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Introduction of a functionally novel consumer to a low diversity system: Effects of the mud crab *Rhithropanopeus harrisii* on meiobenthos

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A B S T R A C T

The Harris mud crab *Rhithropanopeus harrisii* recently expanded into much of the Baltic Sea. This invasion is expected to have significant effects on the structure and functioning of benthic ecosystems due to the lack of native crabs. Habitat type potentially modulates the effects as crabs are expected to behave differently in different habitats. In this study we experimentally evaluated the effect of *R. harrisii* on the species composition and dominance structure of shallow water meiobenthos within common habitat types of the north-eastern Baltic Sea. Among the studied environmental variables *R. harrisii* had by far the strongest effects on meiobenthos. The effects of *R. harrisii* varied among different habitats with the crab mostly modifying taxonomic composition and species abundances of meiobenthic communities on unvegetated soft bottom sediments. Our experiment also showed that boulders provided shelter for *R. harrisii* and thereby reduced their burrowing activity and effects on the adjacent soft bottom meiobenthos.

1. Introduction

Invasive non-native species are one of the biggest threats to nature as they can alter ecosystems and economies (Simberloff, 2011; Strayer, 2012). This is particularly true to ocean ecosystems, primarily near shorelines where human use is exponentially increasing and diversifying (Galil et al., 2014). Although there is no doubt that invasive species have modified marine ecosystems, evidence for most of the reported impacts is still weak (e.g. Ojaveer and Kotta, 2015). However, the impacts of these changes on the structure and functioning of ecosystems and the social and economic consequences that then arise need to be well understood to inform prioritization of management interventions.

Until recently, vast areas of the Baltic Sea hosted no native crabs or other organisms with similar functional roles (Bonsdorff and Pearson, 1999). However, after an invasion of the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) the situation changed dramatically. In the late 2000s and the early 2010s *R. harrisii* was discovered in the northern and eastern Baltic Sea including the Archipelago Sea along the southwestern coast of Finland and the northeastern Gulf of Riga in Estonia. Since then the species has been exponentially increasing its range and density (Kotta and Ojaveer, 2012; Fowler et al., 2013). Owing to the prior absence of any large burrowers and epibenthic predators this introduced species is expected to form a new functional link within existing assemblages and cause pronounced impacts on community structure, food webs and ecosystem functioning. This natural experiment offers an excellent opportunity to observe how communities that evolved without this functional guild react to the presence of *R. harrisii* and thereby better understand the role of crabs in coastal ecosystems in general.

The introduction of *R. harrisii* will likely cause changes in the abundance of organisms across many trophic levels (e.g. Carpenter and Kitchell, 1993). For example, crabs may control the abundance of grazers (Silliman et al., 2004) and thereby modify the growth patterns of micro- and macroalgae. Crabs may also prey on deposit and suspension feeding bivalves and thereby affect the trophic state of sediment (Norkko et al., 2001; Giles et al., 2006; Cranford et al., 2009). Burrowing crabs can lower snails' growth rates due to increased snail burial (Armitage and Fong, 2006) and disturb bivalves' feeding behaviour and damage their shells (Lomovasky et al., 2006). Moreover, chemical cues caused by crab predation may induce prey populations to change their behaviour and such

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alterations may have dramatic consequences for the functioning of benthic ecosystems (Premo and Tyler, 2013). Finally, the mud crab as an effective burrower effectively reworks sediment through bioturbation that affects sediment granulometry and organic matter content (Botto and Iribarne, 2000), sediment biogeochemistry, pore water chemical characteristics and nutrient benthic fluxes (Gilbert et al., 1998; Fanjul et al., 2007, 2011). Most of these issues have not yet been addressed in the Baltic Sea. There exists only one experimental study from the northern Baltic Sea suggesting that *R. harrisii* is already decreasing species richness of littoral hard bottom macroinvertebrate community (Forsström et al., 2015).

Meiofauna (i.e. benthic organisms that can pass through a 500 μm mesh sieve but are retained on a 44 μm sieve; Giere, 2009) represents one of the most abundant and diverse groups of animals and have important functions in marine food webs; nevertheless, they are relatively understudied in many parts of the world (Giere, 2009). Crabs can influence meiobenthos through different mechanisms. Although this is not known for *R. harrisii*, the soldier crab *Mictyris longicarpus* can directly feed on meiofauna (Spilmont et al., 2009). The burrowing activity of crabs can cause physical disturbance that directly alter the abundance and species composition of meiobenthos (Warwick et al., 1990; Rosa and Bemvenuti, 2005). However, the effects are known to vary among taxa. For example, crab burrowing reduces the abundance of ostracods, copepods and turbellarians (Rosa and Bemvenuti, 2005) but not nematodes (Warwick et al., 1990) and in some instances their abundance may even be increased (Shimanaga et al., 2012). Alternatively, crab faecal pellets together with associated bacteria might serve as a new food resource for some meiofaunal taxa. Studies involving *R. harrisii* suggest that their diet consists of detritus to a considerable extent (e.g. Czerniejewski and Rybczyk, 2008) and thereby it is expected that *R. harrisii* may compete strongly for food with some taxa of meiofauna. On the other hand, *R. harrisii* preys to great extent on deposit feeding bivalves (Czerniejewski and Rybczyk, 2008; Ojaveer and Kotta, 2015) thus, they may likely reduce competitive interactions for food among detritus feeding meiobenthos. Moreover, the reduction of macrofauna due to crab predation (e.g. Milke and Kennedy, 2001) may have severe repercussions for meiofauna, as macrofauna are known to have an important structuring effect on meiobenthic communities (Ólafsson, 2003). The evidence above indicates that the potential effects of the crab on meiofauna are diverse and the introduction of *R. harrisii* is likely to disrupt natural meiobenthic communities by establishing new ecological relationships, displacing or completely disassembling native communities, but likely facilitating some native species through the provision of alternative food to native consumers. Considering the vast array of potential impacts and the prior lack of crabs in the northeastern Baltic Sea basin, the effects of *R. harrisii* on meiobenthos are difficult to predict. Moreover, there are virtually no studies on the effects of any invasive species on the Baltic Sea meiobenthos (but see Urban-Malinga et al., 2013).

