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INTRODUCED MARINE CRAB SPECIES IN THE NORTHERN BALTIC SEA: FROM DETECTION TO IMPACTS

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Tiia Forsström

University of Turku

Faculty of Mathematics and Natural Sciences
Department of Biology
Section of Ecology

Supervised by

Professor Veijo Jormalainen
Department of Biology
University of Turku
Finland

Docent Anti Vasemägi
Department of Biology
University of Turku
Finland

Reviewed by

Docent Maiju Lehtiniemi
Leading Research Scientist
Marine Research Centre
Finnish Environment Institute
Finland

Doctor Jonne Kotta
Lead Research Scientist
Estonian Marine Institute
University of Tartu
Estonia

Opponent

Doctor Gregory Ruiz
Senior Scientist
Marine Invasions Research Laboratory
Smithsonian Environmental Research Center
USA

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ABSTRACT

Human mediated species introductions are often irreversible, represent a world-wide problem and are considered one of the threats to marine biodiversity. Invasions can have an impact on the native species and communities, but invasions also affect the demography, dynamics, and genetic composition of the invading species population. Thus, newly introduced species provide a unique opportunity to study different ecological and genetic processes associated with invasions, such as invasion dynamics, build-up of the spatial and temporal population genetic structure, understanding the roles of added or removed functions in an ecosystem and the direct impacts of the invaders.

In my thesis, I studied population demography, dynamics, and the genetics of a newly introduced mud crab, *Rhithropanopeus harrisii*, in the Archipelago Sea in the northern Baltic Sea. In addition, I studied the impacts of this novel invader to the native species and tested whether new molecular tools could be used to detect and monitor this newly introduced species.

The results show that *R. harrisii* has established a relatively stable reproductive population in the invaded area, has spread along the coast, and can be found in several habitats that range from soft sediments to the macroalga *Fucus vesiculosus* having negative impacts on the abundance, richness, and diversity of its prey species. The abundance of the introduced population in the Archipelago Sea is lower than in its native range of North America, although the individuals grow substantially larger in the northern Baltic Sea increasing the reproductive output. The overall abundance of *R. harrisii* appeared to follow the boom and bust pattern with a rapid initial abundance increase and subsequent decline. The population dynamics of *R. harrisii* was mainly driven by changes in the survival of the reproductive females. In addition, environmental variables, such as temperature, was related to the recruitment and growth of juveniles, thus indicating that increasing temperature caused by climate change could potentially increase juvenile recruitment in the future. There was no significant spatial genetic divergence within Finland, which probably reflects the short invasion history of the species in the area. However, the presence of a significant temporal variation between the cohorts (juvenile vs. adult) indicated a lack of temporal stability in this species. Finally, a molecular environmental DNA (eDNA) approach can be used to detect *R. harrisii* from water samples although the detection rate was fairly low. Therefore, more studies are needed to optimize the eDNA method and to evaluate its usability in monitoring.

In conclusion, *R. harrisii* has established a population in the northern Baltic Sea having a negative impact on the native species and communities. However, despite the initial population size increase, the population has declined to the similar size where it was at the beginning of the six-year monitoring. Although the population size seems to be stabilized at the monitoring sites, *R. harrisii* continues to expand its distribution range, and the rapid initial population increase together with the negative impacts, is likely occurring at the newly invaded sites. The results of my thesis provide new information about the population ecology and genetics of a newly introduced functionally novel species that can be used for further research and management purposes in the future.

TIIVISTELMÄ

Ihmistoiminnan aiheuttamat vieraslajien leviämiset ovat peruuttamattomia sekä maailmanlaajuinen ongelma, ja siksi vieraslajeja pidetäänkin yhtenä uhkana merien monimuotoisuudelle. Vieraslajit voivat vaikuttaa paikalliseen lajistoon ja yhteisöihin, mutta vieraslajien kulkeutuminen vaikuttaa myös vieraslajiin itseensä; sen populaatorakenteeseen ja -dynamiikkaan sekä populaation geneettiseen rakenteeseen. Siksi hiljattain levinneet vieraslajit luovat ainutlaatuisen mahdollisuuden tutkia vieraslajien ekologiaa ja geneettisiä prosesseja, kuten vieraslajien populaatiodynamiikkaa, populaation geneettisen rakenteen alueellista ja ajallista muuttumista sekä vieraslajien vaikutuksia paikalliseen lajistoon.

Väitöskirjassani tutkin Saaristomerellä, pohjoisella Itämerellä, hiljattain havaitun vieraslaji liejutaskuravun *Rhithropanopeus harrisi* populaatorakennetta, -dynamiikkaa ja populaation geneettistä rakennetta. Lisäksi tutkin kyseisen uudenlaisen lajin vaikutuksia alueen paikalliseen lajistoon sekä kokeilin sopiiko uusi ympäristö-DNA menetelmä vieraslajin havainnointiin ja seurantaan.

Tulosteni mukaan liejutaskurapu on vakiinnuttanut paikkansa osana pohjoisen Itämeren eliöyhteisöä, levinnyt uusille alueille ja esiintyy useissa erilaisissa elinympäristöissä, kuten pehmeillä pohjilla sekä rakkoleväkasvustoissa vähentävän saaliikseen käyttämien paikallisten lajien runsautta ja monimuotoisuutta. Pohjoisella Itämerellä liejutaskuravun runsaus on alempi kuin lajin alkuperäisellä esiintymisalueella, mutta Itämerellä yksilöt kasvavat huomattavasti suuremmiksi. Lisääntymisikäisten naaraiden elossa säilyvyydellä oli suurin vaikutus liejutaskuravun populaatiodynamiikkaan kuusivuotisen seurannan aikana. Tämän lisäksi ympäristötekijöistä lämpötila vaikutti poikasten elossa säilyvyyteen ja kasvuun. Ilmastomuutoksen seurauksena aiheutuva lämpötilan nousu saattaa parantaa poikasten elossa säilyvyyttä tulevaisuudessa. Saaristomerellä esiintyvillä liejutaskuravuilla ei ollut havaittavissa alueellista geneettistä eriytymistä, mikä selittyy Saaristomerén populaation nuorella iällä. Eri ikäpolvien (poikaset vs. aikuiset) välillä taasen oli merkitsevää vaihtelua geneettisessä monimuotoisuudessa sekä eriytymisessä. Lisäksi totesin, että ympäristö-DNA:han perustavalla menetelmällä pystyy havaitsemaan liejutaskurapuja rapulajia, tosin menetelmä ei vaikuta olevan erityisen herkkä havaitsemaan pohjalla elävää. Lisätutkimuksia tarvitaan optimoimaan menetelmä sekä arvioimaan sen käytettävyyttä vieraslajien seurannassa.

Yhteenvetona, liejutaskurapu on vakiinnuttanut paikkansa osana paikallista lajistoa pohjoisella Itämerellä ja sillä on haitallisia vaikutuksia paikallisiin lajeihin. Kolonisaation alkuvaiheen nopeasta liejutaskurapumäärän kasvusta huolimatta, kuuden vuoden seurannan lopulla rapumäärä oli vähentynyt takaisin lähtötasolle. Vaikka liejutaskurapumäärä näyttää vähentyneen seurantapaikoilla, liejutaskurapu jatkaa leviämistä yhä laajemmalle alueelle pohjoisella Itämerellä ja rapumäärä todennäköisesti kasvaa alkuun voimakkaasti uusilla alueilla aiheuttaen haitallisia vaikutuksia paikalliseen lajistoon. Tulokseni antavat uutta tietoa hiljattain levinneen vieraslajin populaatioekologiasta ja populaation geneettisestä rakenteesta. Tätä tietoa voidaan tulevaisuudessa käyttää tulevien tutkimusten suunnittelussa sekä vieraslajien seurannassa ja torjunnassa.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications and manuscripts, which are referred to in the text by their Roman numerals.

- I Fowler AE, Forsström T, von Numers M & Vesakoski O (2013) The North American mud crab *Rhithropanopeus harrisi* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. *Aquatic Invasions* 8(1):89–96.
- II Forsström T & Vasemägi A (2016) Can environmental DNA (eDNA) be used for detection and monitoring of introduced crab species in the Baltic Sea? *Marine Pollution bulletin* 109:350–355.
- III Forsström T, Ahmad F & Vasemägi A (2017) Invasion genomics: genotyping-by-sequencing approach reveals regional genetic structure and signatures of temporal selection in an introduced mud crab. *Marine Biology* 164:186.
- IV Forsström T, Fowler AE, Riipinen K & Vesakoski O. Post-invasion demography and persistence of a novel functional species in an estuarine system. *Manuscript*.
- V Forsström T, Fowler AE, Manninen I & Vesakoski O (2015) Introduced species meets the local fauna: predatory behavior of the crab *Rhithropanopeus harrisi* in the Northern Baltic Sea. *Biological Invasions* 17:2729–2741.

