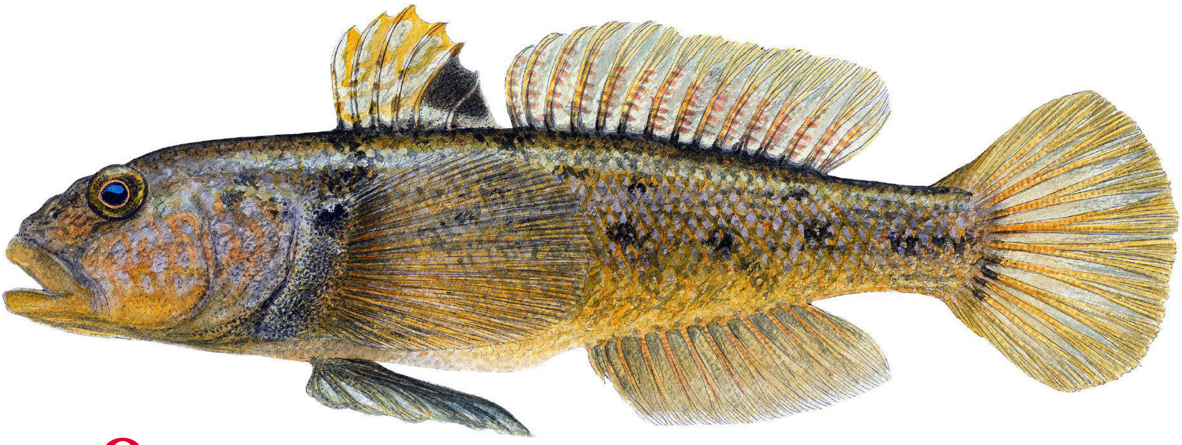
Heidi Herlevi

Implications of the Integration of a Non-Native Fish into Coastal Communities



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Abstract

The Baltic Sea ecosystem is undergoing unprecedented changes in abiotic conditions due to the combined effects of climate change, eutrophication, and bottom-water deoxygenation. Non-native species, introduced outside their native ranges due to human activities, can further impact biodiversity, species composition and food web structure. The Baltic Sea, with its unique brackish water ecosystem and relatively low native species richness, is especially vulnerable to the effects of species introductions. The round goby (*Neogobius melanostomus*), a widely distributed non-native fish in Europe and North America, causes concerns in the Baltic Sea due to its rapid spread, high reproductive capabilities, and potential to affect native species through predation and competition. However, we still lack knowledge of the effects of round goby on community structure and the taxonomic and functional diversity of native fish communities. Assessing these impacts in different invaded areas, particularly in the less-studied northern Baltic regions, is crucial for understanding the overall consequences of species introductions in this naturally low-diverse ecosystem.

In this thesis, I aim to clarify the implications of the introduction of the round goby into coastal communities in the Baltic Sea. I studied the integration in terms of ecological interactions involving the round goby and the impacts of this introduction on the local fish community structure and functioning. I analyzed data from three Baltic Sea populations—Åland (Finland), Karlskrona (Sweden), and Hel (Poland)—which varied in population age, distribution area and abundance levels. By using a combination of stable isotope analysis, diet assessments, and fish community analyses, I studied the positioning of the round goby in the food web, its importance as prey for native predators, as well as consequences for fish community (taxonomic and trait-based) composition and diversity.

The results showed that the role of round goby in the food web is dependent on the ecosystem properties of the invaded area, local population abundances and invasion stage (i.e. population age). The trophic positioning of the round goby varied between the new and old populations, due to local and seasonal prey availability and intra-specific competition. Round goby showed significant isotopic niche overlap with larger perch, but limited overlap with other native benthic-feeding fish in a recently established northern population (Åland). This illustrates its generalist feeding habit and ability to exploit resources on higher trophic levels (e.g. fish eggs), but also resources that were less utilized by native species. This is likely to be a contributing factor to its success as an introduced species but also emphasizes the temporal and spatial variability of its effects on native species.

During the invasion process, from early establishment to population stabilization, populations often undergo large fluctuations in abundance, as also documented in this thesis. When round goby abundances were high, its impacts on native species, in terms of both importance as prey for fish predators and its influence on fish community composition and diversity, were more pronounced. When round goby dominated the fish community in both abundance and biomass, it was also the most important prey species for fish predators (cod, pike, and perch). Simultaneously, native fish species richness in the environment was low, potentially due to displacement effects. However, long-term monitoring indicates that the observed peaks in abundance are temporary, and during periods of lower round goby abundance, fish communities responded positively with increased functional diversity and species richness. I also found that round goby is most abundant in areas where native species richness is high both on a local (shallow sheltered areas on Åland) and pan-Baltic levels (southern Baltic). The population abundances and local (abiotic and biotic) environmental conditions therefore mediate its impact on native species and communities.

My thesis elucidates the role of the round goby as predator, competitor, and prey as well as which factors contribute to the observed impacts of the integration of this species in coastal fish communities. The similarities between populations in different Baltic Sea areas and population stages further our understanding of the ecological implications of the round goby. The different contributing factors highlight the adaptability of this species and the context-dependency which should be considered when assessing the impacts of species invasions at local and regional levels in the Baltic Sea.

Keywords: Species introductions, Non-indigenous species, Trophic interactions, Stable isotopes of carbon and nitrogen, DNA-metabarcoding, Coastal ecosystems, Biodiversity, Functional traits

Sammanfattning (Swedish abstract)

Östersjöns ekosystem genomgår genomgripande förändringar på grund av bl.a. klimatförändring, övergödning och syrebrist i bottenvattnet. Introducerade arter kan ytterligare påverka den biologiska mångfalden, artsammansättningen och näringsvävsstrukturen. Östersjön, med sitt unika brackvattensekosystem och relativt låga artrikedom, är särskilt känslig för effekterna av artintroduktioner. Den svartmunnade smörbulten (*Neogobius melanostomus),* en introducerad fiskart med brett utbredningsområde i Europa och Nordamerika, väcker oro på grund av dess snabba spridning, starka reproduktionsförmåga och potentiella inverkan på bottendjur och fiskar genom predation och konkurrens. Vi saknar dock information om effekterna av den svartmunnade smörbulten på fisksamhällens struktur samt på den taxonomiska och funktionella diversiteten. En bedömning av effekterna av den svartmunnade smörbulten i de mindre studerade norra Östersjöregionerna, är avgörande för att förstå de övergripande konsekvenserna av introduktionen på ekosystemnivå i Östersjön.

Syftet med min avhandling är att klargöra följderna av introduktionen av den svartmunnade smörbulten i kustsamhällen i Östersjön. Jag studerade ekologiska interaktioner som involverar den svartmunnade smörbulten, och effekterna av denna introduktion på det lokala fisksamhällets struktur och funktion. Jag använde data från tre från varandra isolerade populationer i Östersjön: Åland (Finland), Karlskrona (Sverige) och Hel (Polen). Bestånden skiljer sig åt i populationsålder, -storlek och -utbredning. Genom att använda en kombination av stabila isotoper, dietanalys, och analyser av fisksamhällen undersökte jag den svartmunnade smörbultens placering i näringsväven, dess betydelse som byte för fiskpredatorer, samt konsekvenser för fisksamhällets taxonomiska och egenskaps- och funktionsbaserade sammansättning och mångfald.

Resultaten visade att den svartmunnade smörbultens roll i näringsväven är beroende av miljöförhållanden i det invaderade området, populationsstorleken och invasionsstadiet. Den svartmunnade smörbultens födovävsposition varierade mellan en ny och en etablerad population p.g.a. lokal och säsongsberoende bytestillgänglighet och intraspecifik konkurrens. Svartmunnad smörbult uppvisade överlapp i isotopnisch med medelstor abborre, men begränsat överlapp med andra bottenlevande fiskar i den nya populationen (Åland). Detta framhäver dess generalistiska födoval och förmåga att utnyttja resurser på högre trofiska nivåer (t.ex. fiskägg), men även resurser som utnyttjades mindre av andra fiskarter. Detta är förmodligen en bidragande faktor till dess framgång som introducerad art, men antyder även variation i tid och rum i dess påverkan på ursprungsarterna i fisksamhället.

Under invasionsprocessen, från tidig etablering till populations stabilisering, påvisar bestånden ofta stor mellanårsvariation i populationsstorlek, vilket även dokumenteras i denna avhandling. När förekomsten av svartmunnad smörbult var hög var också dess påverkan på andra arter större både när det gäller betydelse som byte för fiskpredatorer och påverkan på fisksamhällens struktur och diversitet. Då mängden svartmunnad smörbult i miljön var stor, dominerade den fisksamhället och var den viktigaste bytesarten för fiskpredatorer (torsk, gädda, abborre). Samtidigt var artrikedom och diversitet av andra fiskarter lågt i miljön, potentiellt på grund av undanträngningseffekter. Långtidsövervakning tyder på att de observerade topparna i förekomst är tillfälliga, och effekterna på fisksamhällen var huvudsakligen positiva för både funktionell diversitet och artrikedom vid något lägre abundanser av svartmunnad smörbult. Jag fann även att svartmunnad smörbult förekom rikligast i områden där artrikedomen är högst både på lokal nivå på Åland (grunda skyddade områden) och Östersjö-nivå (södra Östersjön). Populationsstorleken och lokala (abiotiska och biotiska) miljöförhållanden förmedlar därmed artens påverkan på ursprungsarter och artsamhällen.

Min avhandling belyser den svartmunnade smörbultens roll som predator, som konkurrent och som bytesdjur, samt vilka faktorer som bidrar till de observerade effekterna på kustnära fisksamhällen. Likheterna mellan populationer i olika Östersjöregioner främjar vår förståelse av de ekologiska konsekvenserna av den svartmunnade smörbulten, medan de olika bidragande faktorerna lyfter fram anpassningsförmågan hos denna art och det sammanhangsberoende som bör tas i beaktande vid bedömning av effekterna av artinvasioner på lokal och regional nivå i Östersjön.

Nyckelord: Artintroduktioner, Främmande arter, Trofiska interaktioner, Stabila isotoper av kol och kväve, DNA-metabarcoding, Kustnära ekosystem, Biologisk mångfald, Funktionella egenskaper

Tiivistelmä (Finnish abstract)

Itämeren ekosysteemeissä tapahtuu ennennäkemättömiä muutoksia mm. ilmastonmuutoksen, rehevöitymisen ja happikadon yhteisvaikutusten vuoksi. Näiden lisäksi ihmisen toiminnan seurauksena alkuperäisen levinneisyysalueensa ulkopuolelle kulkeutuneet vieraslajit voivat vaikuttaa Itämeren biologiseen monimuotoisuuteen, lajikoostumukseen ja ravintoverkojen rakenteeseen. Itämeren ainutlaatuinen mutta vähälajinen murtovesiekosysteemi onkin erityisen altis vieraslajien vaikutuksille. Mustatäplätokko (Neogobius melanostomus) on Euroopassa ja Pohjois-Amerikassa laajalle levinnyt vieraskalalaji. Se aiheuttaa huolta Itämerellä nopean leviämisensä ja lisääntymiskykynsä, sekä pohjaeläimiin ja muihin pohjakaloihin kohdistuvien saalistus- ja kilpailuvaikutustensa vuoksi. Tieto mustatäplätokon vaikutuksista kalayhteisöjen rakenteeseen, sekä taksonomiseen ja toiminnalliseen monimuotoisuuteen on kuitenkin puutteellista. Mustatäplätokon vaikutusten arvioiminen Itämeren eri alueilla, erityisesti vähemmän tutkituilla pohjoisilla Itämeren alueilla, on ratkaisevan tärkeää, jotta voidaan ymmärtää lajin yleisiä vaikutuksia Itämeren ekosysteemiin.

Väitöskirjassani pyrin selventämään mustatäplätokon vaikutuksia Itämeren rannikkoyhteisöihin. Tutkin mustatäplätokon ekologisia vuorovaikutussuhteita ja vaikutuksia paikallisen kalayhteisön rakenteeseen ja toimintaan tutkien kolmea eri Itämeren populaatiota: Ahvenanmaalla (Suomi), Karlskronassa (Ruotsi) ja Helissä (Puola). Populaatiot eroavat toisistaan mm. invaasioajankohdan, levinneisyyden ja populaatiokoon osalta. Yhdistämällä vakaiden isotooppien analyysiä, ravintoanalyysejä sekä kalayhteisötutkimuksia pyrin selvittämään mustatäplätokon sijoittumista ravintoverkkoon, sen merkitystä petokalojen ravintona, sekä vaikutuksia kalayhteisöjen taksonomiseen ja toiminnalliseen rakenteeseen ja monimuotoisuuteen.

Tulokset osoittivat, että mustatäplätokon rooli ravintoverkossa riippuu mm. alueen ekosysteemin ominaisuuksista ja paikallisen populaation runsaudesta. Mustatäplätokon sijoittuminen ravintoverkkoon vaihteli uudemman ja vanhemman populaation välillä, mikä todennäköisesti johtui saaliseliöiden paikallisesta ja kausittaisesta esiintyvyydestä ja lajin sisäisestä kilpailusta. Uudessa populaatiossa (Ahvenanmaa) mustatäplätokko osoitti merkittävää päällekkäisyyttä isotooppiarvoissa keskikokoisen ahvenen kanssa, mutta myös rajallista päällekkäisyyttä muiden pohjaeläimiä syövien kalojen kanssa. Tämä korostaa sen monimuotoista ravinnonkäyttöä ja kykyä hyödyntää resursseja korkeammalla trofiatasolla (esim. kalanmäti), mutta myös resursseja, joita muut kalalajit käyttivät vähemmän. Tämä on luultavasti myötävaikuttanut sen menestymiseen vieraslajina, mutta korostaa myös sen alkupersäilajeihin kohdistuvien vaikutusten ajallista ja alueellista vaihtelua.

