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**Rapid Communication**

# Habitat expansion of the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea: potential consequences for the eelgrass food web

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## Abstract

Since at least 2009, the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) has been spreading in the northern Baltic Sea, an area with no native crab species. Thus far, this species has invaded muddy and rocky coastal areas, especially shallow habitats dominated by reeds and the brown macroalga *Fucus vesiculosus* Linnaeus, 1753. Here, we document the first sighting and recruitment of mud crabs in an eelgrass *Zostera marina* Linnaeus, 1753 meadow - a critically important habitat for fish and invertebrate species. We found both adult and juvenile mud crabs in repeated sampling over the summer, suggesting continuous use of eelgrass as habitat for mud crabs and recruitment into the meadow. Given the simple food web structure of the Baltic Sea, this novel predator could lead to new energy pathways with unexpected consequences and potentially important effects on the functioning of the native eelgrass community.

**Key words:** mud crab, invasive species, establishment, *Zostera marina* Linnaeus, 1753

## Introduction

Native to the eastern coast of North America, the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) has successfully invaded fresh and brackish waters around the world including: the Baltic Sea; the Caspian Sea; estuaries in Italy, Japan and Brazil; freshwater lakes in Texas; and the Panama Canal (Grosholz and Ruiz 1996; Mizzan and Zanella 1996; Iseda et al. 2007; Roche and Torchin 2007; Rodrigues and D'Incao 2015). Very little research has been conducted on its ecological impacts in invaded areas, but there is some evidence that it competes with native crab and benthic fish species, preys on native invertebrates, and can be preyed upon by native fishes (Roche and Torchin 2007; and references therein). Although present in the southern Baltic Sea since the 1950s or earlier (Turoboyski 1973), the species more recently expanded northwards and was first recorded in the northern Baltic Sea in the Finnish Archipelago Sea in 2009 (Fowler at al. 2013). At the same time, it also expanded to other areas of the Baltic including the Gulf of Riga, potentially representing multiple invasions (Kotta and Ojaveer 2012). In the following years, *R. harrisii* has spread to >80 sites within a 30 km radius, but has so far remained confined to shallow (<2 m), sheltered areas within the inner and middle Archipelago Sea (Fowler et al. 2013). However, it is known to inhabit deeper depths (up to 20 m) in its native habitat and other invaded areas such as the southern Baltic Sea (Hegele-Drywa and Normant 2007), suggesting it is not necessarily limited to shallow areas.

Invasive crabs have had well-documented effects on biodiversity and ecosystem functioning around the world (e.g., Grosholz and Ruiz 1996; Griffen and Byers 2009), and these impacts are particularly important in systems characterized by low functional redundancy, i.e. few species per functional group (Thomsen et al. 2014). Given the low biodiversity and lack of native crab species in the northern Baltic Sea (due to its low salinity: 5–7 in the Archipelago Sea area), the Harris mud crab could induce important changes in the coastal ecosystem.

Its rapid maturation (0.5 years; Turoboyski 1973) and tolerance to a wide range of salinities and temperatures (0.5–40 psu and 0–34 °C, respectively; Costlow et al. 1966; Forward 2009) also make it an ideal invader.

In its native range, the Harris mud crab is mainly found in estuarine, soft-bottom, habitats, sheltering in woody debris or oyster beds (Turoboyski 1973; Everett and Ruiz 1993; Nurkse et al. 2015). Possibly due to the lack of other crab competitors, in the northern Baltic Sea it has been found to occupy a wide variety of shallow (<2 m depth) muddy and rocky near-shore habitats, though it especially seems to prefer loose-lying or attached bladderwrack *Fucus vesiculosus* Linnaeus, 1753 stands (Nurkse et al. 2015; authors' pers. obs.). This is of particular concern, given *Fucus* is the main habitat-forming macroalgae in the northern Baltic Sea (Kautsky et al. 1992). Crab-induced community shifts in *Fucus*-associated communities could have significant impacts on ecosystem biodiversity and functioning.

In this early stage of the invasion, research into potential impacts on the native community functioning is only beginning. Thus far, studies of mud crab stomach contents in the southern Baltic Sea have reveal that they are omnivores consuming a mix of detritus, green algae, and invertebrates. The common invertebrate prey include amphipods, bivalves, and polychaete worms (Turoboyski 1973; Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009). Recent experiments in the northern Baltic Sea show Harris mud crabs readily consume isopods (Forsström et al. 2015). In the field, experiments have also shown shifts in meiobenthic communities in unvegetated habitats (Lokko et al., in press), as well as a decrease in *Fucus*-associated mesograzers, including isopods, amphipods, and gastropods (Jormalainen et al. 2016), potentially leading to trophic cascades.