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Author contributions (in the order of decreasing contribution) to the original publications

	I	II	III	IV	V
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Field/lab work	TF, AF, OV, MvN	TF	TF	TF, AF, KR, OV	AF, TF, IM, OV
Data analyses	OV, TF	TF	TF, FA	TF	TF
Writing	AF, TF, OV, MvN	TF, AV	TF, AV	TF, AF, OV	TF, AF, OV

TF= Tiia Forsström, AF= Amy Fowler, AV= Anti Vasemägi, FA= Freed Ahmad, IM= Iita Manninen, KR= Katariina Riipinen, MvN= Mikael von Numers, OV= Outi Vesakoski

1. INTRODUCTION

1.1 Introduced marine species

Human-mediated species introductions are a world-wide problem and considered as one of the most important threats to biodiversity, structure, and functioning of coastal ecosystems together with overfishing, habitat loss, pollution and climate change (Ruiz et al. 1997, 1999; Carlton and Cohen 1998; Grosholz 2002; Bax et al. 2003; Molnar et al. 2008; Costello et al. 2010). Introduced species occur outside their native range or the range of their dispersal potential and have been introduced by anthropogenic means either intentionally or unintentionally (Olenin et al. 2010). Introduced species that have negative impacts in the invaded regions and continue to spread further are called invasive species (Olenin et al. 2010). Species introductions can be a consequence of a primary or a secondary introduction. In the case of primary introduction, the species arrive from the native range into a new location, whereas in the secondary introduction, the species arrive from an already introduced area into a new location (Minchin et al. 2009).

Coastal habitats are highly invaded ecosystems due to the multitude of introduction pathways together with the natural and anthropogenic disturbances that make coastal areas prone to invasions (Carlton and Cohen 1998; Ruiz et al. 1999). The number of species introductions have increased in the past decades and continue to increase despite growing awareness, national legislation, and international agreements aimed at reducing species introductions (Seebens et al. 2017). Shipping is the most common pathway for introduced marine species (Carlton and Cohen 1998; Bax et al. 2003; Streftaris et al. 2005; Molnar et al. 2008), as a wide range of organism are transported over long distances in ballast water and/or hull fouling (Carlton and Geller 1993; Gollasch et al. 2000; Chan et al. 2014). Other common pathways for introduced marine species include aquaculture and canal constructions (Bax et al. 2003; Streftaris et al. 2005; Molnar et al. 2008; Minchin et al. 2009). However, not all species transported by anthropogenic means become introduced species. According to the Tens Rule by Williamson and Fitter (1996), only about 10% of all species transported are introduced to a new region; ca 10% of those can establish a population in the invaded region, and ca 10% of those become invasive. Hence, a majority of the transported species die during transportation, or the biological and environmental conditions at the introduced region are unfavorable for the population establishment.

1.2 Species establishment and invasion success

The establishment of an introduced species is dependent on the environmental suitability of the introduced site, propagule pressure, and the resistance of the native community (Elton 1958; Stachowicz et al. 1999; Kolar and Lodge 2001; Lockwood et al. 2005; Simberloff 2009; Britton and Gozlan 2013). Propagule pressure consists of propagule size (the number of arriving individuals) and propagule number (the number of arrival events per time unit) (Simberloff 2009). Large propagule pressure increases

establishment success of a population, as it decreases the effects of demographic and environmental stochasticity and Allee effects (Lockwood et al. 2005; Simberloff 2009; Goodsman et al. 2016). Allee effect occurs in small or sparse populations where population growth is reduced at low densities due to reduced individual fitness, e.g. failure to find a mate in low densities (Allee 1931; Stephens et al. 1999).

Native communities can prevent the establishment of an invader. According to the biotic resistance hypothesis, high biodiversity communities are more resistant to invaders than low biodiversity communities are (Elton 1958; Stachowicz et al. 1999, 2002). In a high diversity community, resources are effectively shared by native species thereby leaving fewer available resources for the invaders (Elton 1958; Stachowicz et al. 1999, 2002). However, some studies have reported that the number of introduced species may actually increase with increasing native species richness (Levine and Antonio 1999; Stohlgren et al. 1999; Zaiko et al. 2007). Recent studies have concluded that the relation of native species richness to the invasibility of a community seems to depend on the studied scale (Byers and Noonburg 2003; Fridley et al. 2007). In small spatial-scale, species richness prevents species invasions due to the lack of available resources, while in larger spatial-scale, native species richness positively correlates with the number of invasions because heterogeneous habitats can support higher species richness including introduced species (Byers and Noonburg 2003; Fridley et al. 2007).

During both introduction and establishment, introduced species may experience genetic bottleneck and/or the founder effect (Roman and Darling 2007; Bock et al. 2015; Dlugosch et al. 2015). These effects can reduce the genetic diversity of the invader and thus potentially decrease invasion success, as genetic characteristics of the invader determine the adaptability and plasticity of the species. However, in many cases, introduced species thrive in the new environment, despite the low genetic diversity (Bock et al. 2015; Dlugosch et al. 2015), and for many species no apparent reduction of genetic diversity is even observed (Roman and Darling 2007; Dlugosch and Parker 2008). Multiple introductions from genetically different source populations can abate the loss of genetic diversity during the invasion (Simon-Bouhet et al. 2006; Roman and Darling 2007; Dlugosch and Parker 2008; Gillis et al. 2009). Thus, occasionally the genetic diversity of an introduced population is higher than that for a native population due to multiple introductions from different source populations (Kolbe et al. 2004; Simon-Bouhet et al. 2006; Gillis et al. 2009). Furthermore, drastic loss of genetic diversity is observed only when the founding population size is small (Uller and Leimu 2011). Taken all together, as subsequent introductions affect the genetic diversity of already-established introduced populations and these organisms are exposed to new selection pressures, the introduced species offer a unique opportunity to study the evolutionary processes that are affecting population genetic divergence, connectivity, and diversity.

Successful introduced marine species, especially those that become invasive, share multiple characteristics. They often have high fecundity, a planktonic larval stage, a wide

tolerance range for temperature, salinity, oxygen levels, and anthropogenic disturbance as well as generalist feeding habits (Ricciardi and Rasmussen 1998; Kolar and Lodge 2001; Streftaris et al. 2005; Hänfling et al. 2011). In addition, according to the enemy release hypothesis, many successful introduced species have escaped from native predators and parasites that constrain the growth and abundance of the species in the native range (Elton 1958; Torchin et al. 2001, 2003; Parker et al. 2013; Jeschke 2014; Prior et al. 2015). Of all the marine species groups, crustaceans and crabs among them are the most successful introduced species worldwide (Carlton and Cohen 1998; Molnar et al. 2008; Vilà et al. 2010), as they possess many of the characteristics of a successful invader (Hänfling et al. 2011).

1.3 Detection of introduced marine species

Species introductions are often irreversible (Bax et al. 2003; Thresher and Kuris 2004), as introduced species are usually observed only after they have established a population in the invaded area (Crooks 2005). Both detection and monitoring of introduced species, especially in the early phase of the invasion, are uncommon (Lehtiniemi et al. 2015). Conventionally, introduced species have been detected either during monitoring programs not targeted on introduced species detection or by chance. Traditional detection and monitoring methods are laborious, time consuming, expensive, need taxonomic identification skills, and are usually targeted toward only certain species, species groups or habitats (Lehtiniemi et al. 2015). To overcome some of the limitations of the traditional detection methods, a new molecular approach that uses environmental DNA (eDNA) to detect and monitor aquatic species has been developed (Ficetola et al. 2008).

In the eDNA approach, the species identification is achieved by detecting DNA fragments that the animals excrete and release in the water. DNA in the water may originate from various sources, including feces, skin cells, epidermal mucus, urine, and saliva. With this eDNA approach, detection and monitoring can be targeted toward a single species (Ficetola et al. 2008; Dejean et al. 2012; Tréguier et al. 2014) or simultaneously detect multiple species from different species groups (Deiner et al. 2015; Port et al. 2016; Evans et al. 2016). During recent years, eDNA has been successfully used to assess the occurrence of a wide range of introduced species, including various amphibians, fish, and molluscan species (Ficetola et al. 2008; Nathan et al. 2014; Smart et al. 2015; Brown et al. 2016).

1.4 Introduced marine species in new communities

Established introduced species often perform better in the introduced range than in the native range (Parker et al. 2013). In the introduced range, the individuals tend to often grow faster and larger, and to have higher survival and reproductive success (Grosholz and Ruiz 2003; Parker et al. 2013; Sargent and Lodge 2014). This enhanced performance of an introduced species seems contradictory, as introduced species are expected to be

adapted to their native rather than to a new environment. However, this observed enhanced performance in the introduced range is believed to be related to the availability of more resources and the absence of predators and/or parasites (Grosholz and Ruiz 2003; Torchin et al. 2003). In addition, several environmental and community level factors such as water temperature and/or salinity, and intraspecific competition can alter the survival and reproductive success of an introduced species.

Some introduced species undergo a lag time after the establishment during which the initial population growth is slow, then followed by a rapid population increase and range expansion (Crooks 2005). Some introduced species, however, undergo the so-called boom and bust pattern wherein a rapid increase phase is often followed by a decline of population abundance that stabilizes at a lower level (Simberloff and Gibbons 2004). Occasionally established populations collapse drastically and even go locally extinct (Simberloff and Gibbons 2004; Lester and Gruber 2016). These declines after an initial increase phase and the population collapses are thought to be caused by intra- and inter-specific competition, the exhaustion of resources and/or the appearance of parasites, pathogens or other unknown causes (Simberloff and Gibbons 2004). Sometimes, native species can regulate the population growth of the invader through predation (Hunt and Behrens Yamada 2003; de Rivera et al. 2005; Jensen et al. 2007), thus decreasing the impacts of the invader as well as the rate of spread and long-term population stability.

