitating native species or function as an important food source for higher trophic-level taxa. An example of an invasive ecosystem engineer providing important ecosystem services are the invasive polychaeta *Marenzelleria sp.* in the Baltic Sea, that improve benthic oxygen conditions through bioturbation (Norkko et al., 2012). In many cases, however, engineering species are not beneficial as alterations to existing habitats can cause physiochemical changes that may result in total regime shifts (Gallardo et al., 2016).

1.2 The importance of littoral communities

Littoral ecosystems, or coastal benthic ecosystems, are near-shore habitats found on the interface between the land and sea, often characterized by significant primary production and high levels of disturbance (Douglas et al., 2022). Globally, littoral ecosystems are very diverse, encompassing habitats like seagrass meadows, mussel/oyster beds, mangroves, coral reefs and kelp forests. Communities inhabiting shallow benthic habitats can be varied and are shaped by physical properties such as sediment type, salinity, temperature, wave exposure and bottom contour (Douglas et al., 2022), as well as ice scour in colder climates (Leppäranta, 2009).

Littoral ecosystems are disproportionately important in supporting aquatic food webs. Due to the high concentration of primary production, coastal habitats can sustain high diversity and consumer biomass. Littoral ecosystems act as crucial nurseries and feeding areas for many pelagic fish species, due to the shelter provided by perennial plants and algae as well as the large amount of available food items (Whitfield, 2016). Therefore, these habitats act as important sources of resources for surrounding ecosystems as well as providing important ecosystem services for humans. The coastal zone is also crucial for the carbon cycling and long-term carbon sequestration in the oceans (Krause-Jensen & Duarte, 2016), making them an important asset for conservation and management.

Coastal habitats are highly susceptible to invasive species due to their high levels of anthropogenic activity. The large number of commercial harbors bring in invasives through ballast water and hull fouling, which are then dumped directly into the surrounding coastal areas

(López-Alonso et al., 2025). In the Baltic Sea, more than half of the introduced species have originated from shipping related pathways; and for successful invaders that value is even higher (57%) (Zaiko et al., 2010). In addition, anthropogenic developments (e.g., building of harbors and wind farms) often result in the degradation of native communities. These factors in addition to littoral ecosystems providing a large variety of habitats for more available niches for invasive species to settle, suggest that coastal habitats are important hotspots for species invasions (Zaiko et al., 2010). In the assessment by Zaiko et al. (2010), they found that most of the widely spread invasives in the Baltic that had a moderate to strong impact on native communities, habitats or ecosystem functioning were species common in shallow habitats.

1.3 The Baltic invasion of the estuarine mud crab (*Rhithropanopeus harrisii*)

1.3.1 The Baltic Sea as a dynamic ecosystem

The Baltic Sea is a shallow continental sea characterized by its brackish water, strong environmental gradients and high anthropogenic impacts. The brackish water is a result of a large catchment area bringing high volumes of fresh water through river runoffs and the saline ocean water pushing into the Baltic through Kattegat and the narrow Danish straights. The input of heavy saline ocean water results in a stable salinity gradient of higher salinity in the south and lower salinity in the north. This is exacerbated near the coastlines where river outputs and slow water exchange create estuary like conditions in many areas. (Leppäranta, 2009).

Strong seasonal variability defines the prevalent conditions in the Baltic. Patterns of annual temperatures, winds and ice cover along the Baltic differ with latitude (Leppäranta, 2009). Generally, the climate can be defined by warm summers with plenty of light and cold or rainy winters. This limits the growing season and seasonally slows down biological processes in the northern Baltic (Leppäranta, 2009; Snoeijs-Leijonmalm, 2017). Ice cover varies annually depending on winter conditions, but the coastlines, bays and basins tend to freeze every year especially in the north. This poses challenges for shallow littoral ecosystems that are subjected to annual ice scouring by melting sea ice rafts that get pushed to shore. High winds and seasonally varying precipitation and evaporation alter the currents and upwelling sporadically altering water temperatures, nutrient concentrations and water clarity. This creates dynamic disturbances in the whole system which can impact many biological processes and species abundance. (Leppäranta, 2009).

On a geological scale the Baltic is a very young sea, that has developed into its current state in just the last few thousand years after the latest glaciation period. The Baltic Sea began as an ice lake around 13-14 000 years ago and has undergone multiple saline and fresh water dominated phases. The present brackish phase of the Baltic gradually developed starting around 8000 years ago as the ocean access through the Danish straights started to open. (Leppäranta, 2009)

The young age of the Baltic holds major biological significance. Because of the short geographic history, most species can be considered newcomers to Baltic ecosystems. The flora and fauna of the Baltic are a collection of both oceanic and freshwater species that have adapted to or tolerate the prevailing conditions. The communities of primary producers and fauna are composed of species that have migrated into the Baltic through oceanic riverine connections and glacial relict species that have remained in the Baltic after the last glaciation period ended. The role and level of evolutionary speciation in the Baltic have been disputed through time, but molecular and morphological studies support ongoing speciation due to the strong selective pressures exerted by Baltic conditions (Snoeijs-Leijonmalm, 2017).

In addition to characteristics defined by the geography and geological history of the Baltic, humans play an important role in shaping ecosystems. The semi-enclosed basin, shallow depth and large catchment area exacerbate anthropogenic impacts (Reckermann et al., 2022). In addition to natural stressors like climate change and invasive species, anthropogenic actions such as land use, shipping and industry have the strongest impacts on the Baltic Sea region. (Reckermann et al., 2022)

The Baltic Sea, like the rest of the world, is going through major shifts in its environmental and ecological conditions driven by anthropogenic and climatic factors. Due to its geography, the Baltic is particularly susceptible to rapid changes. Long time series data from the Northern Baltic shows significant increases in surface water temperatures while salinities have declined (e.g., Mäkinen et al. 2017). Salinity in the Baltic surface water has been projected to decrease as annual rainfall increases, with the potential to alter the distributions of species by up to hundreds of kilometers. Increased rainfall together with open fertilized fields results in an increase of erosion and consequently terrestrial nutrient inputs into the Baltic. As a result of eutrophication, opportunistic filamentous algae become more abundant as they can more effectively incorporate increased nutrients as opposed to slower-growing perennial macroalgae. (Takolander et al., 2017; Viitasalo & Bonsdorff, 2022). This results in an increase in epiphytic algae such as *Pilayella litoralis* or *Ectocarpus siliculosus*. Increased filamentous biomass can shade and smother underlaying habitat forming algae, mainly *Fucus vesiculosus* and *Furcellaria lumbricalis* (Takolander et al., 2017). There is also evidence of large epiphytic growths causing the host to tear off due to the added mass and resistance (D'Antonio, 1985).

Changes in anthropogenic land use can alter ecosystems on a local or catchment level. New anthropogenic developments like wind farms and harbors can destroy pre-existing shoreline habitats. Harbors and man-made channels act as important pathways for new non-indigenous species (NIS) (Cuthbert et al., 2021; Leppäkoski et al., 2002; Rodríguez & Suárez, 2001). Increased anthropogenic action in the form of recreational boating and fishing can also act as vectors spreading NIS on a local scale (Kelly et al., 2013).

Due to the short history of the Baltic along with its' brackish nature and complex structure, it creates a unique environment for possible invaders. Even though the brackish environment can be perceived as a rather hostile habitat for invaders, it must be noted that many of the invasive species transported through maritime traffic originate from estuaries where harbors are located. This helps to explain the relatively high number of marine invasive species present in the Baltic (Leppäkoski et al., 2002). Due to the relatively low species count in the Baltic, invaders often represent a new feeding strategy or functional group in the ecosystem, which can inadvertently restructure food webs (Leppäkoski et al., 2002). That is also the case for the estuarine mud crab (*Rhithropanopeus harrisii;* Gould, 1841) that has been steadily spreading around the Baltic.

1.3.2 Ecology of *Rhitropanopeus harrisii* in the Baltic

Rhithropanopeus harrisii is a small Brachyuran crab originating from the Atlantic coast of North America, from the St. Lawrence Gulf in Canada to Veracruz in Mexico (Rodríguez & Suárez, 2001). *Rhitropanopeus harrisii* is an euryhaline species found in a wide range of brackish environments, but they are commonly found in habitats ranging in salinity from around 1‰ to 25 ‰ (Turoboyski, 1973). Controlled studies have found that crabs can survive and develop in salinities between 1‰ and 40‰ (Costlow et al., 1966). In the Baltic, *R. harrisii* inhabits varying soft and hard sediment habitats from muddy river mouths to mussel beds and rocky littoral shores dominated by algal canopies (Hegele-Drywa & Normant, 2009; Jormalainen et al., 2023).

The mud crab is an opportunistic omnivore known to feed on invertebrates, algae and carrion. A Polish study looking at stomach contents suggested that the crabs readily feed on animal and plant matter as well as detritus with no evidence for food selectivity (Hegele-Drywa & Normant, 2009). Their analysis showed that the crabs preyed mainly on amphipods and bivalves. Studies from the Finnish coast suggest a broader animal diet favoring isopods and gastropods (Forsström et al., 2015). Due to the opportunistic feeding behavior of *R. harrisii* differences in diet compositions can be explained by differing habitats and the invertebrate communities inhabiting them.

Rhithropanopeus harrisii is a functionally novel predator in the Archipelago Sea (Jormalainen et al., 2023). The Northern Baltic Sea has no native brachyurans or similar predators, so native invertebrates are completely naïve to the predation by the crab. *R. harrisii* can establish in new areas quickly and high crab densities along with predatory potential may have strong effects on prey species abundance which can indirectly cause changes in ecosystem functions. Earlier studies have proposed the strong effects that *R. harrisii* has on littoral *Fucus vesiculosus* (Linnaeus) dominated shores (Forsström et al., 2015, 2018; Jormalainen et al., 2016, 2023). These studies suggest that on invaded sites the densities of many invertebrates including important mesoherbivores (e.g. gastropods, isopods) have declined radically. However larger scale quantitative research on the community compositions throughout the entire invasion zone in Finland has yet to be performed.

1.3.3 Invasion history

Rhithropanopeus harrisii was originally introduced to Europe sometime before 1874 when it was discovered in the Netherlands and originally described as a new species. The crab ended up in the Netherlands possibly through oyster farming as Atlantic oysters were transported from America to Europe. It then spread gradually along the European coasts and into brackish water systems. (Rodríguez & Suárez, 2001). The Kiel channel has been attributed to the crab's original invasion of the Baltic, since it was originally discovered in 1936 from the channel (Nehring, 2000). Further spread of *R. harrisii* has likely been facilitated through ballast water, since many initial observations of the crab have been near commercial harbors (for example: Wolff 1954, Turoboyski 1973).

The first observation of *R. harrisii* in Finnish waters was in 2009 near the shipping port of Naantali (Karhilahti, 2010). Based on the location of first observations, ballast water was the likely vector for transporting the crab. The exact origin of the Finnish *R. harrisii* population is not known, since the European crab populations are likely a result of multiple introductions (Fowler et al., 2013). After the initial invasion in Naantali, *R. harrisii* has been consistently spreading through the archipelago (Jormalainen et al. 2023). Currently the crab has established populations throughout most of the Finnish southwestern coastline reaching from Rauma to Hanko, spanning a distance over 200 km. The well documented invasion of the crab has provided an excellent opportunity to study the possible systemic effects of invasions on entire communities and prey responses to completely novel predatory pressures (Jormalainen et al., 2023; Yli-Renko et al., 2022).

1.4 Aim of the study

The aim of this thesis is to compare invertebrate community compositions between the areas affected and not affected by the invasion of *Rhithropanopeus harrisii* in the Finnish archipelago. I will explore the invertebrate communities at rocky littoral habitats dominated by *Fucus vesiculosus* differing in the length of their invasion history. My goal is to describe the effects *R. harrisii* has on invertebrate mesoherbivore community composition and discuss some of the impacts of a possible regime shift.

I hypothesize that (H1) *R. harrisii* has a significant effect on invertebrate community compositions (i.e., species abundance and diversity). I also hypothesize that (H2) soft-bodied or slow-moving species are in lower abundances in areas where *R. harrisii* is present and (H3) less palatable hard-shelled species are in higher abundances. (H4) It is also possible that invasion impacts are strongest in recently invaded sites since native communities are completely naïve to *R. harrisii* predation and *R. harrisii* densities might be higher due to an initial population increase in accordance with a boom-and-bust model (Kondoh, 2006). As the invasion lasts longer, invasion impacts might be mitigated by prey populations’ adaptation against crab predation resulting in a reduction in crab abundance and partial recovery of the native community.