Until now, exposed, sandy, eelgrass *Zostera marina* Linnaeus, 1753 meadows along the Finnish coasts were not considered to be potential habitats for Harris mud crabs, and to our knowledge no records of invasion into eelgrass meadows exist. However, eelgrass meadows are potentially suitable as they provide a complex three-dimensional habitat supporting diverse epifaunal and infaunal communities (e.g. Boström and Bonsdorff 1997; Boström et al. 2006). Because the shoots attenuate waves and stabilize sediments, eelgrass meadows act as particle traps creating sediments rich in organic matter and detritus. As such, they are a critically important habitat, and biological invasions in seagrass ecosystems across the world have been shown to have multiple, negative, impacts on the original community structure and functioning (Williams 2007).

In this paper, we report the first findings of mud crabs inhabiting and successfully recruiting into eelgrass meadows in the northern Baltic Sea (Archipelago Sea, Finland), and discuss potential consequences for the associated community.

## Study site and methods

The invaded site is a semi-sheltered bay in the outer Archipelago Sea (Ängsö, 60°06'31"N; 21°42'45"E; Figure 1). The site includes both dense *Fucus vesiculosus* beds in shallow rocky areas (0–2 m deep) and a ~7-ha *Zostera marina* meadow interspersed with sandy patches at 2.5–5 m depth. Experiments and sampling have taken place in the meadow and the surrounding area since 2004; consequently, the associated epifauna, infauna, and fish species assemblages, as well as the trophic network, are well known (Boström et al. 2006; Gustafsson and Boström 2009, 2014; Duffy et al. 2015). In summer 2015, several different experiments took place within the *Fucus* and *Zostera* habitats of this site, and included collecting epifaunal samples from the various habitats. In early July, 10 epifaunal samples were taken from both *Fucus* and *Zostera* beds. More intensive sampling took place in early September, when epifaunal samples were taken from 42 *Zostera* plots covering the full range of eelgrass shoot densities (20–400 shoots $m^{-2}$) and an area of about 800 $m^2$.

In all cases, we collected epifauna by quickly placing a 100-µm mesh bag around the *Fucus* thalli or *Zostera* shoots, cutting the thalli/shoots at the base, and then tying the bottom of the bag to prevent animals from escaping. The bags had an opening diameter of ~20 cm, thus each sample covered an area of approximately 0.03 $m^2$, allowing us to estimate the density of invertebrates. Similar methods of epifaunal sampling in seagrass meadows have previously been used world-wide (e.g. Connolly 1995; Baden and Boström 2001; Deegan et al. 2002; Arponen and Boström 2012). The samples were then carefully rinsed and weighed, and associated epifauna was sorted and identified to species or genus level. In addition, five baited plastic minnow traps (50 × 25 × 25 cm, with mesh size of 5 mm) were deployed for 24 h in the meadow during late June and early August to determine the presence of mesopredators (both fishes and crustaceans).