Introduced marine species can have various impacts on the local species and communities. The impacts are often pronounced at higher abundances (Grosholz et al. 2000; Ricciardi 2003; Jackson et al. 2015) although the opposite pattern is also observed where these impacts are diminished by the intraspecific competition at high densities (Kornis et al. 2014). The impacts of an introduced species can range from single- and multiple-species impacts to trophic- and ecosystem-level impacts (Grosholz et al. 2000; Grosholz 2002; Hänfling et al. 2011). Introduced species can substantially decrease the abundance and diversity of native species or replace the native species through interspecific competition, predation, or by introducing a new parasite or pathogen to the area (Grosholz et al. 2000; Hänfling et al. 2011; Gallardo et al. 2016). These effects can alter trophic interactions and cascade to both higher and lower trophic levels (Byrnes et al. 2007; Thomsen et al. 2014). Often, the introduced consumers have stronger effects on the native prey/plant species than the native consumers do (Salo et al. 2007; Paolucci et al. 2013). This effect could be due to a lack of co-evolutionary history of the introduced and native species causing prey naïveté i.e. a lack of predator recognition and anti-predator responses by the native species (Cox and Lima 2006; Sih et al. 2010; Carthey and Banks 2014; Gérard et al. 2014).

However, not all introduced species have negative impacts on the receiving community but sometimes the receiving community benefits from the invader. An introduced species can become the main food source for a native predator, thus increasing the abundance of the predator (Marchowski et al. 2015; Pintor and Byers 2015; Cattau et al. 2016), although sometimes the quality of introduced species as a food source might be

lower than that of the native species (Felline et al. 2014; Pintor and Byers 2015). One example of beneficial introduction comes from New England where the introduced European green crab *Carcinus maenas* facilitated the recovery of cordgrass *Spartina alterniflora* by reducing the intense herbivory of herbivorous crab *Sasarma reticulatum*, thereby compensating for the depletion of native predators (Bertness and Coverdale 2013). Another example comes from the Baltic Sea where the introduced polychaeta *Marenzelleria* spp. digs deep holes in the bottom sediment, oxidizing an otherwise anoxic seabed by bioturbation (Wallentinus and Nyberg 2007).

1.5 Introduced species in the Baltic Sea

The Baltic Sea is a young non-tidal brackish-water sea that has steep gradients of temperature (yearly average SST <0–20°C) and salinity (2–25) (Leppäranta and Myrberg 2009). Both the average temperature and salinity decrease when moving from south to north and from west to east. The Baltic Sea consists of species-poor communities, simple food webs and low functional diversity (Bonsdorff and Blomqvist 1993; Elmgren and Hill 1997). The species in the Baltic Sea are mainly euryhaline, and many species live in the margins of their distribution range due to the low salinity for marine species and the high salinity for freshwater species. Many species groups, such as krill and starfish, are thus absent in the Baltic Sea. The Baltic Sea is heavily impacted by anthropogenic stress, such as eutrophication, over-fishing, and anthropogenic hazardous substances, due to a large drainage basin area (4 × the sea area) and a dense surrounding population (~85 million). The low macroscopic species diversity, brackish-water, intense shipping and high anthropogenic stress makes the Baltic Sea particularly prone to species invasions (Leppäkoski et al. 2002; Paavola et al. 2005).

As in many sea areas around the world, the number of introduction events have also increased in the Baltic Sea during the past decades (Leppäkoski et al. 2002; Paavola et al. 2005; Gollasch 2006; Ojaveer et al. 2017). A total of ~130 introduced species have been observed in the Baltic Sea and ~80 of those have established a population (Ojaveer et al. 2017) meaning that 2% of all the macroscopic species in the Baltic Sea are introduced species (Costello et al. 2010). The most common pathway for introductions to the Baltic Sea is shipping followed by aquaculture (Leppäkoski et al. 2002; Paavola et al. 2005; Gollasch 2006; Ojaveer et al. 2017). The most important source areas for the Baltic Sea invasions are the Ponto-Caspian region, the East coast of North America and Southeast Asia which are connected to the Baltic Sea by shipping or manmade canals (Leppäkoski et al. 2002; Paavola et al. 2005). Many introduced species in the Baltic Sea are a consequence of secondary introduction from neighboring regions, and after entering the Baltic Sea, many of these species have spread within the region (Leppäkoski et al. 2002; Ojaveer et al. 2017). Introduced species, especially in a species poor community such as the Baltic Sea, provide a unique opportunity and an excellent natural experiment for studying the evolutionary processes that are affecting population genetic divergence, connectivity and diversity, the population dynamics of invasions, roles of

added and removed functions in the ecosystem and both direct and indirect effects of the invaders.

1.6 Aims of the thesis

The aim of this thesis was to study the different aspects of the marine invasions by covering the detection, population genetic composition, population abundance and structure as well as the impacts of a recently introduced species in the northern Baltic Sea. One such recently introduced species is the mud crab *Rhithropanopeus harrisi*, which is a novel species in the northern Baltic Sea, first observed in 2009 from an area where no native crab species occur and the native benthic communities are naturally low in diversity.

My first aim was to assess the occurrence and habitat use of the newly observed *R. harrisi* population in the northern Baltic Sea and then compare the population demography of the northern Baltic Sea population to an earlier introduced and native population in Poland and the U.S., respectively (I). Second, my aim was to test the suitability of the environmental DNA (eDNA) approach for detecting and monitoring introduced mud crab species (*R. harrisi*) in a brackish-water environment to see whether this approach could be used for detection and monitoring of this introduced species in the near future (II). Third, I wanted to study the genetic structuring and divergence of introduced populations in the Baltic Sea and to explore the effects of invasion on the genetic composition of the introduced species. To achieve this I characterized the genetic diversity, structure and divergence of *R. harrisi* in the Baltic Sea populations at different spatial scales and tested the presence of temporal genetic variation among the cohorts in the northern Baltic Sea by screening 1013 SNP markers (III). Fourth, my aim was to study the population dynamics, demography and the persistence of *R. harrisi* in the northern Baltic Sea with demographic data collected over a six-year monitoring period (IV). Finally, I wanted to reveal the potential impacts of this novel predator to the native species and community associated with the habitat forming keystone macroalga *Fucus vesiculosus* using both laboratory and field experiments (V).

2. MATERIALS AND METHODS

2.1 Study species

North American white-fingered mud crab *Rhithropanopeus harrisi* (Fig. 1) originates from the east coast of North America, and its distribution area extends from Veracruz in the Gulf of Mexico to the southern parts of the Gulf of Saint Lawrence in Canada (Williams 1984). *R. harrisi* is a highly successful brachyuran crab species, and the invaded area currently extends to two oceans, 10 seas and freshwater inland reservoirs covering 28 countries (D’Incao and Martins 1998; Rodríguez and Suárez 2001; Iseda et al. 2007; Roche and Torchin 2007; Bacevičius and Gasiunaite 2008; Kotta and Ojaveer 2012; HELCOM 2015; I). *R. harrisi* has several characteristics that have likely facilitated its invasion success. It has a wide tolerance range to water temperature and salinity, high fecundity, a planktonic larval stage, and omnivorous feeding habits (Turoboyski 1973; Laughlin and French 1989a; Hegele-Drywa and Normant 2009).



Figure 1. The study species *Rhithropanopeus harrisi* and collector crate. Photographs by T. Forsström.

The continuous breeding season of *R. harrisi* lasts from three to five months (Ryan et al. 1956; Turoboyski 1973; Gonçalves et al. 1995a). Females are able to produce eggs multiple times after copulation (Morgan et al. 1983), although, in the invaded areas this multiple oviposition is rarely observed (Turoboyski 1973). *R. harrisi* has a planktonic larval stage and both the survival and duration of the planktonic period are dependent on water temperature and salinity (Costlow et al. 1966; Laughlin and French 1989b; Gonçalves et al. 1995b). In general, higher survival and shorter periods are found in warmer water and higher salinity (Costlow et al. 1966; Laughlin and French 1989a, b; Gonçalves et al. 1995b). The effects of temperature and salinity on the survival and duration of the larval period varies depending on location, as larval adaptations to local environmental conditions have been observed (Laughlin and French 1989a). The larvae have a retention mechanism that prevents the planktonic larvae from drifting away from the hatching sites i.e., the parental population (Cronin 1982; Cronin and Forward 1986). *R. harrisi* is omnivorous (Turoboyski 1973; Hegele-Drywa and Normant 2009), and based on the stable isotopic analyses done in the northern Baltic Sea, adult individuals are secondary consumers (Aarnio et al. 2015).

In Europe, *R. harrisii* was first observed in the Netherlands in 1874. Since then, it has spread to several locations around the North Sea and the Baltic Sea. In 1936, it was observed in the Kiel Canal in Germany (Schubert 1936). In the southern Baltic Sea, *R. harrisii* individuals were first reported in 1951 from Poland (Demel 1953) and 1953 from Denmark (Wolff 1954). After an initial introduction to the Baltic Sea, the spread of *R. harrisii* appeared to cease for almost 50 years, after which the spread continued toward the northern Baltic Sea. In 2000, *R. harrisii* was observed in Lithuania (Bacevičius and Gasiunaite 2008), then in 2009 in Finland (Karhilahti 2010), in 2011 in Estonia (Kotta and Ojaveer 2012) and most recently in 2013 in Latvia (HELCOM 2015). According to genetic studies using mitochondrial DNA data, *R. harrisii* populations in Europe do not form a single panmictic population (Projecto-Garcia et al. 2010) and even on a small geographical scale, they sometimes exhibit significant genetic structuring (Hegele-Drywa et al. 2015).