Invaasioprosessin aikana, varhaisesta esiintymisestä kantojen vakiintumiseen, populaatioissa tapahtuu usein suuria runsauden vaihteluita, joita dokumentoidaan myös tässä työssä. Kun mustatäplätokkojen runsaus oli suuri, myös sen vaikutukset alkuperäislajeihin korostuivat. Mustatäplätokon dominoidessa kalayhteisöä määrällisesti ja biomassaltaan oli se myös tärkein saalislaji petokaloille (turska, hauki, ahven). Samanaikaisesti muiden kalojen lajirikkaus ympäristössä oli alhainen, mahdollisesti mustatäplätokon syrjäyttämisvaikutuksista johtuen. Pitkäaikaisseurannat osoittavat kuitenkin, että havaitut määrälliset runsaushuiput ovat tilapäisiä. Mustatäplätokon runsauksien ollessa pienemmät sen vaikutukset kalayhteisöihin olivat pääosin positiivisia lisääntyneen toiminnallisen monimuotoisuuden ja taksonomisen rikkauden osalta. Havaitsimme myös, että mustatäplätokko on runsain alueilla, joilla alkuperäislajien runsaus on korkeimmillaan, sekä paikallisella tasolla Ahvenanmaalla (matalilla suojaisilla alueilla), että koko Itämeren tasolla (eteläinen Itämeri). Kantojen runsaus ja paikalliset (abioottiset ja bioottiset) ympäristötekijät säätelevät siis mustatäplätokon vaikutuksia alkuperäislajeihin, yhteisöihin ja lajien vuotovaikutussuhteisiin.

Väitöskirjani tulokset selventävät mustatäplätokon roolia saalistajana, kilpailijana ja saaliina, sekä tekijöitä, jotka vaikuttavat havaittuihin muutoksiin rannikon kalayhteisöissä. Populaatioiden samankaltaisuudet Itämeren eri osissa lisäävät ymmärrystämme lajin ekologisista vaikutuksista, kun taas erilaiset vaikuttavat tekijät korostavat tämän lajin sopeutumiskykyä ja sitä kontekstiriippuvuutta, mikä tulee ottaa huomioon vieraslajien vaikutuksia arvioitaessa paikallisella ja alueellisella tasolla Itämeressä.

Avainsanat: Vieraslajit, Trofiset vuorovaikutussuhteet, Hiilen ja typen vakaat isotoopit, DNA-metaviivakoodaus, Rannikkoekosysteemit, Biologinen monimuotoisuus, Toiminnalliset ominaisuudet

List of original publications

This thesis is based on the following three original publications and additional data presented from these.

I. **Herlevi, H.,** Aarnio, K., Puntila-Dodd, R. and Bonsdorff, E. (2018). The food web positioning and trophic niche of the non-indigenous round goby: a comparison between two Baltic Sea populations. *Hydrobiologia* **822**, 111–128. https://doi.org/10.1007/s10750-018-3667-z

II. **Herlevi, H.,** Wallin Kihlberg, I., Aarnio, K., Bonsdorff, E., Florin, A.-B., Ljung, A., Lundström, K., Mattila, J. and Östman, Ö. (2023). Environmental abundances of the non-native round goby *Neogobius melanostomus* influence feeding of native fish predators. *Journal of Fish Biology*, 1–18. https://doi.org/10.1111/jfb.15380

III. **Herlevi, H.,** Bonsdorff, E. and Aarnio, K. The integration of a non-native fish into coastal fish communities increases taxonomic and functional diversity (*Manuscript)*

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Author contributions

	Paper I	**Paper II***	**Paper III**
Original idea/ study design	**HH**, KA, RPD	**HH**, IWK, JM, ABF, KL, KA	**HH**, KA, EB
Field/laboratory work	**HH**, KA, RPD	**HH**, IWK, AL, KA, KL	**HH**
Data analysis	**HH**	**HH**, IWK, ÖÖ	**HH**
Writing and editing	**HH**, KA, RPD, EB	**HH**, IWK, JM, ABF, KL, KA EB, AL, ÖÖ	**HH**, KA, EB

*HH and IWK contributed equally to paper II and share first authorship

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1 Introduction

1.1 Non-indigenous species in coastal ecosystems

Coastal areas are among the most productive areas in the oceans, hosting high habitat diversity with accompanied high biological production (Nixon *et al.,* 1986 Gray, 1997). Coastal areas and seas are also centers for high human activity and are therefore affected by numerous anthropogenic pressures such as eutrophication, habitat destruction, pollution and introduction of species (Halpern *et al.*, 2008; Reusch *et al.*, 2018; Blenckner *et al.*, 2021). These pressures cause changes in the environmental dynamics that drive species community composition (Österblom *et al.*, 2007; Hillebrand *et al.*, 2010; Snickars *et al.*, 2015). The challenge scientists face today is elucidating the, often unpredictable, changes in the ecosystem that are caused by different anthropogenic factors, individually and synergistically.

Non-indigenous species (**NIS**; syn. introduced, alien, and non-native), are species that are introduced, intentionally or unintentionally, outside of their natural distribution ranges due to human activity (shipping, aquarium trade, agri- or aquaculture; Olenin and Minchin, 2011). The number of NIS has increased continuously throughout the 20th century, especially due to increased human mobility and global transfer of goods (Seebens *et al.*, 2017). Not all NIS become *invasive*, (i.e. cause significant negative impacts on ecosystems), but as the number of NIS increases, so does the probability that some of them will become invasive. Non-indigenous species are therefore regarded as one of the main five sources of threats for biological diversity globally, although for marine systems the main drivers of biodiversity loss are direct exploitation (e.g. fishing) and climate change (Jaureguiberry *et al.*, 2022; Viitasalo and Bonsdorff, 2022). Nevertheless, marine NIS have been shown to affect biodiversity, keystone species and habitats, as well as ecosystems functioning in European waters, often negatively (Katsanevakis *et al.*, 2014, 2016; Ojaveer *et al.*, 2021, 2023) and their effects can in many cases be equated to that of other anthropogenic disturbances (Simberloff, 2011; Strayer, 2012; Edelist *et al.*, 2013). Due to the potentially harmful effects of NIS, their impacts have been listed as a factor to be included in environmental status assessments according to the Marine Strategy Framework Directive (2008/56/EC). However, we are still lacking knowledge on the process of integration and ecological impacts of most introduced species in the Baltic Sea, hampering conclusions about cumulative, community- and ecosystem-level impacts of NIS (Ojaveer and Kotta, 2015; Ojaveer *et al.*, 2021).

1.2 The Baltic Sea - a hub for species introductions

The Baltic Sea is a globally unique semi enclosed brackish water system, with many of its unique features also making it especially vulnerable to disturbances. Specifically, the relatively shallow depth (mean 57 m) and slow water exchange rate (~40 years) through the narrow Danish straits has created strong gradients in temperature and salinity, decreasing south to north. This together with the relatively short geological age of the sea (~8000 years) has resulted in a unique mix of freshwater and marine species, but relatively species-poor communities (Snoeijs-Leijonmalm *et al.*, 2017). The species-poor communities together with a high level of other anthropogenic disturbances, are thought to have increased the systems susceptibility to species introductions (Paavola *et al.*, 2005; Olenin *et al.*, 2017).

Species introduction into the Baltic Sea have become increasingly frequent since the mid-20th century (Leppäkoski and Olenin, 2000), mostly due to increased shipping activity (Ojaveer *et al.*, 2018; Zenetos *et al.*, 2022). Altogether 194 NIS (excluding species of unknown origin) have been reported within the Baltic Sea until 2023, of which ca 80 are currently regarded as established (AquaNIS, Editorial Board, 2015). Certain species have even become seasonally or locally dominating, re-structuring benthic (Olenin and Leppäkoski, 1999; Maximov, 2011) and pelagic communities (Gorokhova *et al.*, 2005; Tiselius and Møller, 2017). There are numerous accounts globally of NIS having negative effects on the native communities, through mainly competition and predation (Albins and Hixon, 2013; Paolucci *et al.*, 2013), and by contributing to biotic homogenization across habitats (McKinney and Lockwood, 1999; Toussaint *et al.*, 2016), sometimes even leading to extinction of native species (Nikolaou and Katsanevakis, 2023). Despite significant impacts on food web structure, no native species extinctions have been observed as a result of NIS introductions in the Baltic Sea (Leppäkoski *et al.*, 2002; Zaiko *et al.*, 2011; Ojaveer *et al.*, 2021). On the contrary, the introduced species have on many occasions contributed to increasing trophic and functional diversity in this species poor ecosystem (Norkko *et al.*, 2012; Aarnio *et al.*, 2015; Karlson *et al.*, 2015; Kauppi *et al.*, 2015; Lokko *et al.*, 2015). However, on a regional scale, we are still lacking information on the effects of most NIS in the Baltic Sea, with some 60% of them being ecologically poorly known (Ojaveer *et al.*, 2021). Identifying and describing the changes following the introduction of NIS is especially important in the Baltic Sea as the Baltic Sea ecosystem is simultaneously facing changes due to many other pressures (e.g. eutrophication, hypoxia, pollution) at a faster pace than most other marine areas globally (Reusch *et al.*, 2018), while also subject to alterations in abiotic conditions due to climate change (reviewed in Viitasalo and Bonsdorff, 2022).

1.3 The round goby- a successful invader

The round goby, *Neogobius melanostomus* (Pallas 1814), is among the most successful non-indigenous fish species in Europe, having invaded both fresh- and brackish water systems around Europe, as well as North America (Kornis *et al.*, 2012). Originally from the Black, Caspian and Azov Seas, it was first discovered in the Gulf of Gdansk, southern Baltic Sea, in 1990 (Skóra and Stolarski, 1993) and has since become widely established around the Baltic Sea. It is now the most broadly distributed non-indigenous fish species in the Baltic Sea, having established permanent populations in all countries surrounding the Baltic Sea (AquaNIS Editorial Board, 2015), and is expected to continue expanding its distribution range along all coastal areas of the region (Ojaveer *et al.*, 2015a; Kotta *et al.*, 2016; Ojaveer *et al.*, 2021).

The success of the round goby has been attributed to many suitable functional properties or traits, such as a wide tolerance for a range of environmental conditions (e.g. temperature, salinity, oxygen), aggressive defense behavior, and high reproductive output (reviewed by Kornis *et al.,* 2012 and Cerwenka *et al.*, 2023). Round goby also shows high plasticity in feeding and habitat preferences, with a generalist opportunist feeding habit enabling it to utilize a wide range of prey species (Brandner *et al.*, 2013a; Nurkse *et al.*, 2016). It is able to inhabit both freshwater and near fully marine conditions (29 PSU; Green *et al.*, 2023), as well as riverine habitats and polluted environments (McCallum *et al.*, 2014). Although populations within the Baltic Sea are mainly adapted to brackish conditions (Green *et al.*, 2021), and show highest physiological performance between 0 and 20 PSU (Behrens *et al.*, 2017), the round goby has high potential for local phenotypic adaptation (Björklund and Almqvist, 2010; Green *et al.*, 2020, 2021). It is thus likely to be able to further expand its range in novel salinity conditions.

1.3.1 Ecological impacts of round goby in the Baltic Sea

Due to its success as an introduced species, the ecological impacts of round goby establishment on native species and communities have solicited wide interest in its invasive range (reviewed in Kornis *et al.,* 2012 and Hirsch *et al.,* 2016). In general, negative effects of NIS are more often observed on lower or equal trophic levels to that of the NIS in focus, mainly through predation and competition, while positive effects can be seen for species on higher trophic levels (Thomsen *et al.*, 2014). This has also been shown to be true in the case of the round goby in the Baltic Sea (Liversage *et al.*, 2019), as most negative effects have been observed for invertebrate prey (Henseler *et al.*, 2021; van Deurs *et al.*, 2021; Nõomaa *et al.*, 2022), and indirectly on other benthic-feeding fish (Karlson *et al.*, 2007; Ustups *et al.*, 2016) or even birds (Skabeikis *et al.*, 2019). On the other hand, the round goby has also been shown to create new links in the food web between littoral benthic invertebrates (primarily mollusks) and predatory fish (Almqvist *et al.*, 2010; Liversage *et al.*, 2017; Rakauskas *et al.*, 2020) or fish-eating birds (Jakubas, 2004; Bzoma and Meissner, 2005; Oesterwind *et al.*, 2017). This may enhance individual fitness (Hempel *et al.*, 2016) and ultimately predator abundances (Bzoma and Meissner, 2005) as well as ecosystem functioning through increased food availability for predators (Liversage *et al.*, 2019; Ojaveer *et al.*, 2021).

Currently, most studies on round goby impacts in the Baltic Sea have focused on its role as a predator on macroinvertebrates (Nurkse *et al.*, 2016, 2018; Skabeikis *et al.*, 2019; Henseler *et al.*, 2020, 2021; van Deurs *et al.*, 2021; Nõomaa *et al.*, 2022), thus highlighting the negative effects it may have on native communities. However, the impacts of round goby on native fish have been found to be species, population and ecosystem specific (Hirsch *et al.*, 2016) and the impacts on entire communities in the Baltic Sea remain poorly studied, especially in the northern Baltic Sea (Ojaveer and Kotta, 2015; Liversage *et al.*, 2019; Ojaveer *et al.*, 2021). The high variability in abiotic and biotic structuring conditions across the Baltic Sea, in terms of salinity, temperature, dominating habitat types and native species richness (Ojaveer *et al.*, 2010; Snoeijs-Leijonmalm *et al.*, 2017), make it hard to extrapolate results from one region to another. It is therefore especially important to determine the effects of round goby on the local community in each invaded region to be able to draw any broad scale conclusions of its effects on Baltic Sea ecosystems.

1.4 Studying the consequences of species introductions

A general framework for assessing NIS impacts involves both the abundance and distribution range of the NIS, as well as its per capita impact and community structure of the invaded ecosystem (Ricciardi *et al.*, 2013). There are also many other factors affecting the outcome of species introduction; ecosystem properties of the recipient system (abiotic and biotic), the traits of the NIS, and species interactions within the invaded community (Thomsen *et al.*, 2011a, 2011b, 2014). How these different factors interact during the invasion process to determine the impacts of a NIS is difficult to disentangle. However, assessing as many factors as possible is important for understanding how NIS integrate into a community and which species or ecosystem processes might be most affected (Strayer *et al.*, 2006; Thomsen *et al.*, 2011b).