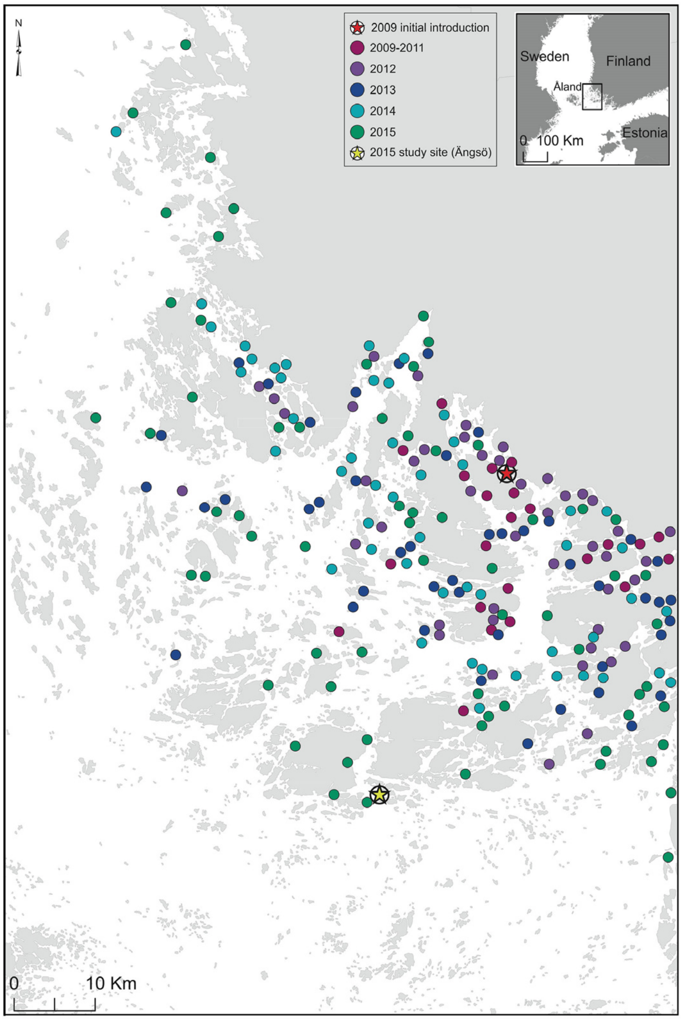


**Figure 1.** Approximate location of initial sighting of mud crabs in the Finnish Archipelago Sea in 2009 (red star), subsequent sightings (coloured circles indicate year of sighting; red: 2009–2011, violet: 2012, dark blue: 2013, light blue: 2014, green: 2015), and our study site Ängsö (yellow star). Map based on data from Fowler et al. 2013, Finnish Biodiversity Information Service – FinBIF 2016, and personal observations (see also Table 1 for details of the sampling in Ängsö).

**Table 1.** Summary of mud crab sampling efforts and results at Ängsö, northern Baltic Sea, June-September 2015. Size (carapace width) and sex of specimens was not recorded for all sampling periods. Each epifaunal sample represents an area of 0.03 $m^2$. Densities were not calculated for mud crabs caught in minnow traps.

| Date | Sampling method | # of mud crabs | Density of mud crabs ($m^{-2}$) | Size (mm) | Sex |
|---|---|---|---|---|---|
| 25 June – 2 July | Epifaunal collection (non-quantitative) | 2 | - | adults 10–12 | male |
| 30 June | Minnow traps in *Zostera* (n=5) | 0 | - | - | - |
| 2 July | Epifaunal sampling in *Zostera* (n=10) | 1 | 3 | adult | - |
| 2 July | Epifaunal sampling in *Fucus* (n=10) | 1 | 3 | adult | - |
| 5 August | Minnow traps in *Zostera* (n=5) | 2 | - | adults 20, 21 | - |
| 3 September | Epifaunal sampling in *Zostera* (n=42) | 8 | 6 | juv. 1–3 | - |

## Results and discussion

In late June and early July 2015, non-quantitative epifaunal collection from the eelgrass meadow revealed the presence of adult Harris mud crabs (two males – carapace width of 10–12 mm; Table 1). Another adult was found during the epifaunal sampling in July from *Zostera* (along with one in the *Fucus)*, suggesting an adult density of ~3 $m^{-2}$ in the eelgrass meadow. Two more adults were then found in the minnow traps in August (carapace widths: 20 and 21 mm; Table 1). During the intensive sampling in early September, eight mud crab recruits (carapace widths: 1–3 mm) were found in 6 out of 42 plots giving a potential density of recruits of ~ 6 $m^{-2}$ (Table 1). Harris mud crabs are known to burrow in sediment, whereas we only sampled the above-ground eelgrass biomass, thus the densities above are likely underestimations.

While this is one the farthest recorded sightings of *Rhithropanopeus harrisii* from its initial introduction point in Finland (~45 km SE from the initial sighting; Fowler et al. 2013), its presence in *Fucus* in this area is not surprising given the high dispersal potential possible due to its long planktonic phase (20–30 days in low-salinity cold waters; Christiansen and Costlow 1975) and the high boat traffic (both commercial and recreational) in the Archipelago Sea, which could promote local spread. Similarly, public sightings of the Harris mud crab in summer 2015 confirmed its spread both southwards and northwards outside of the Archipelago Sea (public sightings recorded through the Finnish Biodiversity Information Facility FinBIF). Most notably, this is the first recorded instance of mud crabs in eelgrass meadows in its invasive range (although it can be found in eelgrass in its native range; JM Hanson, Gulf Fisheries Centre, Moncton, NB, Canada, pers. comm.), and deeper than previous sightings along the Finnish coast. A vertical expansion could be expected as mud crabs can be found at >10 m depths in the southern Baltic Sea (Hegele-Drywa and Normant 2014), and there are no competing crab species. However, food could be limited in deeper waters in the northern Baltic Sea due to high turbidity and decreased algal habitat (Torn et al. 2006).