In Finland, *R. harrisii* was first observed near the Naantali port in 2009 (Karhilahti 2010). After the initial introduction to Finland, *R. harrisii* has spread rapidly along the southwestern coast of Finland, and the distribution area currently extends to the southern Bothnian Sea (Fig. 2) thereby being the northernmost known *R. harrisii* population. In Finland, fish species such as four-horned sculpins (*Myoxocephalus quadricornis*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*) are reported feeding on *R. harrisii* (Puntila 2016).

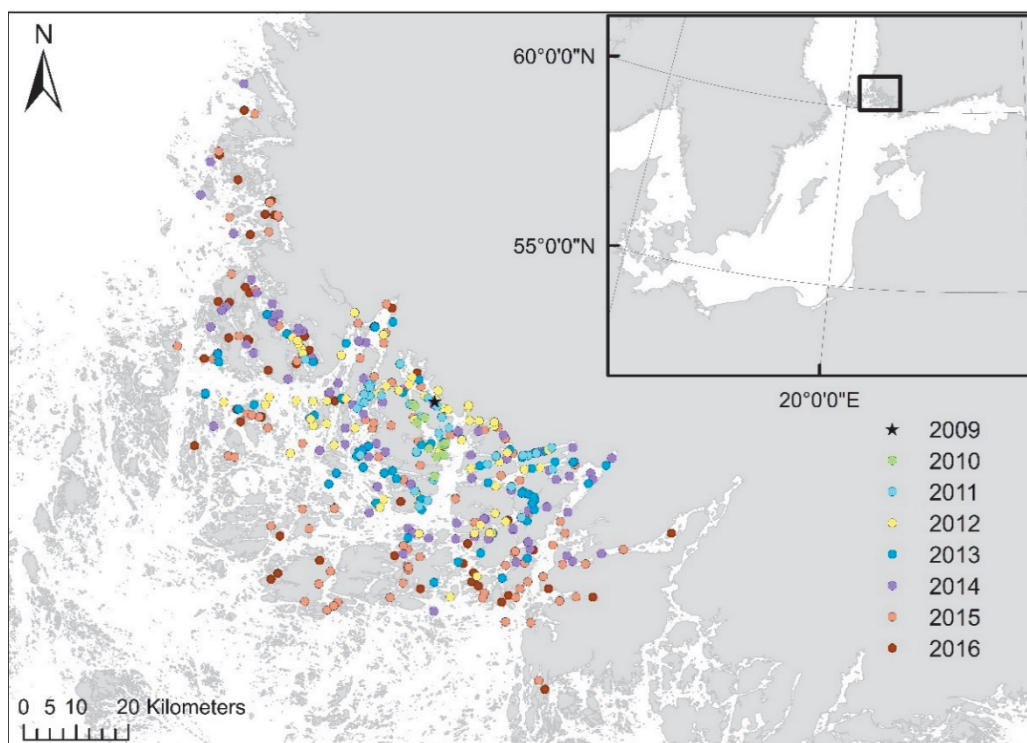


Figure 2. The range expansion of *Rhithropanopeus harrisii* in the Archipelago Sea, the northern Baltic Sea. The distribution area is based on the public observations reported to the Finnish Biodiversity Information Facility (FinBIF) and www.vieraslajit.fi, accessed 10.4.2017.

2.2 Study area

These studies were conducted in the Archipelago Sea in the southwestern Finland (Fig. 3), an area characterized by mosaic landscape with over 50,000 islands, low salinity, low species richness, and strong seasonality. In general, the salinity in the study area is ~ 6 , and surface water temperature varies from <0 to 20°C with the high probability of ice cover during the winter months (Leppäranta and Myrberg 2009). The food webs tend to be simple and consist mainly of the most common species, as the lowest species richness of macroscopic organisms in brackish waters occurs in salinity of 5–7 (Remane 1934). The Archipelago Sea consists of a patchy mixture of soft-bottom and hard-bottom habitats with extensive shallow soft-bottom habitats in the inner Archipelago and deeper hard-bottom habitats more commonly in the outer Archipelago. The keystone species in the northern Baltic Sea is considered to be the bladderwrack *Fucus vesiculosus* as it creates a habitat for several invertebrate and vertebrate species, including gammarids, isopods, snail, mussels, and juvenile fish (Kautsky et al. 1992). In the Archipelago Sea, there are no native crab species (Bonsdorff 2006), and prior to the invasion of *R. harrisi*, other introduced crab species were only occasionally encountered with *Eriocheir sinensis* infrequently and *Carcinus maenas* only twice (Finnish Biodiversity Information Facility) but neither of them are established in Finland.

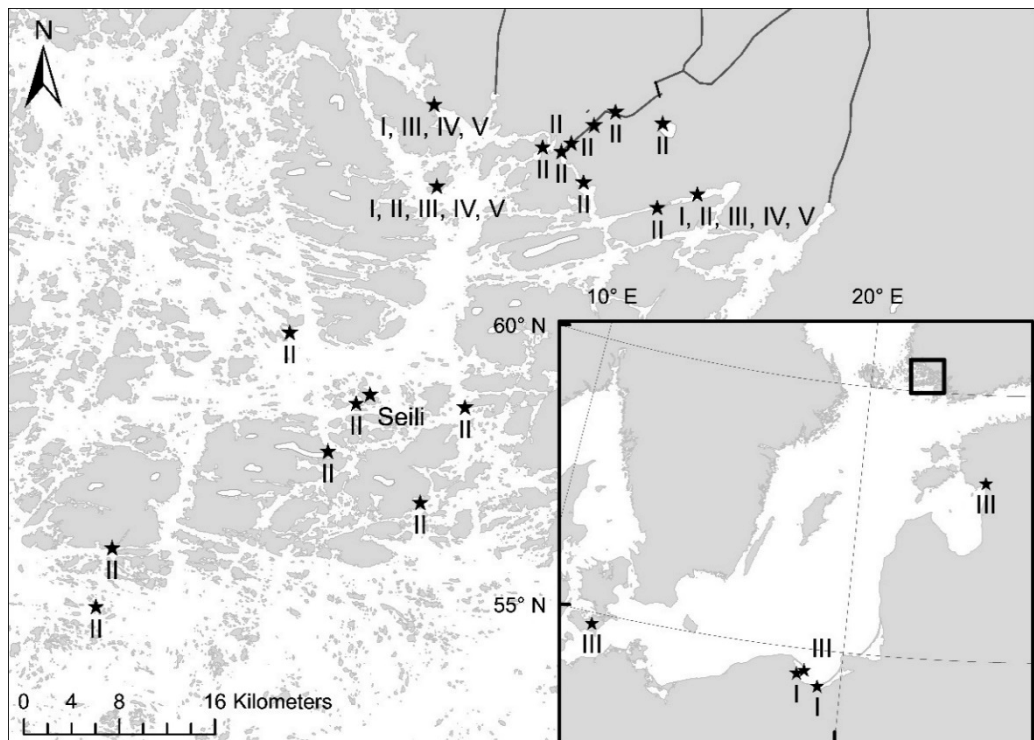


Figure 3. Map of the sampling sites in the Archipelago Sea in Finland, in Estonia and in the southern Baltic Sea. The Roman numerals refer to the chapters of this thesis.

I collected *R. harrisii* individuals for chapters **I**, **III**, **IV**, and **V** from three sites (Kaarina, Lapila and Naantali) in the Archipelago Sea (Fig. 3). These sites were selected from the area where *R. harrisii* were known to occur before the sampling started in 2011 (Fig. 2). All sampling sites are soft sediment habitats with the common reed, *Phragmites australis*, growing on the shoreline. The *R. harrisii* were collected using plastic crates (30 x 30 x 30 cm, Fig. 1) containing autoclaved oyster shells. The crates provides a habitat for both juvenile and adult *R. harrisii*, and the individuals could freely move in and out of the crates. The same sampling method was successfully used in previous *R. harrisii* studies by Roche et al. (2009). For chapter **I**, data from other introduced populations in Poland (Vistula lagoon and Gdynia; Fig. 3) and a native population from Louisiana in the U.S were collected using the same collection method.

For chapter **I**, the data on occurrence based on the public observations of *R. harrisii* were obtained from a web site www.vieraslajit.fi created by the Finnish Game and Fisheries Research Institute and Finnish Environment Institute. In addition, an additional occurrence sampling was conducted in 19 locations in the northern Archipelago Sea in 2011 and 2012. For chapter **II**, I collected water samples from 16 locations in the Archipelago Sea and one additional control sample from Lake Littoinen (Fig. 3). For chapter **III**, in addition to the individuals collected from Finland, I received *R. harrisii* individuals collected from Pärnu Bay in Estonia, the Gulf of Gdańsk in Poland, and Denmark (Fig. 3) as well as samples from one native population from the Ashley River in Charleston, South Carolina, US (**III**). The laboratory and field experiments for chapters **II** and **V** I conducted in the Archipelago Research Institute on Seili Island (Fig. 3).

2.3 Methodological approaches

To study the different aspects of species invasions, I used several approaches that range from basic ecological sample collection and experimental work to molecular approaches (Table 1). To study the occurrence and spread of *Rhithropanopeus harrisii* in a newly invaded area, I used citizen science data in a form of public observations (**I**). To obtain demographic data, I collected monitoring data over six years from three monitoring locations (**IV**). This type of data is rarely collected although it provides fundamental knowledge of the invasion dynamics that is important for evaluating the impacts, interactions and range expansion of the invader. In addition, I used an experimental approach by conducting both laboratory and field experiments to study the potential impacts of the novel species on the native species (**V**).