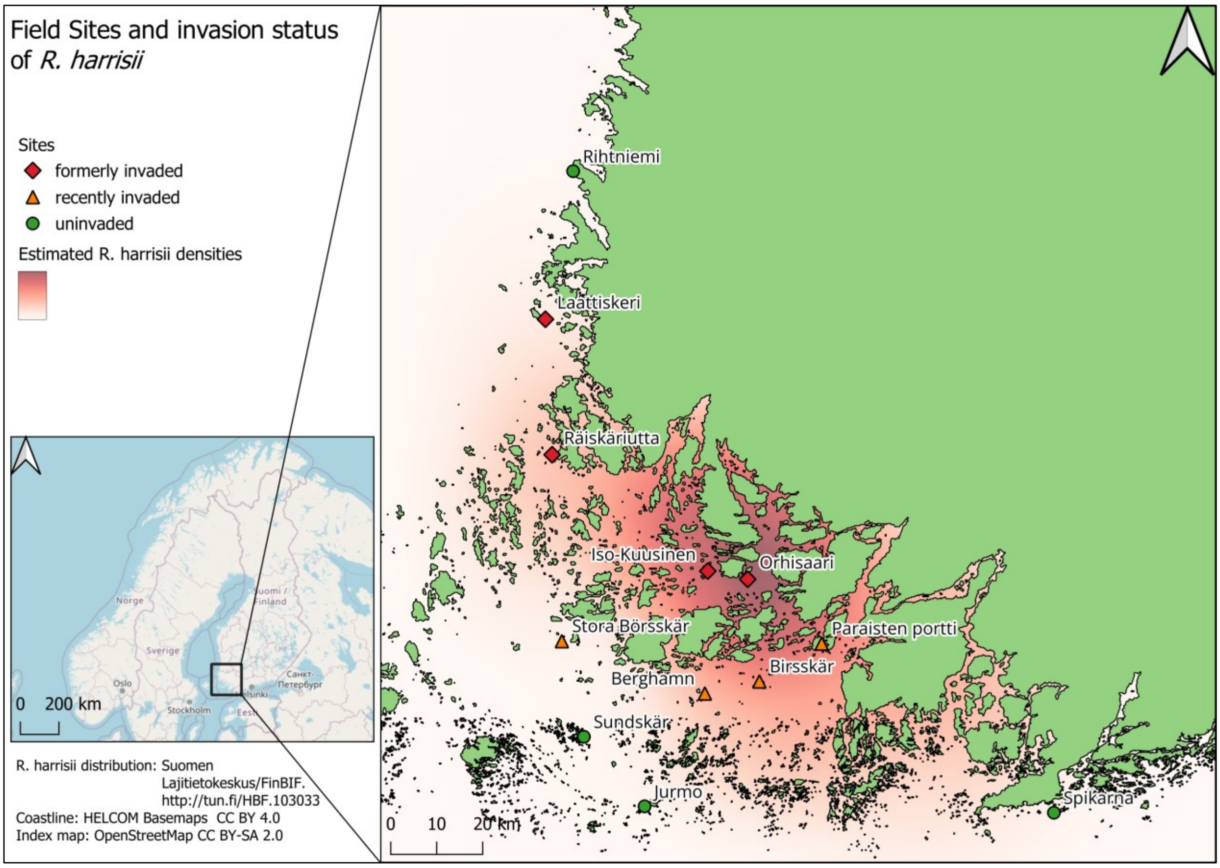
2 Materials and methods

2.1 Study area

The study was conducted on 12 monitoring sites along the Archipelago Sea on the Finnish coast (Table 1). Sites were selected to span the entirety of the current invasion zone of the mud crab *Rhithropanopeus harrisii*. The northernmost sites were in the southern part of the Gulf of Bothnia near Rauma and Uusikaupunki. In the South, the study area stretched out to Jurmo and in the East to Hanko (Figure 1).

Study sites were shallow littoral rocky shores with either bedrock, boulders and/or stones and large gravel, dominated by bladderwrack (*Fucus vesiculosus,* Linnaeus) stands. Sites were selected so that they provided broad coverage across the Finnish coastline within the *R. harrisii* invasion zone as well as ranging from the innermost archipelago to the outer islands. Sites varied geographically from sheltered lagoons to exposed open shorelines. Bottom contours also varied but generally consisted of a slope deepening to around 3–4 meters, where sediments changed from a rocky bottom to softer silt or sand. Some sites were close to relatively high traffic waterways or harbors, while others were more secluded. Sites faced varying levels of anthropogenic disturbance in the form of recreational use, but none of the sites hosted any permanent man-made structures.

Study sites were classified into three classes based on the length of time the area had been invaded by the mud crab relative to 2024. Sites were classified as uninvaded, recently invaded, or formerly invaded. The classification was based on *R. harrisii* observation data from the Finnish Biodiversity Info Facility (FinBIF) open access data repository (laji.fi). Laji.fi database combines data from national and other scientific monitoring programs as well as citizen science observations. Dates of observations as well as a heat map were used to select and classify the sites. In addition to the database, crabs found during earlier invertebrate sampling were used to determine crab presence. To verify the presence of crabs during this study and estimate crab densities, crab trapping was performed in spring on all 12 sites and in late summer for all but two invaded sites (Appendix 1). Sites classified as uninvaded were located on the edges of the known invasion zone, where no crabs had yet been observed. Recently invaded sites were areas where the crabs arrived less than four years ago. Sites in which *R. harrisii* had been documented more than four years ago were classified as formerly invaded.



R. harrisii distribution: Suomen Lajitietokeskus/FinBIF. http://tun.fi/HBF.103033
Coastline: HELCOM Basemaps CC BY 4.0
Index map: OpenStreetMap CC BY-SA 2.0

Figure 1. Map depicting field sites and estimated invasion zone for the Harris mud crab (R. harrisii). Sites have been classified based on how long crabs have been present in the area relative to 2024. Non-invaded sites contained no crabs, recently invaded sites had less than four years of crab exposure, and formerly invaded sites had more than four years of exposure. Heatmap depicting crab abundance is based on the FinBIF data repository observations of R. harrisii until the end of 2023.

Table 1. Field sites with coordinates, invasion status and number of *F. vesiculosus* collected and analyzed.

Site	Coordinates	Invasion status	N
Orhisaari	60°16.443'N, 021°59.547'E	Formerly invaded	16
Iso-Kuusinen	60°17.408'N, 021°50.043'E	Formerly invaded	15
Räiskäriutta	60°31.080'N, 021°12.998'E	Formerly invaded	15
Laattiskeri	60°46.879'N, 021°11.404'E	Formerly invaded	15
Stora Börsskär	60°09.124'N, 021°15.320'E	Recently invaded	14
Berghamn	60°02.921'N, 021°49.348'E	Recently invaded	15
Birsskär	60°04.346'N, 022°02.324'E	Recently invaded	15
Paraisten portti	60°08.840'N, 022°17.149'E	Recently invaded	15
Rihtniemi	61°04.085'N, 021°18.067'E	Non-invaded	15
Sundskär	59°57.772'N, 021°20.557'E	Non-invaded	15
Jurmo	59°49.468'N, 021°35.001'E	Non-invaded	14
Spikarna	59°58.700’N, 023°12.424’E	Non-invaded	15

2.2 Collecting data

2.2.1 Determining *R. harrisii* presence

Site level densities of *R. harrisii* were estimated using traps soaked for 7–9 days in May–July. We used two types of traps: habitat traps and traditional minnow traps (Tucker et al., 2023). The habitat traps were simple metal wire frames filled with rocks or pottery shards and did not have any bait (Outinen et al., 2019). The habitat traps attracted crabs by acting as hiding spots, and crabs could easily move in and out of the traps. For the minnow traps, we used food store-bought turkey sausages as a bait. The minnow traps also caught fish, most notably the invasive round goby (*Neogobius melanostomus*, Pallas 1814).

2.2.2 Collection of *Fucus vesiculosus*

Some of the earlier studies on invertebrate communities have been conducted by collecting *F. vesiculosus* (hereafter: *Fucus*) samples from a boat using rakes to lift it into buckets before sorting through the algae and separating the invertebrates (Jormalainen et al. 2023). However, this methodology causes major disturbance to the bushes before and during collection resulting in difficulty to quantify the part of invertebrates escaping. To increase data accuracy from underwater invertebrate community compositions from *Fucu*s, we collected quantitative samples using SCUBA divers, who gathered individual *Fucus* bushes for further processing, via methods previously used for *Fucus* community data (Korpinen et al. 2010; Jormalainen et al. 2016). This method provides a more comprehensive and realistic estimate of the community composition.

Fifteen individual *Fucus* bushes were collected via diving along transects placed perpendicular to the shoreline from the surface down to a depth of four meters or until the continuous *Fucus* belt ended. *Fucus* was collected starting from the deepest point and taking samples every two meters all the way to the upper limit of the *Fucus* belt. An individual *Fucus* bush was defined as a growth of algae originating from the same distal disc. To ensure representative sampling, 2 or 3 transects placed at least 10 meters from each other were used per site, depending on the depth range and width of the *Fucus* belt. The maximum length for each transect was 30 meters from the shoreline regardless of depth.

Bushes were collected by carefully placing a large mesh bag over the entire bush. Some animals may promptly flee or fall from the algae, so disturbing the algae as little as possible was essential for sample quality. The mesh bag was fastened around the thallus, and the bush was cut into the bag close to the distal disc. Bags were labeled and depths for the collected bushes were recorded.

2.2.3 Invertebrate identification

After *Fucus* bushes were collected, invertebrates were separated from the algae by shaking or picking by hand. Barnacles, *Amphibalanus improvisus* (Darwin, 1854) were removed and counted. Invertebrates were stored in labeled 50 ml vials filled with 70 vol% ethanol and kept in a cold room until processing. Fucus bush wet weight was obtained after separating all invertebrates, and dry weights were obtained after removing attached filamentous algae and drying the bushes at 60°C for a minimum of 24 hours until completely dry.

I identified and counted invertebrate species from each sample using a stereomicroscope (Zeiss Stemi DV4). Species identification was done solely by morphology (Leinikki et al., 2004; Viitasalo et al., 2017), which somewhat limited the taxonomic resolution. Most species were identified to a species level, but some groups were identified to a genus level or higher taxon (Appendix 2) due to laborious or non-viable visual identification. Invasive species found in the samples were identified to a species level except for *Gammarus tigrinus* (Sexton, 1939*)*, which was included in the genus *Gammarus sp*.

2.3 Statistical analysis

Before any statistical analysis, I reviewed the raw abundance data and removed all taxa that had just one observation. Basic abundance data from the whole dataset can be found in Appendix 2. I used Primer 7 version 7.0.24 for the comparisons of community composition between sites of differing invasion histories. I removed *R. harrisii* from the multivariate analysis to avoid circular inference. Samples missing *A. improvisus* abundances were removed, resulting in the final sample size of 165, which was used for all Primer analyses. To account for differences in the size of sampled *Fucus* bushes, I standardized the abundance of individual species by the total abundance of each sample. Because of the large differences in species abundances, I conducted a square root transformation for standardized data, that more evenly weighs both abundant and rare species.

I calculated similarity percentages and species contributions for study groups as well as dissimilarities between groups for the raw abundance data using the SIMPER tool in Primer 7.

I calculated dissimilarities for the three-class invasion histories as well as for a two-class invasion status (invaded, non-invaded). I used the PRIMER 7 Coherence Plot routine to identify species whose abundance patterns were significantly correlated with the multivariate ordination. Significance was assessed using permutation tests on species–axis correlations. Based on this, I constructed a dendrogram for the 20 most significant species using PRIMER's CLUSTER routine to assess species co-occurrence. I calculated similarities using Whittaker's Index of Association based on presence–absence data, to reduce noise from highly variable abundances among species.

Using the standardized and square root transformed data, I created a resemblance matrix using Bray-Curtis similarity. With the resemblance matrix, I created a non-metric multidimensional scaling (nMDS) -ordination plot to visualize community structure with respect to the three-class invasion history. For the nMDS ordination, I tested different transformations, and based on stress values, I selected the square root transformation to be the most representative.

I analyzed statistical differences among invasion history groups using PERMANOVA (9999 permutations) for the resemblance matrix with the three-class invasion history as a fixed factor and site nested under invasion history as a random factor using the sample water depth as a covariate. *Fucus* sample dry weights were not separately included in the model, since differences caused by varying species abundances were already accounted for with standardization. After significant differences were detected for the invasion history, I conducted pairwise PERMANOVA tests to identify which levels differed significantly. The pairwise comparisons used the same resemblance matrix and permutation scheme as the main model. To assess the effects of water depth for community structure between invasion classes, I ran distance based linear models (Primer 7 DISTLM-routine) for the Bray-Curtis resemblance matrix separately for each of the three invasion histories with depth as an explanatory variable.