Increased susceptibility of habitats to species invasions has been linked to both anthropogenic disturbances (Byers, 2002; Crooks *et al.*, 2011) and low diversity of native species (Stachowicz, 1999; Mitchell and Knouft, 2009). The biotic resistance hypothesis predicts that diverse native communities are more resistant to invasion (Levine and D'Antonio, 1999), which at least for some taxonomic groups (e.g. plants) has been shown to mostly be accurate (Beaury *et al.*, 2020). But this hypothesis is also context- and scale-dependent (Olden *et al.*, 2006; Stachowicz and Byrnes, 2006; Fridley *et al.*, 2007), and it seems that factors contributing to high biological diversity, such as habitat heterogeneity, in fact, increase the successful establishment of NIS and coexistence with natives (Melbourne *et al.*, 2007). Nevertheless, ecosystems with low native species richness, especially due to e.g. a short evolutionary history or high levels of anthropogenic disturbances, are often more susceptible to introductions compared to diverse and more pristine systems. This also relates to the concept of vacant niches, where low species richness, especially if reduced due to human disturbance, would lead to unutilized resources and thus vacant niche space favoring NIS establishment (Stachowicz and Byrnes, 2006; David *et al.,* 2017).

When NIS are introduced to a new area, the traits of a NIS can determine both the success of its establishment and the impact it will have on the community. Generally, functional similarity to native communities predicts invasion success, as similar species are more likely to be adapted to local environmental conditions (environmental filtering) (Gallien and Carboni, 2017). However, the response is also dependent on the main community assembly drivers, biotic interactions and resource levels. At finer spatial scales, more similar species may instead be less likely to establish or become invasive due to e.g. competitive interactions and limiting similarity (Gallien and Carboni, 2017). Simultaneously, functional similarity between native and non-native species often predicts stronger impacts on the native species that are most similar to the NIS, again, due to competition (Thomsen *et al.,* 2014). However, NIS that have traits that are dissimilar compared to the native community often show stronger impacts on the native community as a whole compared to NIS with similar traits, which in some cases may be related to e.g. habitat engineering (Troost, 2010; Guy-Haim *et al.*, 2018) or evolutionary naïvité (Ricciardi and Atkinson, 2004; Anton *et al.*, 2020). One such example in the northern Baltic Sea is the North American mud crab *Rhithropanopaeus harrisii,* which is the only crab species established in the area, and has had significant impacts on invertebrate communities in littoral macrophyte habitats (Jormalainen *et al.*, 2016; Liversage *et al.*, 2019).

While NIS traits are important for both establishment success and impacts on the community, trophic interactions within the community are key to describing the role of any species in a community. Predation is a key interaction linking species together within a food web and is often regarded as the main mechanism by which non-native species cause negative impacts on native communities (Salo *et al.*, 2007; Paolucci *et al.*, 2013; Pantel *et al.*, 2017). The effects of introduced species are therefore different depending on the trophic level of the introduced species relative to native species (Thomsen *et al.* 2014). Negative effects are most often observed on lower or equal trophic levels through predation and competition, while positive effects can be seen for species on higher trophic levels when the non-native species acts as a resource. The trophic level of a NIS is therefore regarded as a main predictor of its effects on native species (Thomsen *et al.*, 2014; Bradley *et al.*, 2019).

Predation and competition are also driving biological interactions, determining species community composition within an ecosystem (Hairston *et al.,* 1960; Weis, 2011). NIS can alter the existing interactions in a food web by changing nutrient and/or energy flows through predation on native prey or competition for habitat and food (Antsulevich and Välipakka, 2000; Gorokhova *et al.*, 2005; Almqvist *et al.*, 2010). However, species interactions within a community are not static. Competition and predation pressure are largely density dependent (Hairston *et al.*, 1960) and vary for an individual during its ontogeny (Werner and Gilliam, 1984; Persson and Hansson, 1999) or between species according to population abundances (Bradley *et al.,* 2019). Therefore, the trophic role of a NIS, along with its potential impacts, is expected to change depending on its life stage and population invasion stage; from introduced to established (Crooks, 2005; Brownscombe and Fox, 2013; Masson *et al.*, 2018).

Ultimately, the strength of the trophic interactions exerted on and by a species in a food web determine the role and function the species has in the community. Therefore, these trophic interactions are the key to describing the position of an introduced species in the food web and the effects, whether positive, negative or neutral, this integration has on the ecosystem (Byers, 2009; Thomsen et al., 2014; David et al., 2017).

2 Aims and scope of the thesis

In this thesis, I aim to clarify the implications of the introduction of the round goby into coastal communities in the Baltic Sea. I am focusing on the integration, in terms of trophic interactions involving the round goby, and impacts of this introduction on the local fish community structure and functioning. My thesis describes the role of the round goby under different population establishment phases, which factors contribute to the observed patterns and what the implications are for native species and communities (Fig. 1). The main emphasis is on a relatively newly established and isolated population in the northern Baltic Sea, which is compared to two older and/or more widely distributed populations in southern Baltic Sea. In the more recently established northern regions, round goby populations are less widely distributed (Kotta *et al.*, 2016; Puntila *et al.*, 2018), but as native species and trait richness are lower than in the southern parts of the Baltic Sea (Ojaveer *et al.*, 2010; Törnroos *et al.*, 2015; Koehler *et al.*, 2022), species interactions may be manifested differently. Furthermore, studies on the effects of round goby on functional diversity are largely missing (but see Vivó-Pons et al., 2023b). Therefore, studies focusing on the role of the round goby in a community context are still needed. Knowing which trophic level the round goby occupies and which trophic links it upholds is essential for identifying its realized role in the community. This also helps identifying the species or ecosystem processes that may be affected by the presence of this new species.

The overarching questions in my thesis are (roman numerals refer to papers):

1) What is the trophic role of the round goby in coastal communities as a) a predator (**I**), b) competitor (**I** & **III**), c) prey (**II**), and which native species may be affected?
2) What effect does the round goby have on coastal fish community structure and functioning (**II**-**III**)?

3) Which factors contribute to the observed patterns on a local and regional level (**I**-**III**)?

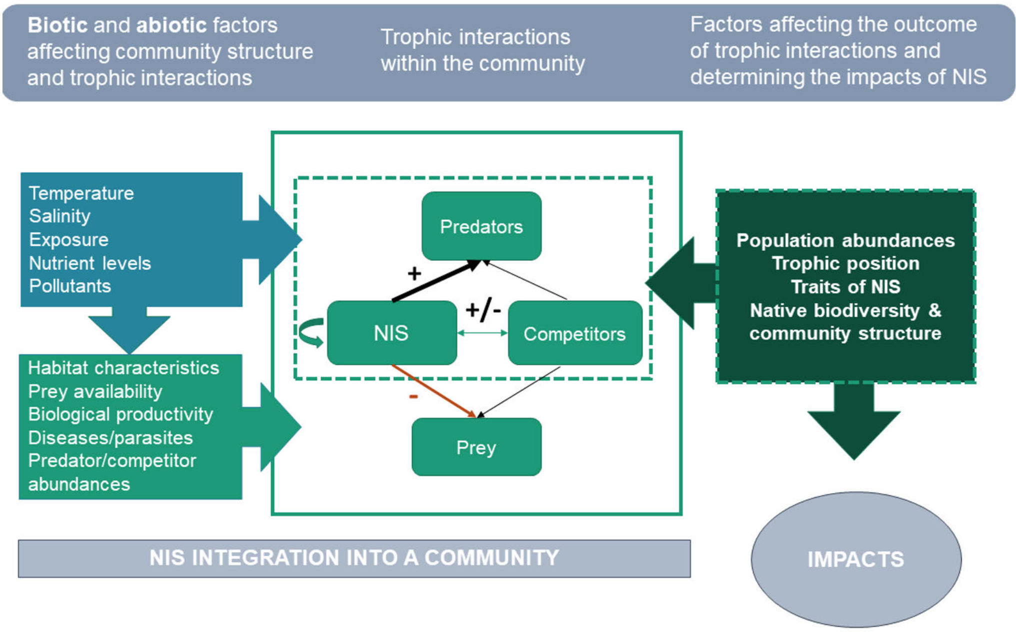

Figure 1. Conceptual figure of factors affecting non-indigenous species (NIS) integration and impacts on native communities, as described in section 1.4. Highlighted here in dashed boxes are the aspects studied in this thesis.

3 Material and methods

3.1 Round goby populations in the study areas

In this section I describe round goby populations and invasion history in the studied areas to set the framework within which these studies were conducted. The studies in this thesis were conducted on three populations of round goby, two in the southern Baltic Proper; Karlskrona (KK, Sweden) and Hel (HEL, Poland), and one in the northern Baltic Proper on the Åland Islands (AL, Finland; Fig. 2). All studies focused on shallow (mostly <10 m) coastal areas in regions of intense shipping traffic and moderate to high cumulative human impacts (Baltic Sea Impact Index;

HELCOM, 2023). However, the regions differ somewhat in terms of environmental conditions such as salinity and sea surface temperature, as well as dominating substrate type and fish species richness. The studied round goby populations also vary in terms of age, population abundances as well as distribution range (Fig. 3; Table 1). The round goby is an opportunistic species, and its diet composition varies according to prey availability (Brandner *et al.*, 2013a), however, in all populations studied here mollusks (bivalves and gastropods) and crustaceans, constitute the most frequently consumed prey (Fig. 4).

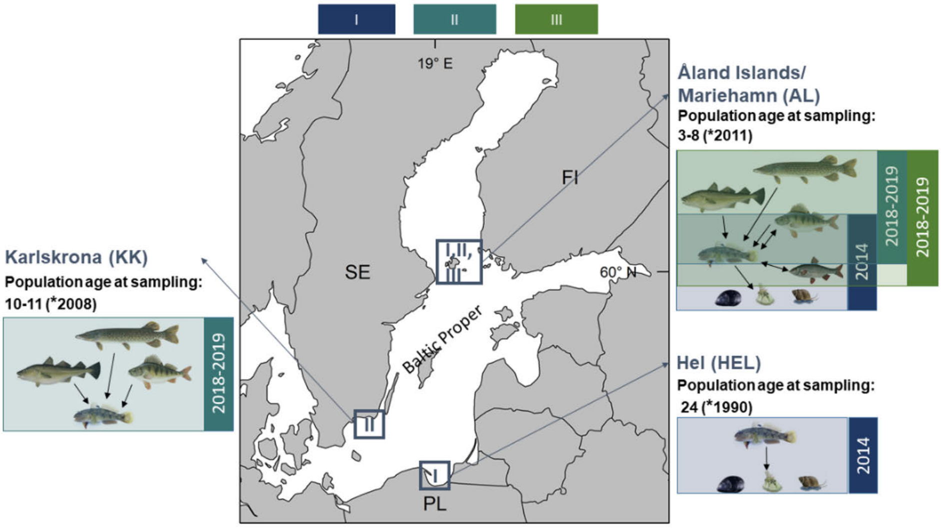

Figure 2. Map of the areas where the studies in this thesis were conducted. Papers marked with roman numerals (I-III). Years of first observations of round goby in each area in parentheses. Focal species groups and sampling years for each study are indicated in colored boxes. Examples of trophic interactions between round goby and other species shown with arrows (down= predation; double sided=competition).

The population in Hel, Gulf of Gdansk, represent the oldest (at the time of sampling ca. 24 years) and most widely established population, with an estimated population range of at least 400 m^2 in the Gulf of Gdansk (Sapota, 2012). In this area, highest round goby population densities have been measured during summer (July-August) and round goby constituted most of the coastal fish abundances in shallow areas from June until November (Sapota and Skóra, 2005), ca. 10 years after the first observations in 1990 (Skóra and Stolarski, 1993). The habitat in the sampling area, Hel harbor basin, is quite uniform, with sparse vegetation and little structural complexity, except for the near-shore human-made pier and embankment structures (Skora and Rzeznik, 2001).