I also used two different molecular approaches: environmental DNA (**II**) and genotyping-by-sequencing (**III**). Environmental DNA is rapidly increasing research area and expected to be a powerful tool for detect and monitor species in the near future. Another modern molecular approach increasingly used utilizes next-generation sequencing (NGS) technologies to study the genetics of a species. With these genotyping-by-sequencing approaches, in my case restriction-site associated DNA

(RAD) sequencing, prior knowledge of the studied species' genome is not needed. In addition, the approaches allow for simultaneous screening of thousands of loci, thus enabling the detection of weak genetic differentiation and loci under selection (Baird et al. 2008; Davey et al. 2011; Sherman et al. 2016).

Table 1. Methodological approaches used in this thesis to study different aspects of species invasions.

Chapter	Approach	Studied factor	Extent of sampling
I	Public observations, demographic data collection	Occurrence, habitat use, demographic comparisons	Three locations sampled 2011–2012, other three locations sampled 2011
II	Environmental DNA	Detection of species	17 locations, experimental and field samples
III	Genotyping-by-sequencing (RAD-sequencing)	Population genetic structure, divergence and loci under divergent selection	7 locations and two cohorts
IV	Demographic data collection	Abundance, demography	Three locations sampled 2011–2016 twice per year
V	Experimental	Impacts of a novel invader	Aquarium and field experiments

2.4 Population ecology and demography

To obtain demographic data for chapters **I** and **IV**, I sexed the collected *Rhithropanopeus harrisii* individuals (Table 1, **I**, **IV**) based on abdomen width and the number of pleopods (Barnes 1980). For chapter **I**, I counted the number of individuals per crate and measured the carapace width (CW) of each individual with electronic calipers to an accuracy of 0.01 mm. These data were used to compare the demographic data of *R. harrisii* in the northern Baltic Sea to the data collected from introduced populations in the southern Baltic Sea and a native population from the U.S (**I**).

For chapter **IV**, I counted the total number of *R. harrisii* per crate as well as the number of females, males, juveniles, ovigerous females in summer, and eggs that each ovigerous female carried (the latter occurred only in 2012, 2014, and 2015). In addition, I measured the CW of each individual with electronic calipers to an accuracy of 0.01 mm. To assess the number of juveniles (young-of-year) in the fall sampling, I determined the cut-off size of the juvenile cohort individually for each site in each year according to the size distribution of the population (**IV**). The maximum size of juveniles ranged between 4.0 and 7.5 mm CW. All individuals in the summer sampling were assigned as adults, as the young-of-year cohort appears later in the summer; therefore, there were no juveniles present at the time of the summer sampling (personal observation; Turoboyski 1973). The collected data were used to determine whether there were changes in the abundance and different demographic characteristics during the six-year monitoring period (**IV**). In addition, I also examined individuals for the presence of an external form of the

rhizocephalan parasite, *Loxothylacus panopei* (Gissler 1884; Van Engel et al. 1966) for chapters **I** and **IV**.

To assess the importance of the different life history stages for the population growth rate and to examine the persistence of *R. harrisii* population in the northern Baltic Sea, I constructed a single sex stage-structured matrix model (Caswell 2000) using the population data collected from the Kaarina and Lapila sites combined in years 2012–2016 (**IV**). In the matrix model, only female individuals were used as the sex ratio of *R. harrisii* is close to 1:1 (Turoboyski 1973; Hegele-Drywa et al. 2014). Hence, it is expected that fertilization of females is not limited by the lack of males. The individuals were divided into three size classes according to CW: juveniles (the same maximum size as described above), young-females (< 9 mm) and reproductive females (≥ 9 mm). Young-females represent small, non-reproductive females, as all ovigerous females collected throughout the six-year monitoring were ≥ 9 mm with two exceptions (CW of 7.5 and 8.74 mm). I used the constructed matrices to estimate the proportional contribution of each life history stage with deterministic and stochastic elasticity values (Caswell 2000) and simulated a stochastic quasi-extinction probability to study the persistence of the *R. harrisii* population in the northern Baltic Sea over the next 50 years (**IV**).

2.5 Using environmental DNA to detect introduced crab species

I tested the suitability of the environmental DNA approach for detecting marine, benthic, introduced mud crab species in a brackish-water environment. First, I designed species-specific quantitative real-time PCR (qPCR) primers and probes that had at least 6 mismatches with the non-target crab species including the two crab species that have occasionally been encountered in the Archipelago Sea (*Eriocheir sinensis* and *Carcinus maenas*). To assess the amount of DNA *R. harrisii* releases in the water and how long DNA persist in the water after the removal of the target species, I conducted an aquarium experiment. Each separate unused plastic aquarium consisted of artificially produced seawater and one *R. harrisii* individual. *R. harrisii* individuals were left in the aquaria for 8 days, then removed. The water samples were collected (**II**) from each aquarium at day 1, 3, 5, and 8 after adding *R. harrisii* and on days 1, 2, 3, 5, and 7 after the removal of the *R. harrisii*. To determine the overall degradation rate of the target DNA in the aquarium samples, I fitted an exponential decay model to the data (**II**) as in Maruyama et al. (2014).

Water in a natural environment usually contains organic material and DNA from a large number of species, all of which may influence the detectability of the target species. Thus, to validate the detectability of *R. harrisii* with the newly designed primers, I collected water samples from a sheltered bay where *R. harrisii* is readily observed (TF, personal observation). I collected 21 water samples (**II**) from near the bottom sediment using sterile syringes and snorkeling. To further test the usability of the eDNA approach to detect and monitor the *R. harrisii*, water samples were collected just below the surface

in 16 locations around the Archipelago Sea, and as a negative control location Lake Littoinen was used (II). *R. harrisii* was known to occur in 10 out of these 16 sampling locations. I considered a detection to be positive when two of the three technical triplicates resulted in a positive target species DNA amplification in qPCR (II).

2.6 Population genetics

For the population genetic study, I extracted DNA (III) from individuals collected from six different sites in the Baltic Sea including three sites in Finland, one in Estonia, one in Poland and one in Denmark together with one site in the native range in the east coast of North America. In addition, I extracted DNA from individuals from two cohorts (adult and juvenile) collected from the three sites in Finland. To attain the DNA sequences from the samples, I used the restriction-site associated DNA (RAD) sequencing approach (Baird et al. 2008). I prepared the four sequencing libraries following the protocol of Elshire et al. (2011) with a few modifications (Pukk et al. 2015; III).

To obtain genotypes for the individuals, I built a *de novo* reference and mapped the sequences to that reference (III). Individuals were genotyped based on the allele ratio according to Hecht et al. (2013). To obtain the 1013 SNPs (a single-nucleotide polymorphism) used for the analyses, I filtered the SNPs to discard any variants that did not fulfill the multiple stringent quality requirements (III). I compared the genetic diversity and divergence of the introduced populations and tested the presence of temporal genetic variation among the cohorts in Finland. To assess the population divergence at different spatial scales, I performed a hierarchical analysis of molecular variance (AMOVA) and determined the pair-wise population differentiation F_{ST} values (III). I compared allele frequencies between the populations together with allelic richness and expected heterozygosity to assess the differences in the genetic diversity (III). To delineate the clusters of individuals, I used the Bayesian approach implemented in STRUCTURE (Falush et al. 2003) and performed a discriminant analysis of the principal components (DAPC) (Jombart et al. 2010). To reveal loci potentially under divergent temporal selection between cohorts in Finland, I performed a hierarchical island model implemented in Arlequin (Excoffier and Lischer 2010) (III).

2.7 Impacts in the new community

To evaluate the impacts of *R. harrisii* on the native species and communities in the northern Baltic Sea, I observed the prey choice of *R. harrisii* in the laboratory and in the field experiments. In order to compare the relative predation pressure of *R. harrisii* on mobile and sessile littoral invertebrate species as well as the impacts of *R. harrisii* on the different life stages (i.e. juvenile and adult) of the prey species, I conducted a series of laboratory experiments (Table 2, V). For a prey species, species associated with *F. vesiculosus* were used as *F. vesiculosus* is considered as a keystone species in the study area due to its functions as habitat for several mobile and sessile species. Thus, impacts of *R. harrisii* to species associated with *F. vesiculosus* could cascade to other trophic

levels. The prey species were isopod *Idotea balthica*, gammarids *Gammarus sp.*, shrimp *Palaemon sp.*, gobies Gobiidae, snail *Theodoxus fluviatilis* and blue mussel *Mytilus trossulus*. In the first and second set of experiments, individual crabs were simultaneously given different prey species one individual per species (Table 2). In the third set of experiment, individual crabs were simultaneously given three different prey species, individuals of three different size classes of each prey species and two individuals of each size class of each species (Table 2). At the end of each experiment, I removed the crabs from the aquaria and recorded the mortality of each prey item.

Table 2. Experimental set-ups of the laboratory assays

Experiment	Prey species	Number of prey individuals per aquarium	Number of aquariums/ crabs per aquarium	Duration (h)
1	<i>Gammarus sp.</i> , <i>Mytilus trossulus</i> , <i>Theodoxus fluviatilis</i> , Gobiidae	4 (1 per species)	29/1	12
2	<i>Idotea balthica</i> , <i>Gammarus sp.</i> , <i>Palaemon sp.</i>	3 (1 per species)	27/1	12
3	<i>Idotea balthica</i> , <i>Gammarus sp.</i> , <i>Mytilus trossulus</i>	18 (6 per species: 2 small, 2 medium, 2 large individuals)	30/1	24

To validate the results of these laboratory experiments, a caging experiment was performed in the field. Bushes of *F. vesiculosus* were attached to bricks and deployed into the water for 3.5 weeks to attain the natural densities of the species associated with *F. vesiculosus*. After 3.5 weeks, a cage (5 × 5 mm mesh) was added on the one set of *F. vesiculosus* bushes (no predation treatment), and on the second set of bushes, a cage and one crab were added (crab predation treatment). The third set of bushes were left open to simulate natural predation in the study area (natural predation treatment) (V). This experiment lasted four days, after which the bushes were retained, together with all the species. I evaluated the impacts of *R. harrisii* on the natural community by comparing the total number of species, the total number of macroinvertebrate individuals, the Shannon-Wiener diversity index (Magurran 2004), the number of *T. fluviatilis*, the number of *Idotea* isopods, the number of gammarid amphipods, and the number of blue mussels for the different predation treatments (V).