Based on the SIMPER analysis and prior studies (e.g. Jormalainen et al. 2016, Hegele-Drywa et al. 2009), I selected species that explained most of the differences in community composition among invasion histories (*Idotea balthica*, *Mytilus trossulus*, *Parvicardium hauniense/ Cerastoderma glaucum*, *Amphibalanus improvisus*, *Theodoxus fluviatilis*, *Radix peregra*, *Hydrobia sp.*, and *Gammarus sp.*) for further analysis. I also included the invasive tanaid *Sinelobus vanhaareni* to test possible co-occurrence between invasive species. I used Rstudio (v4.2.3; R Core Team, 2023) to create generalized linear mixed models (GLMMs) for abundances of individual taxa using the lme4 package (v1.1.32; Bates et al. 2015). I analyzed homoscedasticity and the fit of the error distribution with the DHARMa simulated residuals (v0.4.7; Hartig, 2024). The entire available dataset ($n = 179$) was used for the GLMMs. Using negative binomial error distribution, I tested the effect of invasion history separately for each species' abundance. I selected the error distribution based on overall model fit, overdispersion tests and visual analysis of residual distribution. The number of individuals per *Fucus* bush was used as the response variable, with absences assigned a value of 0. Invasion history was included as a fixed effect, and site as a random effect with sample depth and *Fucus* dry weight as covariates. Depth-by-invasion history interaction was also included. Covariates were centered by subtracting their mean and scaled by their standard deviation using the scale() function to improve model convergence. The statistical significance of model predictors was assessed using type III Wald χ^2 tests. I did pairwise comparisons between invasion histories with Tukey-adjusted t-tests. I additionally tested the co-occurrence between *R. harrisii* and *S. vanhaareni* using a Chi-squared test for a contingency table of presence/absence data. The effect of water depth on the presence of *R. harrisii* in invaded areas was assessed by converting abundance data to presence–absence and fitting a binomial generalized linear model, which was compared to a null model via a deviance test.

I tested the effects of invasion history and water depth on different diversity measures (Shannon-Wiener diversity, H'; total abundance, N; species count, S) using generalized linear mixed models (GLMMs) from the lme4 package (v1.1.32; Bates et al. 2015). Models included a similar variable scheme to the species models. Error distribution was selected based on DHARMa simulated residual tests (Hartig, 2024) including homoscedasticity and overdispersion tests. A gaussian error distribution was used for H' and S, while N used a negative binomial distribution. Type III Wald χ^2 tests were used to test the significance of predictors. I conducted Tukey adjusted pairwise comparisons between invasion histories for measures that had a significant effect on invasion history.

3 Results

3.1 Differences in community composition

Crabs were found from *Fucus* samples in all invaded sites except Laattiskeri (Figure 2). There was large variability between the total number of individuals and proportion of bushes inhabited by *R. harrisii*. The proportion of *Fucus* bushes inhabited by *R. harrisii* varied between 0–60% among sites with the total number of *R. harrisii* individuals found per site ranging from 0–28. No clear patterns emerge between invaded classes, but crab presence seems to be slightly higher in recently invaded sites. Depth had a significant positive effect on the probability of *R. harrisii* occurrence ($\chi^2 = 11.5$, df = 1, $p = 0.0007$), with occurrence increasing with water depth (Figure 3).

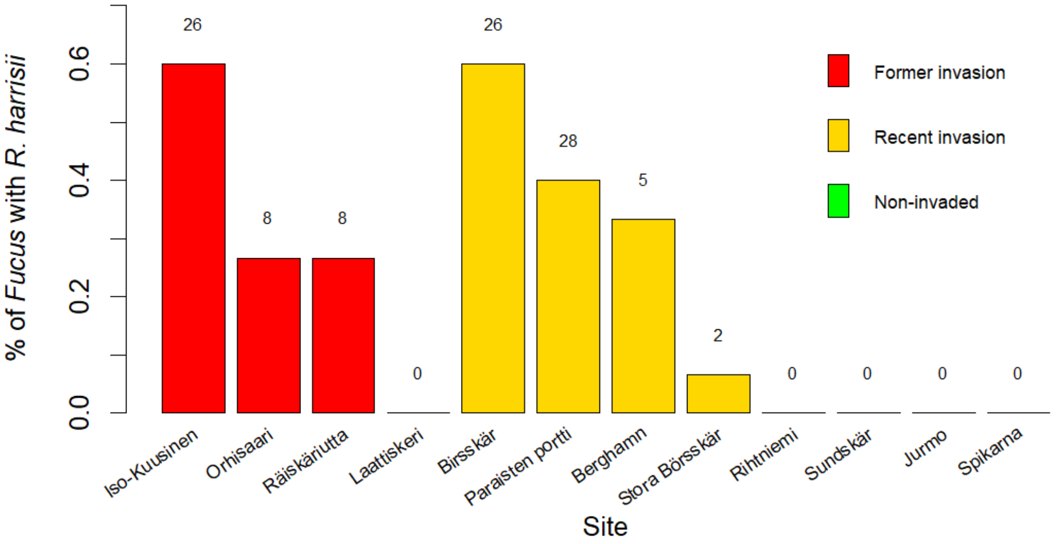


Figure 2. Proportion of *F. vesiculosus* stands, that harbored one or more *R. harrisii* individuals. Above each bar presented the total number of crab individuals found per site

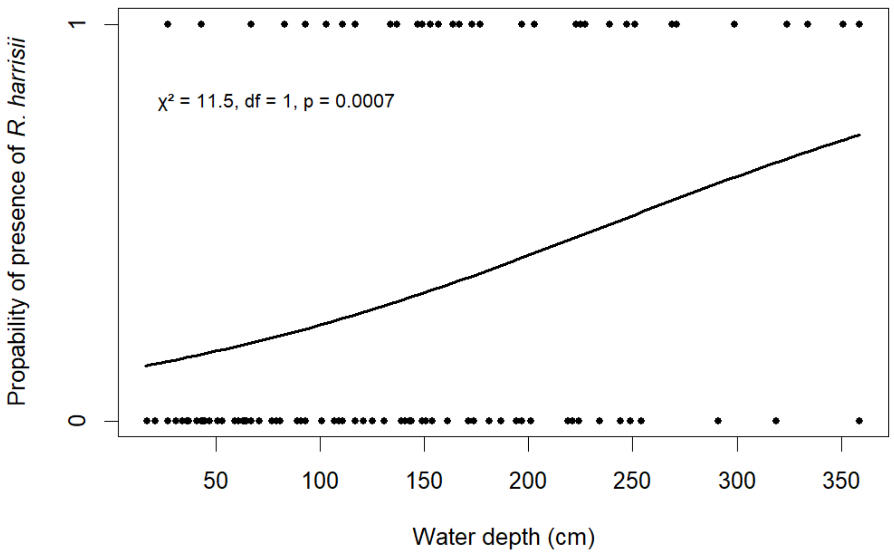


Figure 3. Probability of the presence of *R. harrisii* found from *Fucus* samples across a water depth gradient in invaded areas. Absences were assigned a value of 0 and presences value of 1. Line shows a fitted binomial model with test statistics from a deviance test comparing the depth model to a null model.

SIMPER analyses showed differences in community composition between invasion statuses. Invaded and non-invaded sites had an average dissimilarity of 81.89%. The biggest contributors to dissimilarity between invaded and non-invaded areas were *Amphibalanus improvisus, Theodoxus fluviatilis,* Cockles (*Parvicardium hauniense, Cerastoderma glaucum), Mytilus trossulus, Gammarus sp., Radix peregra* and *Hydrobia sp.* (Table 2).

Table 2. Results of the SIMPER analysis between invaded and non-invaded sites. Table includes mean abundances from non-transformed raw data (number of individuals per *Fucus* bush) for both groups with average dissimilarities and each species' cumulative contribution toward dissimilarity.

Species	**Invaded Average Abundance**	**Non-invaded Average Abundance**	**Average Dissimilarity**	**Dissimilarity / SD**	**Contribu-tion (%)**	**Cumula-tive %**
A. improvisus	143.27	3.25	19.89	0.88	24.29	24.29
T. fluviatilis	34.65	81.79	15.21	1.19	18.58	42.87
P. hauniense / C. glaucum	119.35	16.32	11.27	0.71	13.76	56.63
M. trossulus	57.76	30.95	9.77	0.86	11.93	68.56
Gammarus sp.	8.24	25.88	4.55	0.83	5.56	74.11
Hydrobia sp.	14.94	14.19	4.07	0.68	4.97	79.09
R. peregra	1.26	18.04	3.75	0.51	4.58	83.66

SIMPER analysis for the three classed invasion status showed similar results with pairwise dissimilarities between invasion classes around 75–82%. Within invasion groups, non-invaded sites were most similar with an average similarity of 35.35%. Recently invaded sites had an average similarity of 24.68% and formerly invaded sites 28.98%.

All SIMPER analyses showed common patterns of species composition. Non-invaded sites had higher abundances of *Gammarus sp.*, *T. fluviatilis* and *R. peregra*. In the invaded sites, *A. improvisus, P. hauniense/ C. glaucum* cockles and *M. trossulus* were more abundant. The largest differences in abundance were recorded for *A. improvisus* and cockles (Table 2) There was large variability in the number of cockles within the invaded areas and samples, with some samples having thousands of individuals (Appendix 2). In general, sites differing in invasion status were highly dissimilar, but there was also large variability within grouped sites. Overall, motile and relatively soft-shelled herbivores were lower in abundance in invaded sites while the hard-shelled sessile filter feeders were more abundant.

Clustering supported the results from the dissimilarity analysis. Motile herbivores *Idotea sp.*, *Gammarus sp.* and *T. fluviatilis* were strongly associated together (Figure 4), while filter feeding bivalves including cockles (*P. hauniense, C. glaucum)* and *M. trossulus* clustered together. While not as strongly linked, the gastropods *Hydrobia sp.* showed co-occurrence with bivalves. Overall, results depicted a divide between more motile herbivorous species and filter feeders/ detritivores related to invasion status.

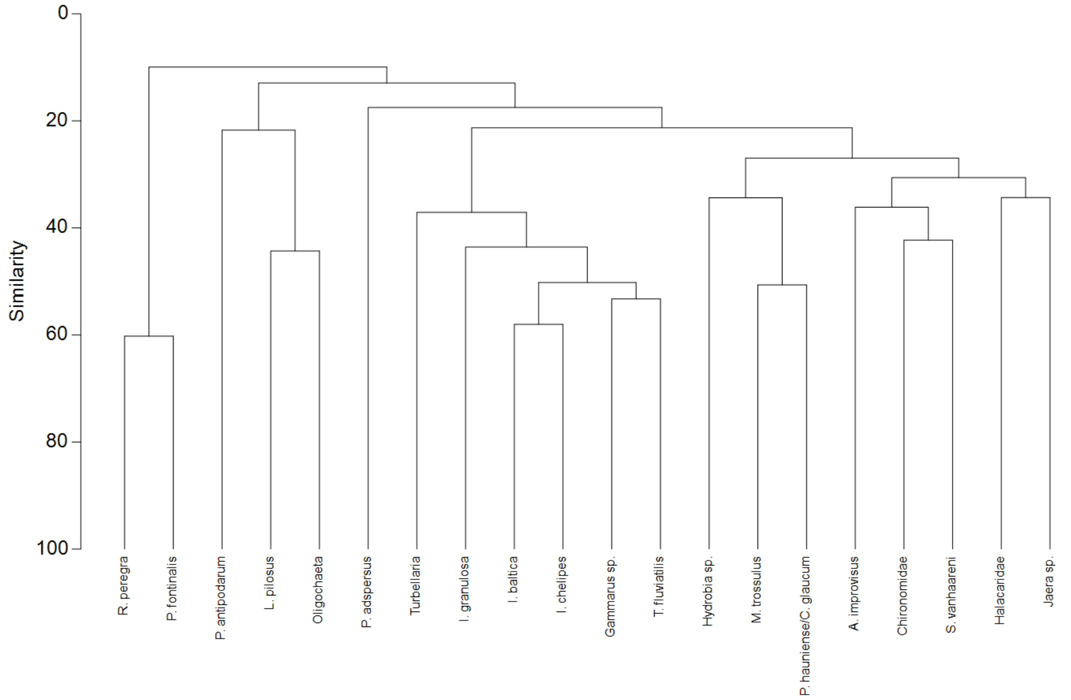


Figure 4. Cluster analysis using for the 20 most significant species whose abundance patterns were significantly correlated with the multivariate ordination. Samples have been standardized by total individuals, and the resemblance matrix is based on Whittaker's index of association.