A single finding of one or two adult specimens in the meadow could be regarded as accidental, but the persistent presence of adults throughout the summer, and the collection of multiple juveniles in the autumn suggests successful establishment in one or both macrophyte habitats and adjacent areas. It is highly likely that the *Fucus*- and *Zostera*-associated populations of Harris mud crabs within the bay are connected due to the short distance between them (20–30 m, separated by sand. The continuous range expansion and population growth in the Archipelago Sea since introduction in 2009 (Figure 1) also suggests that the Harris mud crab population will continue to grow in both the *Fucus* and eelgrass habitats. Globally, crabs are an ubiquitous part of the eelgrass fauna and play an important role as mesopredators (Moksnes 2002). Moreover, the patch complexity and broad-scale structure of the seagrass landscape are known to promote settling and recruitment of a number of pelagic larvae including crab species (Boström et al. 2010), likely facilitating the invasion of eelgrass meadows. In addition, the lack of competing crab species in northern Baltic eelgrass meadows may further facilitate its expansion in this habitat, and lead to a shift in community structure and function.

Stable isotope analysis of mud crabs from *Fucus* and reed habitats along the Finnish coast reveal that large adult Harris mud crabs (>12 mm) have isotopic signatures similar to secondary consumers such as fish, while smaller crabs are more similar to primary consumers (Aarnio et al. 2015). In rocky shore habitats, the presence of Harris mud crabs has led to shifts in community structure, most notably a pronounced decrease in *Fucus*-associated amphipod and isopod populations (Jormalainen et al. 2016). In both *Fucus* beds and *Zostera* meadows, the reduction in abundance of mesograzers could then exacerbate the problems of filamentous algal blooms associated with eutrophication and result in a trophic cascade (e.g. Eriksson et al. 2009).

Given the lack of native decapods, low functional redundancy, and simple food web structure in this area (Elmgren and Hill 1997; Boström et al. 2006; Nordström et al. 2010), a rapid invasion and increase of mud crabs into fully or partially empty niches of vegetated soft-bottom habitats will likely increase the predation pressure on important eelgrass mesograzers such as isopods and amphipods. Adult Harris mud crabs are likely to initially complement native intermediate and top predatory fish such as three-spine stickleback (*Gasterosteus aculeatus* Linnaeus, 1758; a meso-predator), perch (*Perca fluviatilis* Linnaeus, 1758; a mesopredator or top predator depending on its size), and ruffe (*Gymnocephalus cernuus* (Linnaeus, 1758); a mesopredator). An increase in the abundance of mesopredators (three-spine sticklebacks) and the subsequent trophic cascades in terms of decreased herbivory, algal overgrowth and massive eelgrass loss has already been demonstrated along the Swedish west coast (Moksnes et al. 2008; Baden et al. 2003; 2010; 2012). Along the Finnish coast, three-spine sticklebacks are also important mesopredators in eelgrass meadows but their impact is limited to a short period in early summer, after which they move offshore (pers. obs). Thus, increased Harris mud crab abundance could lead to a trophic cascade if abundances of grazers on epiphytes are reduced below some as yet unknown threshold. Potentially counteracting this, Harris mud crabs may also constitute an additional food source for epibenthic fish such as perch, roach *Rutilus rutilus* (Linnaeus, 1758), and four-horned sculpin *Myoxocephalus quadricornis* (Linnaeus, 1758) (Fowler et al. 2013; Ovaskainen 2015).

However, predicting impacts in eelgrass meadows based on studies done in rocky algal habitats is difficult due to the distinct natures of the food webs and community structure between the habitats. Further investigation into the ongoing invasion in eelgrass meadows (including sampling of other eelgrass meadows in the northern Baltic Sea) is needed to determine the scale of the invasion. In addition, habitat-specific experiments are needed to determine how Harris mud crabs can affect eelgrass communities and also whether any management actions should be taken.

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