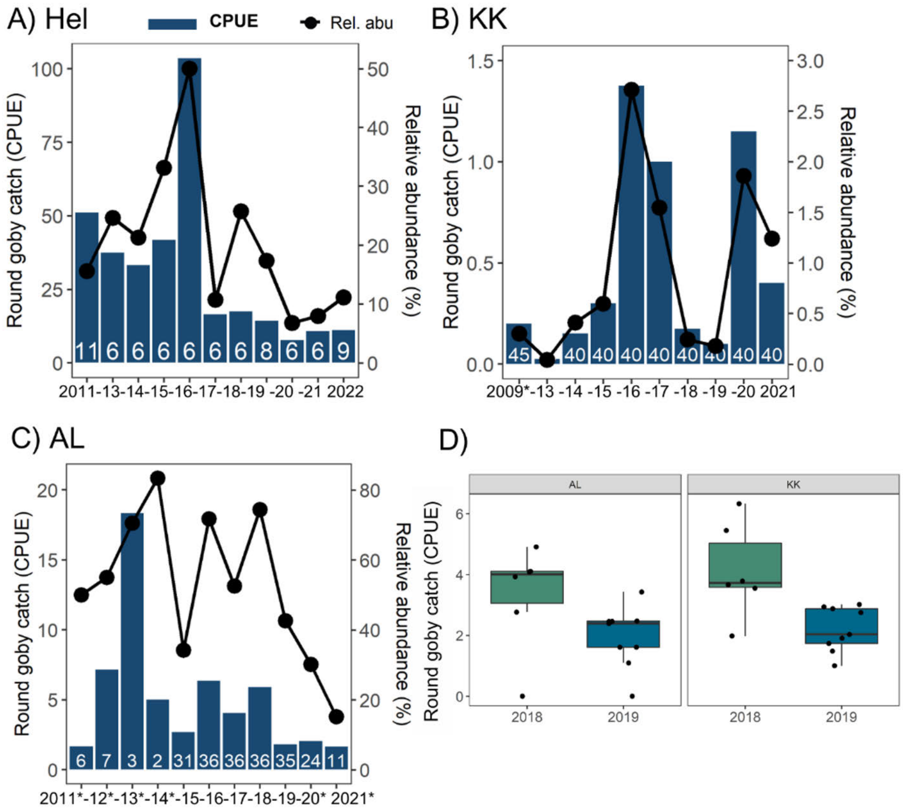

Figure 3. Round goby population development in the three different study areas. Catch per unit effort (CPUE; number of round gobies/total fishing effort per year) and relative abundance (round goby CPUE/ total catch) in A) Hel, Poland (HEL), B) Karlskrona, Sweden (KK), C) Åland Islands, Finland (AL) and, D) in AL and KK in May-June 2018 and 2019 (log-transformed CPUE data from ***paper II****). A) and B) data from coastal fish monitoring surveys conducted in August obtained from A) Polish State Environmental Monitoring program (data from Puck Bay and Hel peninsula) and B) Swedish database for coastal fish monitoring, KUL (SLU; Karlskrona western archipelago), and C) round goby surveys conducted in May-June by the regional government of Åland (K. Ådjers; Government of Åland, 2021). Numbers below bars (A-C) indicate fishing effort per year (# stations). Gear used: Nordic coastal gill nets (KK and HEL; A,B. See HELCOM 2018 and 2019a for a description of monitoring schemes), fyke nets (AL and KK; C&D). NB! Round goby catches differ between gear types and months, therefore the CPUEs are not directly comparable between areas.*data deviates from the standard protocol in B) sampling month (July) and sampling locations in 2009, and C) number of sampled stations 2011-2014 and 2020-2021.*

Some contributing factors to the successful establishment and fast dispersal in the Gulf of Gdansk has been attributed to the degradation of environmental state and changes in species community composition in the decades prior to the arrival of the round goby. A decrease in the abundance of large predatory fish, and an increase in particulate organic matter resulted in the dominance of suspension and deposit feeding bivalves, especially blue mussels *Mytilus trossulus,* in the macrobenthic community (Sapota and Skóra, 2005). The lack of predatory fish and increased abundance of blue mussels, a main prey for round gobies (Skora and Rzeznik, 2001; Puntila, 2016) has been thought to favor the establishment and spread round goby in this area. Between 2011 and 2016, round goby made up 15 to 50 % of the total abundances in coastal monitoring catches, after which there has been a sligt decrease (Fig. 3a). Overall, flounder (*Platichthys flesus*) perch (*Perca fluviatilis*) and Baltic herring (*Clupea harengus membras*), as well as round goby represented the most abundant fish species around the Hel peninsula and Puck Bay (Table 1; HELCOM, 2018).

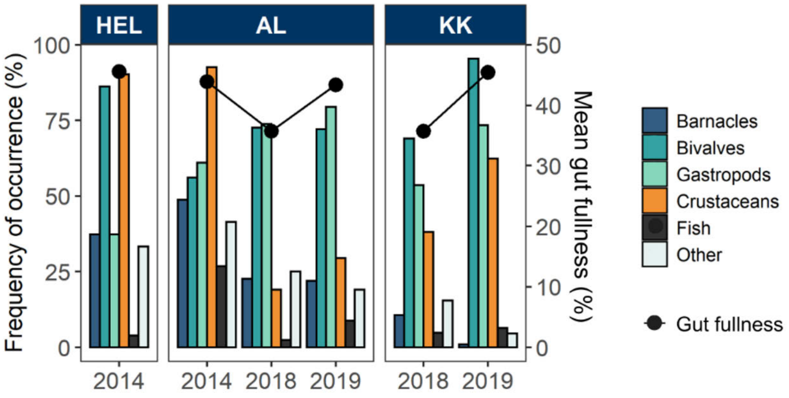

Figure 4. Round goby diet represented as frequency of occurrence (%) of main prey groups in the three study areas and years. Mean gut fullness (%; black dots) for each year is also given. Data from: Puntila, 2016 (2014) and from Wallin Kihlberg et al., 2023 (2018 and 2019).

In Karlskrona (KK), round goby was first observed in 2008, which was also the first observation in Swedish coastal areas. Since then, the round goby has spread widely along the Swedish coast, from Göteborg in the west (Skagerrak) to Örnsköldsvik Municipality in the north (Gulf of Bothnia) (Swedish Species Information Centre; https://artportalen.se/). In the Karlskrona archipelago area, the catches of round goby in coastal fish monitoring, conducted with gill nets in

August, peaked in 2016, after which they started declining (Fig. 3b). The proportion of survey stations where round goby was observed simultaneously increased from 2.5% in 2013 to 55% in 2016, after which it decreased again. This may, however, be a sign that the population range expanded outside the survey area. However, compared to Hel, the catches have remained low (CPUE < 2; Fig. 3b). On the local scale, round goby presence in these areas has been found to correlate positively with both very coarse (bedrock) and very fine (mud) substrates, but less with intermediate substrate types (Florin *et al.*, 2018). Currently, the round goby is widely distributed around the Karlskrona archipelago, with observations covering over 200 km^2 (SLU, Swedish Species Information Centre). The round goby was the 5th most abundant species (~1%) in coastal fish monitoring catches overall from 2013 to 2021, while perch and roach (*Rutilus rutilus*) were the dominating species (>79 % of total catches) (Table 1).

On the Åland Islands (AL), the round goby was first observed in 2011 near the passenger ferry harbor in Mariehamn. This population is relatively isolated, and during the time of first observations, the nearest round goby occurrences were over >100 km away close to the Finnish mainland (Finnish Biodiversity Information Facility; https://laji.fi/). Compared to the other two populations studied here, the dispersal rate has been rather slow (approx. 500 m per year), and the round goby population still mainly occurs in a relatively confined (ca 6 km^2) bay area. Overall, observations around Mariehamn have been made along a 20 km stretch of coastline within 6 km from the first observations (Government of Åland, 2021). After attaining high abundances first in 2013 (only three stations sampled), 2016 and again in 2018, round goby catches have declined and remained relatively low since 2019 (Fig. 3c). A similar decrease in fyke net catches between 2018 and 2019 was observed in both AL and KK (Fig. 3d). Round goby was the 8th most abundant fish species at four stations close to the Mariehamn harbor area (2.4 % of abundances), while perch and roach made up over 50 % of gill net catches in August 2018 and 2019 (Table 1). This population thus represents the most isolated and, although locally abundant, on a regional scale less widespread than the other two populations.

Table 1. Environmental characteristics of the study areas. Mean sea-surface temperature, °C and salinity (min-max; May-August, 2011-2021), fish species richness (local/ basin level).

	Hel	**Karlskrona**	**Mariehamn**
Baltic Sea basin	Gulf of Gdansk	Bornholm Basin	Åland Sea/ Archipelago Sea
Temperature [1,2,3]	10 - 19.1	8.8 - 18.8	9.2 - 19.1
Salinity [2,3]	6.5-7.3	6.5-7.4	5.3-6.5
Main substrate (shallow -> deep) [2,4,5]	Soft (sand -> mud)	Mixed (rocky -> mud)	Mixed (rocky -> mud)
Round goby distribution area [6,7,8]	Wide (> 400 m^2)	Wide (> 200 m^2)	Restricted (< 10 km^2)
Species richness [5,9,10/11]	27/90	29/104	26/71
Most abundant coastal fish species [5,9,10]	Flounder, herring, perch, round goby	Perch, roach, bleak, herring	Perch, roach, bleak, herring

1. NOAA; https://www.seatemperature.org/, 2. Swedish Meteorological and Hydrological Institute, https://www.smhi.se/data/, 3. Government of Åland, coastal monitoring data 4. Herlevi et al., 2018, 5. Own data, 6. Sapota, 2012. 7. Swedish Species Information Centre; https://artportalen.se/. 8. Government of Åland, 2021 9. HELCOM (2018), 10. Swedish database for coastal fish monitoring, 11. HELCOM (2019b)

3.2 General methodology

I assessed different aspects of trophic interactions involving the round goby, and how these interactions relate to round goby population characteristics, environmental conditions, and overall fish community structure (Table 2). Sampling was conducted during early to late summer, when round goby abundances are generally highest in the shallow coastal areas (Brauer *et al.*, 2020; Behrens *et al.*, 2022). Combining traditional biological survey methods (survey fishing, stomach contents analysis; **paper II-III**) with more applied methods, like stable isotope analysis (**paper I**), DNA metabarcoding (**paper II**) and functional trait analysis (**paper III**) enables me to get a comprehensive picture of both the structure (species composition, richness, and diversity) and functioning of the community with regards to the interaction among species in the community. The specific methods used in each paper are described below.

Table 2. Summary of the scale (temporal, geographic, ecological) and main methods used in the three papers of this thesis. For abbreviations, see text.

	Paper I	**Paper II**	**Paper III**
Temporal scale	Week to month August- September	2 years March-June	2 years June-July
Geographic scale	Local- Regional 2 areas	Local- Regional 2 areas	Local 1 area/13 sites
Sampled trophic levels & organisms	Primary producers to secondary consumers (AL), primary and secondary consumers (HEL)	Secondary consumer (round goby) and top predators (cod, perch, pike)	Secondary consumers (round goby, native mesopredatory fish) and top predators (perch)
Ecological interactions	Predation, competition	Predation, top-down & bottom-up regulation	Competition, community composition and diversity
Main method	Stable isotope analysis	Diet analyses: Visual & DNA-metabarcoding	Survey fishing & functional trait analysis
Measured variables	Trophic position (TP), isotopic niche size and overlap (SEA), intra-population variability in isotope values (SDNND, CD)	Diet composition: volume proportion (V%), relative sequence number (S%)	Taxonomic (H', J, S) and functional diversity (Fric, Feve, FDiv, Fspe). Taxonomic (relative biomass) and trait-based (CWM) community composition.
Other relevant factors	Prey availability (*), Round goby population abundances (*), Round goby size (total length)	Round goby population abundances, Predator size (total length)	Round goby population abundances, Local environmental factors (exposure, temperature, salinity)
Data analysis methods	Mann-Whitney U/ T-tests, LM (regression)	Model selection (AIC): GLMM/ LMM	Linear models (GLS), Multivariate: db-RDA

* Not directly measured

3.3 Sampling of species and communities

3.3.1 Sampling for stable isotope analysis (paper I)

Sampling of fish and invertebrates for stable isotope analysis were conducted during the late-summer season in 2014 (August in Hel and September in Mariehamn) at one location in each area. In Mariehamn, AL, we sampled the whole benthic community from detritus, primary-producers, littoral benthic in- and epifauna to fish. Fish, other than round gobies, were caught with two multi-mesh coastal survey gill nets (9 panels, mesh sizes 10, 12, 15, 19, 24, 30, 38, 47, and 60 mm; Appelberg *et al.* 2003). Round gobies were collected using three types of passive gear; minnow traps (mesh size 6 mm), collapsible crayfish traps (mesh size 12 mm) and eel traps (mesh size in cod ends 10, 14, and 17 mm) in each area. These gear have proven most efficient for catching gobies in low-density populations and rip-rap bank habitats (Diana *et al.*, 2006), with this combination of traps providing a better size range of catch than any trap type used alone. In Hel, the sampling was focused on the round goby and potential prey items. The benthic community was sampled using a benthic grab sampler, while round gobies were collected with passive gear as described above for Mariehamn. All sampled organisms were frozen and stored at –20°C prior to further analyses.

Sample preparation

A piece of muscle or other soft tissue was dissected from all sampled animals, while plants were used whole. Samples were dried and homogenized. Small invertebrates and plants were pooled into larger samples to ensure a sufficient quantity of dried material. The dried sample material was analyzed for carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N) stable isotope ratios at the Stable Isotope Facility at UC Davis in California, USA. The results are expressed as a difference in mass (δ) in relation to international standards for carbon (Vienna-PDB, PeeDee Belemnite) and nitrogen (atmospheric nitrogen, N_2) (Peterson and Fry, 1987)

3.3.2 Sampling of round goby and predatory fish (paper II)

Cod, *Gadus morhua*, perch, and Northern pike, *Esox lucius* were sampled in Karlskrona (KK) and on Åland (AL) in May-June 2018 and March-June 2019 corresponding to spring and early summer conditions. Fishing time was one night (12-16 h) on 1-5 fishing occasions per month at 1- 6 locations for each species and area. In AL, cod was caught with gill nets in commercial fisheries approximately

20 km offshore at 80-200 m depth. Perch and pike in AL were fished in both commercial gill net fisheries and in separate sampling campaigns with multi-mesh coastal survey gill nets and regular monofilament gill nets (mesh size 35-60 mm). In KK, predatory fishes were caught with gill nets in commercial fisheries at 6-20 m depths. To estimate round goby abundances in the environment, survey fishing was carried out in the same coastal areas as predatory fishes were collected in May-June 2018 and April-June 2019. We fished with two fine mesh twin fyke nets (in total four houses, house mesh size 8-9 mm and 11-12 mm in leaders and netting bags) at each location for one night each month (~2-5 m depth). Catches were standardized to 12h whenever needed to correct for differences in catches due to varying soak time. Catch per unit effort (CPUE) thus equaled standardized round goby catches in one paired fyke net (4 houses) over 12h.

3.3.3 Sampling of coastal fish communities (paper III)

To study variation in the structure and functioning of coastal fish communities at a local scale in different round goby abundances we sampled the fish community at 13 locations around the Mariehamn peninsula on the Åland islands. The locations were selected based on data from a local round goby monitoring scheme, to reflect a round goby abundance gradient (Government of Åland, 2021). Three locations outside the known distribution range (ca 1- 4 km distance from the nearest known observation) were included as zero abundance locations. We fished in June-July in 2018 (4 sites) and 2019 (all 13 sites; 17 fishing occasions in total). Each site was fished at 2-6 m depth with two joined bottom-set multi-mesh coastal survey gill nets (approx. 12 h/ fishing occasion). All fish were counted and identified, and a subset per species and panel were measured (Total body length, cm), and weighed (Total body mass, g). The total catch per unit effort (CPUE) at each location thus consisted of the total catch (in numbers or biomass, g) in the two joined nets at one fishing occasion. At each fishing occasion the temperature and salinity were measured 1 m above the bottom and wind speed (m/s) at sampling was recorded. The exposure index for each site was calculated based on the simplified wave model (Isaeus, 2004).