PERMANOVA for the standardized and square root transformed Bray-Curtis' similarity matrix revealed that community composition varied significantly with depth ($F_{1,141} = 4.44$, $p = 0.0005$) and invasion history ($F_{2,141} = 2.74$, $p = 0.0114$). There was a significant interaction between invasion history and depth ($F_{2,141} = 4.40$, $p < 0.0001$). Variation among sites within invasion history classes was strong ($F_{9,141} = 24.6$, $p < 0.0001$), which explained the largest amount of the model's variation (43.72% of total variation). Based on the estimates of components of variation, variation among sites was followed by Invasion history (19.97%). Smaller contributions were observed for Depth (2.90%) and its interaction with site (6.72%) and with invasion history (1.88%). Therefore, although depth was highly significant, its contribution to overall variation was smaller relative to the invasion history. Residual variation accounted for 24.86% of the total variation. Pairwise PERMANOVA comparisons showed that both invaded classes differed significantly from non-invaded sites (former – non-invaded: $t = 1.9102$, $p = 0.0001$; recent – non-invaded: $t = 2.17$, $p < 0.0001$), but did not differ among themselves (recent – former: $t = 0.469$, $p = 0,88$)

Distance based linear models (DISTLMs) between individual invasions histories showed differences in the effect of depth. In non-invaded sites, water depth had no significant impact on community structure ($F_{1,55} = 1.28$, $p = 0.25$). For recently invaded sites depth had significant impact ($F_{1,48} = 6.40$, $p = 0.0004$, $R^2 = 0.118$) as well as for formerly invaded sites ($F_{1,56} = 5.24$, $p = 0.0014$, $R^2 = 0.0856$).

The standardized and square root transformed NMDS ordination visualized differences between the invasion groups (Figure 5). Non-invaded sites were most clearly distinguished from the rest. Invaded classes overlapped considerably and showed more variability in community composition, with especially the recently invaded sites forming two partially distinct clusters.

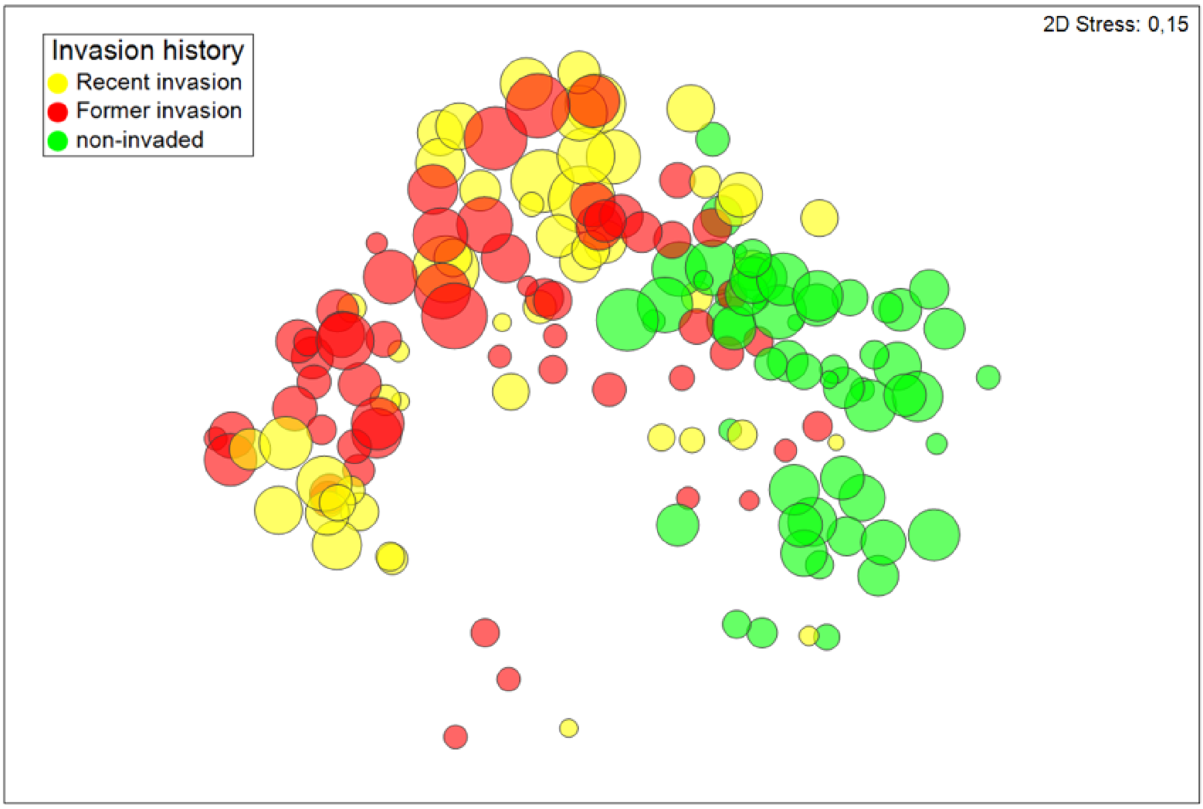


Figure 5. NMDS plot depicts the differences in species composition between different invasion groups. Each bubble represents the invertebrate community inhabiting a single *F. vesiculosus* bush. Samples have been standardized and square root transformed. The resemblance matrix is based on Bray-Curtis similarities. Samples have been classified based on their invasion history. Bubble size increases with sample depth ranging from 0 cm to 400 cm.

GLMs on diversity measures for the entire community data (n = 179) showed that invasion history had a significant effect on the Shannon-Wiener index ($p = 0.0015$; Table 3). Tukey adjusted pairwise comparisons revealed that index values reduced significantly between non-invaded and recently invaded sites ($p = 0.017$), with a small but statistically non-significant increase between recently and formerly invaded sites (Figure 6). Both species richness and total abundance were influenced by *Fucus* dry weight, with total abundance showing a significant dept-by-invasion history interaction (Table 3, Figure 7).

Table 3. Model results for different diversity measures (Shannon-Wiener index H', Species richness S, and total abundance N) with error distributions and test statistics. Statistics include type III Wald χ^2 test values as well as model estimates for covariates. Covariates have been centered and scaled by their standard deviation. n = 179. Statistically significant results are bolded.

Diversity measure	**Error distribution**	**Invasion history** **df = 2**	**Depth (scaled)** **df = 1**	**Fucus dry weight (scaled)** **df = 1**	**Depth-by-inv. history** **df = 2**
H'	gaussian	**χ^2 = 13.0** **p = 0.0015**	β = 0.033 ± 0.046 χ^2 = 0.528 p = 0.47	β = -0.019 ± 0.027 χ^2 = 0.532, p = 0.47	χ^2 = 3.44 p = 0.18
S	gaussian	χ^2 = 0.718 p = 0.70	β = 0.031 ± 0.092 χ^2 = 0.83 p = 0.36	**β = 0.358 ± 0.064** **χ^2 = 17.2,** **p < 0.0001**	χ^2 = 2.11 p = 0.35
N	negative binomial	χ^2 = 2.46, p = 0.29	β = 0.266 ± 0.293 χ^2 = 0.113 p = 0.74	**β = 0.770 ± 0.186** **χ^2= 31.0,** **p < 0.0001**	**χ^2= 11.2,** **p = 0.0037**

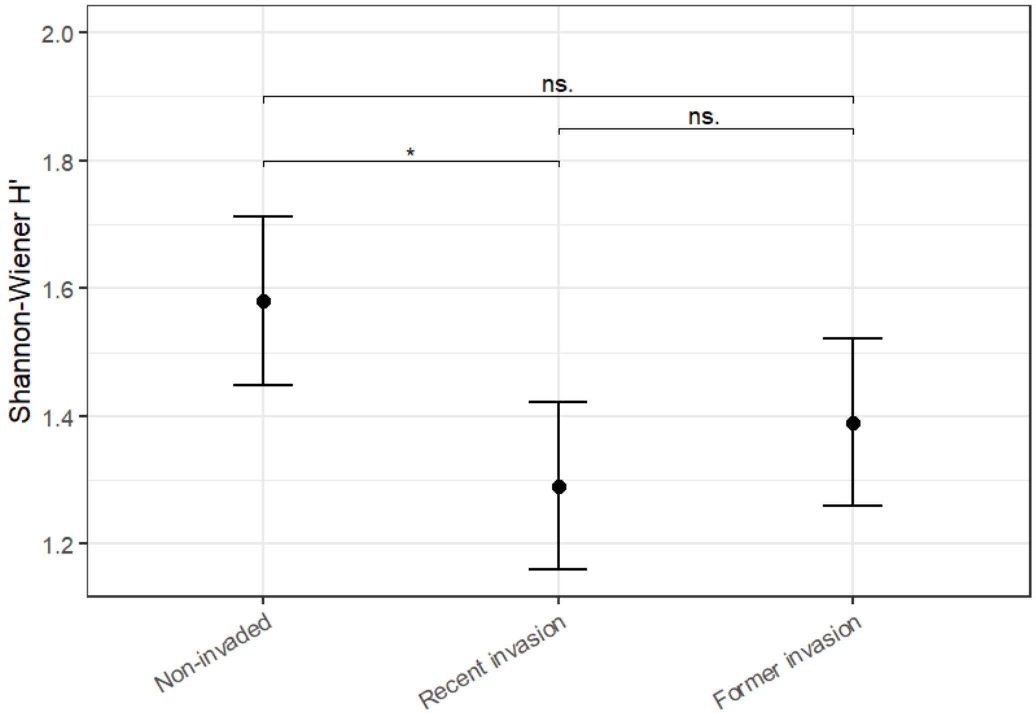


Figure 6. Model estimates for Shannon-Wiener diversity across invasion histories controlling for sample water depth and *Fucus* dry weight. Error bars show 95% confidence intervals. Brackets indicate Tukey adjusted pairwise comparisons, with significance levels (ns. = non-significant, *=p<0.05, **=p<0.01, ***=p<0.001).

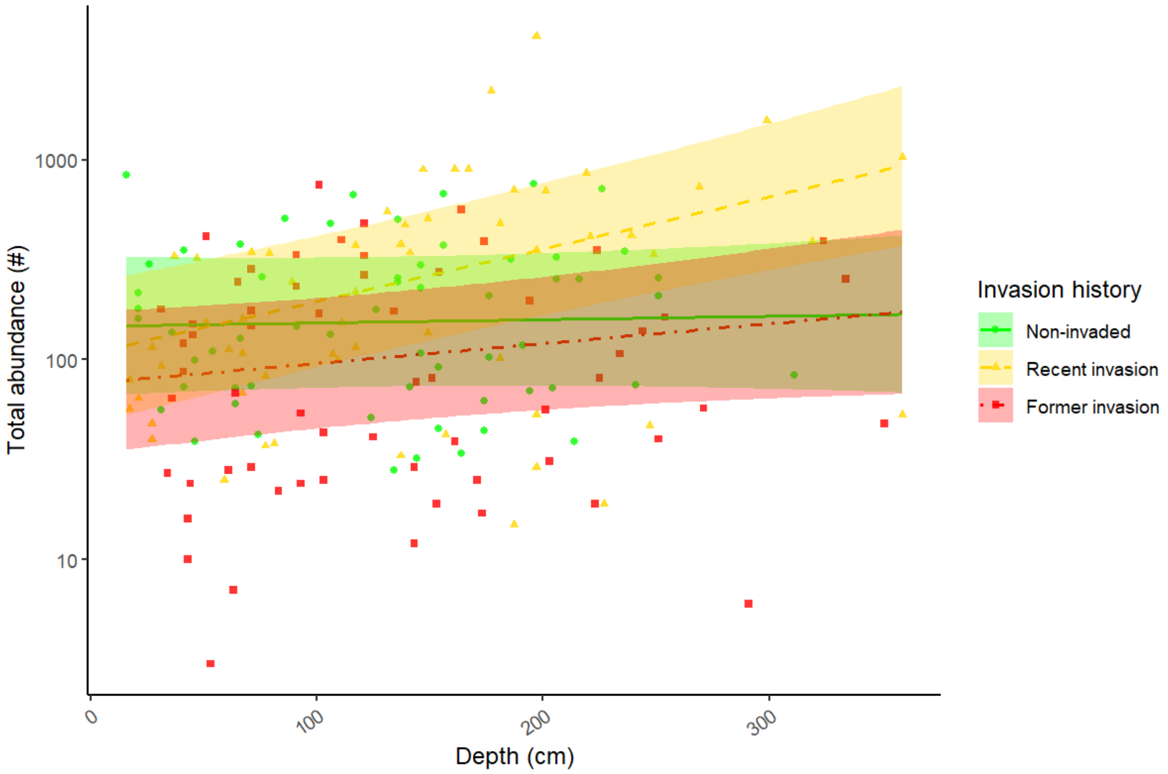


Figure 7. Relationship between the total number of individuals per sample and depth grouped by the invasion history. Lines represent groupwise predicted values with 95% confidence limits. The vertical axis is presented in a log scale.

3.2 *R. harrisii* invasion effects on individual taxa

All GLMM models for individual species converged well and residual analysis showed acceptable model fit. *Idotea balthica* abundance was strongly affected by invasion history (p = 0.013) with a strong depth-by-invasion history interaction (p = 0.003; Table 3). *Idotea balthica* was abundant in non-invaded sites and showed a decline in both invaded classes, although the difference between non-invaded and recently invaded was barely non-significant (p = 0.056; Figure 8A). The abundance of *Gammarus sp.* was affected by invasion history (p = 0.0013) with a positive response to *Fucus* dry weight (p < 0.0001) and a strong depth-by-invasion history interaction (p < 0.0001; Table 3). Pairwise comparisons with Tukey adjustment for *Gammarus sp.* showed that abundance had a reducing trend with increasing invasion history, but the change is statistically significant only between non-invaded and formerly invaded sites (Figure 8B). The abundances of *R. peregra* and *T. fluviatilis* did not vary significantly between invasion histories, but they were affected by *Fucus* dry weight (Table 3; Figure 8F, G).