3. RESULTS AND DISCUSSION

3.1 Population ecology and dynamics

Rhithropanopeus harrisi was observed for the first time in Finland in 2009 near the Naantali port. In the following years, the distribution area of *R. harrisi* grew rapidly, extending ~30 km from the site of the first observation within just three years (I). Since then, the distribution area has expanded and now consists of the majority of the inner- and middle Archipelago Sea and extending to the southern Bothnian Sea (Fig. 2). In the northern Baltic Sea, *R. harrisi* was found in various habitats from soft sediments, hard bottoms and among the macroalgae *Fucus vesiculosus*, and does seem to be opportunistic when it comes to habitat use. Recently, *R. harrisi* has been also found in eelgrass (*Zostera marina*) beds (Gagnon and Boström 2016) and observed to prefer the *F. vesiculosus* habitat (Nurkse et al. 2015). This flexible habitat use behavior suggests that predicting the invasion potential of this opportunistic species should not be based on prior knowledge of habitat preference alone.

Over the six-year monitoring period, a total of 3,288 *R. harrisi* were collected, sexed and measured. Of those, 1,797 were collected from Kaarina, 976 from Lapila and 515 from Naantali. Of the collected individuals, 1,335 (40.6%) were adults (males and females composed 49.7 and 50.3% of adults) with 185 ovigerous females, and 1,953 (59.4%) were juveniles. The sex ratio of the introduced population in the northern Baltic Sea was 1:1 unlike in the southern Baltic Sea where sex ratio is reported to be slightly skewed towards more males (54 and 52% of adults respectively; Turoboyski 1973; Hegele-Drywa et al. 2014). In the native range both male and female skewed sex ratios have been reported with 57 and 47% of males, respectively (Ryan et al. 1956; I) Not a single external form of the parasite *Loxothylacus panopei* was observed, indicating that *R. harrisi* has escaped from the parasite species when invading the Baltic Sea (I; IV; Hegele-Drywa et al. 2014). Lack of the parasite allows crabs to invest more energy in the growth and reproduction, especially as *L. panopei* castrates infected crabs decreasing the reproductive success of the population.

The abundance of *R. harrisi* initially increased rapidly, but then declined although there were differences between the sampling sites (IV, Fig. 4). This type of rapid initial increase in the abundance of an introduced species is commonly observed (Simberloff and Gibbons 2004) and it is thought to be caused by multiple factors such as escape from predators and parasites and access to more resources (Torchin et al. 2003; Simberloff and Gibbons 2004). Despite the initial increase, after six years, the population abundance decreased to almost the same number, as observed at the start of the monitoring. Other introduced populations have also demonstrated this boom and bust pattern, eventually stabilizing at lower abundances than initially observed (Simberloff and Gibbons 2004). Despite the subsequent abundance decline, according to the quasi-extinction probability simulation, *R. harrisi* will persist in the study area at least for the next 50 years.

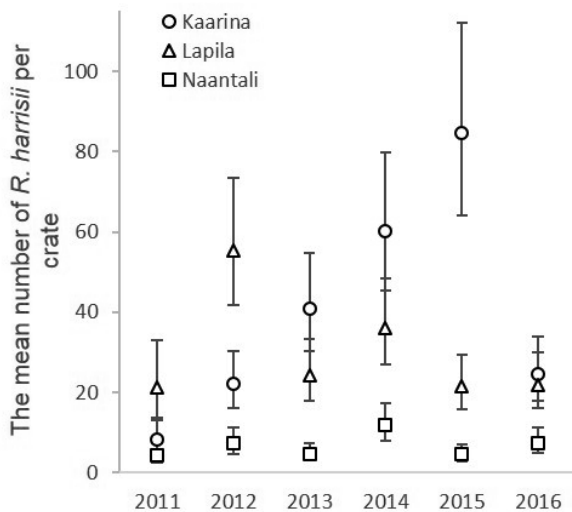


Figure 4. The mean number of *Rhithropanopeus harrisii* individuals per crate during a six-year monitoring period collected from three sites with 95% confidence intervals.

The abundance of *R. harrisii* in the northern Baltic Sea is lower than it is in the native range (I) although in the northern Baltic Sea the individuals grow larger (I). Larger sizes of introduced species in invaded areas is a common phenomenon observed in several species groups (Grosholz and Ruiz 2003; Parker et al. 2013; Sargent and Lodge 2014) and is considered to be caused by increased available resources in the invaded area or an absence of predators and parasites that allows individuals to invest more energy in growth (Torchin et al. 2001; Grosholz and Ruiz 2003; Sargent and Lodge 2014). When comparing the abundance of the introduced population in the northern and southern Baltic Sea, the abundance in the northern Baltic Sea is substantially higher than in the southern Baltic Sea (I). This difference might be caused by either a different stage in the invasion dynamics as the population in the southern Baltic Sea is older than the population in the northern Baltic Sea, a difference in predation pressure, or the more heterogeneous habitats in the northern Baltic Sea that can sustain a more abundant population.

To understand the changes in the population dynamics during the monitoring period and to delineate factors potentially affecting the observed dynamics, I studied several demographic traits and population characteristics of *R. harrisii*. According to both deterministic and stochastic elasticities, changes in the survival of reproductive females has a larger impact on the population growth rate of *R. harrisii* compared to other life stages (IV). This is not surprising given the high reproductive output of females and low survival of larval and juvenile individuals (Costlow et al. 1966; Laughlin and French 1989b). Taken together these results indicate that especially the reproductive females are the drivers of the overall population dynamics of *R. harrisii* in the northern Baltic Sea and factors regulating the abundance of adult females such as predation could regulate the population abundance. In the study area, several fish species such as perch (*Perca fluviatilis*) and four-horned sculpins (*Myoxocephalus quadricornis*) consume *R. harrisii*

(Puntila 2016). These fish predators preferentially consume adult *R. harrisii* between 9 and 16 mm CW (Puntila 2016), thus it is possible that this predation could regulate the abundance of female crabs, and thus the population size of *R. harrisii*.

Overall, in the northern Baltic Sea, female *R. harrisii* were smaller than males (IV). The maximum body-size of both male (CW 23.37 mm) and female (20.21 mm) *R. harrisii* in the northern Baltic Sea seemed to be slightly larger than individuals from other introduced populations elsewhere (the maximum CW of males 17.30–22.10 mm and females 10.90–19.41 mm; Mizzan and Zanella 1996; Roche and Torchin 2007; Hegele-Drywa et al. 2014; Rodrigues and Incao 2015), except for males in one location in Poland (CW 26.1 mm; Turoboyski 1973). However, a reliable comparison is challenging, as the sampling methods were different. On the other hand, larger body sizes in ectotherms occur in lower temperatures where individuals grow slower but larger, and mature at larger body sizes (Angilletta et al. 2004; Kelley et al. 2015). *R. harrisii* in the northern Baltic Sea represents the northernmost known populations that experience some of the coldest water temperatures during winter, factor that might explain the slightly larger body size in the northern Baltic Sea. The larger maximum size of females in the northern Baltic Sea is notable as larger females lay more eggs (IV), potentially increasing the production of offspring to the population compared to other introduced or native populations. In addition, the overall percentage of ovigerous females in the northern Baltic Sea (53%) (IV) was higher than previously reported from the southern Baltic Sea (~30–40%, Turoboyski 1973) indicating a higher reproductive output in the northern Baltic Sea.

I observed a high proportion of recruits (young-of-year) in the northern Baltic Sea population (IV); more than 59% of all the collected individuals were juveniles. This number is more than the 30% of juveniles previously reported from the southern Baltic Sea (Hegele-Drywa and Normant 2014) although the definition of “juvenile” and the sampling methods were different. Hegele-Drywa and Normant (2014) defined all individuals smaller than 4.4 mm CW as juveniles unlike the current study where juveniles were defined separately for each year according to the population size distribution (the maximum size of juvenile range < 4.0–7.5 mm CW). However, the proportion of juveniles in northern Baltic Sea is higher than previously reported even when the 4.4 mm maximum carapace width is used (41%). While sampling methods could explain some of the differences in the proportion of juveniles between studies, the higher female reproductive output observed in northern Baltic Sea may also have contributed to the observed difference. Despite the large proportion of juveniles observed in this study, the majority of them appear not to survive the first winter, indicating that aperiodic cold and long winters may influence the range expansion and population dynamics of this species in the northern Baltic Sea as observed with other species (Canning-Clode et al. 2011; Canning-Clode and Carlton 2017).