Fishing occasions were grouped into impact groups (*High, Low, Absent*) according to their round goby abundances) and sampling year (2018 or 2019). Four out of the 13 stations were sampled in both years, and these stations displayed the highest round goby abundances in the dataset, which yielded 4 stations in each “High” group (High 2018 and High 2019). In terms of recorded round goby abundances at the time of sampling, the High 2019 sites represent intermediate round goby abundances. All other stations, sampled only in 2019, were grouped as “Low” (n=6), except the three stations outside the known distribution range which were grouped as “Absent”.

3.4 Stable Isotope Analysis (Paper I)

We used stable isotope analysis of carbon and nitrogen to determine (1) the trophic position of the round goby, (2) how the trophic position and isotopic niche size, reflecting resource use of the round goby, differs in two populations in different phases of establishment and (3) the ontogenetic changes of isotopic signatures in these two round goby populations. Stable isotope analysis (SIA) is an effective method for understanding trophic relationships, resource-use patterns and studying the role of non-native species in food-webs (Vander Zanden *et al.*, 1999). Stable isotope ratios reflect assimilated diet patterns over longer periods, allowing for the incorporation of temporal variation (Post, 2002). Research shows that the assimilation of carbon and nitrogen isotopes in tissues mostly follows predictable patterns within a food chain, depending on e.g. the tissue type examined (McCutchan *et al.*, 2003). The ratio of heavy to light carbon isotopes (^{13}C:^{12}C) remains relatively stable, with a slight increase from food source to consumer (mean= 0.4 ‰; McCutchan *et al.,* 2003), while the proportion of heavy to light nitrogen isotopes (^{15}N:^{14}N) increases more with each trophic level (3- 4‰), indicating the position of a consumer in the food chain (Peterson and Fry, 1987). Each species in a community thus demonstrates isotopic signatures based on their food sources. The trophic position of a consumer can thus be estimated based on the difference of δ ^{15}N values between consumer and prey (Post, 2002). The trophic position (TP) was calculated for all fish to enable comparison between round goby and other fish (according to Post, 2002). We chose the epibenthic suspension feeding blue mussel *M. trossulus* as our baseline organism. It was deemed as a suitable species as it is a relatively long-lived benthic species present in both sampling areas. It is also one of the main prey species of the round goby in all size classes in the Baltic Sea (Skora and Rzeznik, 2001; Skabeikis and Lesutienė, 2015) as well as important prey for other benthic-feeding fish (Lappalainen *et al.*, 2004). The standard trophic enrichment factor of 3.4 was used to express the mean trophic enrichment of nitrogen between consumers and their prey (Post, 2002).

To further support the interpretation of my results, additional stable isotope data from fish and benthic invertebrates (blue mussels) collected during the fish community sampling in 2018 and 2019 (**paper III**) was included. These were analyzed by a different laboratory (Stable isotopes in nature laboratory, SINLAB) and results may therefore vary slightly. However, the data for the comparison between years were standardized to trophic position (δ 15N; as described above, **paper I**) to enable comparisons between years.

3.5 Diet analysis (Paper II)

We used two diet assessment methods, visual identification (VSCA) and DNA metabarcoding of stomach contents to 1) estimate the contribution of round goby as prey in the diets of cod, perch, and pike 2) relate round goby consumption to its environmental abundances, and 3) describe changes in overall diet composition and feeding strategies of predators in relation to round goby environmental abundances. Combined, these methods make up a new approach in the study of Baltic Sea predatory fish diets. In total, we sampled 595 fishes for diet analysis.

3.5.1 Stomach content analysis: Visual identification (VSCA)

Predator stomach contents were inspected after weighting total stomach content wet mass. Prey items were identified to the lowest possible taxonomic level and all prey items were counted. The contribution of each prey type was visually estimated as a proportion (0-1) of the volume of all prey items in the stomach, excluding non-prey items such as stones or algal material (Hyslop, 1980)

3.5.2 Stomach content analysis: DNA-metabarcoding (DNA)

DNA metabarcoding is a process to identify multiple species in a mixed sample (e.g. samples of soil, water, feces, stomach contents; (Taberlet *et al.*, 2012). We used it as an addition to traditional VSCA (needed to obtain quantitative estimates of diet composition), to get a more comprehensive picture of predator diets, as many organism groups are often underrepresented in VSCA due to e.g. fast degradation and uncertain identification (Nielsen *et al.*, 2018).

For samples that were assigned to both VSCA and DNA metabarcoding, the DNA samples were taken before VSCA to minimize the risk of DNA contamination (See supplement 4 in **paper II** for details about sample selection and DNA sampling methods). DNA metabarcoding (from DNA extraction to sequencing and initial quality control and filtering of sequences) was conducted by SeAnalytics, Sweden, and Eurofins Genomics, Germany. We used the 12S rRNA marker for identifying fish prey (Weigand *et al.*, 2019; Miya *et al.*, 2020). For cod and perch, we additionally used the COI marker for identification of invertebrates (Weigand *et al.,* 2019). Separate PCR runs and sequencing were conducted for the respective markers. Samples with low DNA concentrations (<0.1 ng/µl) and samples that did not yield any sequences were excluded. Rare sequences that comprised <1% of the total sequences in each sample were excluded. The prey datasets for 12S and COI were combined for further data processing and analyses.

3.6 Functional trait analysis (Paper III)

We collected information about eight traits to describe the functional structure of our fish communities (Table 3). We refer to functional traits as any biological i.e. morphological, physiological, behavioral or life-history attribute affecting individual fitness and performance (Laliberté and Legendre, 2010; Villéger *et al.*, 2017). The functional traits selected reflect key biological functions such as food acquisition, mobility, and reproduction (Table 3). These traits describe the role of the species in the community through trophic interactions, behavior, productivity, and resilience to perturbations (Villéger *et al.*, 2017). For each fishing occasion, we calculated a set of seven diversity metrics based on both the taxonomic and trait dataset. To describe taxonomic diversity of fish assemblages we calculated species richness (taxon richness, S) and Shannon diversity index (H') in the *vegan* package (Oksanen *et al.,* 2022). Pielou's evenness (J) was calculated as H'/log(S). The functional diversity (FD) of fish assemblages was described using four indices; Functional Richness (FRic), Functional Evenness (FEve), Functional Dispersion (FDis) and Functional Specialization (FSpe). These indices depict different aspects of the functional diversity of the community and community assembly (Villéger *et al.*, 2008; Mouchet *et al.*, 2010; Mouillot *et al.*, 2013), and may thus respond differently to non-native species inclusion and relative importance in the community (Renault *et al.*, 2022) in this case represented by the abundance of round goby (Round goby impact group). The different FD indices were calculated using the *mFD* package (Magneville *et al.*, 2022) based on the Gower distance matrix (de Bello *et al.*, 2021), computed from trait-pairs of all species within the total trait pool. These were weighted by species relative biomasses per fishing occasion.

Table 3. Traits used to describe the functional structure of sampled fish communities. Main references where the respective traits are used is given.

Trait	Categories	Explanation and relevance
Body size	Continuous (log-transformed)	Average body mass (g) per species. Related to metabolism, trophic status, vulnerability to predation and generation time
Fecundity	Continuous (log-transformed)	Average number of eggs per female per year (Pecuchet *et al.,* 2016, 2017). Related to fitness, productivity and resilience to perturbation.
Maximum age	Ordered categorical: 1:<10 2:10-19 3:20-29 4:30+	Maximum recorded age in Finnish Baltic waters (or elsewhere in the Baltic Sea if not available). Generation time and vulnerability to perturbations (Törnroos *et al.,* 2019).
Egg type	demersal adhering demersal mass clump nest mass demersal scattered pelagic scattered ovoviviparous	Type of eggs and where eggs are laid (Törnroos *et al.,* 2019). Associated with spawning behavior, productivity and habitat as well as parental investment into the survival of offspring. Highest investment for ovoviviparous, i.e. live-bearing, and nest laying (guarding), lowest for pelagic releasing species.
Feeding guild	piscivore invertivore/piscivore invertivore planktivore omnivore	Categories according to trophic level and principal diet composition (Kohler *et al.,* 2022). Reflects food acquisition, trophic status and feeding interactions.
Vertical position	pelagic demersal demersal–pelagic benthic	Position in the water column (Kohler *et al.,* 2022). Associated with habitat use and mobility- affects potential trophic interactions (both with prey and predators).
Body shape	deep compressed elongated eel-like fusiform flat	General body morphology (Pecuchet *et al.,* 2016). Associated with vertical position in the water column, mobility and swimming performance.
Caudal fin shape	forked emarginated rounded truncated continuous	Reflects differences in swimming mode and performance, general mobility, activity and foraging behavior (Pecuchet *et al.,* 2016).

3.7 Data analysis

All data analyses and visualization were conducted in the R environment (R Core Team 2022). All plots were produced using the package *ggplot2* (Wickham, 2016).

3.7.1 Trophic position and isotopic niche (paper I)

Comparisons within and between round goby populations

In **paper I**, we compared the estimated trophic position (TP) of round gobies as well as their isotopic signatures (δ 13C and δ 15N) between benthic-feeding fish (i.e. potential competitors) in the same habitat (AL) and between areas (HEL, AL) using one-way ANOVA's (Tukey's pairwise post hoc test) and t-tests, respectively. A linear regression was performed with carbon and nitrogen isotope values ($\delta\,^{13}C$ and $\delta\,^{15}N$) as a function of total length of all round gobies on Åland (AL) and Hel to detect possible ontogenetic changes and compare the relationship of isotope values to length between areas.

To investigate isotopic niche overlap between the round goby and other fish species in the same habitat, we calculated Standard Ellipse Area's for the most abundant benthic fish in AL with the SIBER package (Jackson *et al.*, 2011). Standard Ellipse Area with a correction for small sample sizes (SEAc), reflects the core isotopic niche of a group (Jackson *et al.,* 2011). The overlap between two species was measured as proportional overlap of the maximum likelihood estimates of SEAc. We considered values larger than 0.60 as ecologically significant overlap, according to Schoener's diet overlap index (Schoener, 1968; Guzzo *et al.*, 2013) . We also used a Bayesian iterative approach in SIBER to obtain confidence intervals for the SEA's (SEA_b: Jackson *et al.,* 2011).

To assess differences in resource use (intra-population variability and diversity), we compared the isotopic niche sizes between round goby and other benthic fish in AL as well as between populations in AL and HEL. The Bayesian Standard Ellipse Areas (SEA_b) were used to calculate a probability for differences in niche size. A significant difference was regarded as a probability of at least 95 %. We also compared four other population metrics to describe the diversity of resource use by round gobies. Carbon and nitrogen range (CR_b and NR_b) describes the breath of resource-use in a population of consumers (Layman *et al.*, 2007; Jackson *et al.*, 2011, 2012), while metric mean distance to centroid (CD_b) was used as a proxy for degree of individual specialization in a population as larger values indicate higher trophic diversity i.e. larger individual differences. The metric standard deviation of nearest neighbor distance ($SDNND_b$) can be used to infer population trophic evenness and is thus also related to the degree of similarity of resource use in a population. Due to the small sample sizes all metrics were bootstrapped (n=10000; indicated with a subscript 'b').

3.7.2 Round goby importance in predator diets (paper II)

In **paper II**, overall diet composition, as well as the contribution of round goby to predator diets, was summarized as relative volume proportion (V %) and relative sequence number (S %) (Deagle *et al.*, 2019), for VSCA and DNA metabarcoding data, respectively.

To assess the influence of round goby environmental abundances on its predation, we ran separate generalized (GLMM) or linear mixed models (LMM) for the respective predator species using the *lme4* package in R (Bates *et al.,* 2015) We selected the best model with lowest AIC and studied changes in AIC, denoted ΔAIC, when removing or adding variables to the best model (Burnham and Anderson, 2002). We calculated ΔAIC for three different dependent variables: a) round goby abundance in predator diets (log-transformed number of round gobies per stomach sample) using LMM, b) volume proportion (V%) of round goby in predator diets per stomach sample using GLMM (binomial distribution) and c) relative prey weight (log-transformed RPW per stomach sample) using LMM. In models a) and c) empty and non-empty stomachs were included (n=359), while in model b) we only used non-empty stomachs (n=300). Relative prey weight (RPW, %) of a predator is a measure of gut fullness and gives the amount (wet mass, g) of prey in a stomach (M_{SC}) relative to the predator body mass (M_{TW}). It was used to describe variation in the amount of ingested prey.

3.7.3 Influence on fish community structure and functioning (paper III)

In **paper III**, I compared fish community taxonomic and functional structure and diversity between round goby impact groups, which represented round goby abundances from absent to high. Furthermore, we compared datasets where round goby was either excluded (Native species only) or included (Native + Rg) to discern the effects of round goby abundances compared to the underlying native community. All analyses were further run with 1) a full dataset with all species (hereafter "full") and 2) a dataset excluding the pelagic, more migratory species, that are only seasonally abundant in the littoral near-shore habitat (hereafter "littoral"). This was done to assess whether the patterns were different for all species and species that are more likely to compete for resources with the round goby in the summer season (i.e. littoral species).