In contrast, the abundance of *A. improvisus* was significantly higher in both invaded classes compared to non-invaded sites (Table 4; Figure 8H) and showed a strong increase with increasing *Fucus* dry weight ($p < 0.0001$; Table 4). A similar yet more subtle increase related to invasion history was present for S. *vanhaareni* ($p = 0.032$; Table 4), as well as in response to *Fucus* dry weight ($p = 0.015$; Table 4). Pairwise comparisons showed that *S. vanhaareni* abundances differed significantly between non-invaded and formerly invaded sites (Figure 7I). A contingency table between presence/absence for *R. harrisii* and *S. vanhaareni* showed strong co-occurrence between the species ($\chi^2 = 20.537$, df = 1, $p < 0.0001$).

While other species were not statistically significantly affected by invasion history alone, the depth-by-invasion history interaction was highly significant for all modeled taxa except *A. improvisus*, *S. vanhaareni* and *Hydrobia sp.*, the last of which was barely non-significant ($p = 0.060$; Table 4). Abundances of taxa showed common patterns along a depth gradient with *I. balthica*, *Gammarus sp.*, *T. fluviatilis* and *R. peregra* having a neutral to slightly positive response to increasing depth in non-invaded sites and a reduction in abundance with depth in invaded sites (Figure 9A, B, F, G). *Gammarus sp.* showed stronger depth-dependence in recently invaded sites. On the contrary, *M. trossulus* and cockles showed a positive depth-dependence in invaded sites, with no clear change in non-invaded areas (Figure 9C, D). For the two taxa, depth dependence was strongest in recently invaded sites. Although not quite statistically significant ($p = 0.060$), *Hydrobia sp.* exhibited a similar pattern of positive depth-dependency in invaded sites (Figure 9E).

Table 4. GLMM results for the species best describing differences between invasion histories. Statistics include type III Wald χ^2 test values as well as model estimates for covariates. Covariates have been centered and scaled by their standard deviation. Sample size was 179 for all taxa except for *A. improvisus* which was 165. Statistically significant results are bolded.

Species/ taxa	**Invasion history df = 2**	**Depth (scaled) df = 1**	**Fucus dry weight (scaled) df = 1**	**Depth-by-invasion history df = 2**
I. balthica	**$\chi^2 = 8.65$** **$p = 0.013$**	$\beta = 0.213 \pm 0.153$ $\chi^2 = 1.95$ $p = 0.16$	$\beta = 0.195 \pm 0.133$ $\chi^2 = 2.14$ $p = 0.14$	**$\chi^2 = 11.3$** **$p = 0.003$**
Gammarus sp.	**$\chi^2 = 13.2$** **$p = 0.0013$**	$\beta = 0.183 \pm 0.121$ $\chi^2 = 2.28$ $p = 0.13$	**$\beta = 0.488 \pm 0.085$** **$\chi^2 = 32.7$** **$p < 0.0001$**	**$\chi^2 = 21.4$** **$p < 0.0001$**
M. trossulus	$\chi^2 = 0.500$ $p = 0.78$	$\beta = 0.077 \pm 0.167$ $\chi^2 = 0.214$ $p = 0.64$	$\beta = 0.201 \pm 0.120$ $\chi^2 = 2.82$ $p = 0.093$	**$\chi^2 = 16.0$** **$p = 0.0003$**
P. hauniense/ *C. glaucum*	$\chi^2 = 0.483$ $p = 0.79$	$\beta = 0.041 \pm 0.186$ $\chi^2 = 0.049$ $p = 0.83$	$\beta = 0.173 \pm 0.129$ $\chi^2 = 1.79$ $p = 0.18$	**$\chi^2 = 24.0$** **$p < 0.0001$**
Hydrobia sp.	$\chi^2 = 0.092$ $p = 0.96$	$\beta = -0.078 \pm 0.250$ $\chi^2 = 0.096$ $p = 0.76$	$\beta = -0.072 \pm 0.132$ $\chi^2 = 0.295$ $p = 0.59$	$\chi^2 = 5.62$ $p = 0.060$
T. fluviatilis	$\chi^2 = 3.31$ $p = 0.19$	$\beta = 0.009 \pm 0.115$ $\chi^2 = 0.0065$ $p = 0.94$	**$\beta = 0.443 \pm 0.085$** **$\chi^2 = 27.1$** **$p < 0.0001$**	**$\chi^2 = 8.81$** **$p = 0.012$**
R. peregra	$\chi^2 = 2.44$ $p = 0.29$	$\beta = 0.249 \pm 0.163$ $\chi^2 = 2.33$ $p = 0.13$	**$\beta = 0.277 \pm 0.163$** **$\chi^2 = 7.42$** **$p = 0.0065$**	**$\chi^2 = 20.4$** **$p < 0.0001$**
A. improvisus	**$\chi^2 = 44.6$** **$p < 0.0001$**	$\beta = 0.285 \pm 0.239$ $\chi^2 = 1.42$ $p = 0.23$	**$\beta = 0.646 \pm 0.154$** **$\chi^2 = 17.5$** **$p < 0.0001$**	$\chi^2 = 2.42$ $p = 0.30$
S. vanhaareni	**$\chi^2 = 6.89$** **$p = 0.032$**	$\beta = 0.103 \pm 0.222$ $\chi^2 = 0.216$ $p = 0.64$	**$\beta = 0.362 \pm 0.148$** **$\chi^2 = 5.97$** **$p = 0.015$**	$\chi^2 = 1.42$ $p = 0.49$

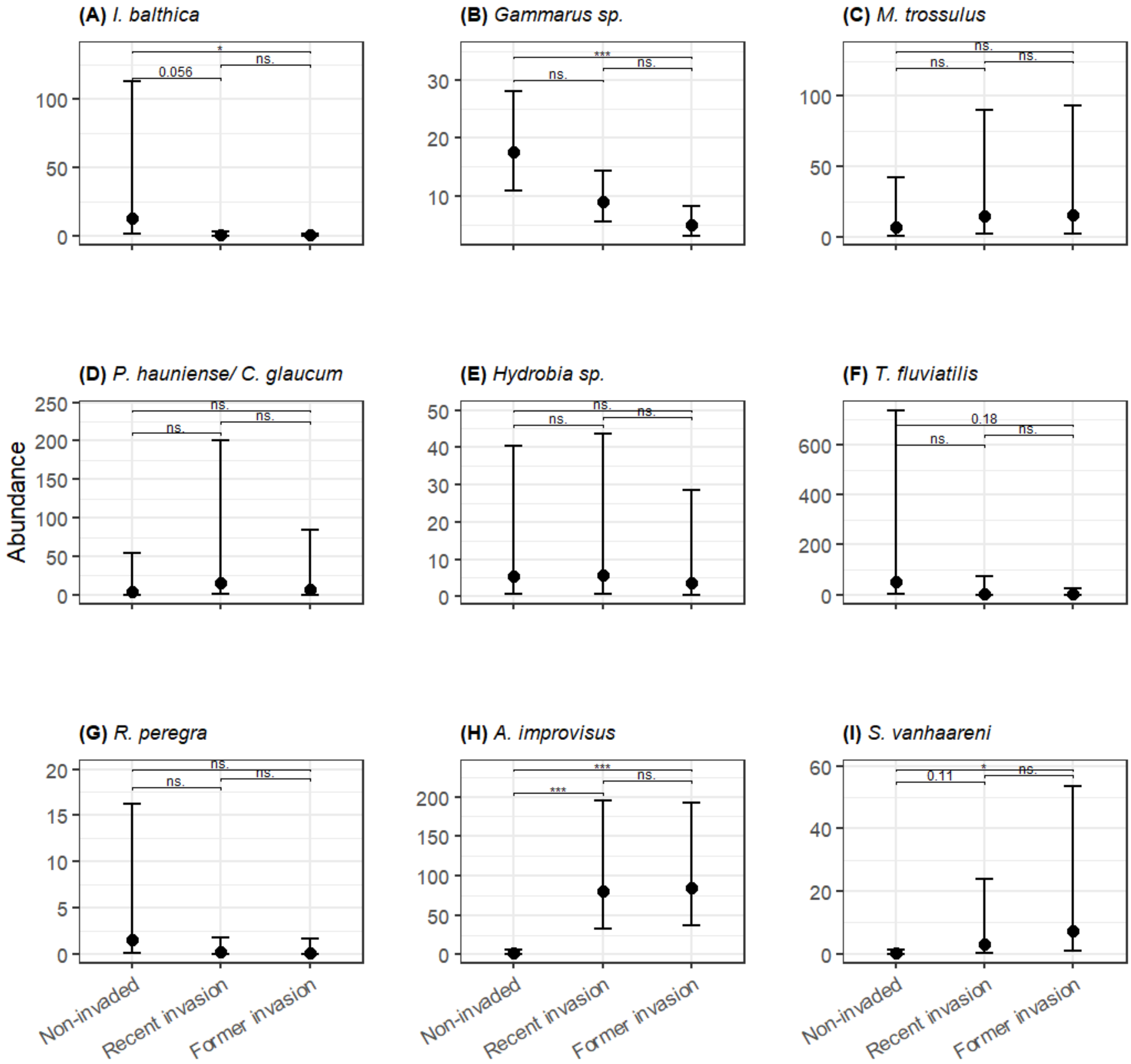


Figure 8. Model estimated abundances for species that best explain differences between invasion histories, controlling for water depth and *Fucus* dry weight. Error bars show 95% confidence intervals. Brackets indicate Tukey adjusted pairwise comparisons, with significance levels (ns. = non-significant, *=p<0.05, **=p<0.01, ***=p<0.001).

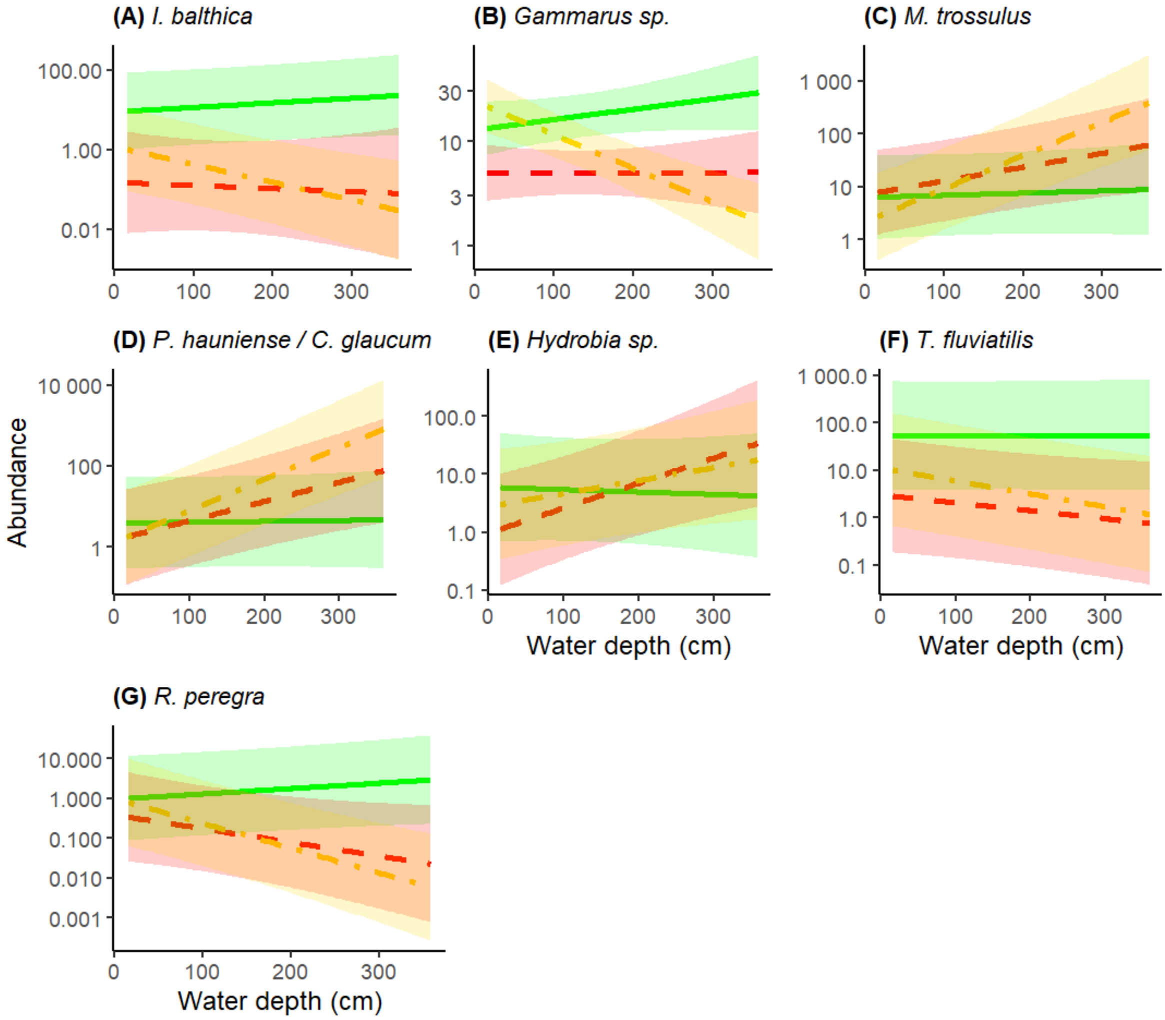


Figure 9. Model-predicted abundances with 95% confidence intervals for species along a water depth gradient among different invasion histories, controlling for *Fucus* dry weight. Site types are indicated by color: green = non-invaded, yellow = recently invaded, red = formerly invaded. Abundances are shown on a log-scale.