In its native range *R. harrisii* is commonly found in habitats that provide some type of shelter from predators either in the form of plants or debris (Ryan, 1956). In its invasive range, however, the species is even more flexible occurring from exposed hard bottoms to sheltered soft bottoms either unvegetated or vegetated (Fowler et al., 2013). In the Baltic Sea *R. harrisii* is abundant both in soft sediment and mixed bottom habitats. On mixed bottom habitats, *R. harrisii* is known to avoid soft sediment and hide either under boulders or among boulders covered with macroalgae (Nurkse et al., 2015). On the other hand, on soft sediment the invasive crab constantly reworks sediment deposits through bioturbation and thereby posing a significant disturbance to the meiobenthic communities. Therefore, the influence of *R. harrisii* on meiobenthos is expected to vary among habitats and such habitat specific interactions need to be experimentally assessed.

The aim of this study was to experimentally investigate the effect of *R. harrisii* on the taxonomic composition and abundance of a shallow water meiofauna community in the north-eastern Baltic Sea. The following questions were asked: (1) Does habitat type modify the effects of *R. harrisii* on meiofauna? Potentially, *R. harrisii* has stronger effect on unvegetated soft bottoms than on other types of environments as such habitat is characterised by low availability of food and microhabitats and thus higher feeding and sediment reworking activity rates. (2) Does *R. harrisii* have variable effects on different meiobenthic taxa? We expect that *R. harrisii* enriches sediment with organic matter and thereby enhances abundances of nematodes, ciliates and disfavours oligochaetes, turbellarians and Gastrotricha. (3) Does *R. harrisii* have variable effects on meiobenthos species composition and total abundance? We expect that *R. harrisii* has a larger effect on meiobenthos species composition than on total abundances and this is because sensitivities of species vary among taxa whereas total abundance is often a function of nutrient availability, the latter being largely unaffected by the presence of crabs.

2. Materials and methods

2.1. Experiment design and set-up

In order to investigate the effect of *R. harrisii* on meiobenthos, a manipulative experiment was conducted in Kõiguste Bay, the north-eastern Baltic Sea in June 2013 (58°22.10′ N, 22°58.69′ E) using 10 l plastic buckets with a diameter of 24 cm. The sediment (fine sand) together with meiobenthos was collected from a shallow water embayment (0.5–1 m depth) adjacent to the experiment site. In order to obtain similar starting conditions, sediment was homogenized prior to the experiment. In the homogenized sediment the medium particle size of sand varied within 2 μm and the content of silt varied less than 2%. Then the buckets were filled with a 6 cm layer of homogenized sand and natural seawater of salinity 6 and were allowed to settle for 6 h. The filled buckets were placed into an outdoor mesocosm facility, assuring ambient light and seawater temperature for all experimental buckets.

Coastal waters of the north-eastern Baltic Sea are dominated by soft and mixed bottom habitats. Owing to habitat-specific behavioural differences the role of *R. harrisii* on meiobenthos is expected to vary among habitats (Nurkse et al., 2015). We used four different habitat types in the experiment. Soft sediments contained homogenized sand only, whereas mixed sediments were generated by adding two similar-sized small stones on the homogenized sands. For vegetated soft sediments the charophyte *Chara aspera* were seeded and on mixed sediment stones overgrown with the green alga *Cladophora glomerata* were placed on sand instead of unvegetated stones. Stones and macroalgae were collected adjacent to the experiment site. In order to start the experiments with similar numbers of species, all stones and macroalgae were inspected for all macroinvertebrates which were then removed from the substrates. In addition, the substrates were carefully rinsed in a bucket of freshwater in order to remove associated motile fauna before introducing them into the experimental buckets.

The density of *R. harrisii* is not well known in the Baltic Sea as current monitoring programs do not target such epibenthic predators due to prior lack of such a function. A pilot experiment deploying artificial reefs in the north-eastern Baltic Sea area has indicated that the number of *R. harrisii* per 1 m^2 seafloor surface area ranges from a few crabs to 1000 crabs and these values (range and density) are still increasing (Fowler et al., 2013; J. Kotta