Fish community structure and diversity

To explore how native fish community structure and diversity is related to round goby abundances (i.e. impact groups) we fit generalized least squares linear models using the *gls* function, from the *nlme* package (Pinheiro *et al.,* 2021). The abundance and biomass, as well as taxonomic (S, H', J) and functional (FRic, FEve, FDis, FSpe) diversity metrics of native fish communities (Native only) were used as dependent variables and round goby impact groups as explanatory factors. We used the *Anova* function (type II, car package, Fox and Weisberg, 2019), to conduct Chi-squared testes on the outputs to assess the overall significance of the impact group on each response variable. When significant differences between groups were detected, we used the *pairs* function from the *emmeans* package (Lenth, 2022) to conduct pairwise comparisons of the estimated marginal means using Tukey's correction for multiple testing. The metrics for the dataset including round goby (Native + Rg) were similarly compared between impact groups to assess whether there were significant overall differences when including round goby in the community dataset. Finally, to assess the influence of round goby inclusion alone on each of the taxonomic and functional diversity metrics, t-test-type pairwise comparisons of the estimated marginal means of the diversity metrics were compared between the round goby included (Native + Rg) and excluded (Native only) datasets for each impact group separately (*Absent 2019* not included), using the *emmeans* function on the gls-models.

Fish community composition

To study the influence of round goby on taxonomic and functional community composition we used distance-based redundancy analysis (db-RDA) to compare the beta-diversity i.e., community composition between impact groups. The db-RDA finds linear relationships between all the Principal Coordinate Analysis (PCoA) axes (summarizing a dissimilarity matrix between samples) and environmental variables (McArdle and Anderson, 2001) For the taxonomic db-RDA the fish community matrix was based on the Bray-Curtis dissimilarity between the relative biomass of fish species in each sample, while the functional db-RDA was run on the gower dissimilarity matrix based on community (biomass) weighted mean values of each trait (CWM; Lavorel *et al.*, 2008) in each sample (fishing occasion). Before calculating the CWM (*functcomp* function in the *FD* package; Laliberté *et al.,* 2014), all categorical traits were transformed into binary traits, with one value (0 or 1) for each trait category (32 trait categories in total), and all traits were scaled to zero mean and unit variance.

To explore the effects of round goby impact group (i.e. round goby abundance) on fish community composition, we ran the db-RDAs with dataset (Native only and Native + Rg), impact group and environmental variables as explanatory factors. We included temperature, salinity, and effective exposure (combination of exposure at each site and wind speed measured at sampling) as environmental variables. All environmental variables were z-score transformed before analysis. We estimated p-values through an ANOVA-like procedure (Legendre *et al.,* 2011) and restricted permutations (n=199) to account for repeated measurements within sites (High group). After a global test for the significance of the full model, sequential tests were run to see whether the addition of each explanatory variable contributes significantly to the explained variation. The interaction of dataset (Native only vs. Native + Rg) and round goby impact group was added last in the model to first account for variation stemming from the environmental factors.

4 Results and discussion

The results of this thesis emphasize the context-dependency of the impacts of non-native species introductions. During the invasion process, from early establishment to population stabilization, populations often undergo drastic fluctuations in abundances, also documented here (**paper II-III**). Similarly, the role of a non-native species in the food web is dependent on the ecosystem properties of the invaded area, local population abundances and invasion stage (**paper I-III**). The population development stage and local environmental abundances therefore mediate its impact on native species and communities. As seen here, when abundances of the round goby are high, also its impacts on native species, in terms of both importance as a prey for predators (**paper II**) and influence on community composition and structure, are more pronounced (**paper III**). This highlights the fact that as non-native species, like the round goby, integrate into the local community, they are linked to other species in the same environment by trophic interactions, and their populations are affected by both other species (predators, prey availability) and the same environmental factors (temperature, exposure) determining species distribution and population abundances of all species in the community.

4.1 Food web positioning and trophic niche of the round goby

In **paper I**, I show that the trophic position and isotopic niche of the round goby, based on stable isotopes of carbon and nitrogen, differs between two Baltic Sea populations in different establishment phases (Fig. 5). These differences can largely be explained by local round goby population abundances and environmental conditions, which in turn affect the availability of prey and both intra- and interspecific competition. Populations in different invasion stages are likely to experience competition at varying degrees depending on their population abundances and distribution range, as well as the abundance of other species in the same habitat (Brandner *et al.*, 2013b; Britton *et al.*, 2018). At the invasion front, populations are generally less widely distributed and thus show lower overall abundances (Brownscombe and Fox, 2012; Cerwenka *et al.*, 2018). However, at a local, site level, abundances may be very high and population increases rapidly due to high reproductive investment (Masson *et al.*, 2016, 2018). When a population threshold is reached, individuals start to migrate to new locations and thus increase the population distribution range, which allows the overall population abundances to increase (Brownscombe and Fox, 2012). In 2014, this was likely the case on Åland (AL) where round goby abundances were generally low and it only occurred at a few locations, but at these locations round goby relative abundances in fyke net catches were relatively high (Fig. 3c). However, round goby abundances in shallow areas are generally highest during the reproductive season in early summer after which they decrease (Sapota and Skóra, 2005; Brauer *et al.*, 2020). Abundances in AL at the time of sampling in September were likely lower than in the surveys in June (shown in Fig. 3c). In the older, widely distributed population in Hel, round goby catches in gill nets (generally lower catchability of round goby in gill nets; Diana *et al.,* 2006) were high even in August 2014 (CPUE> 20; Fig. 3a), which indicates overall higher abundances in this area.

The round goby positioned as a secondary consumer in both populations. However, in the more recently established population in AL, round goby showed a higher estimated trophic position than in the old, widely established population in Hel (TP, Mean ± SD: 3.66 ± 0.15 vs. 2.93 ± 0.26; Fig. 5b). Previous studies have detected similar patterns and Brandner *et al.* (2013b) showed how a newly established round goby population experiencing less intraspecific competition exhibited a more homogenous diet, compared to an established population, where a pronounced ontogenetic diet shift was visible, mirrored in a broad dietary niche. The higher availability of more nutritious prey at the invasion front in their study was also mirrored in a higher trophic position estimate, similar to the difference between populations in our study in 2014 (Fig 5b; AL vs. HEL).

The differences in trophic position and ontogenetic patterns between populations most likely reflect the local habitat and prey availability. In both populations the round goby is likely to experience both intra-and inter-specific competition, but this may manifest itself differently depending on local conditions. Intra-specific resource competition is therefore a possible reason for the size-related change in isotopic composition *i.e.* trophic position ($\delta^{15}N$) and share of pelagic-sourced carbon (more negative $\delta^{13}C$), which increased with round goby size in AL (**paper I**), reflecting an increased contribution of fish and suspension-feeding prey with size. In Hel, the prey community is dominated by blue mussels (Skora and Rzeznik, 2001), which are the main prey item in all size-classes of round gobies (Puntila, 2016; Fig. 4). Intra-specific competition was thus more reflected in high intra-individual variation in isotopic composition, which was seen as higher isotopic diversity (CD_b, $SDNND_b$), and a slightly larger isotopic niche in Hel (2.68) than Mariehamn (1.64; 88% of posterior Bayesian standard ellipses (SEAb)) for adult round gobies (**paper I**).

The trophic position of a non-native species correlates with its impact on native species, with predators showing stronger impacts on native prey populations (Thomsen *et al.,* 2014). As a secondary consumer, round goby may thus have a strong impact on local invertebrate populations, especially mollusks, as has been shown in numerous studies in the Baltic Sea (Henseler *et al.*, 2021; van Deurs *et al.*, 2021; Nõomaa *et al.*, 2022), and other invaded ecosystems (Brookings *et al.,* 2022). However, as a generalist opportunist species (Nurkse *et al.*, 2016; Nagelkerke *et al.*, 2018), round goby is also likely to prey on the most readily available prey. As shown in **paper I** it had a similar isotopic niche size to other common generalist benthic-feeding fish in the northern Baltic coastal areas. In this case, a similar trophic position to larger perch (mean ± SD: 20.77 ± 4.35 cm), whose diet consists of a significant proportion of fish prey in littoral habitats (Mustamäki *et al.*, 2014), indicates that the round goby was likely also feeding on fish prey (as seen in Fig. 4). The share of fish prey in round goby diet has been shown to correlate with high round goby population abundances and thus intra-specific competition (Wallin Kihlberg *et al.*, 2023). As the diet of round goby is affected by intra-specific competition (Wallin Kihlberg *et al.*, 2023) and availability of prey (Brandner *et al.*, 2013b), also it's trophic position is likely to change accordingly. To demonstrate the variability in trophic position of the round goby, I compared it between years on Åland (Fig. 5b). Eight years after establishment in 2019, the trophic position in of round goby is lower than in 2014 in AL, and similar to Hel in 2014 (24 years since establishment). Simultaneously, the trophic position of round goby shifted closer to roach, than perch (Fig. 5a). However, on average round goby had a more pelagic carbon signal than perch and white bream in 2014 and roach in 2019, species that had a similar trophic position to the round goby (Fig. 5a). Low core isotopic niche overlap with most benthic-feeding fish (**paper I**) further indicates that round goby likely also uses resources that are less favored by other species. Stomach content data suggest that one such resource may be the suspension-feeding bay barnacle (*Amphibalanus improvisus*), which was a common prey item at the time of sampling (Puntila, 2016; Fig. 4).

Round goby relative abundances were low in 2019 compared to 2014 in AL (Fig. 3c), which shows that the impact exerted on benthic invertebrates is also mediated by round goby population abundances. At high population abundances and/or low invertebrate prey availability, the impacts of round goby on native fish species may be more pronounced, both through resource competition and predation on fish eggs or larvae (Lutz *et al.*, 2020). These results thus indicate that round goby is likely able to sustain populations in varying habitats and population invasion stages due to its generalist feeding habit and ability to rely on different food sources (incl. fish prey). Low overlap in isotopic values also indicate limited resource competition with other species, although some competition is still likely. Similar conclusions were drawn by Rakauskas *et al.,* 2020 in Lithuanian coastal waters, where low overlap in core isotopic niches were observed, especially in autumn. The local fish and benthic community structure in different seasons and population development phases thus influences the round goby's trophic position. Which native species may be affected varies accordingly.

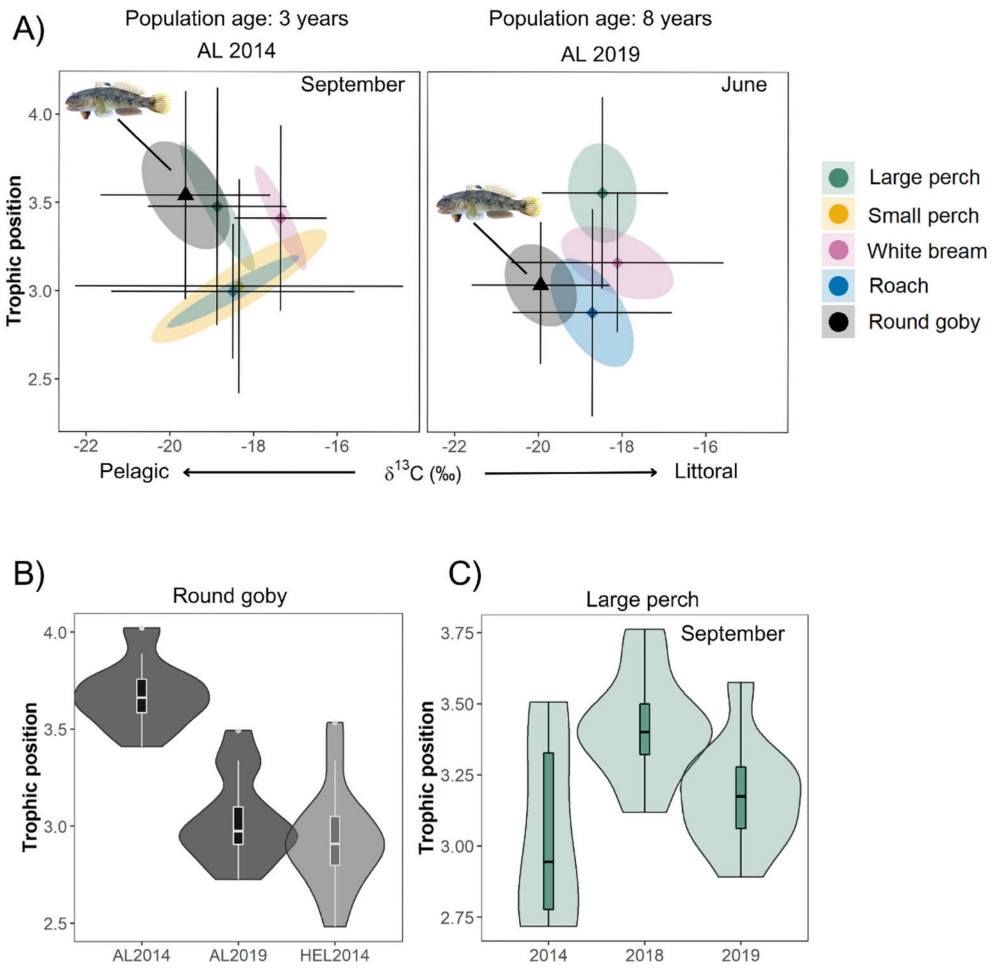

*Figure 5. Trophic position and stable isotope values (mean ± 95% CI) of carbon for A) the fish community sampled in Mariehamn (AL) in 2014 and 2019. Ellipses represent a 40 % confidence interval, encompassing the core isotopic niche. Trophic position compared between B) years (2014, 2019) and areas (AL, HEL) for round goby and C) years for large perch (> 20 cm) in AL. All data from 2014 is from Herlevi et al., 2018 (**paper I**). Additional data from 2018 and 2019 collected during sampling for **papers II** and **III**. In B) round goby from AL 2019 were collected in June (same as right panel in A), while all perch in C) were collected in September. Base-line species from the same months were used in each case.*

4.2 Round goby as prey for native fish predators

Round goby has generally been found to be an important prey for fish and bird predators in the Baltic Sea, in areas where it is established (Almqvist *et al.*, 2010; Oesterwind *et al.*, 2017; Rakauskas *et al.*, 2020). In **paper II**, we show that round goby is also an important dietary component in two, previously unstudied, Baltic Sea areas 7-11 years after the first observations. Most predators in the Baltic Sea are generalist opportunist predators, adapting their diet to the seasonally varying prey abundances and thus preying on the locally most abundant prey (Mattila and Bonsdorff, 1988). This behavior was also observed with regards to cod, pike, and perch predation on round goby, as they predominantly fed on the round goby in a year with high round goby population abundances, although the response to round goby environmental abundances varied between areas and species. The two larger, more piscivorous predators, cod, and pike in KK (where round goby was more abundant; Fig. 3d) showed the strongest response to high round goby abundances. Round goby occurred in up to 100% of stomachs and constituted up to 88% of the total diet volume proportion for cod, while for perch it constituted a maximum 46 % of the diet in volume proportions (averages for both areas shown in Fig. 6). Perch predation on round goby was rather low compared to other studies in the Baltic Sea, while conversely cod predation was relatively high (Almqvist *et al.*, 2010; Liversage *et al.*, 2017; Rakauskas *et al.*, 2020). Whether this is a result of the region specific abundances of round goby, densities of other prey or inter- and intraspecific competition in predator populations remains a subject for future studies. However, we were able to detect some species-specific differences in the importance of other factors such as predator size, general feeding habit and round goby abundances explaining predators' tendency to consume round gobies. For perch, predator size was the most important factor explaining predation, as larger perch fed more on the round goby. The differences between species are also related to main feeding habitat. Cod diet in AL was very similar in both years, mostly dominated by the benthic isopod *Saduria entomon*. This diet reflects feeding in deeper offshore environments (Casini *et al.*, 2016; Haase *et al.*, 2020; Neuenfeldt *et al.*, 2020). In deeper areas prey availability is less varied between years and round goby is not generally found in the summer season (Behrens et al., 2022). However, the DNA analysis, which captured the unidentified fish material in predator diets, showed that round goby may be an occasional diet item in cod diet also in this area. Thus, feeding habits, main feeding environment, body size and environmental abundance of round goby are three important factors explaining round goby importance in predator diets.