4 Discussion

4.1 Impacts on invertebrate communities

Based on the multivariate model and pairwise comparison of invasion histories, I found significant differences in the community compositions of areas invaded by *R. harrisii* when compared to uninvaded sites, supporting the initial hypothesis (H1). As motile herbivores are either preyed upon or indirectly impacted by the crab, especially filter feeders like *A. improvisus* become more abundant. The remaining grazer community in the system changes to one dominated by hard shelled species more resistant to the crab's presence.

My results indicate that in the Northern Baltic isopods, especially *I. balthica,* gammarids and gastropods such as *T. fluviatilis* and *R. peregra* are negatively impacted by crab presence (H2). A clear decline in the abundances of these motile herbivores is evident from both the dissimilarity analysis between invasion statuses (excluding *I. balthica* which was not included in the cumulative dissimilarities due to its low contribution) and the species-specific GLMM predictions. These results support earlier findings from the Northern Baltic that *R. harrisii* is capable of quickly eradicating herbivore species from native communities (Jormalainen et al., 2016, 2023).

The decrease of motile mesoherbivores may be caused by direct predation by *R. harrisii* or be an indirect result of predator avoidance by the native species. Earlier studies from the Baltic have found that *R. harrisii* feeds readily on gammarids (Hegele-Drywa & Normant, 2009) as well as isopods (*I. balthica*) and gastropods (*T. fluviatilis*) (Jormalainen et al. 2023, Pelikan et al., submitted). While no direct food content analysis was performed for the current study, predation is likely a contributing factor to reduced mesoherbivore abundances. However, evidence of predation alone is not sufficient to determine the extent of its ecological effects. It is also possible that prey species are able to, for example, sense the presence of *R. harrisii* through chemical cues (Pelikan et al., submitted) and move out from invaded areas.

While predation by *R. harrisii,* along with its indirect effects, is likely an important driver for reduced mesoherbivore abundances, quantifying these impacts in natural systems is challenging. The crab has been shown to adapt its diet based on available food sources, including algae and detritus when abundantly available (Hegele-Drywa & Normant, 2009). Consequently, spatial variability in prey communities and alternate food sources can modify the ecological effects of *R. harrisii,* complicating the generalization of prior case studies and laboratory experiments to wild communities. Communities inhabiting soft sediments and mussel beds affected by *R. harrisii* (Hegele-Drywa & Normant, 2009) may face very different effects compared to the rocky *Fucus* habitats currently studied. A more detailed study on *R. harrisii* diet in natural communities in the Northern Baltic using stomach content analysis or genetic methods would be crucial for determining the diet of the crab.

This study suggests that while most gastropods and mobile crustaceans show decreasing trends in the presence of *R. harrisii*, bivalves and barnacles flourish in the *Fucus* canopies of invaded areas. Research on other decapod species has shown a preference toward softer-bodied prey due to either limited strength in cracking hard shells (Buck et al., 2003) or avoidance of claw damage (Juanes & Hartwick, 1990). While other gastropods declined, the abundance of small-bodied hydrobiid snails was not affected by the crabs' presence. Hydrobiids are small and relatively hard-shelled compared to other gastropod species, most likely making them low-value prey for the crabs. The same can be said about the cockles *P. hauniense* and *C. glaucum* as well as the barnacle *A. improvisus*, which significantly increased in invaded zones. This supports the original hypothesis (H3), where more unpalatable hard-shelled sessile organisms start to dominate after the invasion.

While certainly possible, high levels of predation by *R. harrisii* do not directly translate into reduced species abundances. For example, earlier results from a controlled study system show that *R. harrisii* readily feeds on *M. trossulus* in the Archipelago Sea (Forsström et al., 2015). However, in the current study *M. trossulus* showed no reduction in abundance in relation to crab invasion. A similar result has been described by Jormalainen et al. (2016). In the current study, the majority of *M. trossulus* individuals in some samples were small juveniles only a couple millimeters long due to the timing of spawning before sample collection (Pierścieniak et al., 2011). Strong recruitment and settlement of juvenile *M. trossulus* might have had a large impact on observed abundances. Studies have also shown preference toward smaller sized individuals within prey species (Forsström et al., 2015; Juanes & Hartwick, 1990). Conversely, it is also possible that for some of the species observed in the current study, juvenile individuals present during sampling were too small for *R. harrisii* to prey on. While this study cannot attest to species specific size preferences, size selectivity by *R. harrisii* might partly explain the lack of differences in the abundance of *M. trossulus*.

When considering changes in community compositions it is important to note the other abiotic factors that could additionally or synergistically impact habitats. In the Archipelago Sea, the mud crab invasion began in the inner archipelago and gradually spread toward the outer islands and reefs. Simultaneously, most environmental gradients such as salinity, temperature, wave exposure and turbidity follow a codirectional pattern with gradients moving outward from the inner archipelago. These factors cannot be separated from the invasion trajectory, and they might have additive or opposing impacts with the invasion. A recent study by (Jormalainen et al., 2023) shows similar reductions in the abundance of *I. balthica* and *T. fluviatilis* on the invasion front from 2020 to 2024. In 2020 when the crab had just arrived in Boskär, *I. balthica* was very abundant. However, by 2024 only a few individuals are present on the nearby island of Berghamn, as shown by the current study. In addition, other studies have shown that the introduction of the crab can rapidly result in changes to community compositions in *Fucus* habitats (Jormalainen et al., 2016). Therefore, while abiotic conditions can help explain site-specific differences in community structures, the presence of *R. harrisii* is the most likely cause for the fast and persistent changes in species dominance.

In addition to species specific responses, some changes in diversity measures (i.e., Shannon Wiener diversity, total abundance, species richness) were detected. There was a significant decrease in Shannon-Wiener diversity in recently invaded areas. Earlier results on diversity impacts are rather similar. In a short-term field study by Forsström et al. (2015) *R. harrisii* presence resulted in significant decreases for species richness and Shannon-Wiener index, while total abundance was not affected. Jormalainen et al. (2016) reported a significant decrease in Shannon-Wiener diversity within few years of invasion. The current study found no impact on species count, while total abundance was significantly affected through the interaction between invasion history and depth. It has to be noted that Forsström et al. (2015) used an experimental setup with full predator exclusion, unlike Jormalainen et al. (2016) and the current study where communities were compared at their natural predation rates.

While diversity reduced in recently invaded sites, total abundance of invertebrates increased significantly with depth. Total abundance and species models as well as the multivariate community model showed common patterns of depth-dependence, with depth having an important impact on abundance and structure, but only in invaded sites. This suggests that the effects of *R. harrisii* are intensified at greater depths in rocky littoral habitats. This is supported by the binomial presence-absence model, where crabs were more likely found in deeper parts of the *Fucus* belt. Very little is known about the depth distribution of *R. harrisii* in its Baltic habitats (Hegele-Drywa & Normant, 2014), but it is possible that the crab favors deeper habitats on the edge of the *Fucus* belt resulting in increased community impacts. It is also possible that the impacts of *R. harrisii* increase in greater depths due to the sparser *Fucus* canopy providing less shelter for motile herbivores. During sample collection we determined that the *Fucus* canopies tended to be densest around 1–2 m and got sparser in deeper bottoms.

Differences in macroinvertebrate community structure between recently and formerly invaded sites were inconclusive and did not differ significantly. These results do not support the boom-and-bust pattern expected to emerge from delayed adaptive antipredatory responses by native prey species (Kondoh, 2006) (H4). It is possible that the temporal resolution of the study has been suboptimal for observing the boom-and-bust dynamic with prey adaptation happening either too quickly or too slowly to be observed between invasion history classes. Anton et al. (2020) estimated across various terrestrial and aquatic taxa that it can take native prey on average around 200 generations to develop appropriate antipredator responses on par with responses to native predators, although the speed of adaptation can vary between functional and taxonomic groups. The invasion in the Archipelago Sea is so recent that sufficiently strong antipredatory responses may not have developed in prey populations even in the oldest invaded areas. Additionally, because the classification of invasion length is mostly based on the FinBIF-repository data, invasion lengths may be underestimated due to incomplete observation records. This may cause uncertainty in the classification of invasion histories, particularly in sites with short invasion histories (< 4 years, classified as recent invasion) or sites classified as uninvaded located close to the invasion front.

A study by Jormalainen et al. (2016) monitored community composition in the inner Archipelago Sea, close to Orhisaari site in the current study, for three consecutive years as the invasion originally spread to that area. While that study documented substantial decreases in herbivore abundance, current data from Orhisaari showed persistently low abundances for motile herbivores (Appendix 2), suggesting a long-lasting change in community composition without notable recovery. On the other hand, the study by Jormalainen et al. (2016) also found a significant decrease in the Shannon-Wiener index from ~1.3 to ~0.7 in the span of three years in response to the invasion. In ten years after the low diversity values were originally recorded the Shannon-Wiener diversity around Orhisaari has returned to pre-invasion values even slightly exceeding them at 1.47, regardless of crab abundances remaining similar since 2014. Apparent differences in diversity values between studies could likely be the result of differences in the size of sampled *Fucus* stands, with smaller *Fucus* bushes sampled in the previous study (V. Jormalainen, pers. comm., 28.11.2025). Another explanation for the difference could be behavioral or physiological adaptations to *R. harrisii* or more likely a demonstration of a regime shift where new species have colonized the habitat after the crab had decimated the original community. An example of post-invasion colonization is the tanaid *S. vanhaareni*, which has become highly abundant in invaded areas and shows strong co-occurrence with *R. harrisii*. While physiological adaptations to decapod predation have been recorded in the past (Brookes & Rochette, 2007) and hypothesized in response to *R. harrisii* (Pelikan et al. unpublished), I consider it is unlikely that adaptation alone has constituted this recovery. This is because community structures and species identities have clearly changed in invaded areas and the time from initial introduction is relatively short when compared to average speeds recorded for the adaptation toward novel predators (Anton et al., 2020). A direct comparison of current community structure to the ones from 2012-2014 (Jormalainen et al., 2016) would be beneficial to increase the temporal scale.

While the direct and indirect negative effects caused by *R. harrisii* on crustaceans and gastropods can most likely be attributed to predation and the threat of predation (Forsström et al., 2015; Jormalainen et al., 2016), it is more difficult to hypothesize on the indirect positive effects on species thriving in invaded areas or larger scale impacts for trophic interactions. Other successful decapod invaders, especially the European green crab *Carcinus maenas* (Linnaeus 1758) in North America, have been extensively studied and their impacts on native communities mirror those suggested for *R. harrisii* (Bissett et al., 2025; Grosholz et al., 2000). There is reliable evidence for direct multitrophic level changes caused by *C. maenas* (Grosholz et al., 2000), which functionally resembles *R. harrisii* as a generalist omnivore.

This study also supports earlier findings (e.g., Kotta et al., 2018) suggesting that *R. harrisii* can shift existing species ratios toward a community typically associated with high eutrophication, indicated here as the increase in bivalves and hydrobiids typically associated with muddier environments. The regime shift toward a filter feeder dominated community enforced by *R. harrisii* is similar to community changes caused by increased nutrient loads and suspended detritus (Kube et al., 1998; Korpinen et al., 2010; Frigstad et al., 2023).