The size of the recruits was dependent on the mean water temperature in June–August (i.e. during the egg development, larval period, and first crab stages) (IV); juveniles grew

larger during warm summers compared to cold summers. Water temperature affects the duration of the planktonic larval stage of *R. harrisii* (Costlow et al. 1966; Laughlin and French 1989b). Hence, juveniles grow to a larger size after a warm summer due to a shorter planktonic larval stage, allowing them to metamorphose into the crab stage sooner. Similar patterns of increased growth rates and decreased intermolt periods in warmer temperatures have been observed in several crab species such as *Callinectes sapidus*, *Chionoecetes bairdi*, *Eriocheir sinensis* and *Paralithodes platypus* (Stoner et al. 2013; Cunningham and Darnell 2015; Ryer et al. 2016; Yuan et al. 2017). Other factors in addition to water temperature, such as juvenile density, may also impact the individual size of juveniles due to intra-specific competition (Donahue 2004; Moksnes 2004).

The abundance of juveniles in fall was more dependent on the temperature at the time of the larval period (July-August) than the reproductive output of the females in summer (IV) indicating that the survival of the planktonic larvae has a large impact on the recruitment of juveniles. As both the survival and growth of larvae are dependent on water temperature, *R. harrisii* may benefit from the warming summer temperatures caused by climate change. In the northern Baltic Sea, the sea surface water temperature is estimated to increase by 4°C over the next 80 years (Meier 2006). This increase in water temperature could potentially increase larval survival, however, salinity is estimated to decrease, although at a slower rate than the water temperature increases (Meier 2006). The larval survival of *R. harrisii* positively relates to both temperature and salinity (Costlow et al. 1966; Laughlin and French 1989b; Gonçalves et al. 1995b); thus decreased salinity in the Baltic Sea may counteract the positive effects of increasing temperature on the planktonic larval stage of *R. harrisii* (Holopainen et al. 2016).

3.2 Using environmental DNA to detect introduced crab species

In chapter II I was able to detect hard-shelled mud crab DNA from environmental water samples collected from both field and experimental aquariums. Aquarium experiments revealed that degradation of *R. harrisii* DNA followed the exponential decay curve (II) as observed with several other species (Thomsen et al. 2012; Barnes et al. 2014; Maruyama et al. 2014). The majority of the DNA (89.9%) degraded during the first two days, however, I was able to detect *R. harrisii* DNA seven days after the individual was removed from the experimental aquarium. In previous studies the degradation speed of the target species DNA has varied substantially from 7 to 25 days (Dejean et al. 2011; Thomsen et al. 2012; Piaggio et al. 2014; Pilliod et al. 2014), as environmental factors such as bacterial composition, UV exposure, temperature and pH affect the speed of DNA degradation (Strickler et al. 2015; Tsuji et al. 2017).

Based on the water samples collected from the sheltered bay at Seili, the overall detection rate of *R. harrisii* from the field samples was not that high (57%), although the consistency of detection among biological and technical replicates was high, thus suggesting that the detection of the target species was reliable using eDNA approach.

Despite of the 57% detection rate when sampling sheltered shallow bay, I was able to consistently detect *R. harrisii* DNA only in a single site of the ten locations where *R. harrisii* was known to occur. Earlier studies have demonstrated that the detection rate of eDNA approach varies depending on the target species from close to 100% for many fish species down to 59% for crayfish species (Thomsen et al. 2012; Tréguier et al. 2014).

The low detection rate of *R. harrisii* in the Baltic Sea samples might be a combination of multiple factors. Previous studies have observed that extracellular DNA persists in seawater only for few hours rather than for days (Dell'Anno and Corinaldesi 2004). Other factors affecting the detection rate include density, age and life-stage of the target species, and environmental factors, such as UV-radiation, salinity, and temperature together with technical factors such as, the amount of sampled water, DNA extraction method and DNA detection approach (Thomsen et al. 2012; Goldberg et al. 2013; Kelly et al. 2014; Mächler et al. 2014; Maruyama et al. 2014; Piaggio et al. 2014; Pilliod et al. 2014; Tréguier et al. 2014; Deiner et al. 2015; Strickler et al. 2015). Therefore, it is hardly surprising that the reported detection rates vary among species and studies. Even though the detection of small mud crab species was possible, the results indicate that the method is not as sensitive when used to detect small, benthic, and hard-shelled species as it is to detect various fish and amphibian species. However, the high detection rates of crustacean species have observed in the latest studies (Dougherty et al. 2016; Agersnap et al. 2017) indicating the usability of the eDNA method to detect and monitor crustacean species. All in all, more studies are needed to optimize the methodological approach, to understand the factors affecting the detection rate of different species groups and to thoroughly evaluate the usability of the eDNA method in monitoring of introduced species.

3.3 Population genetics

In chapter III, I was able to distinguish regional-scale population divergence in the Baltic Sea and small-scale temporal variation in Finland. The Finnish and Estonian *R. harrisii* populations differed from each other substantially according to AMOVA and pairwise F_{ST} values (III). In addition, they were assigned to different clusters based on both STRUCTURE and DAPC analyses (Fig. 5a). As *R. harrisii* individuals collected from Finland and Estonia were genetically divergent, these results suggest that the Finnish *R. harrisii* population is most likely not the source population of the Estonian *R. harrisii* and vice versa, even though these populations are geographically the closest known populations. In addition, even though these two populations were observed for the first time only two years apart, it is conceivable that they do not originate from the same source population.

Nevertheless, both of these newly founded populations possessed similar levels of diversity (III), thus indicating that *R. harrisii* has not experienced a major reduction in genetic diversity during secondary introductions within the Baltic Sea. The maintained genetic diversity might have been one factor facilitating the establishment success of this

species. In both Finland and Estonia the population growth of *R. harrisii* has been rapid following the first observation (Kotta and Ojaveer 2012; I; IV) which can reduce the genetic drift of newly founded populations (Nei et al. 1975; Zenger et al. 2003). As expected, based on the earlier work of Projecto-Garcia et al. (2010), the introduced populations in the Baltic Sea were highly divergent from a native population, thereby reflecting the long geographical distance and the invasion history of this species.

The results indicated, however, that the four Polish individuals are genetically similar to Finnish individuals as they were clustered to the same cluster according to DAPC analysis (Fig 5a). Although these results need to be validated by using a larger number of specimens from the Southern Baltic Sea, it is possible that *R. harrisii* in Finland could potentially have originated from Poland, or these two populations share the same source population. The first observation from Finland was from an area near the port of Naantali, which has received vessels from the Gulf of Gdańsk, Poland where *R. harrisii* has been observed since the early 2000s (Hegele-Drywa and Normant 2014). If indeed the Finnish population originated from the Gulf of Gdańsk, it means that the lag time between the first observation of *R. harrisii* in the Gulf of Gdańsk and the first observation in Naantali was rather short, i.e., a maximum of nine years. A short lag-time between successful invasions also indicates that *R. harrisii* possessed the necessary genetic diversity, adaptive plasticity, and/or tolerance to a wide range of environmental conditions and could rapidly acclimatize or adapt to a new environment (Bock et al. 2015).

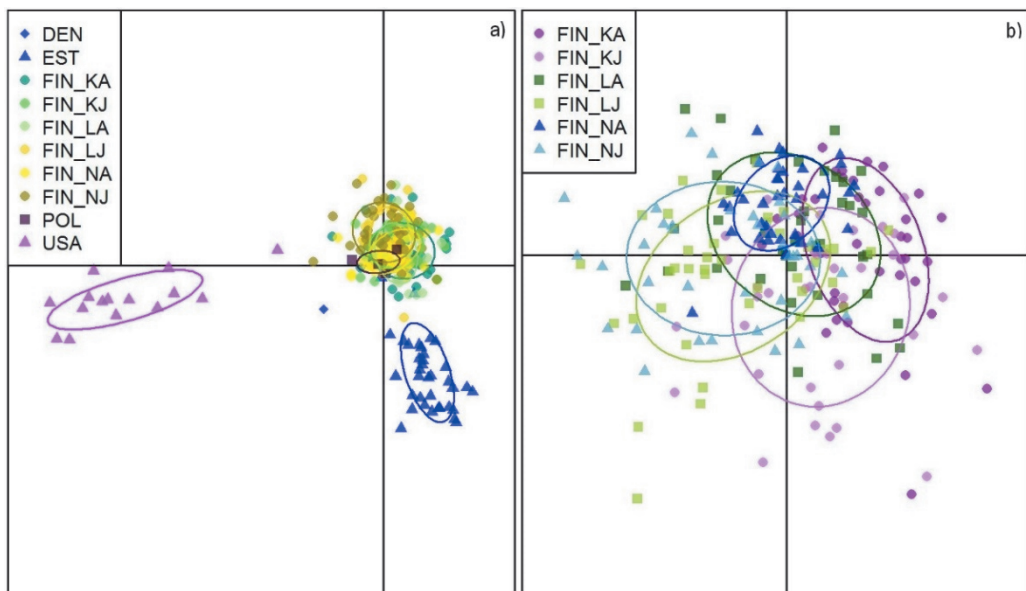


Figure 5. Discriminant analyses of principal components of the genetic structuring a) of all seven locations and b) of the Finnish sites only. Individuals are represented with symbols and sampling sites are color-coded with inertia ellipses. DEN= Denmark, EST= Estonia, FIN= Finland: KA= Kaarina adult, KJ= Kaarina juvenile, LA= Lapila adult, LJ= Lapila juvenile, NA= Naantali adult, NJ= Naantali juvenile and POL= Poland.