As shown previously for cod and perch in the southern Baltic Sea (Almqvist *et al.*, 2010; Rakauskas *et al.*, 2020), we found that when round goby becomes abundant, the predators exhibited more specialized feeding with lower prey richness and a higher degree of piscivory. The diet proportion of especially crustaceans and planktivorous fish was lower at high round goby abundances (Fig. 6). This shift in predator diets thus seems to be consistent throughout the round goby's established range in the Baltic Sea. However, we also showed that the relative weight of ingested prey did not increase with round goby abundances, indicating replacement of other prey, but not higher overall food intake. The high importance of round goby in the diets of native fish predators may thus modify indirect interactions between round goby and native prey species in invaded coastal communities and shifts the energy flow to primarily benthic food sources, compared to a more mixed benthic-pelagic diet when round goby is absent or less abundant in the predators main feeding habitat (Fig. 6).

The change from a mixed, mostly crustacean-based diet prior to round goby establishment, to a more piscivorous round-goby dominated diet has also been shown as an increase in trophic level of perch (Almqvist *et al.,* 2010). When comparing the trophic position of large perch in 2014 (**paper I**) to data from 2018 and 2019 in AL, we saw an increase in trophic position for perch (Fig. 5c). We can thus deduce that as suspected, round goby was likely not an important prey for perch 3 years after its establishment (2014). However, 4 years later, round goby became an important prey item in the diet of perch, increasing the consumption of fish prey (**paper II**). This also shows as an increased trophic position of large perch, which follows the level of consumption of round gobies (i.e. highest TP in 2018; Fig. 5c). An increased trophic level may result in increased condition and growth rate (Hempel *et al.,* 2016), but such effects should be further investigated in the Baltic Sea predator populations.

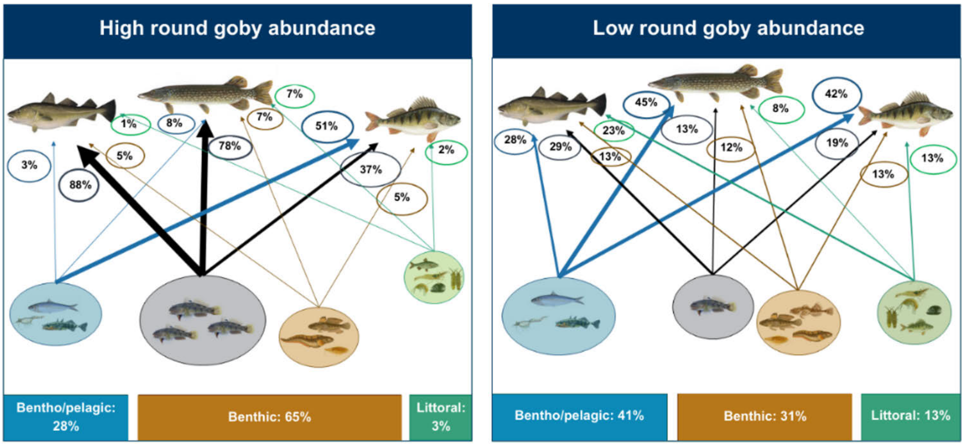

Figure 6. Predator diets summarized for shallow coastal areas (KK: cod, pike, perch, AL: perch, pike) according to the environmental abundance of round goby. The thickness of the arrows reflect the relative importance of prey groups in predator diets and colored bars at the bottom reflect the total share (volume proportion %) of prey items categorized according to their main living environment depicting the change in predator diets.

4.3 Impacts of round goby on fish community structure and diversity

In **paper III**, we show that the influence of round goby on fish community taxonomic and functional structure and diversity is dependent on the abundances of the round goby and whether the effects are measured on the whole fish community (including pelagic migratory fish) or the more stationary littoral species. When round goby abundances were high in 2018, it constituted up to 82 and 87 % of the total and littoral fish community biomass, respectively (mean= 36 and 44% in *High 2018* group). Round goby generally increases taxonomic and functional richness (FRic: volume of the functional trait space), with highest richness found at intermediate to low round goby abundances (*High 2019;* Fig. 7a,b). Moreover, it contributed to increased diversity in terms of increased proportion of extreme trait combinations (concentrated towards the edge of the functional space; Spe; Fig. 7a). As such, it contributes to the diversification of the overall shallow coastal fish communities through increased species richness and influence of distinct trait combinations. However, in the littoral fish community, native fish abundance, biomass, and species as well as trait richness was generally low at highest round goby abundances (*High 2018*) and round goby contrastingly decreased measures of trait distribution in multivariate space, as well as the proportion of specialization along a round goby abundance gradient (FSpe; Fig. 7b). This indicates that within the littoral fish community round goby instead increased redundancy, in terms of the proportion of generalist traits (close to the center of multivariate trait space), despite increasing species and functional richness. However, highest round goby abundances (*High 2018*) were also associated with overall lower native fish richness and abundances compared to the same sites the following year, when round goby abundances were lower (*High 2019*, **paper III,** Fig. 7a,b). As temperature was also shown to affect fish community composition, it cannot be ruled out that this effect was mainly driven by temperature, instead of increased competition and displacement effects of high round goby abundances. Nevertheless, such habitat displacement has been demonstrated before for e.g. flounder (Karlson *et al.,* 2007), and may therefore partly explain the low native demersal fish abundances and richness observed in 2018 (**paper III).**

The most obvious differences in community composition between round goby impact groups was a shift between a roach and cyprinid dominated (*High 2019*), to round goby dominated littoral fish community (*High 2018*). The effects of such a shift, whether it be related purely to environmental factors or also to resource competition, could be manifested in reduced abundances of Hydrobiid gastropods and bivalves (Henseler *et al.*, 2021) which are a main food item of the demersal round goby in this northern Baltic population (Wallin Kihlberg *et al.,* 2023; Fig 4;Fig. 5). While roach also feed readily on bivalves (Lappalainen *et al.*, 2001, 2004), they are more flexible in their habitat utilization (demersal-pelagic vertical position; Fig. 7c) and highly generalist in their diet (**paper I**; Fig 5a; Hayden *et al.,* 2014). The shift from roach to round goby dominance at the high impact sites between years was also related to e.g. fecundity and longevity, with a shift from more long-lived high fecundity species (roach), to a short-lived round goby with lower fecundity (number of eggs per year), but high parental investment (nest-guarding; Fig. 7c). These traits thus mostly reflect species ability to cope with environmental change and perturbations, and may explain why round goby has been able to establish in this area of high human impact and modified habitat (Mariehamn harbor basin), as well as its high abundances in 2018. This supports the conclusions of Vivó-Pons *et al.,* (2023b), who found that parental care and territorial behavior were the most distinctive traits of the round goby compared to native fish in the Baltic Sea, and these traits most likely contribute to the successful establishment of the round goby. Non-native species may thus successfully establish by displaying only a few distinctive traits allowing them to colonize partly vacant niches, while retaining a certain degree of similarity with the natives (Vivó-Pons *et al.,* 2023a, b).

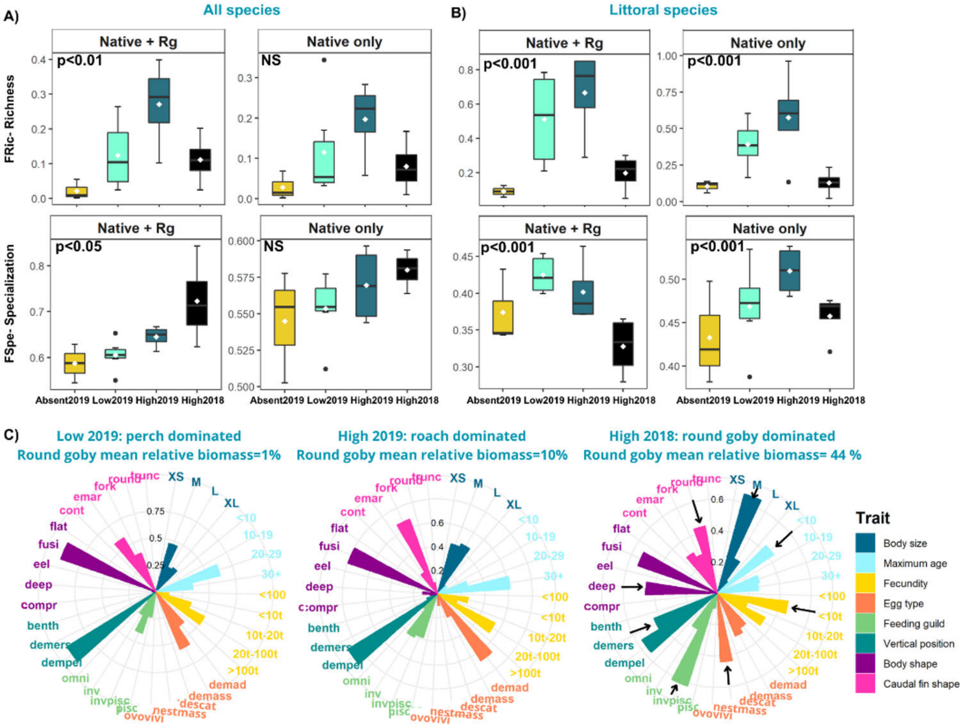

Figure 7. Functional diversity indices shown for A) all species (including pelagic migratory fish) and B) littoral species both including (Native + Rg) and excluding (Native only) the round goby. P-values indicate significant differences between impact groups. FRic= volume of the multivariate trait space, Fspe= proportion of traits (weighted by species relative biomass) located at the edges of the trait space. C) Community biomass weighted mean trait values of littoral fish in different impact groups (continuous traits expressed in categories). Arrows in High 2018 indicate traits expressed by the round goby.

Low species richness and relatively simple food web structures are often regarded as more vulnerable to change, compared to more complex food webs with more complementarity in species and functions (Poisot *et al*., 2013; David *et al*., 2017). Functional redundancy, i.e. the concept of several species contributing with similar traits or ecological functions in a community, is regarded as a key aspect in the buffering capacity that biodiversity brings against species loss and environmental change (Fetzer *et al.*, 2015; Aslan, 2019). Therefore, novel species such as the round goby could increase resilience in low diversity communities by both providing a seasonally abundant prey resource (**paper II**), but also by increasing taxonomic and functional diversity in littoral habitats (**paper III**). However, the overall taxonomic and functional diversity was highest at low to intermediate round goby abundances (*High 2019*), while native species richness and functional diversity were lower when round goby became dominating (Fig. 7). Positive effects for overall biodiversity are therefore strongest at low to intermediate round goby abundances. Data on round goby abundances from the three populations suggest that the high abundances as seen in 2018 are not permanent (Fig. 3), and therefore an increase in taxonomic and functional diversity is more likely in the long term.

4.3.1 The influence of environmental drivers

Non-native species abundances are often thought to be higher in areas with low native species richness (Case, 1990; Levine and D'Antonio, 1999). In the case of the round goby in the Baltic Sea, this does not seem to be the case, as the abundances and distribution range of the round goby is higher in the two southern Baltic populations, where productivity and both taxonomic and functional diversity is higher (Table 1; Törnroos *et al.,* 2015; Koehler *et al.,* 2022). Even on a local scale, sites where round goby was present, native species richness was higher compared to sites where round goby was absent (**paper III,** Fig. 7).

Round goby presence has also been shown to correlate negatively with environmental factor such as wave exposure both on a local (Florin et al., 2018) and regional scale in the Baltic Sea (Kotta *et al.*, 2016; Holmes *et al.*, 2019; Liversage *et al.*, 2019). In **paper III** we identify a similar pattern, as round goby abundances were lowest at the most exposed sites. The relatively slow dispersal in the Åland population compared to the two other populations may thus be due to the relatively high exposure southward, outside the shallowest bays where round goby is established (**paper III;** Government of Åland, 2021). Additionally, a relatively low propagule pressure, as evidenced by low genetic diversity in the Mariehamn population (Green *et al.*, 2023) from other populations could further contribute to slow secondary spread. Kornis *et al.,* (2013) and Coulter *et al.*, (2015) found that higher round goby abundances were associated with sites showing high productivity and species richness. Moreover, on a smaller scale, higher adult and juvenile round goby abundances have been found to be associated with habitats of higher structural complexity in terms of either vegetation, rocks or artificial structures (Sapota and Skóra, 2005; Bauer *et al.*, 2007; Brownscombe and Fox, 2012; Henseler *et al.,* 2020). These observations, together with our results indicate that both on a local and regional scale, round goby may reach the highest densities in areas where biological productivity and species richness is higher, which on a local scale may further be associated with habitats of higher structural complexity (sheltered habitats with more vegetation, **paper III**). Such areas provide e.g. shelter from predation (Liversage *et al.,* 2017) and nesting sites, as well as a potentially larger resource base for both native and non-native species to co-exist (Melbourne *et al.,* 2007).