While the crabs act as efficient predators, they are also readily preyed upon by a variety of fish. Species such as the fourhorn sculpin *Myoxocephalus quadricornis*, common perch *Perca fluviatilis* and ruffe *Gymnocephalus cernua* have been shown to feed on *R. harrisii*. While the crab might be a significant source of food for fish like *M. quadricornis*, predation does not seem to be capable of limiting the spread and abundance of the crab. (Puntila-Dodd et al., 2019). *Rhithtropanopeus harrisii* appears to grow larger in some of its introduced habitats compared to the native range. The lack of predation and parasitism in the introduced habitat has been suggested as an explanation for increased growth (i.e., the enemy release hypothesis). The rhizocephalan parasite *Loxothylacus panopaei,* which parasitizes up to 90% of native populations, is totally absent from the Northern Baltic and all other introduced populations. Release from parasitism can allow the crab to invest more in growth and increase its fecundity (Fowler et al., 2013). High fecundity has been linked to invasion success in other invasive decapods (Epifanio, 2013). On the other hand, as potential predators gradually gain more experience and adapt to use *R. harrisii* more effectively, they could limit crab abundance in the future, if the crab continues to be successful in these introduced populations (Kondoh, 2006).

Rhithropanopeus harrisii is not the only novel invasive species present in the rocky littoral habitats in the Finnish Archipelago Sea. A little studied invertebrate invader, the tanaid *Sinelobus vanhaareni* (Bamber 2014), has been spreading along Finnish coasts since 2016 (Gagnon et al., 2022). The origin and introductory paths of *S. vanhaareni* remain unknown, but it has quickly become abundant in much of the Northern Baltic (Gagnon et al., 2022). Tanaids share a similar niche with the native amphipod *Leptocheirus pilosus* acting as motile filter feeders that live in tube-like burrows among algae (Gagnon et al., 2022; Goodhart, 1939). Based on my current data *S. vanhaareni* seems to be more consistently distributed along the archipelago within the *R. harrisii* invasion zone compared to *L. pilosus. Sinelobus vanhaareni* also appears to strongly co-occur with the crab. Similarly, the invasive barnacle *A. improvisus* is far more abundant in invaded sites. The barnacle is and older invader, originally discovered in Finland in 1886 and likely spread through hull fouling (Meng et al., 2024).

The co-occurrence of *S. vanhaareni* and *A. improvisus* with *R. harrisii* could suggest some form of advantageous or even facilitative relationship between the species. As described by Simberloff & Von Holle (1999), possible invasive-invasive facilitation could further strengthen the regime shift in rocky littoral habitats, as novel invasive species cause synergistic changes to native communities. As so little is known about *S. vanhaareni* or its interactions in the Baltic, no conclusion can be drawn on how these invasive species interact. While synergistic facilitation is possible, there may be more indirect mechanisms such as the crab removing native predators or competitors of *S. vanhaareni* or *A. improvisus*. It is also possible that the co-occurrence is simply a result of shared dispersal pathways resulting in the species sharing many habitats. In the case of the barnacle, it may benefit from the larger scale changes to habitats and energy flows imposed by the crab (section 4.2). These interactions can be further complicated by abiotic factors like salinity, which can limit populations of *A. improvisus*, as well as other invaders, in the inner archipelago (Meng et al., 2024). Overall, more study on facilitative relationships and indirect interactions among invasive species in the Baltic would be necessary to explain patterns of co-occurrence.

4.2 Impacts on rocky littoral habitats

Top-down control of primary production is prevalent in many aquatic littoral systems due to linear food webs and strong trophic interactions (Gruner et al., 2008). Herbivory has a major effect on primary producer biomass in aquatic systems and grazing can remove on average up to 68% of producer biomass in aquatic systems (Poore et al., 2012) as opposed to 4–8% in terrestrial systems (Bakker et al., 2016; Turcotte et al., 2014). Based on the current study, *R. harrisii* can significantly disturb herbivory in rocky littoral habitats possibly causing cascading changes in the energy flows of the system.

Fucus is an exceptionally important species for littoral ecosystems in the Northern Baltic, since it provides shelter and structural complexity. In its optimal growth range *Fucus* can make up 90% of macrophyte biomass (Kautsky & van der Maarel, 1990). Even though *Fucus* makes up the majority of macroalgal biomass, grazing pressure in the Northern Baltic is limited to just a few species. Small *Fucus* recruits are grazed by gastropods (Malm et al., 1999) and some gammarids (Eriksson et al., 2011), but herbivory on mature thalli is essentially limited to just the isopod *I. balthica* (Korpinen et al., 2010). Some cases of major defoliation caused by high densities of *I. balthica* have been reported in the past (Engkvist et al., 2000; Haavisto & Jormalainen, 2014; Nilsson et al., 2004), even though *I. balthica* experiences reduced growth rates when feeding on *Fucus* as opposed to filamentous algae (Jormalainen et al., 2001). Therefore, *Fucus* is not a preferred food source and heavy grazing on the species is likely due to predator avoidance behaviour and shelter provided by the *Fucus* canopy rather than food value. Additionally, it is likely that most herbivores living among the *Fucus* belt do not actually feed on the mature *Fucus* itself, but instead on the ephemeral filamentous algae or microalgae associated with it. Furthermore, due to the low food value of *Fucus* (Jormalainen et al., 2001), even species specialized in grazing on *Fucus* might shift more toward a filamentous diet as ephemeral algae increases with climate change (Takolander et al., 2017).

Based on observed changes in invertebrate community structure, *R. harrisii* elicits strong top-down control on the food web. As mesoherbivores are removed from the system, macrophytes are released from grazing pressure. Without top-down regulation of algal growth, primary producers are only limited by light and nutrient availability. Fast growing filamentous algae tend to benefit from this change by being better competitors when grazing is suppressed, since they prioritize quick growth and nutrient uptake instead of herbivory resistance. In contrast, *F. vesiculosus,* the foundation species on rocky shores, is outcompeted due to its slower growth rate and investment into secondary metabolites such as phlorotannins (Jormalainen & Ramsay, 2009).

Through the high impact on producer biomass, herbivory can counteract the effects of eutrophication. While eutrophication via nutrient addition in aquatic systems leads to higher biomass of filamentous algae, this is only thought to occur in systems lacking grazers (Korpinen et al., 2007b; Worm et al., 1999) As herbivory is especially high on algal recruits and germlings, the lack of grazers allows quick growing algae to colonize and grow. Of all grazers, especially gastropod herbivores were important for maintaining producers' diversity in the environment. Additionally, high densities of gammarids, especially *G. locusta*, can act as efficient controllers of ephemeral epiphytes, but they are prone to predation since gammarids are important prey for many fish (Worm et al., 1999). In another field experiment a strong interaction between the top-down control of grazer predation by fish and the bottom-up effect of nutrient addition for the growth of filamentous algae was described (Korpinen et al., 2007a). Based on these studies I can conclude that while grazing can reduce both filamentous and perennial species, grazer exclusion tends to favor fast growing ephemeral algae. The results from the current study indicate that *R. harrisii* is capable of reducing grazer abundances far beyond the levels of natural predation, which can release algal communities from top-down control, resulting in major cascading changes especially in the inner archipelago where nutrient loads are higher (Korpinen et al., 2007a &2007b).

The reduction of grazers by *R. harrisii* can seriously hinder *Fucus* growth rates through increased fouling. As an example, in mesocosms, *Fucus* growth rate has been shown to nearly double when fouling is removed by *T. fluviatilis* (Honkanen & Jormalainen, 2005). In addition, the increased prevalence of the barnacle *A. improvisus* as well as blue mussels in invaded areas might contribute to adverse fouling for *Fucus*. In large quantities, mussels and barnacles can weigh down algal stands and increase risk of tearing (D'Antonio, 1985). A study by Gutiérrez and Palomo (2016) found evidence for a fouling cascade, where initial introduction of barnacles could facilitate further epiphytic algal growth. Based on field observations from the invaded sites, increased sessile epifaunal mass can also result in large *Fucus* bushes no longer being held upright by the air-vesicles (pneumatocysts).

4.3 Conclusions

A spatially large-scale quantitative study on invertebrate communities in rocky littoral habitats in the Northern Baltic demonstrated that the invasive mud crab *R. harrisii* significantly affects community compositions and species abundances (H1). In response to the invasion, motile mesoherbivores like isopods, gammarids and most gastropods reduced in abundance, likely as a result of direct predation or indirect predation pressure by the crab (H2). In their place, a community dominated by sessile filter feeders and remaining hard-shelled herbivores, as well as some novel invaders, formed (H3). This may be a result of reduced competition or predation for filter feeders as motile invertebrates are removed, or a sign of more complex multitrophic changes imposed by the crab. It seems likely that the crab is capable of suppressing herbivory sufficiently to benefit filamentous algal growth in *Fucus* dominated habitats. Results also showed strong co-occurrence between different invasive species, suggesting facilitation, indirect benefits or shared dispersal pathways between the species. In addition, the Shannon-Wiener diversity was significantly lower in recently invaded sites. On overall strong effect of depth within invaded sites was detected for individual taxa as well as for total abundance. This suggests that the effects of *R. harrisii* are to some extent depth-dependent, likely due to the crabs depth distribution or reduced shelter for prey at greater depths. Taking together, these results suggest that *R. harrisii* might be an important player in the current regime shift in the Northern Baltic.

Communities did not show any significant recovery between recently and formerly invaded sites (H4). Crab densities remained relatively high in formerly invaded sites and macroinvertebrate populations originally diminished by *R. harrisii* did not show signs of increase. I suggest that this is the result of a lack of antipredatory adaptations in prey in response to crab predation due to the short time scale of the invasion or a more permanent regime shift resulting in altered species identities, suppressing mesoherbivores.

More research to determine *R. harrisii* diet and to quantify top-down effects are crucial to understand the crab's impacts in the Norther Baltic. To date, studies on *R. harrisii* in Finland has largely focused on rocky littoral habitats dominated by *F. vesiculosus*, but looking at the two other key habitats, mussel and seagrass beds, would be important for estimating the overall effects of the mud crab across the entire coast. As current results point toward a possible regime shift, I suggest that further study should be focused on the changes to long-term ecosystem functioning in invaded areas. Quantifying the impacts of these crabs is critical for assessing their potential harm to native ecosystems and informing appropriate management actions. At present, *R. harrisii* is included in neither the EU's list of invasive alien species of union concern nor Finland's list of invasive alien species of national concern.

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Appendix

Appendix 1. Crab trapping data

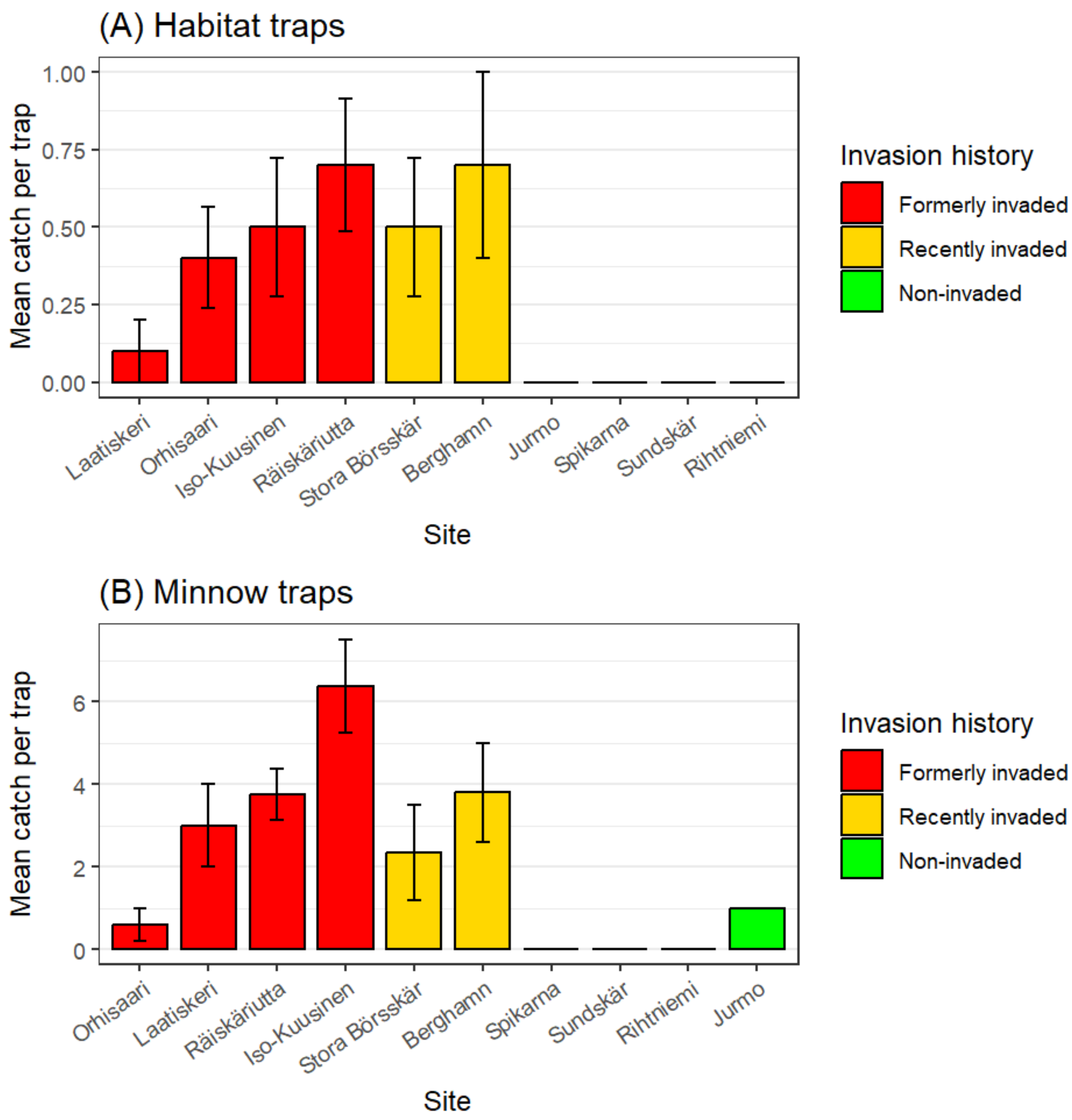

Figure 1 Data collected from crab trappings in June-July of 2024. Results from habitat traps (A) and minnow traps (B) have been separated. Bars represent mean catches with calculated standard deviations. For all sites, 10 habitat traps and 5–8 minnow traps were used.