Within Finland, I observed no genetic divergence among the individuals collected from three geographically close sites (Fig 5b) which was expected due to a recent invasion to the study area (i.e., not enough time has passed to accumulate the genetic divergence between the sites). Despite the lack of genetic divergence among sites, I observed temporal variation between cohorts (adult vs. young-of-year) in genetic diversity and divergence (III). This observed variation between cohorts could be caused by genetic drift or potential selective effects related to a variation in environmental conditions, such as water temperature, during the larval period. Water temperature is known to affect both larval survival and growth (Costlow et al. 1966; Laughlin and French 1989a, b; IV). A similar difference in genetic diversity among the cohorts has also been observed in other species such as polychaete (*Pygospio elegans*), lake sturgeon (*Acipenser fulvescens*) and Hawaiian goby (*Sicyopterus stimpsoni*) (Kesäniemi et al. 2014; Welsh et al. 2014; Moody et al. 2015) and has been linked to environmental stress (Myrand et al. 2002; Ferrer et al. 2016).

I identified a number of outlier loci under temporal divergent selection between cohorts using hierarchical island-model suggesting that contemporary selection in newly established areas may be stronger than selection associated with spatial heterogeneity within the Baltic Sea. Blasting of outlier loci against NCBI database revealed that temporal outliers are involved in collagen biosynthetic process, growth and stress responses. Thus, the functional annotation of outliers support their putative role in adaption to novel environment but in order to characterize the extent and severity of temporal selection in newly established areas availability of better annotated reference genomes from closely related species is needed.

This kind of temporal variation between cohorts, as observed in this study, may be easily interpreted as a fine-scale geographic differentiation if the differences in sampling time and/or age and sex of individuals are not explicitly taken into account. These results demonstrate the importance of considering the temporal perspective when studying fine-scale geographical differentiation in highly mobile marine species to disentangle the spatial and temporal patterns of genetic divergence and diversity.

3.4 Impacts in the new community

In chapter V, I showed that *Rhithropanopeus harrisii* is an effective predator of the most common littoral grazers and has a negative impact on the native species inhabiting littoral habitats dominated by *Fucus vesiculosus*. Omnivorous *R. harrisii* consumed all presented prey species, but showed a clear choice for some species, such as isopods, gammarid amphipods and blue mussels although the feeding choices depended on the availability of prey (V). When *R. harrisii* was offered multiple individuals of the same species, *R. harrisii* consumed mainly isopods and gammarid amphipods and preyed on small and medium sized prey (V). Similar size selective predation of small- and medium-size individuals has been observed with other crab species (Juanes 1992; Mascaro et al. 2003; Smallegange et al. 2008) as well as a preference for consuming softer-shelled

crustaceans (Buck et al. 2003). The result of this size-selective predation of small- and medium- size individuals suggests that *R. harrisii* could alter the prey population size-structure through size selective predation on smaller individuals (Ojeda and Dearborn 1991). In the aquarium experiments, the consumption rate of *R. harrisii* on isopods and gammarid amphipods was high, but it could have partially been due to the naïveté of these prey species to a novel predator and the prey's lack of anti-predator behavior (Cox and Lima 2006; Sih et al. 2010). Although, I cannot exclude the effect of the confined space of an aquarium.

In the field experiment, *R. harrisii* decreased the richness and abundance of its prey species and the Shannon-Wiener diversity index of the macroinvertebrate community associated with *F. vesiculosus* (Fig. 6a, V). From the individual species, the presence of *R. harrisii* only decreased significantly the abundance of *T. fluviatilis* (Fig. 6b), although the relationship could be indirect and the decrease a result of predator avoidance behavior of *T. fluviatilis* snails. These results show that *R. harrisii* can alter the invaded community by reducing the abundance of its prey species, decreasing species diversity, and altering the prey population size-structure through size selective predation. These impacts could be stronger during the early stage of the invasion due to the naïveté of the prey species to a novel predator, the prey's lack of anti-predation behavior toward the predator (Cox and Lima 2006; Sih et al. 2010) as well as at elevated abundance of *R. harrisii* (IV).

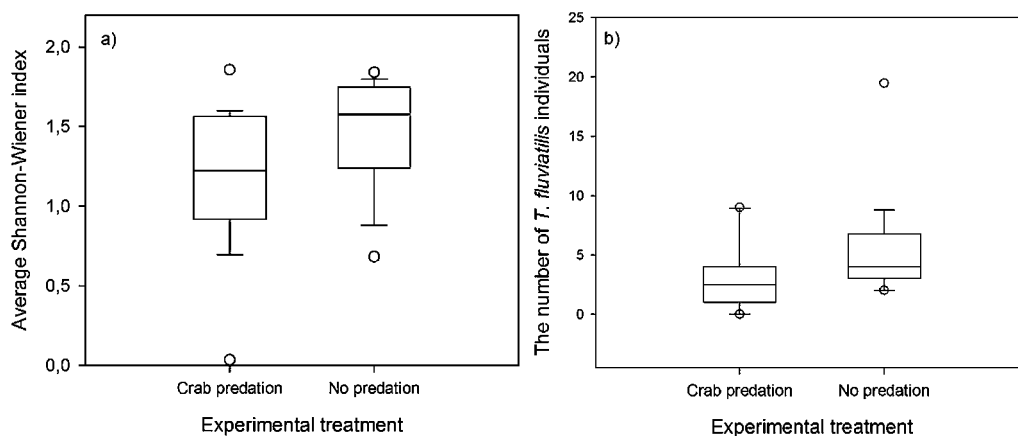


Figure 6. Box plot of the a) average Shannon-Wiener diversity index and b) the abundance of *Theodoxus fluviatilis* in crab predation and no predation treatments. Both comparisons between treatments are statistically significant ($P < 0.05$).

Later, stable isotope analyses positioned adult *R. harrisii* among secondary consumers in the northern Baltic Sea (Aarnio et al. 2015). In addition, similar results of a decrease in species richness and diversity as well as the abundance of gastropods were observed in the natural community of *F. vesiculosus* (Jormalainen et al. 2016). These effects of *R. harrisii* on macroinvertebrates in *F. vesiculosus* community could cascade to other trophic levels as has been observed with other predatory crab species (Silliman and

Bertness 2002; Trussell et al. 2002). These cascading effects might become positive by increasing the abundance of *F. vesiculosus* by reducing the abundance of grazers (Engkvist et al. 2000) or negative by reducing the abundance of *T. fluviatilis* that feed on the fouling organism of *F. vesiculosus* that would otherwise completely cover it (Honkanen and Jormalainen 2005). However, top-down effects of *R. harrisii* are likely modified by top-down effects of fish as several fish species have been shown to predate *R. harrisii* in the study area (Puntala 2016).

4. CONCLUSIONS AND FUTURE DIRECTIONS

The results of my studies show that *R. harrisii* has established a population in the Archipelago Sea (**I, IV**), the northernmost location of its distribution, and has become a part of the local community. The study of *R. harrisii* population ecology revealed the opportunistic habitat use of this species highlighting that the predictions of invasion potential and habitat specific impacts of introduced species cannot be based on the prior knowledge of the habitat occupancy as in the introduced range species might also occupy other habitats than previously recorded. Even though the abundance of *R. harrisii* seems to have followed the boom and bust pattern, the established population will most likely persist in the study area for the next 50 years (**IV**). In the northern Baltic Sea *R. harrisii* grows larger than in the native range or in the other introduced areas (**I, IV**) and has a higher abundance than in the southern Baltic Sea. As seen for many other introduced species, *R. harrisii* has not suffered a major reduction of genetic diversity during the invasion process (**III**), although there are significant differences between the cohorts in diversity and divergence indicating temporal selection in a newly established area. Taken together the results of chapters **III** and **IV** it seems that the genetic diversity and the rapid population growth of *R. harrisii* have facilitated the successful invasion of the northern Baltic Sea.

I was able to detect introduced crab species using environmental DNA approach (**II**) although more research is needed to refine the sample collection and laboratory methodologies to increase the sensitivity of the detection. Recent advances in the studies of eDNA have incorporated eDNA and metabarcoding enabling the faster and more reliable simultaneous detection of multiple species from many different species groups (Brown et al. 2016; Borrell et al. 2017; Trebitz et al. 2017) increasing the usability of eDNA approach for detection and monitoring purposes. According to my results, the population growth rate of *R. harrisii* is most dependent on the survival of the reproductive females (**IV**), hence native predators that feed on adult *R. harrisii*, such as predatory fish, could regulate the population growth of *R. harrisii* in the study area. This information could also be used for management purposes to target the management effort to decrease the survival of reproductive females. The growth and recruitment of juveniles is dependent on the water temperature (**IV**). Therefore warming temperatures in the future caused by climate change is likely beneficial for *R. harrisii*. Finally, in the introduced community this species reduces the abundance of its prey species and lowers the species diversity with possibly cascading effects (**V**). Although, the population abundance seems to be stabilizing at the recently established populations, *R. harrisii* continues to expand its distribution range, and the rapid initial abundance increase is likely also occurring at the newly invaded sites.

My thesis has only scratched the surface of introduced marine species in a species-poor community while opening a door to future studies among this nature's own real-life experiment. In general, this thesis answers certain questions about the population

establishment, genetics, and impacts of an introduced marine species, however, at the same time it raises many more questions that are yet to be answered. Questions such as: How introduced species alter the native community in an ecological and evolutionary perspective? The roles of standing genetic variation, high phenotypic plasticity and rapid local adaptation in a successful species invasions? In the future, new molecular methods will likely create an opportunity for more efficient species detection and monitoring and also provide more detailed information about the position of the introduced species in the food web and the genetic adaptation processes that are needed for introduced species to establish populations in the northern sea areas.

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