Even other environmental factors, such as temperature is likely to affect the abundance of both round goby and other fish species. Round goby, originating from the Black Sea, is thought to prefer warmer temperatures (Kornis *et al.,* 2012), and has high thermal tolerance (Christensen *et al.*, 2021). It has been found to mainly occupy habitats and depths with the warmest temperatures in each area or season (Kornis *et al.*, 2013; Behrens *et al.*, 2022). Therefore, it could be expected that the highest abundances are found at sites with the highest temperatures. However, in **paper III**, round goby abundances, and thus its relative contribution to community biomass composition, varied from very low (< 5 %) at high temperatures (> 15 degrees), to very high (> 80 %) at lower early summer temperatures (< 10 degrees). Our observations of a drop by nearly 90% in round goby abundances from 2018 to 2019 (Fig. 5d; **paper II, III**) coincide with observations of a marine heatwave in the summer of 2018, (Paalme *et al.*, 2020; Kraufvelin, 2021) followed by a disease outbreak in the round goby population (own observations). As the incidence of such heat waves are projected to increase due to climate change (Oliver *et al.*, 2019), the local abundances of the round goby are likely to also show strong variation between seasons and years in the future (Reid and Ricciardi, 2022). This indicates that the influence of the round goby on the local fish and benthic community structure and diversity will vary accordingly due to variation in environmental conditions, such as temperature together with other biotic and abiotic structuring factors such as native species richness, intra-specific competition, predation pressure and habitat characteristics (**papers I-III**).

4.4 Implications for trophic interactions and species dynamics in coastal food webs, now and in the future

Research from the Great Lake-region suggests that in areas where the round goby is abundant and even a dominating benthic fish, it may cause a restructuring of the whole food web as the energy flows are altered and new links between the benthic realm and top predator are created, substituting the previous mainly pelagic energy pathway (Vanderploeg *et al.*, 2002; Johnson *et al.*, 2005). Some indication of this has also been seen in the Baltic Sea as the round goby has become a main prey item for predators such as cod, utilizing both benthic and pelagic food sources (Almqvist *et al.,* 2010, Rakauskas *et al.,* 2020). The results of this thesis also corroborate these findings, and I show that this is the case also in other areas of the Baltic Sea during years or seasons where the round goby occurs abundantly (**paper II**).

When the round goby constitutes the main item in predator diets', it simultaneously substitutes native species (e.g. three-spined stickleback, *Gasterosteus aculaetus* and native gobiids) in predator diets (**paper II**). This could thus lead to relaxed predation pressure on these native species (Hempel *et al.*, 2016; Liversage *et al.*, 2017), but also relaxed competitive interactions with the round goby. For instance three-spined stickleback and sand goby (*Pomatoschistus minutus*) show some isotopic niche overlap with the round goby in Lithuanian coastal areas in spring (Rakauskas *et al.*, 2020). A recent, pan-Baltic increase in three-spined stickleback abundances has also been attributed to predation release, due to lower predatory fish abundances, together with more favorable environmental conditions due to climate change and eutrophication (Eklöf *et al.*, 2020; Olin *et al.*, 2022). The results of this thesis give a further indication of how the round goby could contribute to this predation release on native mesopredators, such as the three-spined stickleback in years of high round goby abundances, when the coastal predatory fish mainly feed on the round goby. Predatory fish are important regulators of ecosystem health and dynamics in the Baltic sea (Eriksson *et al.*, 2009; Östman *et al.*, 2016). Whether a potential predation release could lead to further negative feed-backs on native predator recruitment (Donadi *et al.*, 2020) and population development needs to be further investigated using larger datasets on both round goby and stickleback abundances as well as predator densities and diets.

Several studies from North American lakes have, however, reported positive effects of increased predation on round goby on predator growth rates (Steinhart *et al.*, 2004; Crane *et al.*, 2015; Brooking *et al.*, 2022), despite decreased availability of invertebrate prey, similarly to what has been deduced from the Baltic Sea (Liversage *et al.,* 2019). Indications of increased growth rate and condition factor for pike-perch (*Sander lucioperca*) in the Kiel Canal (southern Baltic Sea) have been observed, post round goby establishment (Hempel *et al.*, 2016). Which effects the increased reliance on round goby as prey has on the growth and reproductive output of fish predators, specifically in the Baltic Sea, should be determined in future studies, as previous studies in other ecosystems have found mixed results (reviewed by Hirsch et al., 2016).

Furthermore, in many Great Lakes regions where round goby has been established for a similar period of time to the Baltic, round goby populations have started to stabilize (Bajer *et al.*, 2019). Some indications of such an effect can also be seen in the Baltic Sea, as recent studies (including data in my thesis) have reported rapid declines followed by stabilized population sizes, after the initial population growth (Kruze *et al.*, 2023; Lewin *et al.*, 2023). In the Great Lakes, this effect has partly been attributed to natural control by native predators (Madenjian *et al.*, 2011; Burkett and Jude, 2015; Bajer *et al.*, 2019). Such evidence is scarce from the Baltic Sea (but see Hempel *et al.,* 2016), and some have suggested that predation by the most abundant coastal predators (perch; Liversage *et al.,* 2017) is not enough considering the poor state of many predator populations in the Baltic Sea. As the population abundances of especially cod and pike show mostly negative population trends in the Baltic Sea (Olsson, 2019; ICES, 2023), there is a need to establish what effects the observed changes in their diet have on the fitness and population growth of these predators. Simultaneously, the potential for predator control of round goby populations by all fish and avian predators combined should further be investigated (Ojaveer *et al.*, 2015b; Oesterwind *et al.*, 2017).

The fluctuations in population abundances of round goby reported in this thesis may also become more pronounced due to climate change induced heatwaves and disease outbreaks (Reid and Ricciardi, 2022). The rapid decreases after initial population increases reported recently for round goby are typical for introduced species' populations (Strayer *et al.*, 2017). This can be a sign that the carrying capacity of the environment has been reached and the population abundances will stabilize in the future. However, round goby also displays distinct seasonal migration patterns from shallow (<25m) coastal waters in spring and summer, to deeper waters (up to 90m) in autumn and winter (Behrens *et al.,* 2022). This migration pattern also entails coupling of the shallow and deep-water ecosystem compartments. This signifies that on one hand, the impacts of round goby on native species in shallow and deep waters, respectively, are likely to be seasonal, but on the other hand it also entails that the impacts are not limited to the shallow coastal areas, where most studies are conducted, but can extend to deeper areas as well (Andres *et al.*, 2020). Thus, future studies should also strive to include the complete yearly depth range of the round goby to assess how strong of an influence it has on the entirety of the Baltic Sea ecosystem and estimate how large the transfer of biomass from shallow to deep areas is.

Ecosystems are dynamic, not static, and thus change is a natural part of ecosystems processes. Intrinsically, change is neither positive, nor negative, but we as humans assign value to it. Arguably, some change can also be negative from an ecosystem perspective, if communities become less diverse and more homogenous, leading to a loss of critical ecosystem functions and resilience (Oliver *et al.*, 2015; Aslan, 2019; Biggs *et al.*, 2020). Often, the response to increased fluctuation in environmental conditions (e.g. due to climate change or eutrophication) is a rise in generality, i.e. a subset of generalist species become increasingly abundant in ecosystems, while specialized species become rare (Clavel *et al.*, 2011; Aslan, 2019). This has already been sown to be a trend in the Baltic Sea, where significant changes in the rates of novelty in abiotic conditions since the 1980's has led to novel species assemblages, from phytoplankton to fish (Ammar *et al.*, 2021). From a food web and functional perspective, this has been seen as increased species richness, generalist feeding and benthic fluxes (Törnroos *et al.*, 2019; Kortsch *et al.*, 2021). I also demonstrate similar patterns on a local scale in a northern Baltic coastal fish population, where round goby is established, i.e. increased species and functional richness, but decreased specialization in the littoral community (**paper III**). Furthermore, at sites where round goby was abundant, the importance of traits related to faster generation cycles (lower maximum age) and increased offspring survival (parental care, nest guarding) were more pronounced, highlighting aspects of the species ecology making it tolerant to environmental change. This may be an advantage also in the future. Thus, it is to be expected that non-native species with suitable generalist traits and high plasticity for environmental conditions, such as the round goby, become increasingly abundant, which in turn can contribute to changes in overall food web dynamics and energy fluxes (Kortsch *et al.,* 2021). A future avenue of research in the Baltic Sea could thus be to explore if communities and species interactions have become more homogenized across the Baltic Sea over time, specifically due to the increased number of widely established NIS with significant food web effects (Ojaveer *et al.*, 2021), and which implications this has for food web stability.

5 Conclusions

5.1 Key findings

Together, the three papers in my thesis elucidate the role of the round goby as predator, competitor and prey in coastal communities as well as which factors contribute to the observed impacts of the integration of this species in coastal fish communities. My results in different areas and stages of invasion further our understanding of the ecological implications of recent invasions at regional and pan-Baltic levels. Specifically, the round goby's integration into coastal food webs and impacts on native species can be seen in Baltic Sea populations in the following ways:

i) Round gobies show a generalist trophic niche and preys on the locally dominant prey. To some extent, it also uses resources that are not fully utilized by other benthic-feeding fish (**I**)
ii) Its food web position, local effects on native biota and the strength of trophic interactions are mediated by local round goby population abundances and environmental conditions (**I**-**III**), which in turn also affect the availability of prey and both intra- and interspecific competition (**I**, **II**)
iii) they are readily preyed on by locally abundant coastal fish predators, especially at high round goby abundances (**II**)
iv) round goby population abundances vary between areas and years, and are affected by local environmental conditions (**II**, **III**)
v) round goby presence increases both taxonomic and functional richness of the fish community, but also the proportion of generalist traits in the littoral community. Displacement effects on native benthic fish may arise when round goby dominates the fish community (**III**)

The Baltic Sea ecosystem has faced many types of human mediated external disturbances, and species introductions are one such example. Round goby is another piece in the puzzle that has already changed shape due to many additive human activities (Reusch *et al.*, 2018; Viitasalo and Bonsdorff, 2022). The round goby is now an integrated part of the Baltic Sea ecosystem in many areas and may be regarded as both a threat and a resource, depending on the species in focus and the values we ascribe to these species. Nevertheless, in the most species poor communities round goby increases both taxonomic and functional diversity which can ultimately increase ecological stability through increased redundancy (Aslan, 2019). In the best-case scenario, round goby thus contributes to increased community stability in the important coastal areas by increasing diversity and expressing traits (e.g. demersal life style, generalist molluscivorous feeding) that may have decreased due to the declining abundances of previously more abundant benthic species such as flounder (Jokinen *et al.*, 2019). Providing food security to important coastal top predators is in itself is also an ecosystem service that we need to learn to take advantage of. Although potential negative impacts on lower trophic levels and especially suspension feeding bivalves (Skabeikis *et al.*, 2019; Nõomaa *et al.*, 2022), with potential cascading effects (Skabeikis *et al.,* 2019), should not be ignored, round goby may become a key player for increased benthic-pelagic coupling and food web stability under future conditions with increased variation in environmental conditions, especially in areas of low native demersal species richness.

5.2 Future directions and management considerations

Many questions still remain unanswered, and more studies are needed to answer e.g. whether the high dietary proportion of round goby in predator diets is simply a manifestation of predatory fishes opportunism and high consumption of the most available prey species, or is it a result of the lack of other prey items due to direct predation by round goby (mollusks or crustaceans, as suggested by Ustups *et al.,* 2016), indirect competition for space (Karlson *et al.*, 2007; Rakauskas *et al.*, 2013) or is it a true preference for the round goby as prey. With this increased piscivory of predators in mind, future studies in the Baltic should also look more into changes in predator fitness, in terms of growth rates and fecundity, in areas with high round goby abundances. Or could round goby predation on fish eggs and invertebrate prey outweigh the potential positive effects on predator populations and lead to predator-prey reversal? Furthermore, the continued population expansion of the round goby could lead to a homogenization of coastal communities and as an extension predator diets and food web structure across Baltic Sea regions. As such we could see a stronger coupling of the benthic and pelagic compartments and a shift from pelagic-dominated to more benthic-sourced food webs. What effects will this have for food web structure and stability?

Round goby abundances have been shown to be highest in disturbed areas, such as near ports (Kotta *et al.,* 2016) and the occurrence in protected areas is relatively low (Holmes *et al.*, 2019). Thus, the strongest effects of round gobies on native biota are likely seen in areas that are already affected by human disturbances. This indicates that continued work for protecting marine (pristine) habitats and promoting healthy ecosystems as a whole, including predator fish populations, is pivotal to ensure diverse coastal communities. These should provide more resistance to negative effects of anthropogenic change (including invasive species). While preventing primary introductions and further secondary spread of round gobies and other NIS, especially into insular freshwater systems, is essential, we as humans also need to adapt to the presence of this new species. The increased use of round goby for human consumption or resource for industry and fisheries would enhance its ecosystem service value to us humans, while also potentially hampering population increases and further spread. Although often advocated by scientists and managers, this is still poorly implemented in most countries around the Baltic Sea.

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Implications of the Integration of a Non-Native Fish into Coastal Communities

This thesis explores how the non-native round goby (*Neogobius melanostomus*) integrates into coastal fish communities in the Baltic Sea, and which factors affect the observed community-level responses in terms of trophic interactions as well as taxonomic and functional diversity.

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