Appendix 2. Full abundance data

Table 1 Summary of the full invertebrate dataset collected from the *Fucus* samples. Means with standard deviations along with minimum and maximum counts are presented for each species in every site (mean ± sd. (min.–max.)).

Species	**Berghamn**	**Birsskär**	**Iso-Kuusinen**	**Jurmo**	**Laattiskeri**	**Orhisaari**	**Paraisten portti**	**Rihtniemi**	**Räiskä-riutta**	**Spikarna**	**Stora Börsskär**	**Sundskär**
A. aquaticus	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
A. improvisus	153.73 ± 382.73 (2–1512)	436.92 ± 549.12 (6–1942)	110.71 ± 129.15 (9–505)	3.31 ± 5.95 (0–20)	49.67 ± 97.12 (0–323)	136.08 ± 163.95 (1–574)	202.58 ± 270.41 (0–920)	1.13 ± 2.50 (0–7)	61.40 ± 72.59 (3–281)	2.93 ± 8.18 (0–31)	6.40 ± 12.49 (0–35)	5.60 ± 5.54 (0–18)
B. tentaculata	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
C. laeviusculus	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
C. obscura	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.29 ± 0.61 (0–2)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.21 ± 0.58 (0–2)	0.40 ± 1.06 (0–4)
C. volutator	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
Chironomidae	5.53 ± 8.66 (0–34)	20.67 ± 35.25 (0–131)	2.73 ± 2.87 (0–8)	3.07 ± 2.06 (0–7)	10.07 ± 6.26 (1–27)	15.07 ± 34.40 (0–105)	30.67 ± 22.21 (6–75)	3.80 ± 7.08 (0–26)	2.80 ± 3.55 (0–13)	0.20 ± 0.56 (0–2)	7.07 ± 7.38 (0–23)	3.47 ± 4.37 (0–17)
Coenagrionidae	0.07 ± 0.26 (0–1)	1.00 ± 1.56 (0–5)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
Gammarus sp.	9.00 ± 5.32 (1–23)	12.93 ± 11.00 (1–43)	1.73 ± 1.71 (0–6)	13.64 ± 11.76 (2–41)	11.20 ± 8.90 (1–32)	6.53 ± 5.90 (0–18)	11.33 ± 14.51 (0–43)	8.47 ± 9.54 (0–33)	3.73 ± 4.28 (0–16)	29.47 ± 33.35 (0–110)	10.43 ± 15.65 (1–55)	48.87 ± 32.28 (8–113)
H. diversicolor	0.00 ± 0.00 (0–0)	0.60 ± 1.55 (0–6)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.14 ± 0.36 (0–1)	0.27 ± 0.59 (0–2)
Halacaridae	13.27 ± 16.17 (0–49)	0.60 ± 2.32 (0–9)	0.53 ± 1.25 (0–4)	0.07 ± 0.27 (0–1)	5.20 ± 4.81 (0–19)	4.73 ± 3.63 (0–10)	6.00 ± 5.62 (0–18)	4.07 ± 3.41 (0–10)	1.27 ± 2.12 (0–7)	0.07 ± 0.26 (0–1)	0.14 ± 0.36 (0–1)	0.13 ± 0.35 (0–1)
Hydrobia sp.	25.20 ± 24.52 (1–88)	11.87 ± 16.82 (0–64)	0.20 ± 0.56 (0–2)	16.86 ± 20.07 (0–57)	27.33 ± 47.73 (0–128)	8.00 ± 10.76 (0–37)	0.07 ± 0.26 (0–1)	0.20 ± 0.41 (0–1)	8.53 ± 25.13 (0–99)	6.33 ± 13.78 (0–54)	47.00 ± 54.89 (0–153)	31.93 ± 46.94 (2–174)

Species	Berghamn	Birsskär	Iso-Kuusinen	Jurmo	Laattiskeri	Orhisaari	Paraisten portti	Rihtniemi	Räiskäriutta	Spikarna	Stora Börsskär	Sundskär
Hydroptilidae	0.07 ± 0.26 (0–1)	0.53 ± 1.25 (0–4)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.47 ± 0.52 (0–1)
I. baltica	0.93 ± 1.87 (0–7)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	8.57 ± 14.96 (0–56)	11.93 ± 9.90 (1–29)	0.00 ± 0.00 (0–0)	0.13 ± 0.35 (0–1)	7.53 ± 6.74 (0–21)	0.13 ± 0.35 (0–1)	11.73 ± 13.58 (2–46)	8.93 ± 8.43 (1–25)	45.80 ± 26.36 (6–88)
I. chelipes	0.20 ± 0.56 (0–2)	0.27 ± 0.80 (0–3)	0.00 ± 0.00 (0–0)	2.14 ± 2.63 (0–9)	0.53 ± 0.83 (0–3)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	3.33 ± 4.13 (0–12)	0.00 ± 0.00 (0–0)	5.07 ± 4.25 (0–17)	0.57 ± 1.40 (0–5)	6.33 ± 3.98 (1–14)
I. granulosa	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.93 ± 1.44 (0–5)	0.53 ± 0.92 (0–3)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	3.93 ± 6.97 (0–28)	0.00 ± 0.00 (0–0)	0.93 ± 1.28 (0–4)	0.29 ± 0.73 (0–2)	2.47 ± 1.92 (0–6)
Jaera sp.	2.00 ± 3.63 (0–13)	0.80 ± 1.57 (0–5)	0.00 ± 0.00 (0–0)	2.36 ± 2.21 (0–6)	1.60 ± 1.68 (0–5)	3.60 ± 6.99 (0–24)	0.07 ± 0.26 (0–1)	0.53 ± 0.92 (0–3)	0.60 ± 0.91 (0–3)	0.20 ± 0.41 (0–1)	0.50 ± 1.09 (0–4)	1.60 ± 1.84 (0–5)
L. capitata	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.20 ± 0.56 (0–2)	0.13 ± 0.52 (0–2)	0.00 ± 0.00 (0–0)	0.40 ± 1.30 (0–5)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.00 ± 0.00 (0–0)
L. pilosus	0.00 ± 0.00 (0–0)	51.47 ± 98.13 (0–329)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	1.27 ± 1.79 (0–6)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	2.53 ± 3.50 (0–13)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
M. affinis	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
M. trossulus	146.53 ± 180.61 (1–633)	64.00 ± 123.72 (0–493)	1.80 ± 2.76 (0–9)	23.93 ± 19.93 (4–67)	59.20 ± 62.47 (1–211)	7.00 ± 8.95 (0–34)	0.53 ± 0.74 (0–2)	0.47 ± 0.64 (0–2)	101.20 ± 85.09 (4–318)	2.87 ± 2.64 (0–10)	75.00 ± 97.23 (0–289)	92.33 ± 123.98 (4–445)
M. truncata	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
Marrenzellaria sp.	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.13 ± 0.52 (0–2)	0.00 ± 0.00 (0–0)	0.13 ± 0.52 (0–2)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
N. integer	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
Oligochaeta	0.00 ± 0.00 (0–0)	1.93 ± 5.51 (0–20)	0.00 ± 0.00 (0–0)	0.57 ± 1.45 (0–4)	0.67 ± 1.11 (0–4)	0.47 ± 0.92 (0–3)	0.47 ± 0.74 (0–2)	0.07 ± 0.26 (0–1)	0.13 ± 0.52 (0–2)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.07 ± 0.26 (0–1)
P. adspersus	0.40 ± 0.63 (0–2)	0.80 ± 1.42 (0–5)	0.13 ± 0.35 (0–1)	0.00 ± 0.00 (0–0)	0.47 ± 0.64 (0–2)	0.27 ± 0.80 (0–3)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.27 ± 0.46 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.20 ± 0.56 (0–2)

Species	Berghamn	Birsskär	Iso-Kuusinen	Jurmo	Laattiskeri	Orhisaari	Paraisten portti	Rihtniemi	Räiskä-riutta	Spikarna	Stora Börsskär	Sundskär
P. antipodarum	0.07 ± 0.26 (0–1)	0.73 ± 1.16 (0–4)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	1.33 ± 2.87 (0–10)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.13 ± 0.35 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
P. elegans	0.07 ± 0.26 (0–1)	0.13 ± 0.35 (0–1)	0.13 ± 0.35 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.13 ± 0.35 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.20 ± 0.77 (0–3)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
P. flexuosus	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.29 ± 0.83 (0–3)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
P. fontinalis	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	7.47 ± 9.01 (0–28)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
P. geometra	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)
P. inermis	0.20 ± 0.41 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.50 ± 1.16 (0–4)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.13 ± 0.35 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.14 ± 0.53 (0–2)	0.00 ± 0.00 (0–0)
P. hauniense/ C. glaucum	242.00 ± 261.05 (0–818)	525.93 ± 804.65 (0–3001)	1.27 ± 1.53 (0–5)	21.64 ± 35.23 (0–131)	50.53 ± 71.95 (0–265)	0.87 ± 1.46 (0–4)	0.07 ± 0.26 (0–1)	0.13 ± 0.35 (0–1)	57.07 ± 72.29 (0–283)	3.27 ± 3.95 (0–11)	73.00 ± 94.51 (0–261)	38.53 ± 28.85 (8–91)
R. harrisii	0.33 ± 0.49 (0–1)	1.73 ± 1.79 (0–5)	1.73 ± 2.22 (0–6)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.53 ± 0.99 (0–3)	1.87 ± 3.85 (0–14)	0.00 ± 0.00 (0–0)	0.53 ± 0.99 (0–3)	0.00 ± 0.00 (0–0)	0.14 ± 0.53 (0–2)	0.00 ± 0.00 (0–0)
R. peregra	0.13 ± 0.35 (0–1)	7.20 ± 11.55 (0–41)	0.20 ± 0.56 (0–2)	0.50 ± 0.76 (0–2)	0.73 ± 1.33 (0–5)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.53 ± 0.64 (0–2)	62.60 ± 43.56 (15–157)	0.29 ± 0.47 (0–1)	7.73 ± 4.06 (0–15)
S. entomon	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
S. vanhaareni	7.00 ± 9.81 (0–39)	26.53 ± 41.03 (0–125)	10.47 ± 9.40 (0–34)	11.14 ± 10.01 (0–38)	2.87 ± 8.13 (0–32)	9.60 ± 8.83 (0–27)	6.13 ± 6.64 (0–26)	0.00 ± 0.00 (0–0)	6.53 ± 5.24 (1–20)	0.00 ± 0.00 (0–0)	0.07 ± 0.27 (0–1)	0.13 ± 0.35 (0–1)
T. adspersa	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
T. fluviatilis	27.33 ± 28.59 (3–112)	15.87 ± 19.94 (0–72)	0.07 ± 0.26 (0–1)	40.50 ± 33.46 (3–128)	106.20 ± 57.27 (26–262)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	24.20 ± 12.39 (7–47)	25.40 ± 32.67 (2–109)	73.87 ± 53.28 (7–178)	92.86 ± 95.62 (5–328)	180.73 ± 101.20 (51–412)
Trichoptera	0.00 ± 0.00 (0–0)	0.07 ± 0.26 (0–1)	0.07 ± 0.26 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)

Species	Berghamn	Birsskär	Iso-Kuusinen	Jurmo	Laattiskeri	Orhisaari	Paraisten portti	Rihtniemi	Räiskä-riutta	Spikarna	Stora Börsskär	Sundskär
Turbellaria	1.53 ± 3.07 (0–9)	0.07 ± 0.26 (0–1)	0.80 ± 1.15 (0–3)	0.93 ± 1.38 (0–5)	0.80 ± 1.37 (0–5)	0.20 ± 0.41 (0–1)	2.20 ± 2.11 (0–8)	0.13 ± 0.35 (0–1)	1.67 ± 2.38 (0–8)	4.33 ± 2.66 (1–10)	1.21 ± 2.86 (0–10)	4.13 ± 5.15 (0–14)